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COLOR VISION

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■ **Abstract** Color vision starts with the absorption of light in the retinal cone photoreceptors, which transduce electromagnetic energy into electrical voltages. These voltages are transformed into action potentials by a complicated network of cells in the retina. The information is sent to the visual cortex via the lateral geniculate nucleus (LGN) in three separate color-opponent channels that have been characterized psychophysically, physiologically, and computationally. The properties of cells in the retina and LGN account for a surprisingly large body of psychophysical literature. This suggests that several fundamental computations involved in color perception occur at early levels of processing. In the cortex, information from the three retino-geniculate channels is combined to enable perception of a large variety of different hues. Furthermore, recent evidence suggests that color analysis and coding cannot be separated from the analysis and coding of other visual attributes such as form and motion. Though there are some brain areas that are more sensitive to color than others, color vision emerges through the combined activity of neurons in many different areas.

INTRODUCTION

Color is frequently defined as the sensation that allows us to discriminate uniform surfaces of equal brightness. Although this definition is correct, it does not do justice to the importance of color in primate vision. First, there are not many natural surfaces totally devoid of texture. Second, most of these surfaces differ in brightness as well as in color. Presumably, the highly complex process of color vision did not evolve to perceive stimulus configurations unlikely to appear in our natural environment. Figure 1*A* shows a color photograph of a natural scene, Figure 1*B* a version in which each pixel was assigned the same luminance value, and Figure 1*C* a black and white version of the same scene. The latter image contains only luminance information, the former only color information, and the sum of the two results in the original image. It is apparent that the black and white image contains all the fine structure and object boundaries. Nevertheless, it is very difficult to distinguish the petals from the leaves. When color is added, the

distinction between petals and leaves becomes effortless and immediate. In line with these observations, recent psychophysical experiments on scene recognition and long-term memory have shown that the main benefits of having color, in addition to luminance information, are to recognize things faster and to remember them better (Gegenfurtner & Rieger 2000, Wichmann et al. 2002).

Here we review current physiological studies that investigate the neural signals for chromatic processing in primates. In recent years, our understanding of the chromatic properties of cells in the early stages of the visual pathways, the retina, and the dorsal lateral geniculate nucleus (dLGN) has increased considerably. Much less is known about the processing of color information in the cerebral cortex. First, we summarize the retinal and geniculate stages of visual processing, and then we review current knowledge of color processing in primate cortex. We mostly present data from macaque monkeys, whose trichromatic visual system is highly similar to the human (DeValois 1965, Jacobs 1993), and we refer to studies with human subjects whenever possible.

COLOR CODING IN THE CONES

The spectral absorption functions of the three different types of cone photoreceptors are the hallmark of human color vision. Grassmann (1853) was the first to formally state that there are three degrees of freedom in normal color matching. This was verified by Maxwell (1855). A few years later, König & Dieterici (1886) were the first to propose an experimental estimate of the cone absorption spectra. They derived estimates from the idea that red-green color-blind observers (deuteranopes and protanopes) lack exactly one class of cone, whereas the other cone classes are identical to those of color-normal observers. The estimates made by König & Dieterici (1886) more than a century ago are remarkably close to recent ones (Vos & Walraven 1971, Smith & Pokorny 1975). They differ very little over the range where the cones are most sensitive, but recent estimates significantly extend the range over which the spectra have been measured. Figure 2 shows the most recent and precise cone fundamentals by Stockman & Sharpe (2000). Advances in microspectrophotometry (Dartnall et al. 1983), recordings of cone electroretinograms (Jacobs et al. 1996), and suction electrode recordings (Schnapf et al. 1987) have provided physiological verification of the earlier psychophysical measurements, albeit at lower precision.

TRICHROMACY AND UNIVARIANCE

The three classes of cones drastically reduce the dimensionality of color vision. Whereas the light stimulus is determined by its intensity at an infinite number of wavelengths between 400 and 800 nm, the output of the cones can be characterized by only three numbers. This is the principle of trichromacy. Light is absorbed in the cones and converted by a complex photochemical reaction into an electrical signal (see Jindrova 1998 for a review), which corresponds to the number of

photons absorbed by each cone. The reduction to three dimensions results in a loss of wavelength information. Photons of different wavelength have different likelihoods of being absorbed by the three cone classes, denoted long- (L-), middle- (M-), and short-wavelength-sensitive- (S-) cones. Once absorbed, the only remaining information is the photon count in each cone, not the wavelength of the absorbed photons: a principle termed univariance by Rushton (1972). An increase in photon count can thus be due to an increase in light intensity, a change to a more favorable wavelength, or both. For example, an increase in the L-cone signal can signify that the light's wavelength came closer to the peak of the L-cone absorption spectrum, that the light became more intense, or a combination of both. Therefore, to compute the color of an object unambiguously, the magnitudes of the output signals of the three cone classes have to be compared. This happens at the next stage of processing, which is performed by horizontal cells and ganglion cells in the retina. Note that we only dealt with the cone receptors in our discussion of photoreceptors. Rods contribute to vision only at low light levels. Although they are known to have an effect on color perception in the mesopic range (Stabell & Stabell 1998, 2002; Knight et al. 1998), their influence is small and can be ignored here.

There are several characteristics of the cone absorption spectra shown in Figure 2 worth noting. First of all, cones are sometimes referred to as red, green, and blue cones. This is highly misleading because all types of cones are sensitive to a large range of wavelengths. The L- and M-cones are sensitive to the whole visible spectrum. The S-cones have their peak at a wavelength that would appear violet under neutral viewing conditions, and the L-cones have their peak at a wavelength that would appear yellowish.

A more surprising aspect of the cone absorptions is the large overlap between L- and M-cone absorption spectra. Their peaks, characteristically at about 535 nm and 565 nm in humans, are only about 30 nm apart, whereas the S-cone absorption spectrum is clearly separated from the M- and L-cones, its peak being 440 nm. The consequence of the L- and M-cone overlap is a high correlation in the photon catches of the two cone classes, as illustrated in Figure 3. Considering that color vision must compare M- and L-cone signals (see above), the small difference in L- and M-cones signals seems to be a disadvantage. Although this argument is valid when the color system is considered on its own, one has to keep in mind that the visual system also extracts information about other aspects of the scene. To achieve the highest possible acuity at the center of the fovea, the visual system treats L- and M-cones equally, ignoring the difference in their absorption spectra. Therefore, any such difference leads to a deterioration of the luminance signal (Osorio et al. 1998). Thus, the small separation between L- and M-cone spectra might be a compromise between the needs for high-contrast color vision and high-acuity luminance vision. This argument is consistent with the fact that there are no S-cones (with their vastly different absorption spectra) in the foveola, the central 30 arc minutes of the fovea where visual acuity is highest.

Another reason for the close spacing of L- and M-cone absorption spectra is their genetic origin. Both cone types are assumed to have evolved recently (about

35 million years ago) from a common ancestor. The S-cones and rod receptors presumably split off from the ancestral receptor much earlier. The evolution of L- and M-cones has been (and still is) the topic of intense research (see Nathans 1999, Sharpe et al. 1999 for reviews). In brief, the L- and M-cone photopigment genes lie juxtaposed on the X chromosome (Nathans et al. 1986) and are 98% identical at the DNA level. Their origin is probably due to a duplication of the ancestral opsin gene and subsequent mutations. The effect of such mutations can still be seen in the population. Several varieties (alleles) of the L- and M-cones are present in normal and color-deficient observers (Neitz et al. 1993). The location of the genes for the M- and L-cone pigments on the X-chromosome explains why color deficiencies are more common in males, who have only one X chromosome.

The introduction of a third cone type must have offered enormous evolutionary benefits because it required massive reorganization at the geniculate and cortical levels as well. The exact nature of these benefits, however, is still a matter of intense debate. Initially, it was proposed that the red-green system mostly enabled our ancestors to discriminate ripe fruits from green leaves (Polyak 1957, Walls 1942, Mollon & Jordan 1988). Indeed, the spectral sensitivity of the red-green color mechanism is finely tuned to differences between leaves and fruit (Osorio & Vorobyev 1986, Regan et al. 2001). A diet of fruit could free metabolic energy from digestion and make it available to expand brain resources (Allman 1999). However, trichromacy has also evolved in several species that eat leaves only, and trichromacy is equally well suited to discriminate different types of leaves (Dominy & Lucas 2001). It may well be that the evolutionary advantages of color vision are more general and that detecting ripe fruits was only one of several benefits.

RETINAL GANGLION CELLS AND LATERAL GENICULATE NUCLEUS

Information from the cones is sent to the lateral geniculate nucleus (LGN) in the thalamus and the superior colliculus via axons of the retinal ganglion cells in the optic nerve. Coding in the optic nerve is highly efficient: The number of nerve fibers is kept to a minimum, maybe to keep the size of the optic nerve, and with it the size of the retinal "blind spot" (about 5° wide by 7° high), as small as possible. An important aspect of efficient coding is that the signals traveling along the optic nerve should be uncorrelated. Information from neighboring parts of natural scenes are highly correlated spatially and therefore highly predictable (Kersten 1987). Lateral inhibition between neighboring retinal ganglion cells minimizes this spatial correlation, thereby improving efficiency. Additionally, as seen in Figure 3, cone signals—especially from L- and M-cones—are also highly correlated because of the large overlap of their absorption spectra. In this case, coding efficiency is improved by combining the cone signals to minimize this correlation. Mathematically, principle components analysis (PCA) can be performed to achieve this goal. PCA looks iteratively for the dimension that explains the largest amount

of unaccounted variance in a data set, with the *n*th component being orthogonal to the previous *n*-1 dimensions. Buchsbaum & Gottschalk (1983) used this scheme on the cone absorption functions, and more recent studies applied it to naturally occurring spectra (Zaidi 1997, Ruderman et al. 1998). The principle dimensions in the space of cone excitations produced by natural objects are: first, a luminance axis where the L- and M-cone signals are added; second, a red-green opponent axis where the difference of L- and M-cone signals is taken; and third, a blue-yellow color opponent axis where the S-cone signal is differenced with the sum of the L- and M-cone signals. These channels—derived on purely computational grounds—happen to coincide with the three retino-geniculate channels discovered in electrophysiological (DeValois et al. 1966, Lee et al. 1988, Derrington et al. 1984) and inferred from psychophysical experiments (Krauskopf et al. 1982).

In psychophysical experiments, Krauskopf and colleagues (Krauskopf et al. 1982) showed that there are three independent channels in color vision, which they called cardinal directions of color space. In addition to a luminance direction ("black & white"), they found two color-opponent cardinal directions, illustrated in Figure 4. Krauskopf et al. (1982) habituated their subjects for 30 seconds to a uniform field changing color along a particular direction in color space. Following the habituation they measured thresholds for detecting lights in the same or other directions of color space. When subjects habituated along one of the cardinal directions, thresholds were elevated for test lights along the same cardinal direction and unaffected for test lights along the other cardinal directions. For example, habituating to the red-green cardinal direction (the L-M axis in Figure 4) would increase thresholds for reddish test lights but not for test lights along the other cardinal directions (blue-yellow or black and white). One interesting aspect of these results is that the cardinal directions do not coincide with the color opponent mechanisms that were proposed previously by Hering (1878) and Hurvich & Jameson (1957). These mechanisms are associated with the so-called unique or pure hues, e.g., a blue that contains neither red nor green. The cardinal directions differ significantly from these hues, as shown by the labels on the perimeter of Figure 4, which represent the outcome of a color naming experiment. The importance of cardinal directions for color vision was shown in a whole series of experiments by Krauskopf and colleagues (for review, see Krauskopf 1999). Although the cardinal directions appear fundamental to color vision, a number of studies show significant departures from a processing scheme based solely on mechanisms tuned to these directions (e.g., Webster & Mollon 1991, Gegenfurtner & Kiper 1992, Zaidi & Shapiro 1993). Therefore, in addition to the three second-order (cardinal) mechanisms, higher order chromatic mechanisms are required to account for color perception.

Physiologically, the chromatically opponent cardinal directions correspond closely to the response properties of neurons in the parvocellular layers of the LGN. Derrington et al. (1984) showed that the preferred color directions of LGN cells cluster around two axes of color space, which correspond to the psychophysically defined cardinal directions of Krauskopf et al. (1982). Furthermore, the response of

LGN neurons can be predicted by the dot product of the stimulus color with the preferred color direction of the neuron. Cells representing the three cardinal axes are not only distinct in their functional and chromatic properties, but also project from retina to visual cortex via three mostly independent anatomical pathways.

First, cells in the magnocellular (M-) layers of the LGN receive input from retinal M-cells (not to be confused with the M-cones), which in turn receive their signals from diffuse bipolar cells. The diffuse bipolar cells receive synergistic inputs from L- and M-cones (Derrington et al. 1984). The receptive fields of M-cells are composed of a center and a surround, which are spatially antagonistic. An ON-center receptive field, which we denote +L+M receives, in its center, excitation from both L- and M-cones. It has a surround receiving inhibition from L- and M-cones (−L−M). Conversely, OFF-center receptive fields receive inhibition (−L−M) in the center and excitation (+L+M) in the surround. Geniculate M-cells have high-contrast sensitivity for luminance stimuli, but their responses exhibit a null at some combination of L–M opponent inputs (Shapley 1990). However, because the null points of different M-cells vary slightly, the population response is never really zero—a property that is passed on to cortical areas with predominant M-cell inputs (Dobkins et al. 2000).

The parvocellular (P-) pathway originates with the individual L- or M-cone inputs to midget bipolar cells. The midget bipolar cells provide input to retinal P-cells. In the fovea, the receptive field centers of P-cells are formed by single L- or M-cones. The structure of the P-cell receptive field surround is still debated. A simple and elegant solution would be to have a random mixture of L- and M-cone signals in the surround (Lennie 2000), but most of the current data indicate that the surround consists of a specific cone type (Reid & Shapley, 1992, 2002; Martin et al. 2001). Both arrangements result in a receptive field structure that is spatially opponent for luminance stimuli, as can be seen in the bandpass spatial tuning function in Figure 5. For isoluminant stimuli the response is best for spatially extended patterns, resulting in a lowpass spatial tuning function. The parvocellular layers contribute about 80% of the total retinogeniculate projections (Perry et al. 1984).

Finally, the recently discovered koniocellular (K-) pathway (Casagrande 1994) carries, to a large degree, signals from S-cones. Groups of S-cones project to special "blue-cone" bipolar cells, which in turn provide input to small bistratified ganglion cells (Dacey & Lee 1994). These also receive input from diffuse bipolars thus forming chromatically opponent S-(L + M) cells, which are usually not spatially opponent. The axons of the small bistratified ganglion cells project to thin (intercalated) layers of the LGN adjacent to the parvocellular layers (for a recent review see Hendry & Reid 2000).

Thus, there are three channels of information from retina to cortex, which are distinct from each other not only in their chromatic properties but also in their anatomical substrate. These channels pose important limitations for basic color tasks such as detection and discrimination, but a direct correspondence between their physiological properties and behavior is not the rule. This would, after all, be surprising, because there is a lot of subsequent cortical processing. Nonetheless,

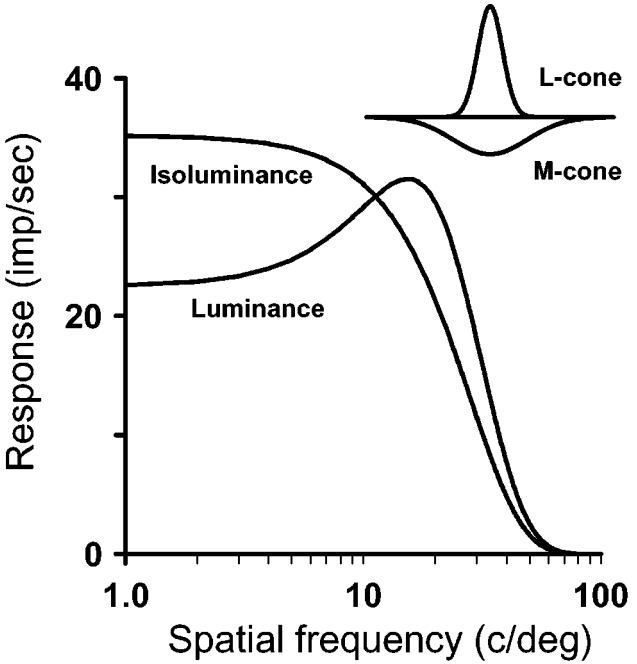

Figure 5 Spatial frequency tuning curves for a typical LGN parvocellular, red-green, color-opponent neuron. The inset in the top right corner shows a schematic representation of the receptive field's sensitivity profile: The cell receives inhibitory inputs from M-cones in the whole receptive field and excitatory inputs from L-cones in the center. The sign difference between the cone inputs gives this neuron its color-opponency. The difference in spatial extent between the inputs produces its spatial opponency. The cell is lowpass for equiluminant stimuli and bandpass for luminance.

two very basic psychophysical measurements—heterochromatic flicker photometry and unique yellow adjustments—correlate well with the physiology of retinal ganglion or LGN cells.

Flicker photometry is used to define the concept of luminance (Lennie et al. 1993). The relative luminous efficiency curve $V(\lambda)$ specifies the efficiency of light of a particular wavelength in exciting the visual system. The human luminance channel adds L- and M-cone signals with a weighting of 2:1, similar to the way most magnocellular neurons combine cone-inputs (Lee et al. 1988). Unique yellow—a yellow that contains neither red nor green—is used to define the red-green color opponent channel and typically represents the point where L- and M-cone signals are weighted 1:1. Both types of measurement, flicker photometry and unique yellow, were suspected to correlate with the relative number of L- and M-cones in the retina (e.g., Otake & Cicerone 2000, Krauskopf 2000). Because L- and M-cones are quite similar in most respects (see above), it was for a long time impossible

to discriminate the two in human retinae. Recently Roorda & Williams (1999), in a stunning application of modern optical engineering, managed to image all three different types of cone in the living human retina. Contrary to expectations they found vastly different relative cone numbers in different observers, yet all these observers had seemingly normal color vision. Precise testing, combined with a genetic analysis of each observer's cone photopigments revealed that the relative number of L- and M-cones, ranging from 0.25:1 to 9:1, had essentially no effect on perception (Brainard et al. 2000). The second stage mechanisms of color vision seem to adjust themselves, to some degree even on the timescale of a few days (Neitz et al. 2002), to the input signals from the first stage, the cones.

In the cortex, the projections from the magno-, parvo-, and koniocellular pathways terminate in different layers of the primary visual cortex (see Callaway 1998 for a review). The magnocellular fibers innervate principally layer 4Cα and layer 6. Parvocellular neurons project mostly to 4Cβ, and layers 4A and 6, and koniocellular neurons terminate in the cytochrome oxidase– (CO-) rich blobs in layers 2 and 3, as well as in layer 1. Several authors proposed that these pathways remain segregated in V1 and extrastriate cortex (Livingstone & Hubel 1987a, 1988; DeYoe & Van Essen 1985; Roe & Ts'o 1999). In V2, the M-pathway would coincide with the thick CO-rich bands (Hubel & Livingstone 1987), the P-pathway with the pale interbands and the thin CO-rich bands, and the K-pathway with the thin CO-rich bands. In that scheme, the discrete anatomical channels have a functional counterpart, with motion and depth being treated in the thick bands, form in the pale, and color in the thin bands. Beyond V2, signals carried by these pathways give rise to the "what" and "where" functional streams described in extrastriate cortex (Ungerleider & Mishkin 1982). It is thus of great interest not only to study the processing of color signals in the visual cortex and investigate how they relate to color perception, but also to determine how color signals are treated relative to other visual attributes such as form, depth, or motion. In the next paragraphs, we first review the chromatic properties of cells in V1 and V2, then discuss the proposal that color is analyzed by a dedicated, independent color system that extends throughout the visual cortex.

CHROMATIC PROPERTIES OF V1 AND V2 CELLS

In many respects, the chromatic properties of cells in cortical areas V1 and V2 are very similar. In both V1 (Dow & Gouras 1973, Gouras 1974, Yates 1974, Thorell et al. 1984, Johnson et al. 2001) and V2 (Baizer et al. 1977, Levitt et al. 1994a, Yoshioka et al. 1996, Gegenfurtner et al. 1996) about 50% of the cell population is selective for color. The majority of color-selective cells in these areas, like those of the dLGN, sum their inputs in a linear fashion. Indeed, most V1 (Lennie et al. 1990) and V2 (Kiper et al. 1997) cells' responses to chromatic modulations are well accounted for by a model postulating a linear combination of the signals derived from the three cone classes. This model had been proposed, as described above, by Derrington et al. (1984) to describe the responses of dLGN cells. Although there are some V1 cells that are more selective for color than

predicted (Cottaris & DeValois 1998), the model adequately fits the responses of the majority of V1 cells. In V2, the proportion of cells more selective than predicted by the model is significantly larger. Kiper et al. (1997) used sinusoidal gratings with a moderate, fixed luminance contrast and varying color, modulated around a fixed, white adapting point, to measure the chromatic selectivity of V2 cells. The modulation directions spanned the range of colors shown in Figure 4 in regular intervals. Figure 6 shows representative examples of responses. The responses of most cells (Figure 6*A*) are well captured by the linear model where

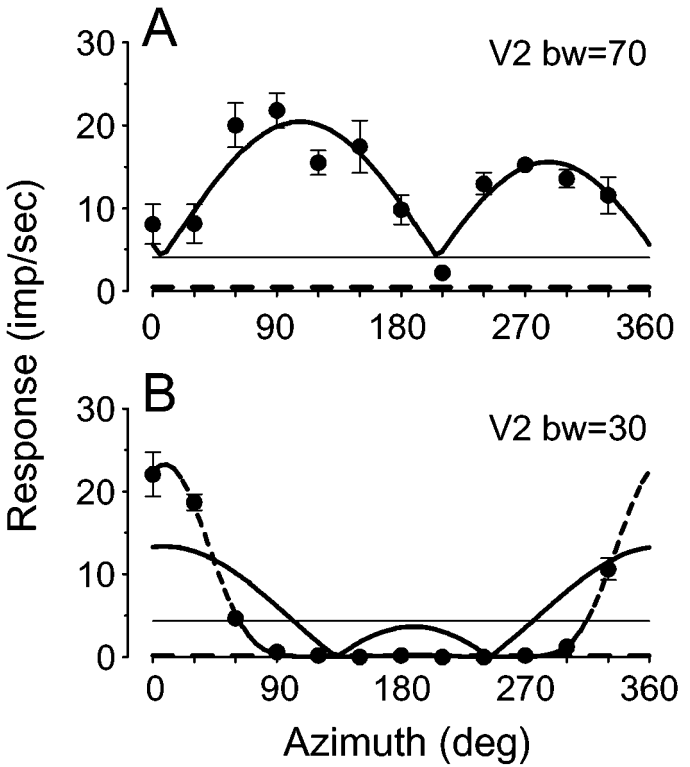

Figure 6 Responses of two V2 neurons to drifting gratings of varying colors, plotted on the abscissa as the azimuth in Derrington-Krauskopf-Lennie (DKL) space. The gratings all had a small luminance contrast (∼10%) and were modulated in color around the white point. The cell shown in (*A*) follows the predictions of the linear model (*solid curve* in *A* and *B*) quite closely. The neuron shown in (*B*) has a much narrower bandwidth (bw) of tuning in color space (bw $= 30^\circ$ compared to bw $= 70^\circ$ for the neuron shown in *A*) and requires a fit that includes a nonlinear stage. The fit of the nonlinear model is shown as a dashed curve in *B*. The horizontal solid lines show the cells' responses to a black-and-white grating having the same luminance contrast as the colored gratings. The horizontal dashed lines show the response to a blank screen, with a luminance equal to the space-averaged luminance of the other stimuli.

the response is proportional to the angle between stimulus color and the neurons' preferred color (*solid curve*). Other cells, like the one shown Figure 6*B*, respond to a range of colors narrower than predicted by the linear model. For these cells, an extended model that includes a nonlinear stage is necessary to fit the data. The parameters derived from these models allowed the authors to compute the cells' bandwidth of tuning in color space. Whereas two thirds of the cells in V2 have a bandwidth close to that predicted by the linear model (60°), the bandwidth of the other third of color-selective cells is significantly narrower. A further difference between LGN and cortical cells is the distribution of preferred colors. The preferred colors of V1 (Lennie et al. 1990, Cottaris & DeValois 1998) and V2 cells (Kiper et al. 1997) do not cluster around the three cardinal directions found in the LGN (Derrington et al. 1984). Instead, cells often prefer colors that lie intermediate to these cardinal directions. These tuning characteristics of cortical cells possibly relate to the elaboration of color categories, which are known to occupy a narrow range in color space (Komatsu 1997) (see Figure 4).

Most color-selective cells in V1 (Johnson et al. 2001) and V2 (Kiper et al. 1997) also respond vigorously to luminance variations, a property that seems ubiquitous in the visual cortex. This illustrates the fact that color selectivity does not imply color opponency. A response to stimuli containing chromatic but no luminance information (isoluminant stimuli) does not imply that the neuron receives opponent inputs from two or three cone classes. For example, a hypothetical neuron that receives inputs from the L-cones only will respond to an isoluminant stimulus that modulates the contrast in the L-cones, for example a red-green isoluminant grating. True color opponency can be deduced in neurons that give stronger responses to isoluminant than to luminance stimuli, provided that the stimuli are equated for cone contrasts (Schluppek & Engel 2002). Johnson et al. (2001) measured the cone contributions directly using cone isolating stimuli. They found a large proportion of cells that gave robust responses to both isoluminant and luminance stimuli (their color-luminance cells). Whereas most of these cells did receive color-opponent inputs, some had L- and M-cone inputs of the same sign. Most likely there is a whole continuum of cells ranging from strict color opponency to strict luminance.

PROCESSING OF COLOR AND OTHER VISUAL ATTRIBUTES

Following the modular concept developed after the discovery of functional ocular dominance columns and orientation domains in V1, and considering the anatomical segregation between the P-, M-, and K-pathways described above, it was suggested that there is a specialized system within the visual cortex devoted to the analysis of color information (Livingstone & Hubel 1987b, 1988). The notion of a specialized color system is consistent with the observation of a patchy segregation of cells in the upper layers of V1 that represent color and luminance processing, respectively. Cells in CO-rich regions of layers 2 and 3, the cytochrome oxidase blobs, were

found in some studies to have a preponderance of unoriented, color-selective cells (Livingstone & Hubel 1984, Ts'o & Gilbert 1988, Roe & Ts'o 1999, Landisman & Ts'o 2002b, Shipp & Zeki 2002). Cells within one CO-rich blob tend to share the same chromatic properties, resulting in red-green and blue-yellow blobs. Cells with intermediate preferred colors are located within patches of cortex that bridge blobs of similar or different opponency (Ts'o & Gilbert 1988). This proposed arrangement is supported by recent studies that combined electrophysiological recordings of cell activity with mapping of the cortical surface using optical imaging of intrinsic signals (Landisman & Ts'o 2002a,b). In V2, unoriented, color-selective cells were reported in the thin CO-bands (Livingstone & Hubel 1988, DeYoe & Van Essen 1985). Thus, color signals would be processed, within V1 and V2, by a population of unoriented neurons, located primarily in the CO-rich blobs of V1 and the thin bands of V2.

Beyond V2, the modular view of the extrastriate visual pathways was strongly advocated by Semir Zeki (Zeki 1978, Shipp & Zeki 1985, Zeki & Bartels 1998, Bartels & Zeki 1998). In a very influential series of papers, Zeki suggested that visual motion processing proceeded through V1 to extrastriate visual area V5, also called the middle-temporal area (MT) (Zeki 1980; Shipp & Zeki 1985, 1989a,b), a view that is currently well substantiated. Color information on the other hand was thought to be processed mainly in extrastriate visual area V4 (Van Essen & Zeki 1978; Zeki 1983a,b,c), but this has received rather little support from subsequent studies (Schein et al. 1982, Schein & Desimone 1990). About a decade later, Ungerleider & Mishkin (1982) proposed two extrastriate processing streams: ventral and dorsal. The ventral pathway, including parts of V2, V4, and inferotemporal cortex, is thought to be involved with processing what the objects were—their shape, size, and color. The processing of object color in area V4 was considered to be an essential part of the ventral pathway. The dorsal pathway, areas V3, MT, and the middle-superior-temporal area (MST), was thought to be involved primarily in analyzing where objects are located in the environment and their motion.

In contrast to this modular view of functional organization in the cortex, several studies failed to find a strong segregation of functional properties between V1 (Leventhal et al. 1995) and V2 CO compartments (Levitt et al. 1994a, Peterhans & von der Heydt 1993, Gegenfurtner et al. 1996). Figure 7, for example, shows the relation between color and orientation selectivity within the CO compartments of V2 (Gegenfurtner et al. 1996). Each cell's selectivity was quantified by computing a selectivity index for orientation and color (see legend of Figure 7). In all three V2 CO compartments, most cells are selective for both the orientation and the color of the stimulus. Furthermore, there is no correlation between these two properties. Similar results have now been reported by Friedman et al. (2002) in a large sample of V1 and V2 cells of awake-behaving monkeys. Although Lennie et al. (1990) and Johnson et al. (2001) reported that about 10% of V1 cells that respond preferentially to color were spatially lowpass and tended to be unoriented, they showed that the vast majority can also encode the spatial properties of the stimulus. Moreover, some

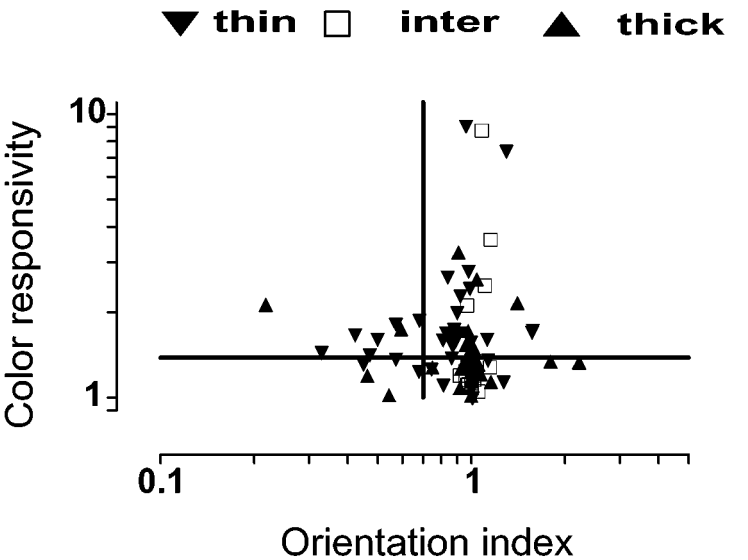

Figure 7 Color versus orientation selectivity for a population of V2 cells. Different symbols indicate location within different V2 CO compartments. Orientation and color selectivities were quantified for each cell by an index. The color index was (R_{col}-b)/(R_{white}-b) where R_{col} is the best response to a color stimulus, R_{white} the response to a white stimulus of equal luminance to the colored ones, and *b* is the cell's spontaneous firing rate. The orientation index is 1- (R_{ortho}-b)/(R_{pref}-b), where R_{pref} is the response to a stimulus at the cell's preferred orientation, and R_{ortho} when the orientation is orthogonal to the preferred. Cells located above the horizontal line were classified as color selective (color index >1.4), cells to the right of the vertical line were classified as orientation selective (orientation index >0.7). Color and orientation selectivities are not correlated in V2.

color-selective cells that code not only orientation but also direction of motion have been reported in V1 (Leventhal et al. 1995), V2 (Gegenfurtner et al. 1996), and V3 (Gegenfurtner et al. 1997). These results contradict the idea that color information is treated solely by a dedicated, specialized population of neurons in V1 and V2. They agree with a large number of psychophysical studies showing that the processing of form defined by color is limited only by retinal factors—the contrast in the cones—but not by subsequent processing (e.g., Webster et al. 1990).

In our view, the conflicting results arise mostly from the method used to classify cells as color selective. For example, most authors concluding that color-selective cells are unoriented and clustered in CO blobs rely on qualitative criteria to classify cells into different categories (color, luminance, oriented, unoriented, motion selective, etc.) This often leads to classifications that are difficult to match to those from quantitative studies because, as described above, individual cells can code for several visual attributes. The resulting sample of color-selective cells probably

contains only cells at the extreme of the color-opponency spectrum and tends to ignore all others. When quantitative, objective measures are used to classify cells, the results of different studies agree remarkably well. Such biases probably also explain why early studies of the primary visual cortex reported only a small proportion of color-selective cells, about 10% (Hubel & Wiesel 1968). The view that color is only weakly represented within V1 was so prevalent that recent fMRI results showing a strong activation of human V1 to color stimulation (Kleinschmidt et al. 1996, Engel et al. 1997) came as a surprise to many. The remarkable agreement between V1 activation levels seen in fMRI images and the subjects' perceptual reports (Engel et al. 1997) shows that V1 makes a major contribution to color perception. The role of V1 has been further illustrated by Engel & Furmanski (2001), who studied chromatic adaptation in V1 using fMRI techniques. They showed that V1 activity elicited by chromatic patterns was reduced if the observer had been previously exposed to a high-contrast chromatic pattern, compared to that obtained after exposure to a luminance pattern. Conversely, prolonged exposure to a luminance pattern reduced subsequent activity evoked by a luminance but not a chromatic pattern. Thus, the activity of V1 neurons can account for the phenomenon of chromatic adaptation, which had been observed in numerous psychophysical experiments. Finally, recent work has reconciled, to some degree, the fMRI activation and the predicted activation from the neuronal population (Schluppeck & Engel 2002). The use and development of fMRI techniques in combination with psychophysics and single-unit recordings is thus extremely promising and will undoubtedly help us to better understand the role of areas such as V1 and V2 in color processing.

The lack of a functional segregation between the V1 and V2 CO compartments is consistent with anatomical findings that reveal the existence of considerable crosstalk between the P-, M- and K-pathways within V1 (Sawatari & Callaway 1996) and V2 (Levitt et al. 1994b). Moreover, recent data show that the pattern of projections between V1 and V2 does not conform to the proposed segregated scheme. Indeed, Sincich & Horton (2002a,b) showed that, contrary to previous descriptions, V1 outputs are segregated into two kinds. The first one originates from the CO-rich blobs and terminates in the thin bands of V2. The second originates outside the V1 CO-rich blobs and innervates both the thick and interbands of V2. The notion that the CO-rich compartments of V1 and V2 represent the anatomical basis for three functional streams is thus considerably weakened. The predominant role of CO-rich regions in color vision has been further questioned by studies of nocturnal primates who possess well-defined CO blobs but lack trichromatic color vision, such as owl monkeys (Horton 1984, O'Keefe et al. 1998).

COLOR CONSTANCY

One of the most important properties of our color vision system is color constancy, the ability to assign colors to objects, irrespective of changes in illumination conditions. In the early 1980s, Zeki (1983a,b,c) described two populations of color-selective cells in area V4. He used stimuli that were irregularly sized,

adjacent rectangles of different colors (like a Mondrian painting) that could each be independently illuminated by a controllable light source. One neuronal population (wavelength or WL cells) responded to colored stimuli in a way that can be predicted by the wavelength composition of the stimulus. A second population (color-coded or CC cells) gave responses that cannot be predicted by the wavelength composition of the stimulus. Instead, their responses correlated with color appearance, as defined by human observers. These cells were therefore thought to provide the basis for color constancy (but see Schein et al. 1982 and Schein & Desimone 1990 for a challenge of these data based on methodological grounds). Color-coded cells were reported absent in earlier stages of the visual pathways by Zeki (1983a,c), including area V2 (Moutoussis & Zeki 2002), which provides a major input to V4.

In addition to the methodological problems raised by Schein and collaborators, the notion that V4 is the primary locus of color-constant cells has been weakened by recent reports confirming the existence of double-opponent cells in the primary visual cortex. Such cells, observed by Michael (1978a,b,c, 1979), have receptive fields that resemble the circular, concentric receptive fields of parvocellular dLGN neurons, but both center and surround show color opponency. As a result, a change in illumination that would, for example, result in an increase of the center response would produce a simultaneous, compensatory increase in the surround response and vice versa. In other words, double-opponent cells are potentially important for the computations underlying color constancy because their receptive field organization enables them to maintain constant responses despite global changes in the illumination of their receptive field. After a number of quantitative studies performed on large samples of cortical cells had failed to find significant numbers of double-opponent cells (Thorell et al. 1984, Lennie et al. 1990), interest in them was reawakened by recent studies of the chromatic properties of V1 cells (Conway 2001, Johnson et al. 2001). Johnson et al. (2001) found a significant number of cells that were chromatically opponent and spatially bandpass for both luminance and isoluminant stimuli. The latter observation indicates that their receptive field must contain spatially segregated and antagonistic subregions, which are themselves color opponent. These are, by definition, double opponent, even though they did not have circularly symmetric receptive fields. Thus, cells capable of achieving some degree of color constancy exist in V1 already, contrary to Zeki's original report (1983c). In another study, Conway (2001) used cone-isolating stimuli to map the receptive field of individual V1 neurons of awake macaque monkeys. He found that many of the neurons he selected had circularly symmetric, double-opponent receptive fields. Unfortunately, Conway did not maintain the cells in a constant state of chromatic adaptation in these experiments, which makes his results difficult to interpret (Shapley & Hawken 2002). Overall, the results of numerous psychophysical experiments imply that there is no single mechanism by which color constancy is achieved. Rather, color constancy depends on a number of computations, both in the retina and in the cortex (Kraft & Brainard 1999).

IS THERE A "COLOR CENTER" IN THE CORTEX?

Early evidence for the existence of a unique color center in the visual cortex came from single-unit recordings of macaque monkey area V4. Zeki (1983a,b,c) argued that area V4 is uniquely specialized for color because it contains an unusually large proportion of color-selective cells, some of which exhibit the property of color constancy. Initial estimates of the proportion of color-selective cells in V4 were as high as 100% (Zeki 1973). Subsequent studies found significantly lower estimates, some as low as 20% (Schein et al. 1982). Although a consensual estimate is still lacking, it is likely that V4 contains approximately the same proportion of color-selective cells as V1, V2, or V3. Moreover, the color selectivity of V4 cells appears to be similar to that of neurons in earlier areas. Schein & Desimone (1990) showed that most V4 neurons are not more narrowly tuned in their wavelength selectivity than retinal ganglion or LGN cells. However, a subpopulation of V4 neurons exists that is more narrowly tuned. In that respect, V4 is not different from V1 or V2.

The major argument against V4 as the color center of the monkey brain comes from lesion studies. Lesions of extrastriate area V4 do lead to mild deficits in color vision (Heywood & Cowey 1987; Walsh et al. 1992b, 1993; Schiller, 1993) and to a variety of other visual deficits. Monkeys with V4 lesions are severely impaired in shape discrimination (Walsh et al. 1992a, Merigan 1996), object recognition (Schiller 1995, Merigan & Pham 1998, Walsh et al. 2000), texture discrimination (Merigan 2000), and in their ability to focus attention (De Weerd et al. 1999). Lesions to the next processing stage, inferotemporal (IT) cortex, seem to mimic the human condition of cerebral achromatopsia, i.e., a specific loss of color perception. However, the color deficit depends on the removal of all of IT cortex, which has a variety of other dramatic effects on higher level vision (Heywood et al. 1995, Cowey et al. 2001). In IT cortex the proportion of color-selective cells is believed to be high as well—somewhere between 48% (Gross et al. 1972) and 70% (Komatsu et al. 1992, Komatsu & Ideura 1993). Komatsu et al. (1992) also reported a rather uniform distribution of preferred colors in IT cortex, as well as a subpopulation of cells selective to a very narrow range of colors. These results prompted Komatsu (1997) to suggest that IT cortex could be involved in the elaboration of perceptual color categories.

In humans, it has long been reported that bilateral cortical damage to the lingual and fusiform gyri on the ventromedial side of the occipitotemporal lobe could lead to severe color vision deficiencies (for reviews see Meadows 1974, Zeki 1990). In analogy to earlier single-unit studies in monkey V4, this area has been called human V4. Brain imaging studies show this part of visual cortex to contain a representation of the contralateral, upper quadrant of the visual field and to be highly active during a variety of color vision tasks (Lueck et al. 1989, Corbetta et al. 1991, Gulyas et al. 1994, Kleinschmidt et al. 1996, McKeefry & Zeki 1997). Recently, Hadjikani et al. (1998) also discovered high activity to color stimuli in a region at roughly the same cortical coordinates but argued that it was not

homologous to monkey V4 and therefore gave it a new name, V8. Although the homology between monkey and human brains—especially V4 (Merigan, 1993)—might be impossible to solve, it is likely that V8 is not a separate, new color area, as shown by a new analysis of the topographic representation of the visual field along the human ventral pathway (Wade et al. 2002). In this study, the authors report the existence of a complete contralateral hemifield representation anterior to human V3 that can be considered the human equivalent of V4 (hV4). However, they do not find an additional hemifield representation adjacent to hV4, as reported by Hadjikani et al. (1998). They conclude that Hadjikani's data should be interpreted as evidence for a complete representation of the contralateral visual hemifield in hV4.

Whereas all these results imply that some region of the visual cortex, whether it is called V4 or V8, has a high sensitivity to color relative to luminance, no single experiment has shown evidence for a region that does respond to color only. Similarly, the visual world of patients with cerebral achromatopsia is not the world of black and white movies. The patients typically show a variety of severe object- and pattern-recognition disorders. We think it more likely that color perception is the result of the simultaneous activity of neurons belonging to several cortical areas. The fact that different aspects of color perception can be differentially affected by cortical lesions lends support to this view. Indeed, Clarke et al. (1998) and Rüttiger et al. (1999) have reported on several patients with lesions outside the primary visual cortex, who had impaired color constancy but no deficits in color discrimination. Similar results had been reported for monkeys with V4 lesions (Walsh et al. 1992b, 1993; Schiller 1993). In addition, Schoppig et al. (1999) showed that color memory and color constancy can be differentially affected in humans suffering from cortical lesions. Thus, as is the case for most other visual attributes, our experience of color probably depends on the activity of neurons belonging to a number of different cortical areas. This notion is further supported by the observation that many visual cortical areas are activated by exposure to chromatic stimuli (see Wade et al. 2002 for a review). Additional experiments using modern imaging techniques in monkeys will help to clarify the exact relationship between the color responses in the monkey brain, where single neurons have been studied extensively, and the color responses in the human brain, where only imaging data are available.

COLOR PROCESSING IN THE DORSAL PATHWAY

Of the areas in the dorsal stream, perhaps the best known is area MT. Early reports suggested that MT, an important area for the analysis of visual motion, lacks color selectivity (Zeki 1983c). Albright and collaborators, using a combination of physiological and psychophysical techniques, later showed that color information does contribute to the responses of MT neurons (Croner & Albright 1999, Thiele et al. 1999, Dobkins & Albright 1994). Moreover, Gegenfurtner et al. (1994) showed that most MT neurons do respond to chromatic variations, although much less vigorously than to luminance modulation. As described above, larger responses

to luminance than to isoluminant stimuli of equal cone contrast suggest that these cells are not truly color opponent. Rather, most of the responses evoked by color variations in MT cells can be explained by the fact that individual cells behave like poorly calibrated photometers. They do sum L- and M-cone inputs similarly to the human photopic sensitivity curve V(λ), but different neurons use slightly different weights. Gegenfurtner et al. (1994) used stimuli consisting of achromatic gratings of various contrasts and a fixed, high-contrast, red-green, isoluminant grating. The achromatic gratings were displayed either alone or with the isoluminant grating superimposed. If a cell simply responds to the luminance component of the stimulus, its response should be the same to the achromatic and to the heterochromatic grating of the same luminance contrast. Thus, when the luminance contrast is zero, the response should be zero as well. Nearly all cells did exhibit such a zero, or point of isoluminance, but frequently the zero point did not correspond to that predicted by V(λ). For these cells, a small amount of luminance contrast needs to be added or subtracted to the isoluminant grating to obtain a zero response. On the other hand, cells that receive color-opponent inputs should respond well to all color stimuli regardless of their luminance contrast. These cells should not have a null response for any of the chromatic stimuli in this experiment. Only 1 out of 51 cells responded in this manner. Because the individual zero points of MT cells differed slightly, the average response of all MT cells never became zero (Figure 8).

Thus area MT, as a whole, gives responses to isoluminant stimuli, even though it contains few, if any, color-opponent cells. The existence of residual responses at photometric isoluminance (the 0 point on the abscissa of Figure 8) in cortical areas that do not contain many color-opponent neurons has important implications for the interpretation of studies that use isoluminant stimuli to isolate the cortical mechanisms involved in color perception (see Logothetis et al. 1990). If such studies use stimuli that are at photometric isoluminance, they will evoke responses in areas that are expected to remain silent. Even in a typical motion area like MT, there is a clear average response. This observation has been confirmed by fMRI responses in the human MT/MST complex (Tootell et al. 1995, Wandell et al. 1999).

Furthermore, when comparing the average response of MT neurons to the stimuli used by Gegenfurtner et al. (1994) to that obtained in other areas (V1, V2, and V3), no significant differences are observed (Gegenfurtner & Kiper 2003). The response at isoluminance drops to about 30% of the maximal response in all areas. The response does not go to zero and is just as big in MT as in V1 or V2. Because all areas show a clear dip at isoluminance in the population average response, it is not surprising that many perceptual functions show a similar degradation at photometric isoluminance (Livingstone & Hubel 1987b, Cavanagh & Anstis 1991, Kingdom et al. 1999).

In their study of MT responses, Gegenfurtner et al. (1994) demonstrated that the residual color responses produced by macaque MT cells are nonetheless insufficient to account for the animal's perceptual thresholds. A trained monkey can detect drifting, chromatic gratings with color contrasts lower by a factor of three than can be detected by even the most sensitive MT cells (Gegenfurtner et al. 1994).

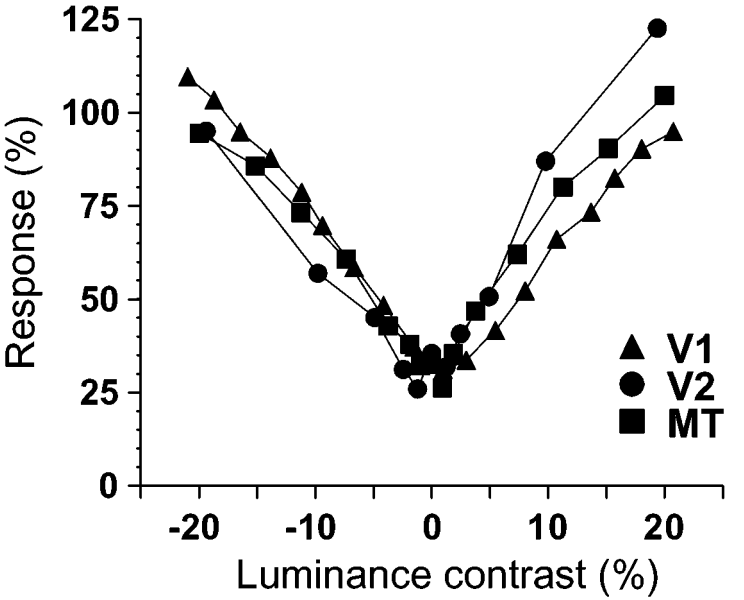

Figure 8 Averaged responses to stimuli with a fixed chromatic—but different luminance—contrasts (see text). Each neuron's baseline firing rate was subtracted from the responses. The responses are plotted relative to the response to the gratings with a luminance contrast of 20%. Negative and positive luminance contrasts on the absicssa indicate that the luminance grating was superimposed in- or out-of-phase with the chromatic grating. Averaged population responses from simple and complex cells in V1 ($N = 319$; courtesy of M. Hawken, personal communication), V2 (averaged across CO compartments, $N = 33$; Kiper et al. 1997), and MT ($N = 51$; Gegenfurtner et al. 1994) are indicated by different symbols.

Thus, although area MT has the potential to see all stimuli irrespective of their color, it certainly does not play a significant role in assigning colors to objects. Other areas more sensitive to color variations are more likely to limit performance in color vision tasks.

One of these areas is V3, which used to be considered the first stage of the dorsal pathway. However, it has prominent connections not only with MT but also with V4, which is part of the ventral pathway. V3 is an area known to contain many direction-selective neurons (Felleman & Van Essen 1987). Indeed, fMRI studies of human subjects show that the human V3 complex is active in numerous tasks, particularly those involving moving stimuli (Singh et al. 2000, Kaas & Lyon 2001). In a recent study of the chromatic properties of V3 in macaque monkeys, Gegenfurtner et al. (1997) used methods similar to those described above (Kiper et al. 1997). Both the proportion of color-selective cells and their properties are similar to what has been found in area V1. About half of the V3 cell population

can code for color. The responses of almost all V3 cells are well described by the linear model, and the preferred color of cells seems uniformly distributed in color space. In contrast to other areas, V3 does contain a significant proportion of cells that are selective both to color and to direction of motion. These cells do respond to moving isoluminant stimuli. These response properties make V3 a candidate area for the processing of motion defined by color. A further characteristic property of V3 is the existence of numerous cells that are mainly responsive to luminance (even at high temporal frequencies) and direction selective, but which receive a small input from S-cones (Gegenfurtner et al. 1997). Similar cells have recently been observed in area MT (Seidemann et al. 1999). A contribution of S-cones to neurons in the magnocellular pathway, however small, could ensure that visual motion can be reliably detected for all possible stimuli, even those containing only S-cone contrast. Psychophysical results confirm this notion (Lee & Stromeyer 1989).

CONCLUSIONS

The perception of color is a central component of primate vision. Color facilitates object perception and recognition and plays an important role in scene segmentation and visual memory. Moreover, it provides an aesthetic component to visual experiences that is fundamental to our perception of the world. Despite its enormous importance, and the long history of color vision studies, much has still to be learned about the physiological basis of color perception. The treatment of color signals in the retina and LGN is relatively well documented, but the existing data on cortical chromatic properties are scarce and often controversial.

There are two possible conclusions one can draw. The first is that a great deal of the processing for color vision is done early, at the stages of the retina and the LGN. The color signal is then transmitted to the cortex, where it undergoes transformations related to the color appearance of the visual stimuli. This contrasts with the widely held view that the form of an object is processed first, with color being subsequently filled in. This view is known as the "coloring book" hypothesis. It is not supported by most recent findings showing that processing of color signals occurs early in the visual pathways, that color is treated by the same populations of cells that analyze other visual attributes, and that computations necessary for functions as sophisticated as color constancy can already take place in primary visual cortex. Color processing occurs at an early level of visual processing and therefore should be important for early visual processes.

The second conclusion is that we need to study mechanisms of color processing in the cortex with higher resolution techniques. Indeed, as described above, most cortical areas, taken as a whole, appear quite similar in their chromatic properties. It is only with careful, quantitative studies of individual neurons' response properties that the particular contribution of each area to color vision can be revealed. The chromatic properties of cells have to be studied more closely, at the level of circuits rather than at the level of columns.

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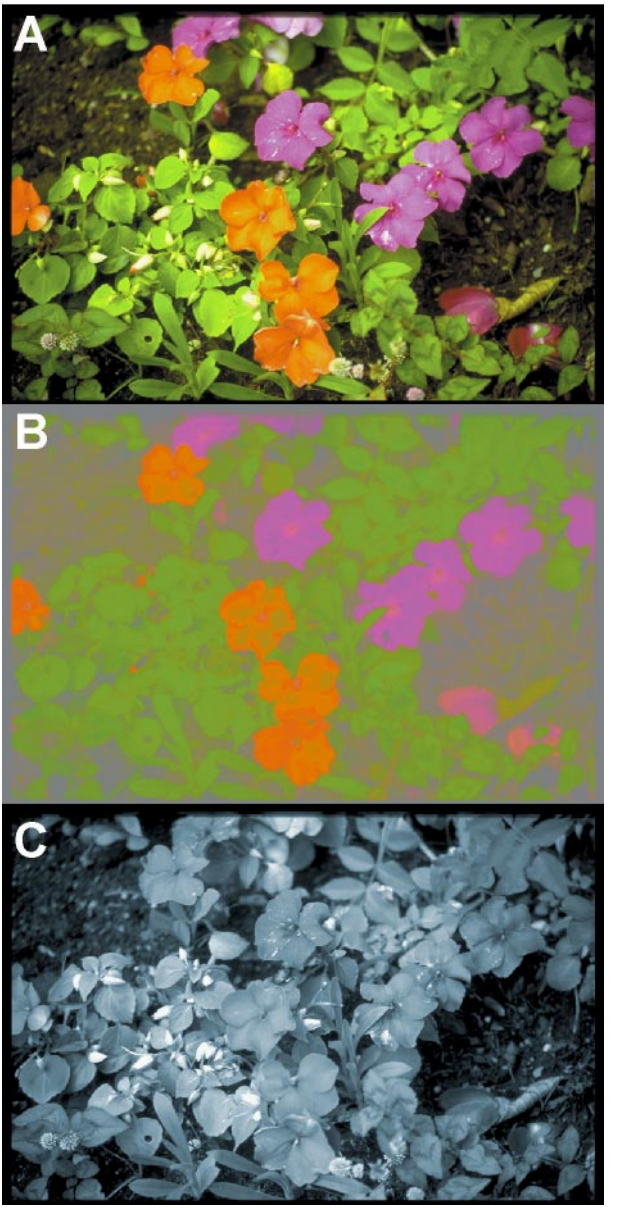

Figure 1 (*A*) Decomposition of a color photograph of a scene with flowers into its (*B*) color and (*C*) luminance components. The isoluminant image (*B*) has the same luminance value across all pixels. Reproduced from Gegenfurtner (2001).

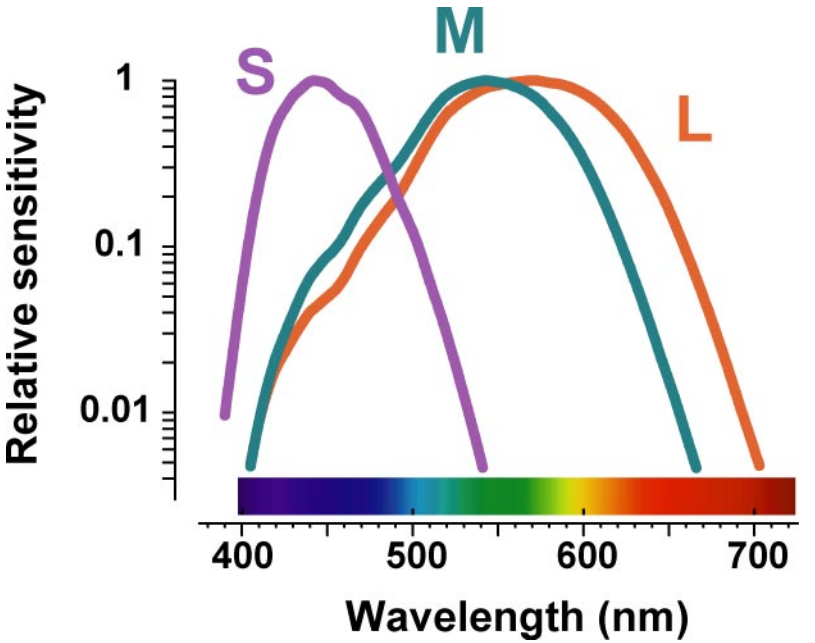

Figure 2 The relative sensitivities of the Short- (S), Middle- (M), and Long- (L) wavelength sensitive cones as a function of wavelength. Each curve was normalized to its maximum. The curves show the cones sensitivity profiles derived by Stockman & Sharpe (2000). The M- and L-cones' sensitivities overlap to a large extent and include almost the entire visible spectrum.

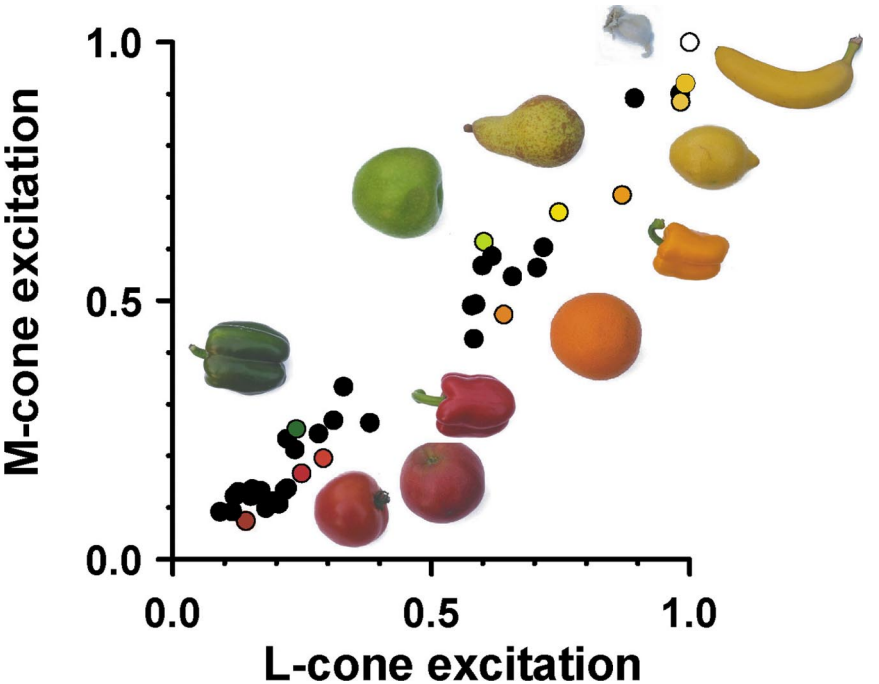

Figure 3 Excitations produced in L- and M-cones by various fruit objects. Measurements were taken in a small area of each fruit with a Photo Research PR 650 spectroradiometer. The spectra were then multiplied with the cone absorption functions and normalized to the maximum excitations in each cone type, which was caused by a clove of garlic (appearing white under daylight conditions).

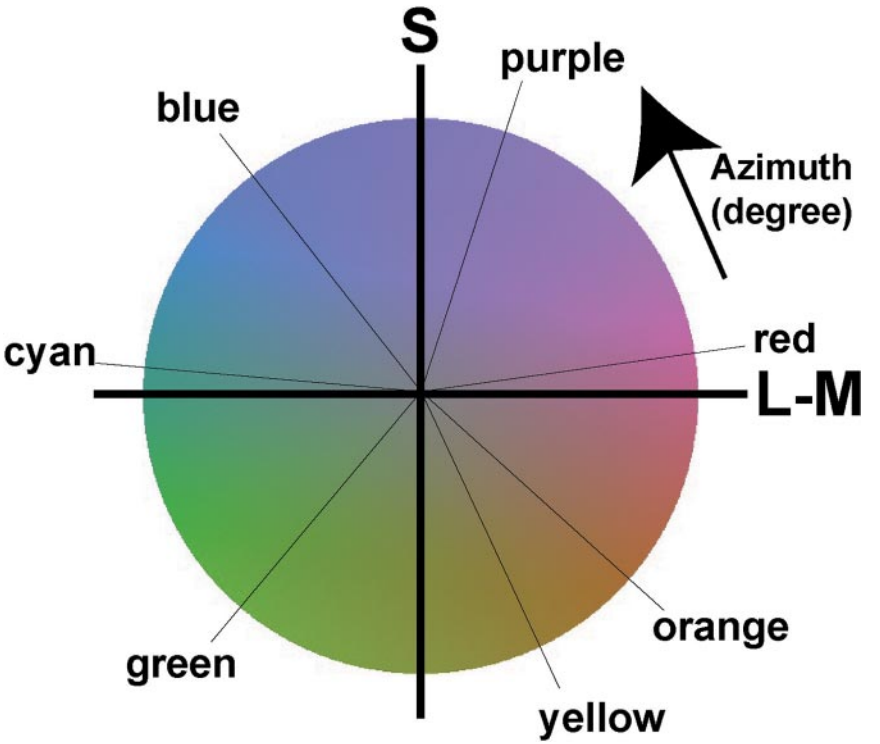

Figure 4 Isoluminant plane of the DKL color space proposed by Derrington et al. (1984). At the center is a neutral white. Along the L-M axis, the excitation of the L- and M-cones covary to keep their sum constant. Along the S axis, only the excitation of the S-cones varies. The thin lines show the location of various basic colors in this space, as determined by a color naming experiment. The DKL color space also includes a luminance (S+M+L, not shown in this figure) axis, going through the origin and perpendicular to the other two. Along the luminance axis, the excitation of the three cones varies in proportion. A light in DKL space is specified by its elevation, the angle between a vector joining it to the origin, and its projection onto the isoluminant plane, and by its azimuth, the angle between its projection on the isoluminant plane and the L-M axis.

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