# Computational Neuroimaging: Color Representations and Processing *

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**Abstract**

Establishing the relationship between neural activity and private experience requires reasoning that links psychological and neural measurements. Because the experimental variables in these two disciplines differ, rigorously linking the data requires a quantitative analysis of the information represented in corresponding psychological and neural measurements. Color appearance is a good psychological domain for working out the link because several quantifiable rules, such as trichromacy, light adaptation, opponent-colors responses, and low spatiotemporal resolution for color, are well-characterized. In this chapter, these fundamental color appearance properties are described. Then, current hypotheses linking color appearance and neural activity are

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Figure 1: Color appearance is a neural computation. When uniformly illuminated, the pair of squares on the left and right send the same number of photons to the eye. The pair on the left appears lighter because neural computations of brightness interpret including information from the surrounding regions, and not just the photon absorptions from the object itself.

discussed. Finally, recent experiments using functional magnetic resonance imaging to analyze the relationship are reviewed.

# Introduction

The brain interprets the retinal image as a collection of objects having various perceptual features, including color, motion, and texture. One important goal of vision science is to discover the computational principles and specific neural mechanisms used by the brain to infer the presence of objects and their properties from the retinal image. This chapter reviews the main ideas concerning how color appearance is derived from the signal encoded within the retina.

Illusions remind us that our visual experience is not a measurement of the physical stimulus, but a rather a neural computation. Some visual illusions offer significant insight into these neural computations. The illusion in Figure 1 demonstrates that even a sensation as simple as brightness is an interpretation of the image and not just a measurement of the number of photon absorptions. The square patches on the left side of the figure appear light; the square patches on the right side appear dark. In fact, the squares patches on the left reflect the same amount of light and cause the same number of photon absorptions as those on the right. The appearances differs because of neural computations.

The illusion suggests that brightness is a perceptual explanation of surface reflectance. The number of photons reflected from an object confounds the reflectance of the object and the ambient illumination level. The brightness of the squares is better explained as a comparison between the patch and the background. If we assume that the background reflectance is constant across the page, this

comparison estimates the reflectance: Were the background constant, the patch on the left would be more reflective than the one on the right. It is a reasonable guess that the neural computations incorrectly treat the large background as uniform and that the difference in photon absorption rates are caused by an illumination gradient. Hence, we experience the two patches as having different brightness even though they send equal numbers of photons to our eyes.

For two reasons, color appearance is a useful model system for exploring the neural basis of visual experience. First, a great deal is known about the biological basis of color encoding in both human and animal vision (Wandell, 1995). Because we understand many of the fundamental rules concerning the encoding of color, we can begin with a firm understanding of how color information enters the visual pathways. Second, when compared to many other visual sensations, color appearance is simple. Color sensations can be well-described using only a few primitive terms – such as hue, saturation and brightness. By studying the neural basis of color appearance, we may be able to deduce some principles about the neural basis of visual awareness.

In this chapter, I will explore some of the current hypotheses of how color appearance is computed within the visual pathways. The first part of this review summarizes the basic principles of color appearance. The second part introduces recent working hypotheses about the neural computations underlying these color appearance principles.

A central conclusion of the chapter is this: information about the wavelength composition of light must be represented throughout much of visual cortex. Information about the wavelength composition of the retinal image is used by neural circuits engaged in image segmentation, object recognition, motion, and other important visual tasks. In this way, color information is part of the vast array of unconscious visual processing. To identify the neural circuitry specifically associated with color appearance, we must identify the specific color signals that share the properties of behavioral color appearance judgments. I will suggest some ways functional magnetic resonance imaging can be used to measure cortical signals in human observers and discriminate neural signals that correlate with appearance from those that provide wavelength information for other visual circuits.

## Principles of color appearance

Human color appearance judgments are based on three fundamental principles: trichromacy, opponent-color representations, and color constancy. This section contains a brief review of these principles and some discussion of their neural basis.

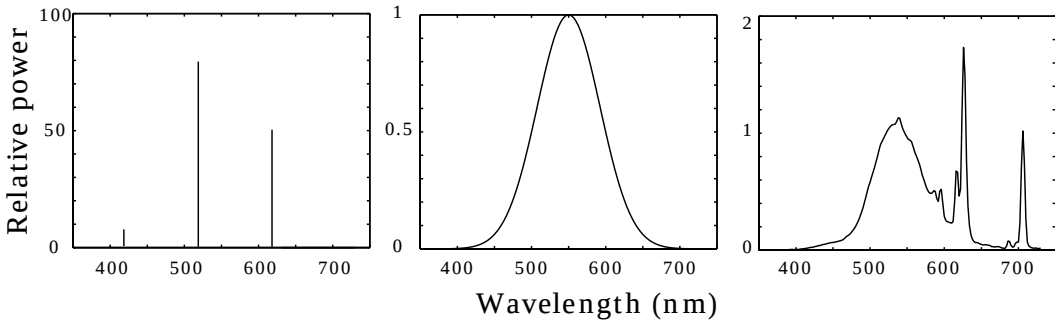


Figure 2: Three different spectral power distributions that have the same color appearance are shown. (A) The sum of three monochromatic lights, (B) a Gaussian spectrum, and (C) light emitted from a typical television monitor.

## Trichromacy

The neural representation of the visual world begins with the responses of four interleaved photoreceptor mosaics: three types of cone photoreceptors. and one type of rod photoreceptor. These mosaics simultaneously encode information about pattern, motion and many other aspects of the visual world. The rods function primarily under very low light levels, where human observers are monochromats, so that any pair of lights can be matched to one another simply by adjusting their relative intensities. Signals initiated within the cones permit us to discriminate between lights of different spectral composition. Hence, in the remainder we will focus on signals initiated by the cone mosaics.

When other factors such as the spatiotemporal properties of the stimuli and ambient viewing conditions are held equal, two lights that cause same number of absorptions in the three cone classes appear identical. Because there are only three cone types, people have only a modest ability to discriminate among lights with different *spectral power distributions.* The spectral power distribution (SPD) of a light source measures how much power there is at each wavelength. The SPD is commonly used to specify the wavelength composition of a light. When studying color vision, spectra are ordinarily specified over a range from about 370 to 730 nanometers (nm). Figure 2 shows the spectral power distributions of three lights that, despite the obvious differences in their SPDs, cause the same number of cone absorptions. These lights are metameric to one another.

Two lights that cause the same number of absorptions in each cone class, but have different spectral power distributions, are called *metamers.* With only a few caveats, it is possible to arrange a match between any test light and a second light that is the sum of three, fixed, primary lights. The ability to arrange a color match using three primary lights is called *trichromacy* and flows from the presence of three cone types. Because photopigment absorptions follow nearly linear rules over a large range of

intensities, it has been possible to develop a complete characterization of the set of metameric lights. The ability to control and create metamers is a key aspect of most color reproduction technologies (Brainard 1995; Wandell, 1995).

The trichromatic character of color-matching is a fundamental principle color appearance. But there is no immediate connection between color-matching and common color appearance terms, such as hue terms like red and green, or general terms like light and dark. This is because many factors, including the spatiotemporal structure of the stimulus and the ambient background, strongly influence the perceived color appearance. Thus, the retinal encoding by three cone types defines a fundamental limit on the range of color experiences, but there is much more to be understood about color appearance than simple matching.

To see this point, consider that during the color-matching measurements the observer never describes the stimulus appearance, but only establishes a match between a pair of stimuli. The difference between setting match and judging appearance is implicit in Figure 1. Suppose that we set a color match between a pair of square targets, such as the upper and lower squares on the left. These two squares cause the same pattern of cone absorptions, so they still match in appearance when they are shifted to the right. While the match between the two squares is preserved, the color appearance of both squares changes. Hence, from the point of view of color-matching nothing changes as the position shifts from the left to right. From the point of view of color appearance, there is a significant change.

Thus, a theory of color appearance requires more information than a theory of color matching. Matches between two common spatial temporal patterns, seen within a common framework, can be explained by knowing only the light absorptions within the cone outer segments. But, measuring and explaining color appearance requires much more.

## Opponent colors

A second key concept in color appearance is our inability to experience certain hue combinations. While logically possible, these hue combinations are beyond the scope of our neural apparatus and are never offered as a visual explanation of the retinal image. These forbidden color combinations are called *opponent-colors*.

To understand this phenomenon, first consider a pair of color sensations that can co-occur, red and yellow. We have no difficulty perceiving these two components within a single color; orange is the common name for such a color. Nor do we have any trouble identifying hues that appear both reddish and bluish at the same time; purple is the common name for such a color. But, observers never identify a hue as being reddish and greenish at the same time. Similarly, people never report seeing a color that is yellow and blue at the same time. A spot may appear yellow *or* blue or

neither. But a spot never appears yellow *and* blue. There is no logical or physical reason that there should be such opponent-colors. The cause must be how the brain encodes color appearance.

Since Hering's (1905) initial description of opponent-colors, there have been many behavioral and theoretical studies of opponent-colors. One way to demonstrate the significance of an opponent-colors representation is to ask subjects to name the colors of spectral test lights. The words red and green are essentially never used together, nor are the words blue and yellow. Other combinations, such as red and yellow, do occur frequently (Boynton and Gordon, 1965).

A second way to see the effects of the opponent-colors representation is to measure the detection threshold of various colored test lights. The points in Figure 3 show the L and M cone contrast levels at detection threshold, and the solid curve is an ellipsoid drawn through these points. These data were measured using a spatially blurry spot whose contrast increased and then decreased slowly over time, as shown by the insets.

To understand why these data suggest a powerful opponent-colors signal, consider how much contrast is needed to see an L cone stimulus, and M cone stimulus and an L plus M cone stimulus. A test light that excites only the L or M cones can be seen at less than 1 percent contrast. But a test light that excites the L and M cones together requires 6 percent contrast in both cones, considerably more. Hence, stimulating the M cones reduces the visibility of an L cone signal. This opposition of the signals suggests an L-M opponent-colors neural representation. Other sensitivity measurements also suggest a blue-yellow opponency (e.g., Pugh, 1976; Pugh and Mollon, 1979; Mollon, 1982).

Behavioral experiments suggest that color information is represented in an opponent-colors a format comprised of three neural pathways. One pathway encodes the red-green dimension of color. An increase, say, of activity in this pathway corresponds to a red percept while a decrease of neural activity corresponds to a green percept. A second opponent-colors pathway represents blue-yellow, and a third neural pathway represents light-dark. This neural format explains opponent-colors appearance: If different sensations are coded by increments (red) and decrements (green) within a single set of neurons, then red and green cannot be experienced at the same location and time. Similarly, blue and yellow are a forbidden combination.

To study one of the three neural pathways, it is necessary to silence the other two. To do this, it is essential to identify the set of stimuli that *fail* to excite each pathway. Then, by finding a signal that fails to excite, say the red-green and the light-dark pathways, we can isolate the blue-yellow pathway. A stimulus that appears neither red nor green is said to be in red-green equilibrium. Such a stimulus might appear blue, yellow, or a achromatic.

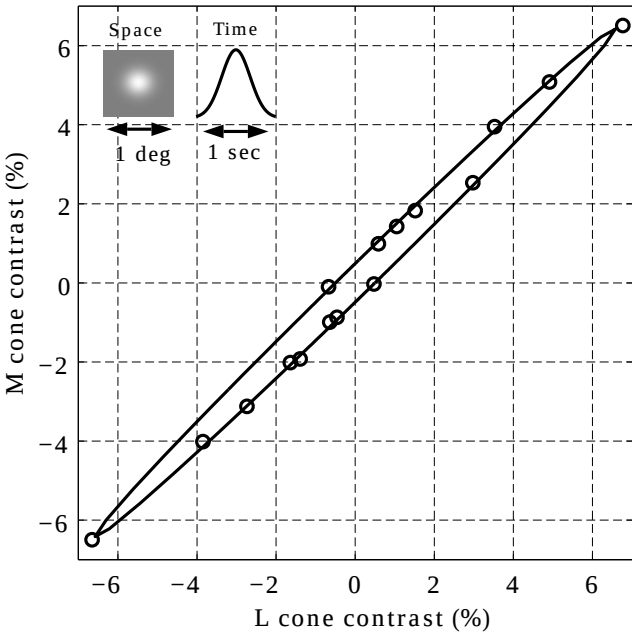


Figure 3: Detection threshold contour for colored stimuli. The horizontal and vertical axes measure L and M cone contrast levels. Threshold measurements are shown by the open points. When the stimulus modulates only the L cones (horizontal axis) or only the M cones (vertical axis), threshold is much lower than when the stimulus modulates both the L and the M cones (upper right direction). The lowest cone contrast levels occur when the L and M cones are modulated with opposing signs (upper left direction). The solid curve shows an interpolated ellipsoidal curve. The insets in the upper left show spatial and temporal representations of the test stimulus. Source: Wandell, 1985.

The collection of red-green equilibrium stimuli can be characterized using simple geometric figures. To see how, first consider Figure 4A. This drawing shows a method of representing colored stimuli as three-dimensional points. In the representation used in this figure, the stimuli are described in terms of the red, green and blue phosphors intensities, relative to the background. Second, consider a surface that passes through the points representing stimuli red-green equilibrium stimuli; Figure 4B shows four different views of such a surface. This red-green equilibrium surface divides those stimuli that appear reddish (concave side) from those that appear greenish. The surface is shaded to suggest the bluish and yellowish appearance of the equilibrium stimuli. Because the equilibrium stimuli appear neither red nor green, they should be invisible to neurons coding red-green color appearance. Hence, the shape of this surface can be used to identify the properties of neurons that might carry the opponent-colors appearance signal for red-green. ( Burns et al., 1984; Chichilnisky and Wandell, 1995; Ejima et al., 1985; Mausfeld and Niederee, 1993).

**Spatial resolution.** Based on these and other opponent-colors measurements, it is possible to present observers with simple patterns that stimulate one of the three color pathways and fail to stimulate the other two. By isolating such mechanisms, it is possible to study their spatial and temporal properties. Studies of the spatial sensitivity of the red-green and blue-yellow pathways demonstrate that opponent-colors pathways have very poor spatial resolution compared to the light-dark pathway. Consequently, fine spatial patterns (higher than 30 cpd) invariably *appear* to be a light-dark variation around the mean no matter what their true physical composition. Red-green spatial variation does not exceed roughly 20 cpd (correcting for the optics) or 10 cpd (through natural optics). Blue-yellow spatial spatial variations extend only to 5 or 6 cpd. Figure 5 summarizes measurements of spatial sensitivity of the red-green opponent-colors pathways from three different laboratories.

At high spatial frequencies, observers have reduced contrast sensitivity to the red-green patterns compared to light-dark patterns. At low spatial frequencies, observers are relatively more sensitive to red-green targets. The same spatial frequency dependence holds for the blue-yellow opponent-color dimension. The poor spatial responsivity of the eye to color is a very large effect. Consequently, it is used widely to create efficient image representations in color imaging applications (Zhang and Wandell, 1996, Zhang et al., 1997). Hence, the spatial resolution of a neural population should serve as a useful marker for identifying the population of neurons carrying the opponent-colors signals. Neurons carrying the blue-yellow opponent colors image should have relatively large spatial receptive fields and their receptive field centers should sample the retinal image sparsely. Neurons carrying the light-dark image should have small receptive fields and sample the image finely. Neurons carrying red-green information should have an representation intermediate

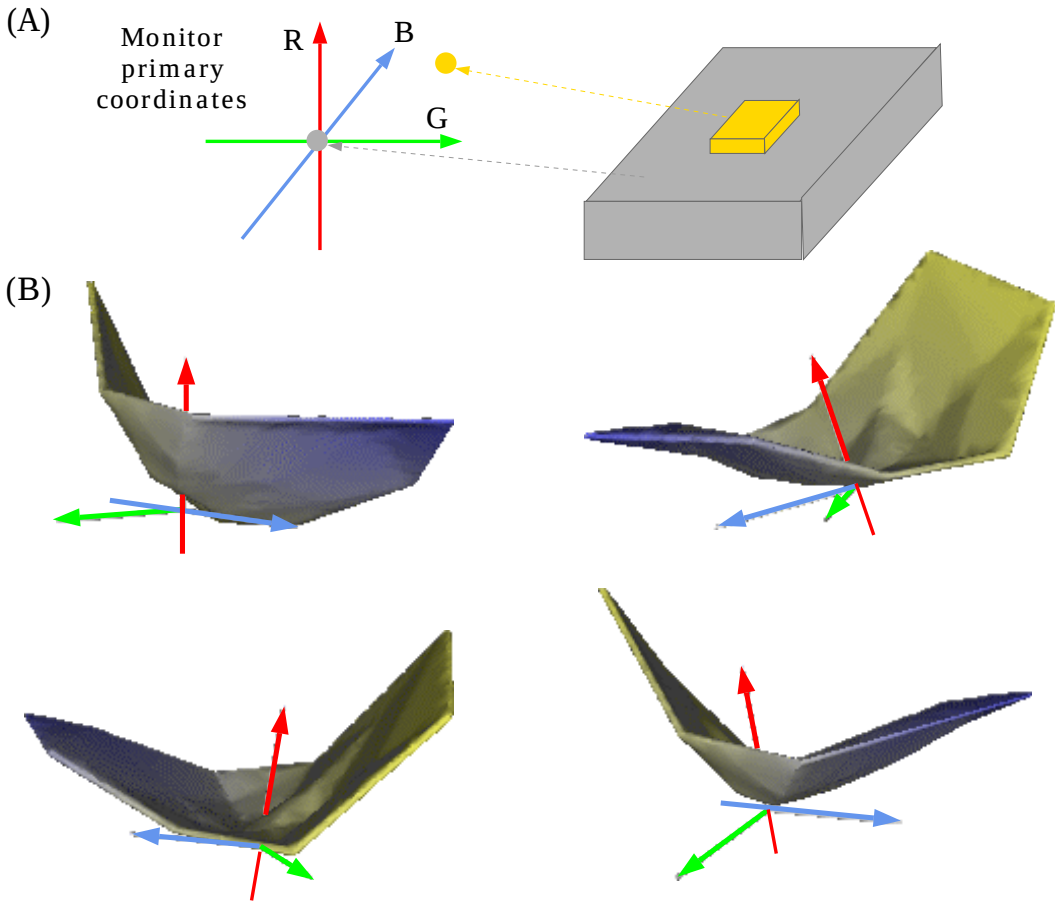


Figure 4: A geometric description of colored stimuli that appear neither red nor green. (A) The test stimulus is a square patch shown on a uniform background. The background is plotted at the origin of the three-dimensional coordinate system. The test stimulus is represented in a three-dimensional color space in terms of the intensities of the three display primaries relative to the background. The arrows on the three axes indicate the direction of increasing intensity. (B) A surface passing through red-green equilibrium stimuli is shown from four separate views. Stimuli represented on the surface appear blue, yellow, or achromatic. The surface is shaded with these colors to provide a rough guide about their color appearance (Source: Chichilnisky and Wandell, 1999)

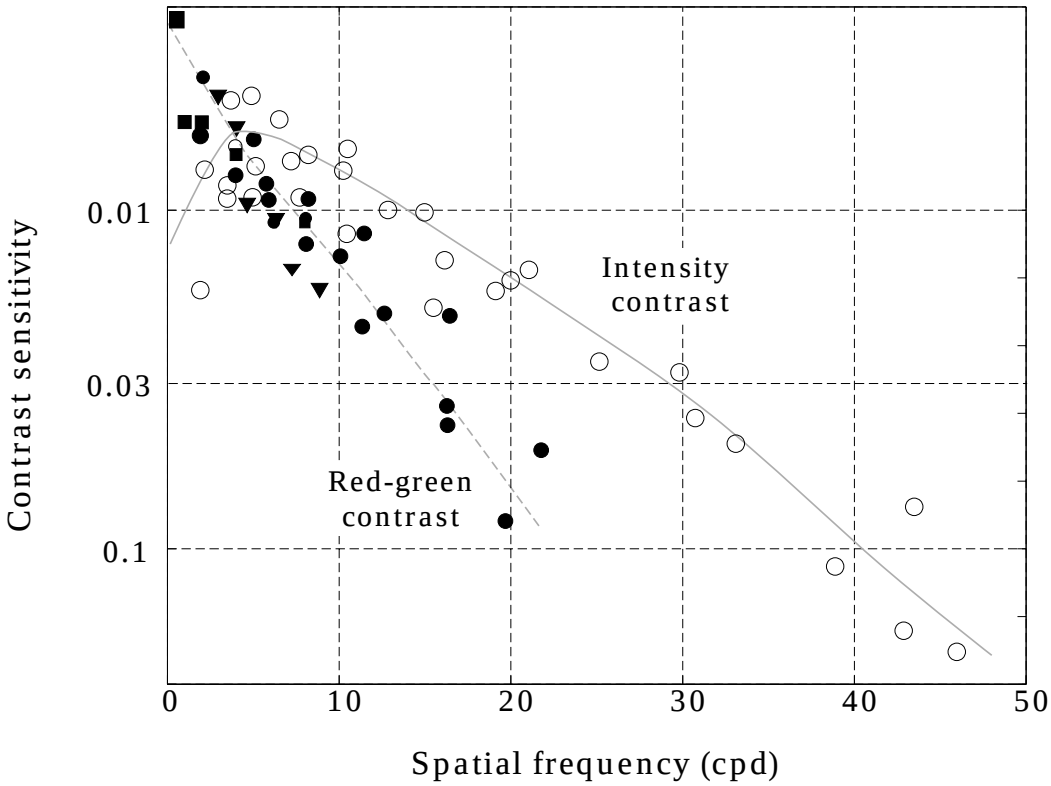


Figure 5: Comparison of red-green and intensity spatial contrast sensitivity functions. The filled symbols show contrast sensitivity measurements made using stimuli visible mainly to the red-green opponent-colors mechanisms. The data from Anderson et al.(1991; inverted triangles) and Sekiguchi et al. (1993; circles) show absolute contrast. The data from Poirson and Wandell (1993; squares) were obtained using a method that does not permit estimation of the absolute sensitivity. These data have been shifted vertically and should be compared only with respect to the fall-off in sensitivity. Measurements by Sekiguchi and Anderson et al. compensated for the chromatic aberration of the eye. The Poirson and Wandell measurements did not, but at the relatively low spatial frequencies (below 7 cpd) where the three data sets overlap red-green chromatic aberration is not a large factor (Marimont and Wandell, 1993). The open circles show contrast sensitivity measurements from three observers to light-dark patterns (Sekiguchi et al., 1993). The shaded curves were drawn by hand to emphasize the higher spatial resolution of the light-dark variation measurements.

between the other two populations.

## Contrast, adaptation, and constancy

A third fundamental aspect of color is that appearance depends strongly on the spatial and temporal context (see e.g., Figure 1). The significance of the spatial and temporal context for color appearance judgments represents an important part of the computational structure of the visual pathways.

Various contextual conditions influence color appearance, and several of these conditions have been given special names. Changes in appearance caused by the immediately surrounding spatial region are usually called *contrast* effects. Appearance effects caused by the eye's adaptation to large, steady backgrounds are called *color adaptation* effects. Appearance shifts caused by changes in the ambient illumination used to view a collection of surfaces are called *color constancy* effects. These stimulus conditions are commonly separated in the literature; but, there is no powerful evidence to show whether these effects are produced by different or similar neural mechanisms.

As stimulus conditions, color adaptation and color constancy have much in common. Both are appearance changes caused by a contextual shift that is spread over large regions of the image and that is stable across time. One important difference between the two conditions is that adaptation is usually associated with conditions in which the target is presented on a uniform background, while color constancy involves a patterned background. Given the significance of edges for visual perception, this difference may be important. There is no widely agreed upon method for incorporating both pattern and illumination variation in a single theory. But, some general rules have been observed in cases in which there are relatively few edges in the image and the main effects we must explain are the change in the characteristics of the illumination.

The visual pathways adapt to illumination level changes that span many orders of magnitude and very large changes in the illuminant spectral power distribution. Thus, both the the overall level of absorptions and the relative cone absorption rates from a surface change under different illuminants. In recent years, a number of studies have shown that the appearance changes caused by changes in the intensity or spectral composition of a uniform background can be approximated by simple rules that modestly extend a proposal from J. von Kries, made in the early 20th century, and sketched in Figure 6 (von Kries, 1902).

Consider the simple visual stimulus shown in Figure 6. The stimulus is comprised of a uniform background field and a superimposed target. In this case the target is shown as an increment, though in other cases it might be a decrement of the mean field. Modern explanations of von Kries adaptation explain how the background

and target interact by assuming that based on spatial and temporal properties the target causes one signal in the photoreceptor array, shown by the main signaling path in the figure. Photons from the background establish the gain, say $G_L$, $G_M$ and $G_S$ of the three cone pathways in the main signaling path. For example, increasing the background absorptions in the L cones, reduces the gain in the L cone signal.

It is worth spending a moment to consider the implications of this hypothesis rigorously. Stating the rule using symbols is important because the rule contains some surprising subtleties. Suppose that a target, t, is presented on a background, B. Suppose that the background causes a mean level of cone absorptions, (L,M,S), which must be all positive. The target causes a change in the mean level of (l,m,s), and these values may be negative, positive, or zero. Von Kries' suggested that *any* target t seen on background B will match a second target, t' = (l',m',s'), seen on a second background, B' = (L',M',S'), when the target cone absorptions are related by

$$l'/l = G_L/G_{L'}, m'/m = G_M/G_{M'}, s'/s = G_S/G_{S'}$$

One important part of this hypothesis is this: The cone absorptions ratios, say $l'/l$, are the same for any pair of matching lights seen on backgrounds B and B'. Hence, many different matches can be predicted once we know the scalar values associated with each cone class. The von Kries hypothesis has been tested on several occasions and serves as a good approximation (Bäuml, 1995, Brainard and Wandell, 1992; Chichilnisky and Wandell, 1995).

There is a second important part of the hypothesis that has been rarely studied: How do the gain values, $G_L$, depend on the background photon absorptions? As the hypothesis is drawn, the value of $G_L$ depends only on the L cone signals. Hence, with this form of the hypothesis test matches can be predicted by scaling within cone types. It may be the case, however, that the gain values depend on the backgrounds in more complex ways.

The two parts of von Kries hypothesis are open to empirical examination. When measured on simple, uniform backgrounds, the first part of von Kries hypothesis holds well for decremental targets and coarsely for all targets. Significant improvements in the predictions of color matches can be obtained by applying different rules to incremental and decremental test targets (Chichilnisky and Wandell, 1996; Mausfeld and Niederee, 1993). The further problem of understanding how the gain factors depend on the spatial pattern of the background or the scene interpretation is not understood.

While open problems remain, enough is known about adaptation on uniform backgrounds so that one can make preliminary comparisons between neural and behavioral measurements. The predictions of von Kries adaptation are powerful, and we may find that not all neural substrates follow its form. Hence, von Kries can be very helpful when we seek those neural substrates that mediate color appearance.

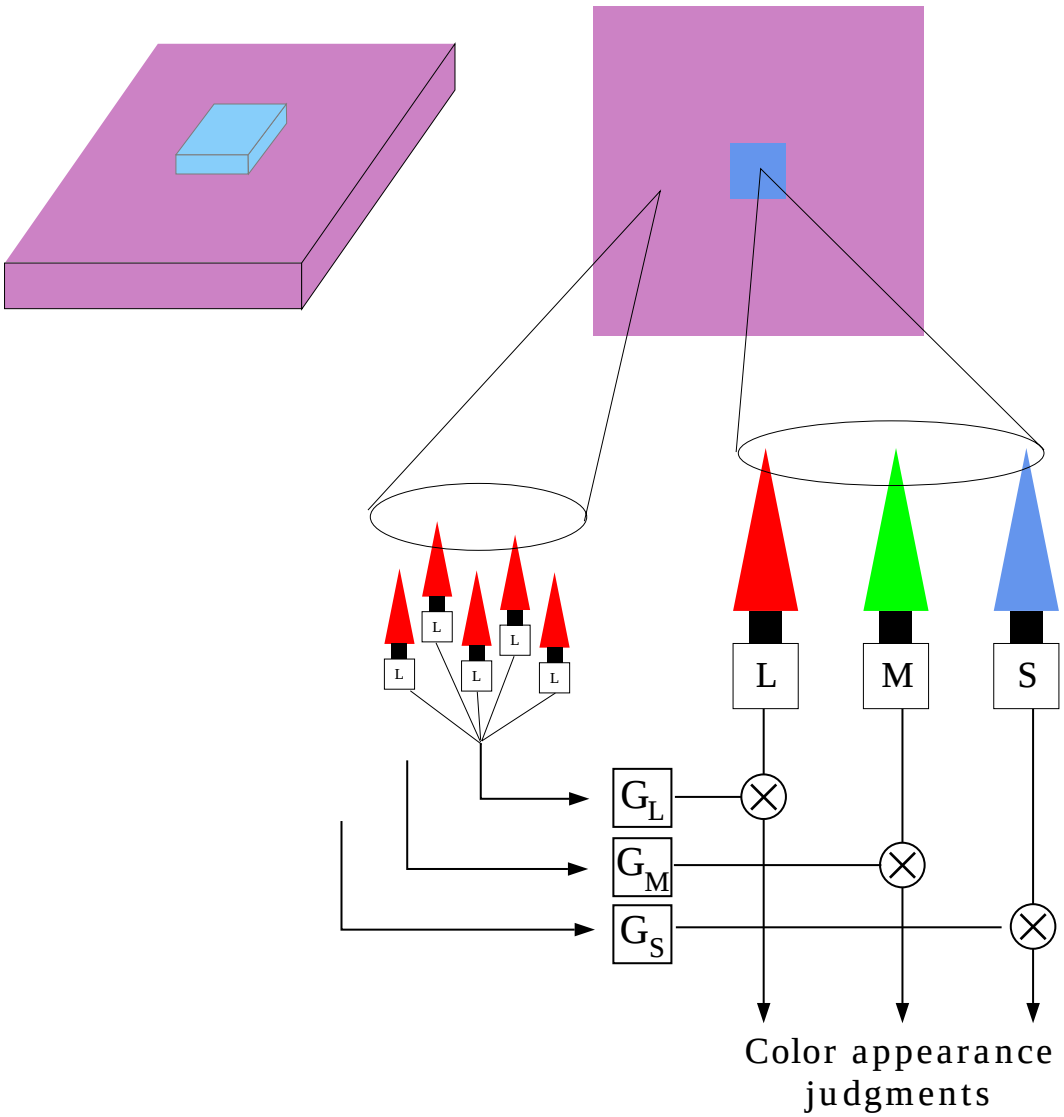


Figure 6: Schematic of the von Kries model of adaptation. The stimuli are shown as a uniform background field and a small incremental test. Light from the background establishes the gain of the cone signals. Light from the test perturbs the cones. In this version of von Kries adaptation, only background photons absorbed in the L cones influence the gain of the L test signal, and incremental and decremental signals are treated the same. Neither of these assumptions is precisely correct (e.g., Chichilnisky and Wandell, 1996; Mausfeld and Niederee, 1993).

# The neural basis of color appearance

Two main hypotheses that have been proposed concerning link between neural activity and color. One hypothesis emphasizes the flow of information from the retina into cortex. The second emphasizes regions in cortex that may play a special role in color perception.

## Retinal origins

Information is sent from the retina to cortex along several distinct populations of neurons, or pathways. These pathways can be distinguished based on the morphology of the cells, their connections within the retina, and their central projections (see Figure 7). At present, three fundamentally different pathways have been clearly established. The *P pathway* leaves the retina via the midget ganglion cells. These cells comprise both on- and off-center neurons, and both on- and off-center cells are driven by the single foveal L and M cones. Based on anatomical studies, it appears that the S cones appear to contribute only to an off-center midget ganglion cell (Klug et al. 1993). It appears, though is not yet certain, that the opposing surround signal is controlled by signals from a mixture of the other cone types (Sterling 1998; but see Reid and Shapley, 1992). The midget ganglion cells project to the parvocellular layers of the lateral geniculate nucleus, and then to layer 4Cb of primary visual cortex.

The M pathway leaves the retina via the parasol cells. These neurons projects to the magnocellular layer of the LGN. The L and M cone signals contribute with a common sign to both the center and surround responses of neurons in the M pathway. The output of the parasol cells is sent to layers 4Ca and 4B of primary cortex.

The *K pathway* leaves the retina via the *small bistratified retinal ganglion cells.* These neurons receive an excitatory S-cone center and an inhibitory L and M cone surround. They project to *koniocellular* layers of the lateral geniculate nucleus, layers that fall in between the parvocellular and magnocellular layers. The neurons in the koniocellular layers project to the superficial layers of visual cortex.

The receptive field and anatomical connections of neurons within these pathways suggest they each have different specializations for transmitting color information. The clearest association is between the K pathway and blue-yellow color appearance. In addition to their opponent-colors signal between the S and (L,M) cones, these neurons also have low spatial resolution (Dacey and Lee, 1994; Sterling,1998).

It is often said that color is coded by the P-pathway, and luminance is coded in the

Pathway properties

| Pathway | Cone inputs | Ganglion cell type | LGN layer | V1 input layers |
|---|---|---|---|---|
| P | central: single L,M,S center, mixed surround<br>peripheral: mixed center, mixed surround | midget | parvocellular | 4Cb |
| M | LM center and surround | parasol | magnocellular | 4Ca |
| K | S on<br>LM off | small bistratified | koniocellular | 2,3 |

Figure 7: Some properties of the parvocellular, magnocellular, and koniocellular pathways.

M-pathway (e.g., Spillmann and Werner, 1990). The principal experimental evidence for this hypothesis is that foveal midget ganglion cells centers are driven by signals from a single cone while the surround is driven by an opposing signal that includes the other cone type. Thus, an L cone center midget cell receives an opposing M cone signal from the surround. The opponency between the L and M cone signals can be measured using large stimuli that cover both the center and surround of the receptive field (Derrington, Krauskopf and Lennie, 1984). Neurons in the M pathway are not a candidate for representing an opponent-colors signal because they receive a mixture of L and M cone signals in both the center and the surround. Moreover, their properties seem very well-suited to carrying high temporal frequency information called the *luminance* signal (Lee et al., 1990; but see Smith et al., 1992).

There are some problems with this segregation of tasks between the P and M pathways. First, the number and spacing of the mosaic of neurons making up the P pathway is significantly higher than any other retinal mosaic. In the fovea, for example, each cone sends its output to two neurons in the P pathway (one on- and one off-signal). In fact, the midget ganglion cell mosaic that carries the P pathway signal contains 70% of the 1.25 million human retinal ganglion cells (Rodieck, 1998). Consequently, this mosaic is the only one that can represent the high resolution signal used for achromatic vision. Second, it seems likely that neurons in the K pathway carry blue-yellow signals. This pathway contains a full representation of

the visual field, and the spatial receptive field of the pathway matches the blue-yellow signal well. Third, it is odd to argue that the P pathway represents all of blue-yellow color vision given that it contains only an off-center S-cone driven cell type and the primary on S-cone signal exits via the K-pathway.

At present, there appear to be several possibilities concerning the distribution of color signals. First, the blue-yellow signals may be carried on both the P and K pathways. Second, a new retinal pathway carrying the red-green signals may be found. Third, the signals within the P pathway may code both achromatic and red-green signals and the perceptual red-green representation may be formed through a recombination of these signals in cortex. For example, if P-pathway neurons with L and M cone inputs can be distinguished at the level of cortex, then P-pathway signals could be recombined to create both a light-dark and a red-green representation (Ingling and Martinez, 1983; Lennie et al., 1990). What the basis for this discrimination between these types of neurons might be, and how the cortical creation of achromatic and red-green signals can be integrated with other novel cortical receptive field properties such as direction selectivity, orientation and disparity tuning, remains to be worked out.

## Cortical centers.

The second widely discussed hypothesis about the neural basis of color is that there is a cortical "color center." A cortical center for a perceptual feature, such as color or motion, means that visual experience of that feature is represented by the activity of the neurons within that center (Zeki, 1990; Zeki 1993).

In monkey, two cortical locations have been suggested for a putative cortical color center. Zeki has argued that in monkey area V4 is the color center because single-unit recordings in area V4 CO-varied with color appearance, and not the wavelength composition of the test light (Zeki, 1993). These measurements have not been repeated, and there has been some disagreement concerning V4's role in color (Schein and Desimone, 1990). For example, Cowey and Heywood (1995) have convincing evidence that area V4 is not essential for color constancy, an important appearance task. They suggest that processing in a nearby area, TEO, is essential.

The modern focus on a human color center is rooted in a seminal paper by Meadows (1974) who reviewed descriptions of individuals with cerebral disturbances of color appearance. Several different types of disturbances exist, and he sketched a pathway and lesion sites where damage might impair performance on several different types of color tasks, including discrimination, appearance language. Human neuropsychological and neuroimaging measurements suggest that damage to a cortical region on the ventral surface of the occipital lobe, in the fusiform gyrus, interferes with normal color processing (Meadows, 1974; Zeki, et al., 1991).

Neuroimaging studies about this hypothesis are reviewed below.

## FMRI measurement methods

By juxtaposing the retinal and cortical hypotheses, one can see that to understand the neural basis of color appearance requires tracing the flow of information from retina through cortex. Selecting stimuli that preferentially stimulate one retinal pathway or another, and then measuring the color responses across cortex, can provide important data for a general theory of the neural basis of color appearance. But, how can we trace the neural activity of the color pathways in the human brain?

Functional magnetic resonance imaging (fMRI) is a neuroimaging method that can be used to make inferences about the neural activity in the alert, performing human brain. The physical basis of the method, as well as some recent advances, are reviewed elsewhere ( Moseley and Glover, 1995; Tootell et al, 1996; Wandell, 1999). Briefly, the fMRI signal is an indirect measure of neural activity. The fMRI signal varies as a function of the local blood oxygen content which, in turn, covaries with modulations in the neural activity. In some portions of the brain, particularly near primary visual cortex, changes in blood oxygen mirror the spatial pattern of neural activity at a spatial resolution of less than 2 mm (Engel et al., 1997a). The signal to noise ratio (SNR) of the fMRI signal is somewhat higher than earlier neuroimaging methods, and it can be used to measure stimulus-response functions of active cortical regions in the brains of individual subjects.

To integrate fMRI measurements with the extensive literature on the activity of single-units in monkey brain, it is useful to co-locate the neuroimaging measurements with visual areas. The spatial resolution of fMRI and certain advances in visualization methods have made it possible to identify retinotopically organized visual areas in individual observers' brains (DeYoe, 1996; Engel et al., 1997a; Sereno and Dale, 1995; Smith et al., 1998). Hence, the neuroimaging results can be compared to single-unit measurements from corresponding areas in animal models.

Two developments have made identification of retinotopically organized areas possible. First, a simple class of stimuli have been developed to permit efficient measurement of the retinotopic organization in several visual areas (Engel et al., 1994). Second, novel methods for visualizing the spatial distribution of activity on the cortical surface have been developed (Dale and Sereno, 1993; DeYoe et al., 1996; Drury et al, 1996; Engel, et al., 1997; Goebel, 1996; Teo et al., 1997). The visualization methods permit one to to segment gray and white matter and reconstruct three-dimensional images of the gray / white boundary (Figure 8A). Using the segmentation it is proven useful to create flattened representations of the gray matter in order to appreciate the retinotopic organization (Figure 8B). In those cases described below when a visual area is mentioned, its location was determined using

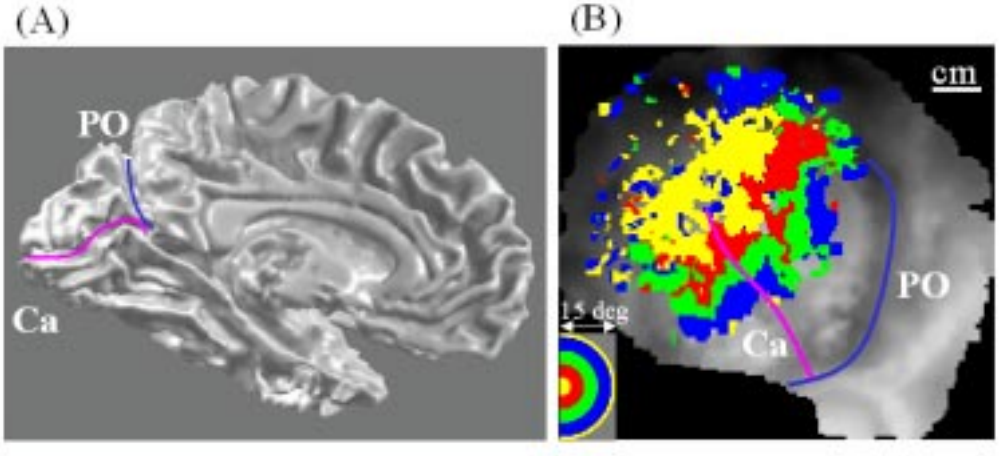


Figure 8: Methods of visualizing the human brain. (A) A three-dimensional rendering of the gray/white boundary of a human brain is shown. The rendering was created by segmenting gray and white matter and creating a connected representation of the gray matter (Teo et al, 1997). This medial view shows the location of the calcarine (Ca) and parieto-occipital (PO) sulci. This image was created using software developed by R. Taylor in our laboratory. (B) Distances within the connected gray matter can be measured using Dijkstra's algorithm. From these distances, it is possible to create a flattened representation of the gray matter that a minimizes the difference between distances measured along the curved gray matter surface and distances on the flattened representation. The underlying gray image represents the gray matter, shaded so that light and dark measuring position along the medial to lateral axis. The colored overlay shows the retinotopic organization with respect to distance from fixation (see the legend at the lower left). A description of the methods as well as software for segmenting and flattening can be obtained from the web-site (http://white.stanford.edu/wandell.html).

retinotopic mapping and flattened representations.

## Color fMRI measurements

Zeki et al. (1991; McKeefry and Zeki, 1997; Sakai,et al. 1995) have used both PET and fMRI to measure color-related activity in the human brain. In a widely cited set of papers, they measured the difference in activity caused caused by an achromatic and colored stimulus (Lueck, et al. 1989; McKeefry and Zeki, 1997;Zeki et al., 1991). The achromatic version of the spatial stimulus is shown in Figure 9A, and the colored version has the same lightness but adds various hues. The initial reports were that "the only area showing a significant change of activity was in the region of the

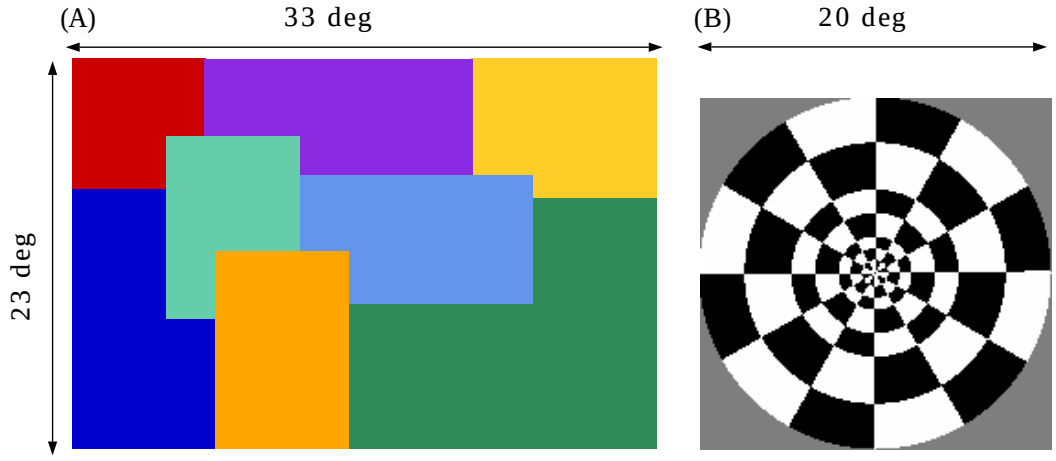


Figure 9: The spatial structure of (A) the Mondrian stimulus used by McKeefry and Zeki (1997) and (B) the contrast reversing checkerboard used by Engel et al. (1997b).

lingual and fusiform gyri. This area lies outside the striate cortex and is the same area implicated in achromatopsia (cerebral color blindness) [Zeki et al., 1991]".

This report was puzzling for the following reasons. The achromatic and colored stimuli have equal achromatic signals but different opponent-colors signals. Hence, if we accept the logic of the subtraction methodology, comparisons of the activity caused by the two stimuli should produce activity in all brain regions that respond to opponent-colors signals. The absence of an opponent-colors signal in early cortical areas is puzzling because the parvocellular and koniocellular pathways should respond to such a signal, and these pathways represent a large fraction of the neurons in primary visual cortex. Why wasn't their response measured? The absence of a signal in primary visual cortex poses the further question of how these opponent-colors signals reach the fusiform gyrus on ventral occipital surface?

This puzzle has been solved by new results from several laboratories showing that opponent-colors signals can be measured in early visual areas (e.g., Kleinschmidt, et al., 1996; Engel et al., 1997b; McKeefry and Zeki, 1997; Tootell et al., 1998). For example, Engel et al. (1997b) showed that for certain stimuli, the most powerful responses in area V1, per unit cone contrast, are caused by lights that excite opponent-colors mechanisms.

Figure 10A shows the color tuning measured in area V1 using a contrast reversal rate of 1 Hz and with with the spatial pattern shown in Figure 9B. The color tuning is plotted using a format that can be compared with behavioral detection thresholds (see Figure 3). The solid line in the fMRI color tuning curve shows the L and M cone contrast levels that produced the same fMRI signal. The dashed curves are 80 percent confidence intervals. The iso-response curve qualitatively matches the detection threshold contour measured with the same stimulus.

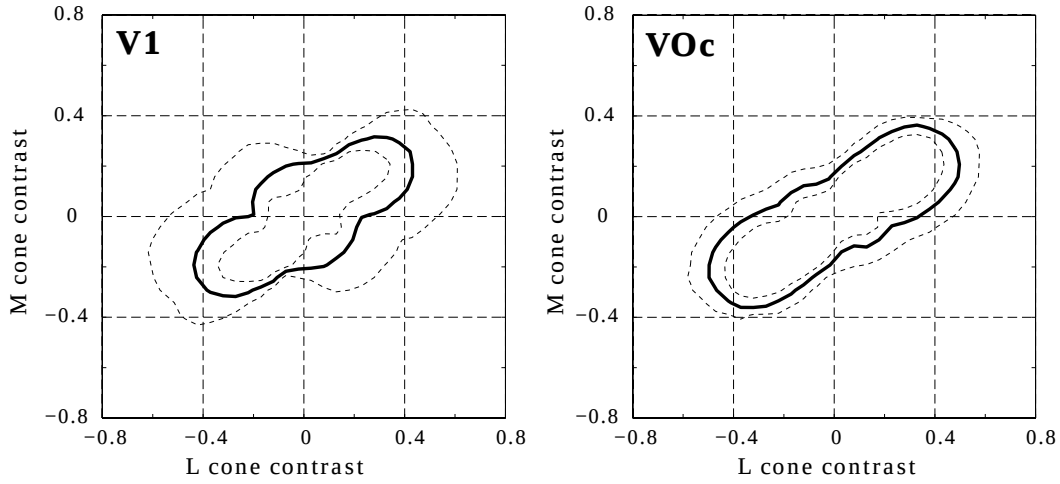


Figure 10: Comparison of the color tuning in area V1 (left panel) and an active region located in the ventral occipital region, VOc (right panel). The solid curves show stimuli that evoked an equal fMRI response. Stimuli with opposing L and M cone contrasts (opponent-colors signals) are more effective at evoking a response than stimuli with covarying L and M cone contrasts. The two regions share a common color tuning; separate measurements suggest that the signal in VOc is slightly stronger.

The original observation of a strong response to chromatic signals within the fusiform gyrus is also confirmed by all groups, and studies of this region may tell us more about the flow of cortical color signals. The retinotopic organization of this region has been probed by McKeefry and Zeki (1997) and by Tootell et al. (1998). Both groups find that this location on the ventral occipital surface represents and entire hemisphere. The main difference in their analysis is that McKeefry and Zeki refer to the area as V4, in homology with monkey V4. Tootell et al. (1998) suggest the color responsive area falls beyond the fourth retinotopically organized human area and that it should be called V8, and not V4. For the present, the neutral and temporary name *VOc* will be used to refer to the location in ventral-occipital cortex.

Does the color tuning of area V1 differ from that of VOc? Were the opponent-colors signals substantially more powerful in VOc than V1, one might still argue for an enhanced color representation in VOc. Wandell et al. (1998) measured the iso-response curve in VOc to the same stimulus shown in Figure 9B. For these conditions, they found that the color tuning in VOc and V1 are quite similar. Of course, it remains possible that by selecting other spatial patterns, or by choosing different tasks and viewing conditions, differences will emerge.

Measurements with contrast-reversing lights and simple rectangular patterns reveal a powerful opponent-colors signals along the pathway from V1, V2 and VOc. But, these are not the only cortical locations that receive opponent-colors signals. Moving stimuli, seen only by opponent-color mechanisms, evoke powerful activations in

motion-selective areas located at the lateral portion of the parieto-occipital sulcus (ffytche et al., 1995; Poirson et al., 1997). Hence, cortical responses to opponent-colors stimuli, presumably carried by the parvocellular and koniocellular inputs to cortex, appear widely distributed in cortex. The powerful opponent-colors signal in V1, V2, VOc and motion-selective cortex represent only a portion of the distribution of color signals in cortex

The ability to make complete color tuning measurements using fMRI offers us one way to measure cortical signals in human observers. By making these measurements with a broader array of stimuli, we should be able identify the neural signals that correlate with appearance and understand the computations that take place at different cortical locations.

# Conclusions

Several quantitative principles describe human color appearance judgments. Color appearance represents three perceptual dimensions (trichromacy); color appearance computations adjust to changes in the ambient illumination, so that appearance depends more on the relative cone absorptions than the absolute number of absorptions; color appearance is organized into one achromatic and two opponent-colors representations; the spatial resolution of the opponent-colors mechanisms is substantially lower than that of the achromatic mechanism.

Using fMRI, it is possible to make measurements of the color sensitivity in various parts of human visual cortex. While visual cortex contains many different signals coding the spectral composition of the retinal image, these signals do not all match the quantitative principles of human color appearance. The signals measured so far may be significant for color appearance, but no region has been clearly identified as a unique color appearance center. Rather, it seems likely that by expanding the range of measurements, and comparing the quantitative responses in visual cortex with the fundamental properties of human color judgments, it may be possible to find a series of neural computations that, taken together, result in our experience of color.

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