

Representation of Color[☆]

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Wavelength and Color

Intuition tells us that color is a property of objects in the physical world, but in fact, color exists only in our internal, perceptual worlds. The physical world contains lights, which are composed of many wavelengths, and it contains surfaces, which reflect and absorb these lights to varying degrees. The wavelength composition, or spectrum, of light entering our eyes thus contains information about light sources and surface reflectances, and our visual systems analyze this information so that we can interact productively with our environment. Color is the quality of visual perception associated with this analysis.

The spectrum of a light is closely related to its color. A bright light with a flat spectrum looks white and the absence of light looks black. Colored lights have nonflat spectra: Long-wavelength lights tend to look reddish and short-wavelength lights tend to look bluish (Fig. 1; [Rechtsteiner and Ganske, 1998](#)).

If we take a light with a fixed spectrum and double its intensity (doubling the photon flux at every wavelength) it looks brighter, but its color changes little, if at all. In this case, we say that we have doubled the luminance of the light but kept its chromaticity constant. Changing chromaticity without changing luminance is a more complex operation because luminance depends on both the spectrum of the light and the spectral sensitivity of the human visual system. By convention, two lights have the same luminance if they appear equally bright to the average human observer when they are shown in rapid alternation.

It is tempting to ignore luminance when considering the neural basis of color vision. This would be a mistake because the processing of luminance and chromaticity are tightly linked in the early visual system, as evidenced by the first stage of visual processing, the photoreceptors.

Cone Photoreceptors

In daylight, vision begins with the absorption of photons by three classes of cone photoreceptor at the back of the retina. This section describes how light is encoded by the cones and how cone signals are combined into the channels that provide the basis of color vision.

[☆]*Change History:* April 2016. Akihiro Eguchi and Samuel Neymotin added section on “Computational Modeling of Color Representation” and updated References section.

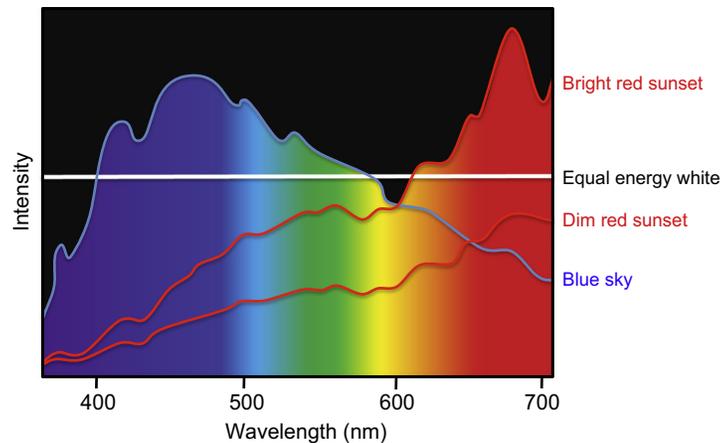


Figure 1 Spectra of a bright red sunset, a dim red sunset, a blue sky, and a light with equal energy at all wavelengths (equal energy white). Adapted from Rechtsteiner, G.A., Ganske, J.A., 1998. Using natural and artificial light sources to illustrate quantum mechanical concepts. *Chem. Educ.* 3, 3, Fig. 3, with kind permission of Springer Science and Business Media.

Light Coding in Cone Photoreceptors

The probability that a photoreceptor of a given class absorbs a photon depends on the wavelength of the photon. The three classes of cone photoreceptor are named after the wavelengths to which they are maximally sensitive: Long-wavelength cones, or L-cones, are maximally sensitive to long-wavelength photons (560 nm); M-cones are maximally sensitive to medium-wavelength photons (530 nm); and S-cones are maximally sensitive to short-wavelength photons (420 nm) (Fig. 2; Brown and Wald, 1964; Rowe, 2002).

There exists an infinite array of physically different lights that stimulate the cones identically. Pairs of such lights are called metamers and are visually indistinguishable. Metamers are the foundation of many common visual displays. For example, the lights generated by a color television have spectra that differ profoundly from those in the natural world, but because television-produced and natural lights can affect the cones in the same way, they give rise to indistinguishable color percepts. Lights that look reddish tend to excite L-cones well, and lights that look blueish tend to excite S-cones well. It is thus tempting to think of each cone class as leading directly to a corresponding color percept (e.g., L-cone excitation = red). It is easy to see that this is incorrect. A flat spectrum light, which looks white, excites L-cones moderately well. Doubling the intensity of this light doubles the excitation of the L-cones, and yet the light continues to appear white, not reddish. Our perception of redness is thus not strictly a function of L-cone excitation alone.

To a first approximation, changing the intensity of a light affects all three cone classes identically; increasing light intensity increases the number of photons caught by each cone. Changes in light intensity thus preserve the relative levels of excitation across cone classes and, as mentioned previously, the color of the light. These observations suggest that color perception depends on a comparison of excitation across the cone classes.

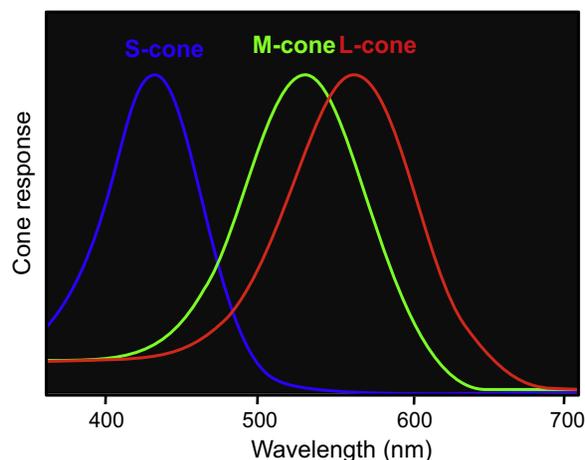


Figure 2 Spectral absorption functions of the three cone photoreceptors.

Cone Opponency: Theory

Comparing excitation across cone classes makes good sense from a computational perspective. L- and M-cones have broad and overlapping spectral sensitivities, so most lights excite them to similar degrees. The visual system emphasizes the small differences that exist between the L- and M-cone signals, however, by subtracting them. This subtraction facilitates the discrimination of very small differences in wavelength around ~ 550 nm, where the L- and M-cone absorption spectra overlap (Rowe, 2002).

Cone difference signals carry important information about the world around us. For example, the nutritional value of a leaf is better indicated by the difference in L- and M-cone signals than by either one alone (this fact has been suggested as a significant pressure in the evolution of opponency between L- and M-cone signals in Old World primates). This signal, however, is quite small with respect to the absolute levels of L- and M-cone excitation, which depend on ancillary factors such as whether the leaf is in direct sunlight or shadow. The differential signal is immune to the absolute levels of cone excitation and is therefore useful for finding nutritious leaves irrespective of the illumination.

Cone Opponency: Implementation

The biological substrate for the comparison of cone signals is a group of cone-opponent retinal neurons, which are excited by some cones and inhibited by others. Midget bipolar cells receive antagonistic input from L- and M-cones so their output reflects the difference between L- and M-cone excitation. Small bistratified ganglion cells are excited by S-cones and inhibited by a combination of L- and M-cones (De Valois, 1960).

Cone-opponent signals in the retina are transmitted along the optic nerve to the lateral geniculate nucleus of the thalamus (LGN), where they are preserved faithfully (Martin, 2004). Neurons in the LGN are arranged in layers, each of which receives input from a different population of retinal ganglion cells (Casagrande, 1994). In an individual layer, neuronal cell bodies have a characteristic size after which they are named. Parvocellular neurons ("parvo" meaning "small") receive input from the midget pathway and are thus described as having "L versus M" or "L - M" tuning. At least some koniocellular neurons ("konio" meaning "dustlike") receive input from small bistratified ganglion cells and are thus described as having "S - (L + M)" tuning. A third population of cells, the magnocellular neurons ("magno" meaning "large"), is not cone opponent. These cells are excited by both L- and M-cones and are thus described as having "L + M" tuning.

Magnocellular neurons have been proposed to be responsible for our sensation of luminance, and parvocellular and koniocellular neurons have been proposed to be responsible for our sensation of chromaticity. This model is supported by three observations. First, magnocellular neurons respond more vigorously to changes in luminance than do either parvocellular or koniocellular neurons. Second, luminance flicker can be detected at much higher frequencies than chromatic flicker, and magnocellular neurons are particularly sensitive to high-frequency flicker. Third, at least two cone-opponent channels are required to account for human color perception, and neurons with L - M and S - (L + M) tuning are attractive candidates for these channels.

However, the truth appears to be more complex. Neurons in all three categories respond to changes in chromaticity as well as to changes in luminance, albeit to different degrees. Furthermore, the spatial resolution of these cell types conflicts with predictions from human psychophysics. Human observers can easily see fine spatial patterns defined by luminance modulations but have difficulty seeing similarly fine chromatically defined spatial patterns. One might thus expect that neurons with L + M tuning would have small receptive fields, implying high spatial resolution, and neurons with L - M tuning would have large receptive fields, implying low spatial resolution. The truth is exactly the opposite: Magnocellular (L + M) neurons have larger receptive fields than parvocellular (L - M) neurons.

This apparent paradox is elegantly resolved by the receptive field organization of a subclass of parvocellular neuron (Lennie and Movshon, 2005). Parvocellular type I neurons are excited by one cone class in the receptive field center and suppressed by another cone class in the receptive field surround. Type II neurons, in contrast, are excited by one cone class and suppressed by another cone class throughout the receptive field. A type I neuron with an L-cone-dominated excitatory center and an M-cone-dominated inhibitory surround responds well to a change in light that increases L-cone excitation and decreases M-cone excitation, and this is true throughout the receptive field. The same neuron, however, responds differently to lights that modulate L- and M-cone excitations together. Such a light drives the cell poorly if it covers the entire receptive field because center and surround contributions cancel, but a small L + M spot restricted to the center drives the cell quite well. Type I neurons thus carry information about chromaticity at coarse spatial scales and luminance at fine spatial scales, illustrating again the close relationship between luminance and chromatic processing in the early visual system (Fig. 3).

Cone Opponency: Relationship to Opponent Colors

Although wavelength is naturally represented on a line, our perception of hue wraps around on itself, creating the familiar color circle. Red and green appear at opposite sides of the color circle because they are mutually exclusive hues: A single light never appears at once reddish and greenish. The same can be said of blue and yellow. On the other hand, bluish-reds (purple), yellowish-reds (orange), bluish-greens (turquoise), and yellowish-greens (lime) are easily seen.

In 1878, the German physiologist Ewald Hering hypothesized that the perception of any color derives from a combination of four elemental sensations: red, green, blue, and yellow (Hering, 1878). According to Hering's model, these sensations are the result

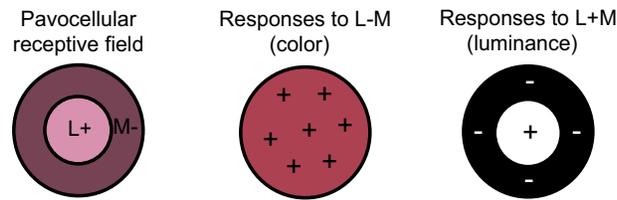


Figure 3 Schematic receptive field structure of a type I parvocellular LGN neuron (top). L – M modulations excite the cell throughout the receptive field (middle), whereas L + M modulations are excitatory in the center and suppressive in the surround (bottom). A relatively small M-component to the receptive field center has been omitted from the figure for clarity.

of two independent physiological processes: a red-green process and a blue-yellow process. The red-green process cannot be in the red and green states simultaneously, and the blue-yellow process cannot be in the blue and yellow states simultaneously, which accounts for the mutual exclusivity of opposite hues. Hering's idea, that color vision is founded on four primary sensations, was thought originally to be incompatible with the view championed by [Hermann von Helmholtz \(1852\)](#) and [Thomas Young \(1802\)](#) that color vision was based on three sensors in the eye. Today, the ideas can be reconciled: The three sensors of Helmholtz and Young correspond to the cones, and the two opponent processes of Hering correspond (roughly) to the cone-opponent neurons in the retina and LGN.

Cone-opponent neurons in the LGN behave similarly to the opponent process channels predicted by Hering. L- and M-cone signals cannot be dominant simultaneously in L – M neurons just as the red-green process cannot be in the red and green states simultaneously. Likewise, S- and (L + M) cone signals cannot be dominant simultaneously in S – (L + M) neurons just as the blue-yellow process cannot be in the blue and yellow states simultaneously. Because of these relationships, L – M neurons are sometimes referred to as “red-green cells” and S – (L + M) neurons are sometimes referred to as “blue-yellow cells.” It is important to note, however, that LGN neurons differ in important ways from the processes predicted by Hering. LGN cells are not tuned to the unique hues, which are the particular shades of red, green, blue, and yellow that human observers agree are pure and uncontaminated by other hues. Thus, a change in the blueness of a light affects activity in both the S – (L + M) and L – M pathways. Together, these observations suggest that cone opponency at the level of the retina and LGN is important for the mutual exclusivity of complementary hues, but additional processing of color signals in the cortex may also play an important role.

Color Processing in the Cortex

Color processing in the cerebral cortex is an active area of research ([Gegenfurtner, 2003](#)). This section describes some of the better understood aspects of cortical color processing.

Signal Mixing in V1

The three major cell types in the LGN project to distinct layers of the primary visual cortex (area V1, which is also called striate cortex). Magnocellular neurons project primarily to layer 4C, parvocellular neurons project primarily to layer 4C β , and koniocellular neurons project primarily to layers 2/3. Lower layer 3 receives information about increases in S-cone excitation, and upper layer 4A receives information about decreases in S-cone excitation. Whether these signals have a koniocellular or parvocellular origin is unclear ([Chatterjee and Callaway, 2003](#); [Douglas and Martin, 2007](#)).

The segregation of LGN inputs to V1 is not maintained long because intracortical connections within V1 mix signals across pathways. The nature of this mixing is beyond the scope of this article, but it is worth noting that some of the underlying intracortical circuitry is highly stereotyped and some of this signal mixing is likely important for color vision.

In principle, the mixing of LGN signals in V1 could account for the differences between the color tuning of LGN cells and perceptually opponent unique hues. For example, by mixing L – M and S – (L + M) signals in the appropriate proportions, the brain could create discrete classes of V1 neurons whose activity mimics the human perception of redness, greenness, blueness, and yellowness. Again, however, the truth appears to be more complicated: The distribution of preferred colors in V1 appears to be more or less random, implying indiscriminate mixing of LGN signals.

The apparent randomness of preferred colors in V1 may be a manifestation of the complexity of processing that occurs here. Neurophysiologists make simplifying assumptions about the computations that neurons perform because the full range of possibilities cannot be tested during an experiment of realistic duration.

One common assumption is that V1 neurons add and subtract LGN inputs but do not perform more complex operations. LGN neurons, in turn, can be modeled as adding and subtracting cone signals, so this assumption is formally equivalent to asserting that V1 neurons add and subtract cone signals. In this case, the color tuning of a V1 neuron can be described by a set of weights with which it combines cone signals ([Komatsu, 1998](#); [Komatsu and Goda, 2009](#)). Cone weights estimated from the activity of V1 neurons are nearly random, consistent with actual random color tuning or, alternatively, with complex, orderly color tuning that is not yet understood.

Double Opponency in V1

V1 is the earliest stage of the primate visual system to contain cells that are excited by some wavelengths and inhibited by others in the center of their receptive fields and have the reverse spectral sensitivity in the surround. These cells are called double opponent because they exhibit both wavelength and spatial opponency (Michael, 1978). The receptive fields of some double-opponent cells are nearly circularly symmetric, rendering them sensitive to spatial color contrast irrespective of orientation. Other double-opponent cells have receptive fields with elongated, side-by-side subunits, rendering them sensitive to edges of a particular orientation and chromaticity. Many double-opponent cells respond to both color and luminance modulations, again illustrating the close relationship between color and luminance processing in the early visual system (Fig. 4).

Cytochrome Oxidase (CO) Blobs in V1/V2

In area V1 and V2, clusters of color-selective neurons have been reported, as mapped with optical imaging and electrophysiological recordings (Landisman and Ts'O, 2002). This specialization for color processing in V1 derives from the location of the cone-opponent neurons. Layers 2/3 of V1 contain small, regularly spaced regions that stain darkly for the enzyme cytochrome oxidase (these regions are called cytochrome oxidase blobs). Many neurons in the blobs are cone opponent and many receive a strong koniocellular input. Koniocellular input is consistent with a role in color processing because S-cone signals, at least some of which are carried by the koniocellular pathway, play a greater role in chromatic vision than they do in luminance vision. Many neurons in the blobs project to a subcompartment of area V2, which is the next stage of cortical visual processing.

Area V2 can be divided into three subcompartments, which are named the thick, thin, and pale stripes after their appearance when stained for cytochrome oxidase. Neurons in the thin stripes receive input preferentially from V1 neurons in the cytochrome oxidase blobs, suggestive of a role in color vision.

Spatial Organizations and Off-Response Cells in V2

Our understanding of color processing in V2 is less developed than our understanding of color processing in V1. Nevertheless, a comparison between these areas reveals that color processing in V2 is even less linear than in V1; many V2 neurons respond to an extremely narrow range of colors that is inconsistent with a weighted sum of cone signals. There are two interesting distinctions that arise in these areas.

First, strongly color-responsive V2 neurons are spatially arranged according to their color tuning. For example, V2 neurons that are excited by purple are physically close to those that are excited by blue and others that are excited by red. This physical arrangement of neurons thus reflects our perception of hue similarity (Xiao et al., 2003).

Second, clusters of off-response cells emerge in V2 (Roe and Ts'O, 1995). Some of those cells also respond during the on-phase of stimuli of the preferred colors as well as at the offset of stimuli of colors opponent to the preferred colors, which is known as opponent color coding (De Valois, 1965). For example, such a cell may give on-responses for yellow and off-responses for blue (Friedman et al., 2003).

Color Constancy in V4

Neurons in the thin stripes of V2 project to area V4, which was once considered a color center in the monkey brain. Early studies reported an unusually high proportion of color-tuned neurons in V4, but recent studies have reported unexceptional proportions. Lesions of V4 impair a variety of visual functions including, but not restricted to, color perception. V4 is thus unlikely to be specialized for color processing exclusively. On the other hand, some V4 neurons compensate for the spectrum of illumination in a manner similar to human color perception (human observers compensate effortlessly for surprisingly large changes in illumination, as described later) (Wild et al., 1985). V4 is unlikely to be single-handedly responsible for this important feature of color perception but may contribute to it.

Two factors largely determine the cone excitations produced by illuminated objects. Consider an apple; the first factor is the reflectance of the skin of the apple. Red Delicious and Granny Smith apples reflect different wavelengths of light with different

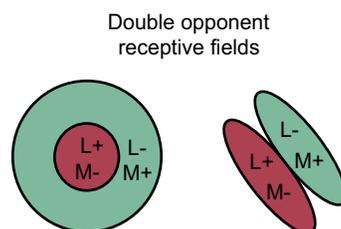


Figure 4 Schematic receptive field structure of double-opponent cells.

efficiencies. Red Delicious apples reflect long-wavelength light better than do Granny Smith apples, making Red Delicious apples appear red and Granny Smith apples appear green under normal illumination.

The second factor affecting cone excitation is the spectrum of the illumination. Incandescent bulbs produce more long-wavelength light than do fluorescent bulbs. Thus, apples of both varieties reflect more long-wavelength light when lit by an incandescent bulb than when lit by a fluorescent bulb. Nevertheless, Red Delicious apples continue to look red and Granny Smith apples continue to look green under either illuminant. This consistency of color perception, which is called color constancy, implies a mechanism in the visual system that discounts the spectrum of the illumination (Zeki, 1983).

Color constancy is likely a consequence of several physiological processes. Cone responses adapt over time, and this adaptation can partially account for color constancy. Some V1 neurons have been shown to exhibit a degree of color constancy which may be a consequence of double-opponent receptive field organization. Cognitive factors, such as an observer's knowledge of the physical layout of a visual scene, also play a role in color constancy. Elucidating the neural mechanisms underlying color constancy remains an important goal.

Color Processing in MT

The middle temporal area (area MT) of primate cerebral cortex is specialized for the analysis of visual motion. Neurons in this area respond well to moving luminance patterns but poorly to moving patterns defined solely by chromatic contrast. Perhaps as a consequence of this fact, moving luminance patterns are more easily seen than moving chromatic patterns.

The chromatic sensitivity of MT neurons may derive from at least three sources. First, a heterogeneous population of magnocellular neurons provides the dominant input to MT. On average, magnocellular neurons integrate L- and M-cone signals with roughly equal weight, but individual magnocellular neurons weight L- and M-cone inputs unequally. As a result, stimuli that modulate L- and M-cones with equal strength and opposite sign minimize the magnocellular population response while still driving some individual magnocellular neurons reasonably well. Second, many individual magnocellular neurons respond well to chromatic edges without regard to the colors on either side of the edge. The signals transmitted by these neurons are thus sufficient to mediate the computation of motion direction of a chromatic edge, but they are not sufficient to identify the colors on either side of the edge. Third, MT neurons receive modest inputs from koniocellular and parvocellular pathways which may provide overtly cone-opponent signals.

Color signals in different parts of the brain are probably used to perform different tasks. Color signals in MT are likely used to determine the locations of object boundaries for the analysis of visual motion but are unlikely to be important for the identification of surface properties. This task is likely performed by neurons in the ventral temporal lobe.

Color Processing Beyond V4/MT

Human patients with damage to a small region of the ventral temporal lobe suffer from a disorder called acquired cerebral achromatopsia. These patients report that the colors they see in their day-to-day lives are washed out. In the laboratory, they perform poorly on tasks that require color naming or arranging stimuli according to their colors.

The part of the brain damaged in acquired cerebral achromatopsia was originally thought to be the human homolog of monkey area V4 but is now believed to be several centimeters more anterior. Currently called VO or V8, this area is strongly modulated by colored stimuli in functional imaging experiments, further suggesting its participation in color vision.

Determining whether a VO (V8) homologue exists in the monkey brain is an important direction for future research. Anatomical considerations suggest that such an area may exist in the inferior temporal cortex. Some neurons in this part of the brain respond to single hues. Others respond to multiple perceptually dissimilar hues. Some respond to highly saturated colored stimuli—in some cases irrespective of hue. Lesions of this area create a syndrome in monkeys that is similar to cerebral achromatopsia in humans. Furthermore, recent studies have revealed that the color such as “Gold,” with which traditional color science cannot deal, is also represented in V4 by integrating the representations of hue and the specular reflectance which are both developed along the ventral visual pathway (Komatsu et al., 2013).

The weight of the current evidence thus suggests that a cortical area in monkeys and humans anterior to V4 is specialized for the analysis of color, but we do not yet know what processing occurs here, how this processing is implemented, and what functions it serves.

Computational Modeling of Color Representation

In this section, we introduce some of the computer modeling studies that allow us to make predictions on the function and developmental origins of several features observed in visual cortex *in vivo*, including orientation and color *maps*. Computer modeling of neuronal networks with biologically-plausible learning rules allows us to elucidate the origin of connectivity patterns observed in the brain. These types of studies are important because it is not possible to observe the state of all neurons in the brain along with microcircuit wiring changes at different stages of development.

Rao and Xiao (2012) have recently used a rate-coded neural network model to investigate some of the principles discussed in *Signal Mixing in V1*. They used anatomically realistic projections incorporating two color opponent channels and a luminance channel and successfully produced maps of orientation and color selectivity in their network. Eguchi et al. (2014) later

incorporated spiking neurons to further investigate the self-organization of various kinds of representations of color in the early stages of visual processing. In this model, each color input presented to the network was first decomposed into an RGB representation in digital images, which determined the activation of the three kinds of photoreceptors: S, M, and L cones. Generated spikes were then transmitted to the visual cortex via a simulated optic nerve in a luminance channel (MC pathway) and red-green (PC pathway) and blue-yellow opponent color channels (KC pathway). The model of the early visual system consisted of multiple topographically-arranged layers of excitatory and inhibitory neurons, with sparse intra-layer connectivity and feed-forward connectivity between layers. For consistency with physiology, the MC and PC pathways project their output to V1 L4, the KC pathway terminates in V1 L2/3, and many neurons in L2/3 project excitatory connections to the neurons in V1 L5 (Fig. 5).

Synaptic weights were randomized and learned using spike-timing-dependent plasticity (STDP), a biologically-plausible learning rule. After training with natural images, the neurons displayed heightened sensitivity to specific colors. Information-theoretic analysis revealed mutual information between particular colors and responses, and that the information reaches a maximum with fewer neurons in the higher layers, indicating that estimations of the input colors can be performed using the output of fewer cells in the later stages of cortical processing. In addition, cells with similar color receptive fields clustered together to form spatial organization and exhibited temporal color opponency with ON/OFF response cells, a phenomenon observed in V2.

Conclusion

Color processing in the early visual system has been reasonably well described, but many fundamental questions remain: How are LGN signals combined in the cortex and what are the functional consequences of these combinations? How is color constancy achieved? What is the physiological basis for the unique hues? The difficulty in understanding how the brain processes color information arises in part from the fact that color and other aspects of visual processing are closely related. As discussed in this article, the processing of chromaticity and luminance is tightly linked in the early visual system. Modulations of chromaticity and luminance often derive from different physical sources, and they give rise to different perceptual experiences. Nevertheless, both types of information are processed by the same neural hardware in the early visual system, and fixing one while varying the other in an experiment can lead to a confusing pattern of results.

Other examples abound. Psychophysical studies in humans have shown that the spatial, temporal, and chromatic context of a light can have dramatic effects on its color. This complicates the study of color processing: the spatial and temporal properties of the stimuli used in neurophysiological experiments, which are usually treated as nuisance parameters and fixed arbitrarily, affect color tuning measurements. This complication has a silver lining, however, because the relationships among visual attributes may

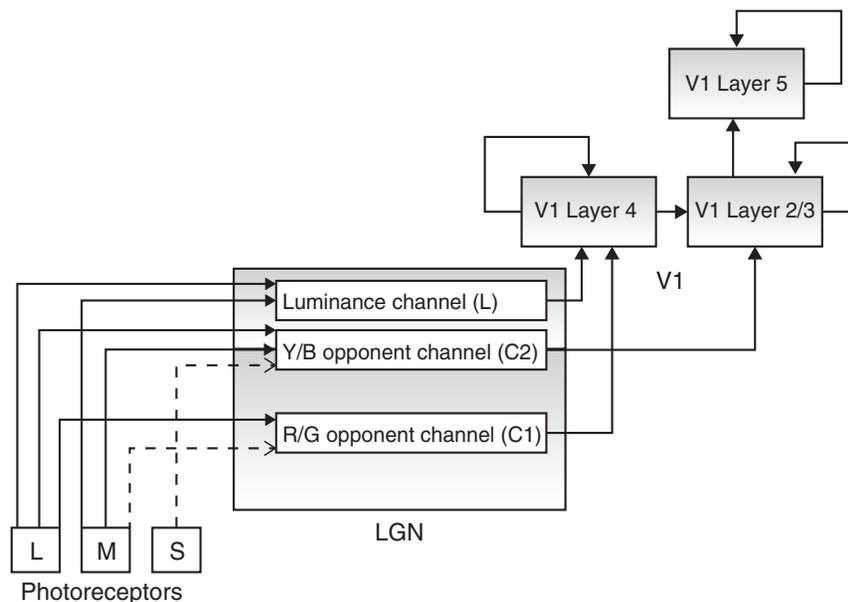


Figure 5 The pathways along which color information from the photoreceptors is conveyed to cortical area V1 (*solid lines* represent excitatory connections and *broken lines* represent inhibitory connections). Each color input is represented by a specific combination of corresponding firing frequencies of trichromatic cones. Each signal is projected to the anatomically appropriate layer in LGN forming a luminance channel and two color opponent channels. The output is then projected to the appropriate layer in V1. Reproduced from Eguchi, A., Neymotin, S.A., Stringer, S.M., 2014. Color opponent receptive fields self-organize in a biophysical model of visual cortex via spike-timing dependent plasticity. *Front. Neural Circuits* 8 (16).

provide valuable leverage into the problem. For example, the neural signals that underlie color perception should vary with the spatial and temporal properties of a stimulus in the same way that color perception does. Exploiting these relationships may help reveal how electrical signals in the brain give rise to color perception.

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