Annual Review of Vision Science

Signals Related to Color in the Early Visual Cortex

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Annu. Rev. Vis. Sci. 2020. 6:287–311

The *Annual Review of Vision Science* is online at vision.annualreviews.org

https://doi.org/10.1146/annurev-vision-121219-081801

Keywords

color, neuron, cortex, cone-opponency

Abstract

Visual images can be described in terms of the illuminants and objects that are causal to the light reaching the eye, the retinal image, its neural representation, or how the image is perceived. Respecting the differences among these distinct levels of description can be challenging but is crucial for a clear understanding of color vision. This article approaches color by reviewing what is known about its neural representation in the early visual cortex, with a brief description of signals in the eye and the thalamus for context. The review focuses on the properties of single neurons and advances the general theme that experimental approaches based on knowledge of feedforward signals have promoted greater understanding of the neural code for color than approaches based on correlating single-unit responses with color perception. New data from area V1 illustrate the strength of the feedforward approach. Future directions for progress in color neurophysiology are discussed: techniques for improved single-neuron characterization, for investigations of neural populations and small circuits, and for the analysis of natural image statistics.

INTRODUCTION

The chain of events that links the activation of peripheral receptors to perceptual experience is poorly understood in any domain. Color may be uniquely suited for exposing the mechanics of this process. Color has been investigated by scientists for centuries and by artists for millennia (Henshilwood et al. 2001, Mollon 2003). Our collective fascination with color has produced a wealth of knowledge regarding signal processing in the eye and about color perception. The current generation of scientists is now poised to discover mechanisms of color processing in the visual cortex, a key step toward understanding how these mechanisms mediate perception.

In everyday life, terms related to color, and the word color itself, are used to describe both visual stimuli and perception. A fire engine is red (a description of an object in the world) because the light that it reflects into our eyes produces the sense of redness (a description of our perceptual experience). This can be confusing. A major goal of visual neuroscience is to understand the mapping from distal stimuli (e.g., the fire engine and the light that it reflects into our eyes) to perception, and using the same words for the input and output of this mapping obfuscates an already perplexing process. In this article, I attempt to reserve color terms for perceptual phenomena and acknowledge explicitly when I am using them instead to describe visual stimuli.

PERCEPTUAL DESCRIPTIONS OF LIGHT

The words hue, saturation, and brightness were originally used to describe perceptual experiences but these days are often used to describe visual stimuli too. The perception-based terms are qualitative and intuitive. Brightness describes the perceived intensity of a light. It depends on the physical radiance of the light and its spectral power distribution; an infrared light, no matter how intense, cannot be bright because it lies beyond the range of human vision. Hue refers to the aspect of light that we describe as red, blue, green, and so forth, and saturation refers to the vividness of color. The blue sky may have the same hue and brightness as a blue LED but is less saturated.

Hue, saturation, and brightness (or lightness or value) can also refer to three scalar quantities computed directly from light spectra. These quantities predict, to some degree, the perceptual experiences described above but are only approximate. Hue, saturation, and brightness, in the perceptual sense, are affected profoundly by the spatial and temporal aspects of light, but these influences are not incorporated into the standard formulas that use the same words to describe stimuli.

Both brightness and luminance are attempts to quantify how strongly light affects the human visual system as a function of wavelength. A key difference between them is that luminances add (the luminance of two lights combined is the sum of each light's luminance), whereas brightnesses do not. This property of luminance is convenient mathematically, but it comes at a price: The spectral sensitivity function on which luminance is based must be measured under somewhat contrived conditions, for example, using rapidly alternating lights. Despite this definition, luminance is frequently used to describe the static stimuli typically used in neurophysiology experiments, an application whose utility derives mostly from conventionality.

LUMINANCE AND SATURATION IN NEUROPHYSIOLOGICAL EXPERIMENTS

Luminance and saturation (in the stimulus sense, not the perceptual one) are often treated asymmetrically in neurophysiological experiments. Saturation may vary across stimuli in uncontrolled

ways, whereas luminance is more often fixed across stimuli and matched to the background. Saturation is rarely equated across stimuli because no single set of stimuli can be equated for all of the equally reasonable definitions of saturation (Schiller et al. 2018). Luminance, conversely, has a single, well-accepted, formal definition, and equiluminant stimuli are easy to construct (Lennie et al. 1993).

The rationale for using equiluminant stimuli in neurophysiological experiments may appear reasonable at first glance but is hard to justify upon deeper inspection. Most neurons in the early visual system are sensitive to luminance, hue, and saturation (in the stimulus sense), and luminance, hue, and saturation (in the perceptual sense) are interrelated (Valberg et al. 1991). Without varying luminance, important aspects of neuronal responses could be missed, and hue and saturation are unlikely to be a particularly useful stimulus parameterization for understanding signal processing in the early visual system.

COLOR LABELS IN NEUROPHYSIOLOGY

Much of what we know about the neural representations of visual stimuli comes from functional imaging and single-neuron electrophysiological recordings. This review focuses on single-neuron studies; the reader who is interested in functional imaging studies is directed to recent reviews (Conway 2014, Moutoussis 2015).

To study the neural representation of images, the classical neurophysiologist inserts a microelectrode into the brain of an experimental animal, shines light into the eyes of that animal, and records the resulting action potentials. By manipulating the light and observing changes in neuronal response, the experimenter measures stimulus tuning. By moving the electrode from neuron to neuron, the experimenter assesses consistency or diversity of stimulus tuning across neurons.

Summarizing the results of such an experiment calls for concise description of the stimuli that excite each neuron. A standard description for a single neuron is a record of the stimulus that evoked the strongest response, which is called the preferred stimulus. While this description is certainly concise, the preferred stimulus is at best impractical for understanding color processing in the early visual system, and at worst misleading, for at least four reasons.

First, the preferred stimulus is agnostic to the range of stimuli to which a neuron responds. The broader this collection of stimuli is, the less informative the preferred stimulus is. Second, how strongly a stimulus activates a neuron is determined by its contrast. A nonpreferred stimulus can sometimes be made preferred by increasing its contrast. Standard measures of contrast do not apply equally well to all possible spectral deviations from a background. Cone contrast can be used in some special cases, but contrast can differ across cone types, simplifying the problem of comparing spectrally distinct stimuli but not solving it. Additionally, the convergence and divergence of signals downstream of the cones raise the deeper question of what it means for two spectrally distinct stimuli to have the same contrast in the first place. Third, the preferred stimulus can promote the idea that each neuron contributes to vision by signaling the presence or absence of its preferred stimulus, an idea that is probably wrong in the early visual system. Finally, a neuron might respond strongly to a contrived stimulus in a neurophysiological experiment but, under natural circumstances, may contribute to vision by encoding a distinct class of stimuli. For example, many neurons in the lateral geniculate nucleus (LGN) respond strongly to a bright red spot on a dark green background, but these neurons appear to contribute to many aspects of chromatic and achromatic vision (Al-Hashmi et al. 2011, Merigan & Eskin 1986, Wiesel & Hubel 1966).

Labeling neurons with color names is a common practice in neurophysiology. This practice fosters the idea that each neuron contributes to vision by promoting a particular color percept.

This idea is probably wrong, which makes the convenient shorthand descriptions of neurons as red–green or blue–yellow misleading. In general, descriptions of stimulus tuning that focus on feedforward signals have the advantage of making few assumptions about neural readout, which is rarely known.

WHAT WE TALK ABOUT WHEN WE TALK ABOUT COLOR

The study of pain provides a useful guide for how we might choose to talk about color-related signals in the early visual system (Finlay 2019). Both pain and color are triggered by sensory stimulation and are the product of significant neural signal processing. A key difference between them is that top-down influences on pain are evident through introspection. A stimulus can be painful in one context but not another, and this fact helps us to think and talk about pain and pain-producing stimuli clearly and distinctly. The top-down influences on color, conversely, contribute to the stability of object color perception in the face of changes in the sensory inputs (Hansen et al. 2006, Hasantash et al. 2019, Land 1959). This stability makes color seem, deceptively, like an aspect of the external world.

The word nociception is valuable for talking about pain. It refers to neural responses to stimuli capable of damaging tissue whether or not they produce pain. A word or concise phrase that fills the same role in the field of color would be valuable. The phrase "signals that are precursors to color" is presumptuous and wordy. The term "spectral signals" comes close but sounds distinct from spatial signals, which is undesirable given how interwoven the processing of spatial and spectral information are in vision (Brainard 2019, Moutoussis 2015).

CONES

A common current practice is to describe stimuli in terms of their effects on the long (L), medium (M), and short (S) wavelength–sensitive cone photoreceptors in the retina. Individual cones are color blind in the sense that a change in light intensity or spectrum can produce identical responses. A comparison of signals across cone types resolves this ambiguity. Changes in light intensity affect photon absorption in all three cone types similarly, whereas changes in light spectra can produce differential signals across cone types. When signals are compared across cone types, spectral and intensity differences can be dissociated, which is a key step in the construction of color.

The characterization of the cone absorption spectra catalyzed significant progress in our understanding of color (**Figure 1*a***). Before this advance, visual stimuli were described in terms of their dominant wavelength, spectral power distribution, or appearance to the experimenter. Today, they are usually described in the concise and physiologically meaningful terms of cone excitation, cone excitation differences from background, or cone contrast. The utility of this new convention is clear: Understanding a complex, hierarchical system, like the visual system, is simplified when inputs to a poorly understood stage are specified in terms of the output of an earlier, better-understood stage.

RETINAL GANGLION CELLS

The output of the primate retina is conveyed by 17–20 classes of retinal ganglion cells (RGCs) (Masri et al. 2019, Nassi & Callaway 2009). RGCs within each class have receptive fields (RFs) that

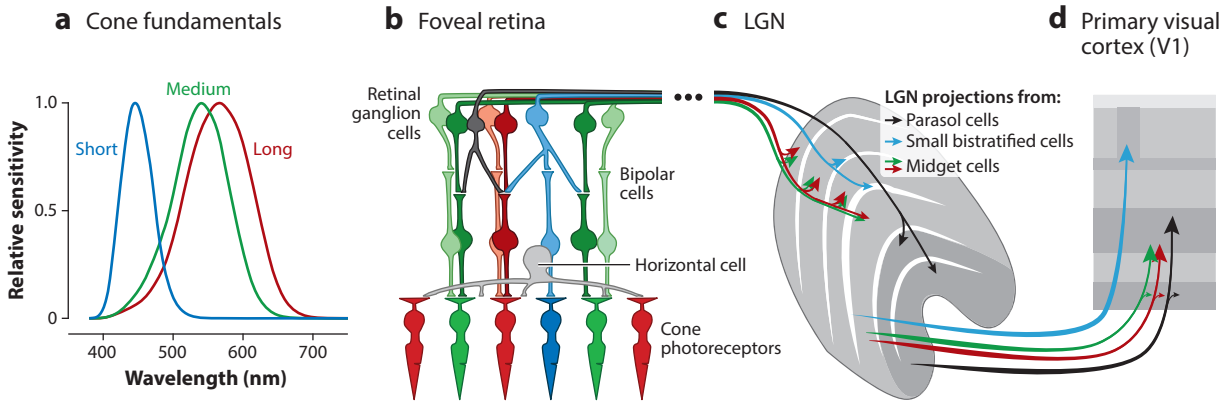


Figure 1

(*a*) Absorption spectra of the short (*blue*), medium (*green*), and long wavelength–sensitive cones (*red*). (*b*) Schematic of the foveal retina. Cone photoreceptors (*bottom*) drive horizontal cells (*gray*), ON bipolar cells (*light ink*) and OFF bipolar cells (*dark ink*). Bipolar cells drive retinal ganglion cells (*top*), which in turn project to the lateral geniculate nucleus (LGN). (*c*) LGN projections from midget cells (*red* and *green arrows*), parasol cells (*black arrows*), and small bistratified cells (*blue arrows*). (*d*) Projections from the LGN to the layers of area V1. Dark gray represents cytochrome oxidase reactivity.

form a mosaic pattern, tiling visual space with minimal redundancy (Gauthier et al. 2009). Light responses of neurons within a class are impressively homogeneous, and the residual heterogeneity can, in many cases, be attributed to variation in the arrangement and type of cones in each neuron's RF (Field et al. 2010, Wool et al. 2019).

In primates, three types of RGC account for approximately 70% of the total (Dacey 2004). Parasol cells pool signals from the L- and M-cones with the same sign (either ON or OFF). These cells are therefore sensitive to increments or decrements in light intensity and are a major contributor to luminance (Lee et al. 1988). Many midget cells are also sensitive to stimulus luminance, having inherited the luminance sensitivity of the cones. Near the fovea, midget RGCs are driven primarily by a single cone (Calkins et al. 1994, Kolb & Dekorver 1991) and can therefore be classified into four categories on the basis of dominant cone type and response polarity: L-ON, L-OFF, M-ON, and M-OFF (**Figure 1*b***). Some midget cells carry S-OFF signals in addition to L-OFF or M-OFF signals (Field et al. 2010, Wool et al. 2019). Curiously, few if any midget cells carry S-ON signals. Instead, S-ON signals are carried by a specialized population of small bistratified RGCs (Dacey & Lee 1994). These neurons are S-ON, L-OFF, and M-OFF, a spectral sensitivity that is usually written S-(L+M). Other less well-characterized pathways also carry S-cone signals (Marshak & Mills 2014).

THE LATERAL GENICULATE NUCLEUS

Most RGCs project to the LGN (**Figure 1*c***). The transformation of visual signals between RGCs and LGN neurons appears to be minimal under the conditions of most neurophysiological experiments (Usrey et al. 1999). Parasol RGCs project to magnocellular neurons, midget RGCs project to parvocellular neurons, and small bistratified RGCs and other less well-characterized types project to koniocellular neurons (Hashemi-Nezhad et al. 2008, Hendry & Reid 2000, Roy et al. 2009). Each LGN compartment projects, in turn, to a unique set of targets in the primary visual cortex (V1) (**Figure 1*d***).

Lesions of the dorsal (parvocellular and koniocellular) layers of the LGN have larger effects on color vision than lesions of the ventral (magnocellular and koniocellular) layers (Merigan 1989, Schiller et al. 1990). The distinction between parvocellular and koniocellular neurons was not widely appreciated when these lesion studies were conducted, and lesions that were intended only to affect parvocellular neurons also affected some koniocellular neurons. The relative contribution of parvocellular and koniocellular neurons to color remains debated (Neitz & Neitz 2017).

MEASURING THE SPECTRAL TUNING OF NEURONS

The spectral tuning of a neuron is typically measured by recording responses to a small set of spectrally distinct lights at the neuron's RF. Ideally, these measurements would be sufficient to accurately predict responses to another set of spatiotemporally identical lights that had not been shown. This is not yet generally true, even in V1, which is a testament to how rudimentary our understanding of color processing in the cortex is.

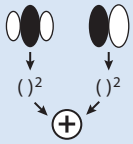
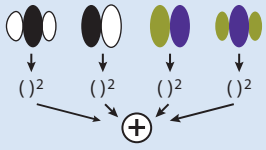
The inability to generalize spectral tuning measurements to novel stimuli is closely related to uncertainty about how to summarize neurophysiological data. Data summaries may eliminate information. What information can be eliminated, and what must be preserved, for the purposes of quantifying neuronal stimulus tuning depends on how stimuli are encoded by neurons. Only once we understand how stimuli are encoded can we summarize data without risk of losing information. We thus find ourselves in a catch-22: Our reason for summarizing neurophysiological data is often to learn the thing that we need to know to summarize the data without information loss.

For neurons that combine cone inputs approximately linearly, cone weights are sufficient to describe spectral tuning, and details about the stimuli used to measure these weights are extraneous. Once measured, the spectral tuning of these neurons can be described in convenient shorthand [e.g., L-M, S-(L+M), L+M, or the broader cone-opponent or nonopponent].

These shorthand descriptions, however, fail to capture a complexity that is critical for complete neuronal characterization. The contribution of each cone type to downstream neurons usually depends on its location in the RF. At the finest level of granularity, this is trivially true because the cones are laid out in a two-dimensional array, and each cone occupies space. Fortunately, for neurons that combine cone inputs linearly, the contribution of each cone type to each part of the RF can be measured independently.

Midget RGCs combine cone signals approximately linearly. Near the fovea, many midget RGCs are driven dominantly by one cone at the center of their RFs and are weakly inhibited by a combination of cone types over a wider area. Consequently, the spectral sensitivity of a midget RGC depends on the spatial pattern of light used to measure it. A well-understood consequence of this fact is that midget RGCs respond to cone-opponent modulations at coarse spatial scales and nonopponent modulations at fine spatial scales (Ingling & Drum 1973). Similar tradeoffs occur in the temporal domain (Gouras & Zrenner 1979).

Neurons in the visual cortex combine cone signals nonlinearly, which complicates neuronal characterization (Hanazawa et al. 2000; Horwitz & Hass 2012; Horwitz et al. 2005, 2007; Solomon & Lennie 2005; Solomon et al. 2004). Measuring nonlinear cone signal combination requires stimulating multiple cone types together in a variety of proportions. The functional cone inputs to one part of the RF may depend on stimulation at other locations. Which stimuli should be presented, or even just how many, to characterize the spectral tuning of nonlinear neurons to a desired level of accuracy is unknown. The convenient shorthand for describing linear cone signal integration fails to capture the tuning of these neurons. Such neurons may receive both cone-opponent and nonopponent input and thus cannot be described as belonging to either class.

Type label	Cone-opponent?	Idealized RF map	Notes
			Linear versus nonlinear
Linear	–		Linear neurons combine signals from different parts of their RFs approximately as a weighted sum
Nonlinear	–	?	Nonlinear neurons combine signals in other ways
			Simple versus complex
Simple	No		Simple cells combine signals across their RFs approximately linearly; complex cells do not
Complex (nonopponent)	No		Most, if not all, complex cells respond to cone nonopponent modulations
Complex (mixed opponency)	–		Cone-opponent neurons are excited by one cone class and suppressed by another Cone nonopponent neurons receive same-sign (or zero) input from all three cone types Some complex cells respond to nonopponent modulations, cone-opponent modulations, and combinations thereof
			Single-opponent versus double-opponent
Single-opponent	Yes		RFs of single-opponent neurons have a single homogeneous subfield
Double-opponent	Yes		RFs of double-opponent neurons have >1 subfields

ON regions OFF regions Cone-opponent regions

Figure 2

Physiological categories of primary visual cortex (V1) neurons. Mutually exclusive categories are grouped. Definitions and relationships among categories are provided in the notes (*right*). Idealized receptive field (RF) maps schematize the computation that each type performs on visual input. Linear neurons have RFs consisting of ON subfields (*white*), OFF subfields (*black*), or cone-opponent subfields (*purple* or *yellow*). Idealized complex cells sum the squared output of linear cells.

TAXONOMIES OF PHYSIOLOGICALLY DEFINED V1 CELL TYPES

The distinction between neurons that combine cone signals linearly and those that do not is a major bifurcation in the taxonomy of physiologically defined cortical cell types (**Figure 2**). The discreteness of this binary division remains contentious, but it is useful from a variety of perspectives. Discrete, physiologically defined neuronal types provide a structure for organizing data, for identifying motifs of signal convergence between the cones and the cortex, and for developing theories about how cortical neurons might contribute to perception. Ultimately, any coherent theory of signal processing in the cortex must account for the observations upon which the types were established. Below, I describe the major physiologically defined neuronal types in V1, their defining characteristics, and the methodological subtleties that can cause a neuron to be assigned different classifications by different investigators.

Simple Cells

The simple cell is perhaps the best-understood neuronal type in V1. Simple cells respond to increments of light in one RF location and decrements of light in another, and they combine signals across these regions approximately linearly. The linearity of spatial integration in simple cells is due largely to a mechanism called push–pull inhibition, whereby excitation from the ON pathway is spatially paired with inhibition from the OFF pathway and vice versa (Tolhurst & Dean 1990).

Simple cells were originally discovered in cats, which have a dichromatic visual system, and with isochromatic stimuli, which excite both cone types together. Later, when simple cell spectral sensitivity was measured in trichromatic monkeys, strong, nonopponent inputs from the L- and M-cones and weaker input from the S-cones were found. Cone-opponent neurons may have also been classified as simple cells in some studies, but these are more usefully defined as double-opponent cells.

Double-Opponent Cells

Double-opponent cells are defined by two properties: They are cone-opponent, being excited by one cone type and suppressed by another within local regions of their RFs, and they are spatially opponent, having opposite spectral sensitivity at different locations inside their RFs. Some double-opponent cells have RFs consisting of side-by-side subunits of opposite spectral sensitivity that produce responses of a similar magnitude at similar latency (Johnson et al. 2008). Others have RFs that consist of a large central region and a diffuse surround that may have a longer latency (Conway & Livingstone 2006). One possibility is that multiple types of double-opponent cells exist in V1, some of which receive feedforward inputs from neighboring regions of visual space with opposite spectral sensitivity, and others of which have a surround that is mediated predominantly by lateral connections or feedback (Angelucci et al. 2002).

Double-opponent cells have been proposed to contribute to the perceptual phenomena of simultaneous color contrast and color constancy (Conway 2001, Shapley et al. 2019) (**Figure 3*a–c***). Simultaneous color contrast is the repulsive effect that one light has on its neighbor with respect to color, and color constancy is the stability of perceived object color despite changes in illumination. Double-opponent cells signal chromatic differences across space and are relatively insensitive to spatially uniform changes in light spectra. Human observers are also relatively insensitive to these changes. Double-opponent cells respond strongly when the light spectrum on one side of an edge is changed (e.g., more short-wavelength light) or when the spectrum on the other side of the edge is changed in the complementary fashion (e.g., more long-wavelength light). Both manipulations cause human observers to perceive similar chromatic transitions across the edge.

Simple cells may contribute to simultaneous lightness contrast and lightness constancy in the same way that double-opponent cells may contribute to simultaneous color contrast and color constancy (Rudd 2017) (**Figure 3*d–f***). Simple cells and at least some double-opponent cells may be close relatives, differing primarily in the signs of input that they receive from the three cone types. Consistent with this idea, some double-opponent RFs are oriented (Johnson et al. 2008), have push–pull inhibition (Conway & Livingstone 2006), and could be wired from LGN afferents in the same way that is posited for simple cells (Johnson et al. 2008).

Different laboratories classify double-opponent cells on the basis of different criteria. Double-opponent cells were initially defined as cells that responded with opposite polarity (ON versus OFF) to lights of different spectra at the RF center and had the inverted spectral sensitivity in the surround (Daw 1968). Livingstone & Hubel (1984a) extended this definition to include neurons with cone-opponent RF centers and suppressive surrounds. In addition to classically defined

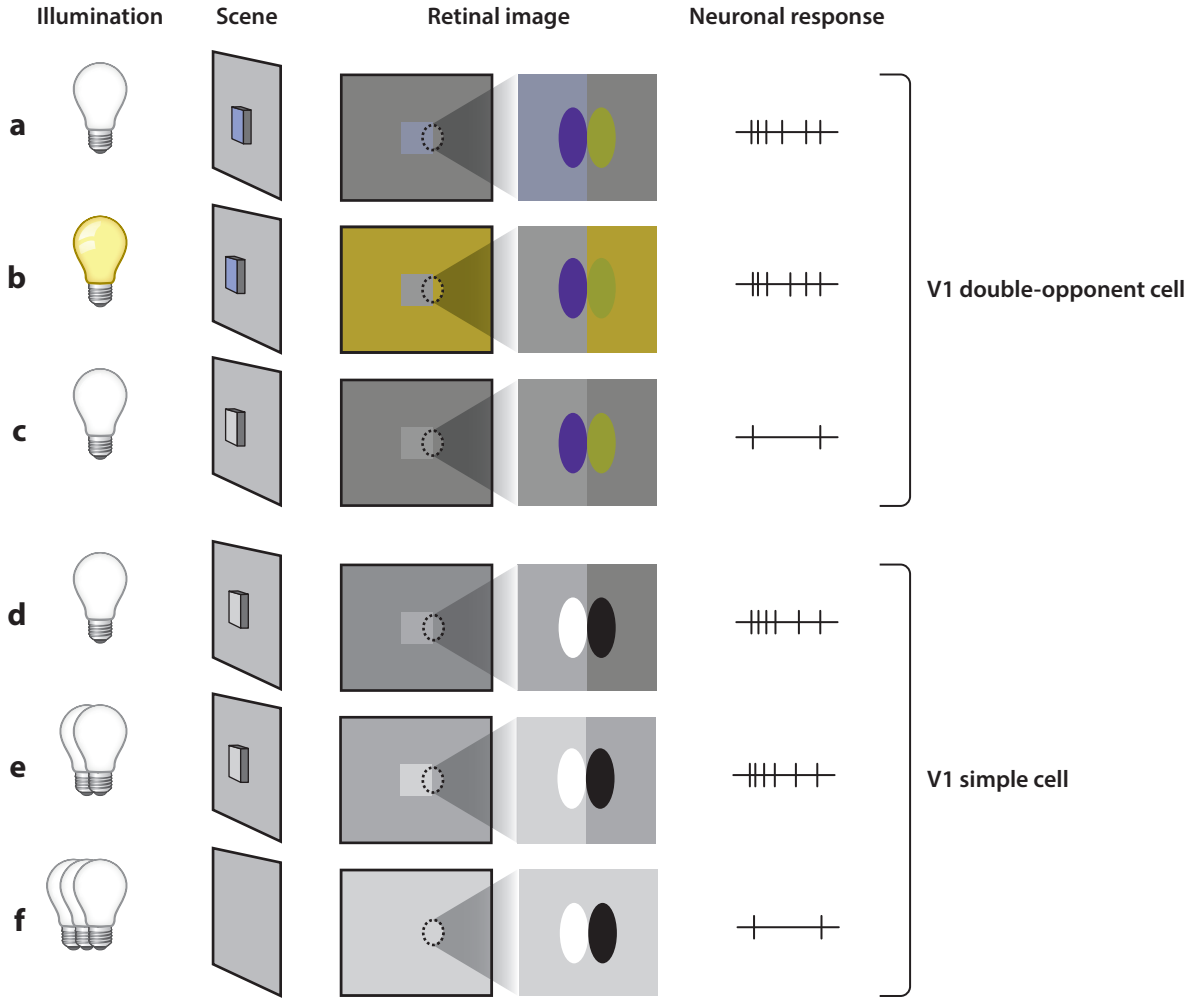


Figure 3

Idealized responses of a primary visual cortex (V1) double-opponent cell (*a–c*) and a simple cell (*d–f*) to illuminated scenes. Each row shows a lightbulb illuminating a square object against a larger, rectangular background (*left*); the retinal image produced by the scene (*middle*); a close-up of the edge between the object and the background; and a hypothetical spiking response of a neuron with a receptive field spanning the edge (*right*). (*a*) Broadband illumination of an object that reflects more short-wavelength light than the background. (*b*) Identical to panel *a* but with the illumination shifted to longer wavelengths, which increases the long-wavelength light reflected by both object and background. Note the similarity of neural responses in panels *a* and *b*. (*c*) Illumination is identical to panel *a*, but the object no longer reflects more short-wavelength light than the background, and neuronal response is weak. The squares in the retinal images in panels *a* and *b* may appear similar, but those in panels *b* and *c* are physically identical. (*d*) Simple cell response to broadband illumination of an object with a greater reflectance than the background but the same reflectance spectrum. (*e*) Identical to panel *d* but with more intense illumination. Note the similarity in neural response in panels *d* and *e*. (*f*) Illumination is further increased, and object reflectance is identical to background. The ink used to represent squares in the retinal images is identical in panels *e* and *f*.

double-opponent cells, this definition admits neurons with nonselective surrounds, called modified type II cells (Ts'o & Gilbert 1988).

Johnson et al. (2004) identified double-opponent cells on the basis of their responses to drifting red–green gratings. Cone-opponency was established with a color exchange test. The luminance of the green bars varied relative to the red bars, and neurons that responded to all of

these variations were classified as cone-opponent (nonopponent neurons fail to respond at some relative luminance). Spatial opponency was established on the basis of spatial frequency tuning; neurons with bandpass tuning were classified as spatially opponent. Double-opponent neurons, classically defined, are cone-opponent and spatially opponent by these criteria. However, so are some complex cells (Conway & Livingstone 2006, Vladusich 2007). Double-opponent cells carry information about the contrast polarity across an edge, and complex cells do not. Lumping both cell types together obscures this functionally important difference.

Complex Cells

Complex cells combine inputs from the cone photoreceptors nonlinearly. They are traditionally identified on the basis of their responses to a drifting sinusoidal grating of optimal spatial frequency and orientation. Whereas simple cells have approximately cosine-tuning for spatial phase, complex cells respond similarly to all spatial phases. Under a classic model, complex cells achieve phase invariance by pooling the outputs of simple cells with the same orientation preference but disparate RF positions or preferred spatial phases. If this pooling were restricted to nonopponent simple cells, a nonopponent complex cell would result. The fact that direction-selective simple cells in V1 appear to be exclusively nonopponent raises the testable hypothesis that nonopponent complex cells are more often direction selective than other types of complex cells (Horwitz & Albright 2005).

Complex cells carrying exclusively nonopponent signals are common in V1, and those carrying exclusively cone-opponent signals appear to be absent (Horwitz et al. 2007, Yoshioka et al. 1996). Some complex cells, however, carry a mixture of cone-opponent and nonopponent signals (Horwitz & Hass 2012, Horwitz et al. 2007). These neurons respond to edges largely irrespective of the lights on either side (Gouras & Kruger 1979, Hubel & Livingstone 1990, Yoshioka et al. 1996). The broad spectral tuning of such complex cells can be captured by a simple extension of the classic model. These neurons may receive input from simple and double-opponent cells with the same orientation preference and a variety of RF positions or preferred spatial phases. This model accounts for the lack of a response null in color exchange experiments (Johnson et al. 2004), the near-invariance of orientation and spatial frequency tuning across color directions (Johnson et al. 2001), and the ellipsoidal shape of isoresponse surfaces of some complex cells in cone contrast space (Horwitz & Hass 2012). The alternative miscalibrated photometer model fails to account for this third point (Johnson et al. 2001).

Single-Opponent Cells

Single-opponent cells in V1 are excited by at least one cone type, are suppressed by at least one other, and have roughly the same spectral sensitivity throughout their RFs. These neurons are untuned for orientation and are lowpass for spatial frequency, so they respond as strongly to a full-field light as to a smaller-field one. The spectral sensitivity of single-opponent cells is presumably not completely independent of the spatial structure of a stimulus, but this is a good approximation for the types of stimuli that are typically used in neurophysiological experiments. Like linearity, separability of tuning for the spatial and spectral aspects of a stimulus is a mathematical ideal that is never achieved by real neurons.

Single-opponent neurons likely comprise multiple types. For example, some neurons in the input layers of V1 have RFs that resemble those of their LGN afferents (Hubel & Wiesel 1968). The cytochrome oxidase (CO) blobs in upper layer 2/3 also contain single-opponent cells, but these neurons are likely at least two synapses away from cells in layer 4Cβ and have larger RFs (Hubel & Livingstone 1987, Sawatari & Callaway 2000, Yabuta & Callaway 1998b).

MODIFIED TYPE II AND 3/4 DOUBLE-OPPONENT CELLS

The cone-opponent modified type II and 3/4 double-opponent neurons in V1 are distinguished by the spectral sensitivity of their RF surrounds. By definition, modified type II cells have nonselective surrounds (Ts'o & Gilbert 1988), and 3/4 double-opponent neurons have surrounds that lack one of the two cone systems present in the center (Livingstone & Hubel 1984a). For example, a neuron with an L-ON, M-OFF RF center would be 3/4 double opponent if it had a pure L-OFF surround and would be modified type II if it had a nonselective surround.

The descriptions of surrounds as nonselective (modified type II) and cone type–specific (3/4 double-opponent) are unlikely to be completely accurate. No neuron is equally sensitive to all possible light modulations, so even a nonselective surround has some degree of spectral sensitivity. Similarly, no pathways through the LGN carry signals exclusively from a single cone type, making cone type–specific surrounds in V1 unlikely.

Other Qualitative Types

Some cone-opponent V1 neurons integrate signals across space in ways that remain poorly understood (see sidebar titled Modified Type II and 3/4 Double Opponent Cells). Some are preferentially suppressed by nonopponent modulations outside of the classical RF (Solomon et al. 2004). This observation is consistent with the idea that the RF surround is mediated by a network of inhibitory neurons that combine signals across cone types with the same sign. Importantly, stimulation of the nonclassical surround reduces responses without changing the spectral sensitivity at the RF center, providing substantial leverage for characterizing the joint spectral tuning of classical and nonclassical RF compartments (Solomon et al. 2004; but see Wachtler et al. 2001).

Neurons that do not fit any of the aforementioned categories abound in V1. Some cell types might represent failures in ideal wiring of better-understood types (Billock 1991). Some might occupy the tails of a continuous distribution; the concept of a physiologically defined cell type may be useful for organizing experimental observations but not beyond. Alternatively, a finite number of physiologically distinct cell types may exist in V1, but the response properties of some types may be sufficiently complex that they are described in different ways by different investigators.

In the next section, I describe a group of neurons that are consistent with this last possibility. The spectral tuning of these neurons, like those in the LGN, depends on the spatial properties of the stimuli used to probe them. Unlike LGN neurons, however, they combine input across cone types nonlinearly, which stymies some conventional approaches to characterization.

Nonopponent Facilitation of S-Cone-Opponent Signals in V1

In previously unpublished experiments, I recorded the responses of V1 neurons in an awake monkey to an array of lights that changed randomly and independently every 13 ms (for a description of these experiments, see Horwitz et al. 2005). Stimuli preceding each spike were analyzed by averaging and by principal components analysis (**Figure 4*a***). Spike-triggered averaging from a single experiment revealed a neuron that responded to a decrease in S-cone contrast opposed to a combination of L- and M-cone contrasts (**Figure 4*a***, *top*).

Principal components analysis of the spike-triggering stimuli revealed sensitivity to high-spatial-frequency luminance contrast (**Figure 4*a***). The qualitative difference in the appearance of the spike-triggered average (STA) and first principal component (PC1) reveals that this neuron combines cone signals nonlinearly (Horwitz et al. 2005, Schwartz et al. 2006).

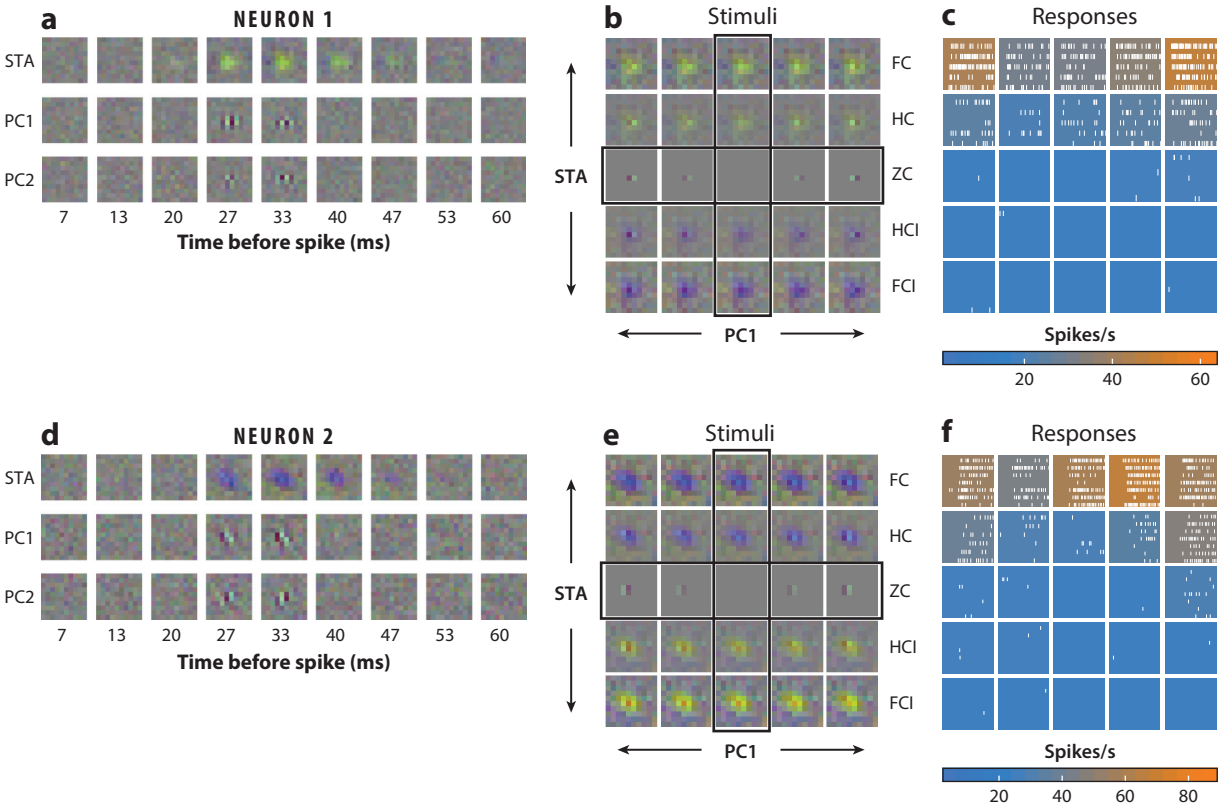


Figure 4

Nonopponent facilitation of S-cone-opponent signals in V1. V1 neurons in a rhesus monkey were stimulated with white noise. (*a*) The spike-triggered average stimulus (STA) (*top*), first principal component of the spike-triggering stimuli (PC1) (*middle*), and second principal component (PC2) (*bottom*) were calculated for a single neuron. Numbers indicate time in milliseconds relative to the spike. Following white noise stimulation, neurons were stimulated with static images synthesized from the STA and PC1. (*b*) Five variants of the STA were constructed (*middle column*): full contrast (FC), half contrast (HC), zero contrast (ZC), half contrast and inverted (HCI), and full contrast and inverted (FCI). The same five variants of the PC1 were constructed (*middle row*). Each pair of STA and PC1 variants were superimposed to create a battery of 25 stimuli. Only pixels near the receptive field center were used to calculate the PC1. (*c*) Responses to repeated presentations of each of the 25 stimuli. Color indicates mean firing rates (*color bar*). Rasters are plotted from stimulus on (*left edge* of each panel) to stimulus off (*right edge* of each panel). (*d–f*) Identical to panels *a–c*, respectively, but showing data from a second neuron.

To probe the stimulus tuning of this neuron more thoroughly, I presented 25 static images for 500 ms each (**Figure 4*b***). Each image was created by selecting an individual frame from the STA and PC1 movies, manipulating their contrast, and superimposing them.

The main result of this experiment was that the neuron was excited maximally by the superposition of the STA and PC1 (**Figure 4*c***, *top left* and *top right corners*). The STA drove moderately strong responses by itself (**Figure 4*c***, *top row*, *middle column*) except when its contrast was inverted, whereupon the neuron fell silent (**Figure 4*c***, *bottom row*, *middle column*). The PC1 drove weak responses irrespective of contrast polarity but only when the STA was permissive (**Figure 4*c***, *left* and *right columns*). The STA therefore reflects a half-wave rectified driver of neural activity, and the PC1 reflects a full-wave rectified signal that boosts the response but differs in spatial and spectral sensitivity from the dominant driver. A second neuron responded similarly, but its STA revealed

sensitivity to S-cone increments, not decrements (**Figure 4*d–f***). These data confirm that some V1 neurons respond to S-cone-opponent modulations superimposed on higher-spatial-frequency, nonopponent modulations, a combination of response properties that does not fit with any of the established types.

Discreteness of V1 Cell Types

Whether neurons in the early visual cortex are more usefully thought of as belonging to discrete types or a multidimensional continuum continues to be debated. The prospect of a finite number of discrete types is bolstered by recent progress in other fields. RGCs were once thought to belong to two types, ON and OFF, with substantial heterogeneity within each. Today, we know that a greater number of RGC types exists in primates, with only modest heterogeneity within each type when eccentricity is held fixed. Further support comes from studies of the mouse visual cortex, which have revealed a finite number of transcriptomic types that are predictive of electrophysiological properties (Cadwell et al. 2016, Tasic et al. 2016).

Several factors may conspire to make neuronal types in primate V1 less obvious than RGC types. V1 contains more transcriptionally distinct neuronal types than the retina. Neural circuitry is more complex in V1 than in the retina. V1 neurons are more difficult to characterize physiologically than RGCs. The clusters observed in V1 transcriptomic data, the stereotyped circuitry of V1, and the absence of neurons with certain combinations of physiological characteristics (e.g., cone-opponent complex cells and cone-opponent, direction-selective simple cells) are evidence in favor of discrete physiological types in V1.

FUNCTIONAL ANATOMY OF V1

A complement to the standard single-unit approach to understanding cortical signal processing is to consider cortical anatomy and mesoscopic physiology. This alternative approach has provided several useful clues regarding the signal transformations for color occurring in V1.

The major projections from the LGN to V1 include the koniocellular projections to layer 2/3, the parvocellular projections to layer 4Cβ, and the magnocellular projections to layer 4Cα (Nassi & Callaway 2009) (**Figure 1*d***). Electrophysiological measurements have revealed an S-OFF signal in layer 4A whose anatomical basis has yet to be been determined precisely (Chatterjee & Callaway 2003). Within the first few synapses in V1, signals segregated in the LGN mix across pathways via circuitry whose structure appears highly organized but whose function is poorly understood (Callaway 1998, 2005; Malpeli et al. 1981; Nealey & Maunsell 1994).

Several transformations occur between the LGN and V1. First, signals from the two eyes converge. Second, low-spatial-frequency information is consolidated from many neurons to few. Most LGN neurons with receptive fields within the central 10° of visual angle respond strongly to low-spatial-frequency stimuli. Given the prevalence of low spatial frequencies in natural scenes, V1 is usually under a barrage of action potentials from the LGN. Nevertheless, the baseline firing rate of most V1 neurons is low, which is presumably because of the push–pull inhibition that mediates simple cell linearity and prevents most simple cells from responding to full-field lights (Miller 2003). This inhibition has been linked to gamma-frequency oscillations in the local field potential and may account for the high-amplitude, gamma-frequency oscillations in V1 that are produced by full-field stimuli (Buzsaki & Wang 2012, Peter et al. 2019, Ray et al. 2013, Shirhatti & Ray 2018).

The circuitry that mediates these two transformations produces two orthogonal maps tangential to the layers of V1. Ocular dominance varies along one axis, and orientation tuning, which is rooted in the convergence of ON and OFF signals, varies along the other (Hubel & Wiesel

1977, Kremkow et al. 2016). These functional specializations have intriguing relationships to cone-opponency.

ORIENTATION TUNING AND CONE-OPPONENCY

In cats, ON and OFF signals merge in the main input layer of V1 to produce simple cells (Hubel & Wiesel 1962). In the monkey, the situation appears similar but is likely more complicated (Kremkow et al. 2016). Monkeys, unlike cats, have a parvocellular pathway and excellent color vision. The construction of orientation-tuned neurons in monkey V1 requires circuitry that is sensitive to the differences between subtypes of parvocellular neurons. Pooling L-ON with M-ON signals (and L-OFF with M-OFF) may produce simple cells with broadband (L+M) spectral sensitivity, whereas pooling L-ON with M-OFF (and L-OFF with M-ON) may produce double-opponent cells. The segregation of L-ON, M-ON, L-OFF, and M-OFF parvocellular afferents and the subsequent merger into cone-opponent and nonopponent channels may require an additional processing step that cats lack.

OCULAR DOMINANCE AND CONE-OPPONENCY

Ocular dominance columns are related to spatial frequency and cone-opponency. Low spatial frequencies are represented at the centers of ocular dominance columns, and high spatial frequencies are represented where dominance switches from one eye to the other (Nauhaus et al. 2016). Low-spatial-frequency, cone-opponent modulations are easier to detect than low-spatial-frequency, nonopponent modulations (Mullen 1985). This psychophysical observation suggests that neurons near the centers of ocular dominance columns might be preferentially cone-opponent. Indeed, neurons in the CO blobs, which are located at the centers of ocular dominance columns in layers 2/3, respond particularly strongly to full-field, chromatic stimuli and weakly to isochromatic stimuli (Garg et al. 2019, Livingstone & Hubel 1984a, Lu & Roe 2008, Tootell et al. 1988, Ts'o & Gilbert 1988).

CYTOCHROME OXIDASE BLOBS

The CO blobs in layers 2/3 of V1 are so called because they stain positively for the enzyme CO. Neurons in the blobs, unlike most in V1, respond strongly to full-field lights and may be major contributors to the net spiking activity in V1 produced by these stimuli (Garg et al. 2019, Livingstone & Hubel 1984a, Schluppeck & Engel 2002). They are particularly sensitive to L-M modulations, consistent with the parvocellular input that they receive (Callaway & Wiser 1996, Garg et al. 2019, Lachica et al. 1992). They also receive direct input from the koniocellular pathway that presumably carries S-(L+M) signals (Fitzpatrick et al. 1983, Hendry & Yoshioka 1994). Some blobs also receive input from layer 4A (Callaway & Wiser 1996, Yoshioka et al. 1994), which carries S-OFF signals (Chatterjee & Callaway 2003). Interestingly, the blobs also receive substantial input from the magnocellular pathway, which is not classically thought to contribute much to color vision and may underlie the broadband sensitivity of some neurons in the blobs (Callaway & Wiser 1996, Garg et al. 2019, Lachica et al. 1992, Livingstone & Hubel 1984a, Tootell et al. 1988). Attesting to their anatomical specialization, CO blobs are interconnected via lateral projections that bypass the intervening cortex (Livingstone & Hubel 1984b, Yabuta & Callaway 1998a).

Neurons in the blobs are arranged with respect to their spectral preferences and are spatially lowpass (Xiao et al. 2007, Garg et al. 2019). The failure of high-acuity form vision at equiluminance

may be related to the poor orientation tuning of these neurons (Livingstone & Hubel 1987). However, neurons immediately outside of the blobs also respond to equiluminant modulations and are tuned for orientation (Garg et al. 2019).

S-CONE SIGNALS IN V1

Most LGN neurons do not carry S-cone signals, but most V1 neurons do (De Valois et al. 2000; but see Johnson et al. 2004). This observation is consistent with the idea that S-cone signals are amplified between the LGN and V1 (Mullen et al. 2008, Xiao 2014). However, comparing the magnitude of S-cone-driven signals in V1 and in the LGN is difficult for several reasons. First, the spatial structure of the stimulus matters. Some V1 neurons respond to lower-spatial-frequency S-cone modulations than L- and M-cone modulations (Johnson et al. 2001). Thus, the choice of stimulus spatial structure may augment or diminish the appearance of S-cone signals in V1. Second, V1 responses to full-field S-cone modulations tend to be slow, especially in the output layers of V1 (Cottaris & De Valois 1998). Finally, signals originating in S-cones and in L- and M-cones interact in V1 in ways that are incompletely understood (Horwitz et al. 2005) (**Figure 4**).

OVERREPRESENTATION OF THE DAYLIGHT AXIS IN V1

A surprisingly high proportion of V1 neurons are excited by stimuli that modulate the S- and M-cones together and the L-cones in opposition (a spectral sensitivity denoted S+M−L) (Conway 2001, Horwitz et al. 2007, Lafer-Sousa et al. 2012, Solomon & Lennie 2005). Why V1 should be preferentially sensitive to S+M−L modulations is unclear. The suggestion has been made that this represents an adaptation to the spectra of natural light (Lafer-Sousa et al. 2012). Individual neurons can represent this variation only crudely because of their finite dynamic ranges and noisy responses. Perhaps the high proportion of V1 neurons dedicated to encoding S+M−L signals serves to compensate for this fact. However, humans are relatively insensitive to S+M−L signals under some conditions, which is difficult to reconcile with their cortical overrepresentation (Bosten et al. 2015, Krauskopf & Gegenfurtner 1992). Sensitivity to modulations along the orthogonal axis might be more useful for discriminating materials independently of variations in natural illumination spectra, a feat at which humans excel (Aston et al. 2019, Brainard et al. 2018, Delahunt & Brainard 2004).

Modulations along the daylight axis have an orange–cyan appearance to human observers. Inverting the sign of S-cone modulations relative to L- and M-cone modulations changes the appearance to lime–magenta. Orange–cyan and lime–magenta stimuli are thought to drive LGN neurons in a similar manner, so differences in how they affect cortical activity and perception may reveal specializations that arise de novo in the cortex (but see Tailby et al. 2008).

Functional imaging studies have reached conflicting conclusions about how strongly orange–cyan and lime–magenta modulations affect activity in V1. Lafer-Sousa et al. (2012) found greater V1 responses to orange–cyan stimuli, whereas Goddard et al. (2010) found greater responses to lime–magenta. This may represent a difference between primate species: Lafer-Sousa et al. studied rhesus monkeys, whereas Goddard et al. studied humans. Alternatively, the difference may be related to stimulus spatial structure. Lafer-Sousa et al. used moderately high-spatial-frequency stimuli that extended into the retinal periphery, whereas Goddard et al. used lower-spatial-frequency stimuli closer to the fovea. One possibility is that V1 response to lime–magenta modulations drops relatively quickly with spatial frequency, similarly to psychophysical detection thresholds (De & Horwitz 2017, Hass & Horwitz 2013).

SIGNALS RELATED TO COLOR IN V2

The processing for color by individual neurons in V1 and V2 appears similar—a fact that may have more to do with the conditions tested than with actual functional similarity between the areas. Many neurons in V1 and V2 respond strongly to equiluminant modulations and are poorly tuned for orientation (DeYoe & Van Essen 1985, Hubel & Livingstone 1987, Lennie et al. 1990, Levitt et al. 1994). Neurons in both areas respond to chromatic and isochromatic modulations, and they do not fall into discrete categories on the basis of their spectral tuning (Kiper et al. 1997, Levitt et al. 1994).

Some systematic differences between V1 and V2 neurons have been noted with regard to how they process color-related signals. In particular, the linear model of cone signal integration, which fails to describe the responses of many V1 neurons, fails even more decisively in V2. Some V2 neurons have spectral tuning that is too narrow to be captured by the linear model (Kiper et al. 1997). Complex-unoriented cells respond to a spot of a preferred size anywhere within a larger RF, which also violates the linear model (Hubel & Livingstone 1985, 1987). Many complex-unoriented cells are sensitive to the sign of chromatic contrast, responding more strongly to a red spot on a green background, for example, than to the reverse. When a spot of light on an equiluminant background is enlarged beyond a preferred size, V2 neurons are suppressed more strongly than V1 neurons (Solomon et al. 2004).

CYTOCHROME OXIDASE DOMAINS IN V2

V2 can be partitioned into three compartments on the basis of CO staining: thin stripes, thick stripes (which are difficult to distinguish from thin stripes histologically in macaques), and interstripes. Each compartment contains a complete representation of the visual field and has unique functional specializations (Hubel & Livingstone 1987, Nasr & Tootell 2018, Roe & Ts'o 1995).

Processing in the thin stripes appears to be closely related to color. A large fraction of thin-stripe neurons respond to chromatic contrast in a polarity-specific manner, are poorly tuned for orientation, and are spatially lowpass, similar to neurons in the CO blobs of V1 (Hubel & Livingstone 1987). These properties are consistent with the inputs to the thin stripes, which come directly from V1 blobs and cocolumnar neurons in the deeper layers (Livingstone & Hubel 1984a, Sincich et al. 2007). V2 also receives direct projections from the koniocellular layers of the LGN, but whether these projections target the thin stripes specifically is unknown (Bullier & Kennedy 1983).

Neurons in V2 thin stripes, but not thick or interstripes, are clustered according to their spectral tuning (Ts'o et al. 2001). Within a thin stripe, spectral tuning is consistent across cortical layers (Ts'o et al. 2001) and varies systematically tangential to the layers (Xiao et al. 2003). This tangential variation creates maps of spectral differences from the background that are similar to those found in V1 blobs but on a larger scale. Some of the heterogeneity in the projections from V1 blobs to V2 thin stripes is probably related to these maps (Roe & Ts'o 1999).

Other regions of thin stripes are excited by full-field achromatic (bright or dark) stimuli (Wang et al. 2007). Regions sensitive to bright or dark are spatially segregated, in apparent contrast to the smooth transitions in the representations of equiluminant lights. This may reflect two aspects of the same underlying architecture. A variety of spectral changes may be represented across V2 thin stripes, with departures from the background in opposite directions represented at distant locations. This would explain why the representations of bright and dark, or L-M and M-L, are spatially distinct.

Thick stripes and interstripes differ anatomically and physiologically from each other and from thin stripes (Livingstone & Hubel 1988, Sincich & Horton 2005). Thick stripes contain maps

for visual motion direction and retinal disparity. Interstripes contain maps for orientation, and many interstripe neurons have small, end-stopped RFs. Largely nonoverlapping populations of V1 neurons project to the thick stripes and interstripes, but the specialization of input from V1 to the thin stripes appears to be the most distinct (Sincich & Horton 2002).

The simple textbook characterizations—thin = color, thick = motion and disparity, interstripe = form—is a useful first-order description, but it belies the diversity of neuronal tuning in each compartment. Orientation-tuned, luminance-sensitive complex cells abound in all V2 CO compartments (Hubel & Livingstone 1987, Levitt et al. 1994). Many thin-stripe neurons are tuned for orientation but are not organized spatially with respect to this parameter (Lim et al. 2009). Thin stripes contain more cone-opponent neurons than the other two, but color cells have been found in all compartments. Some studies reported more color cells in the thick stripes (Peres et al. 2019, Shipp & Zeki 2002) and others reported more in the interstripes (DeYoe & Van Essen 1985, Levitt et al. 1994). Part of the discrepancy likely stems from different definitions of what defines a color cell.

BEYOND V2

A dense and largely mysterious network of color-related cortical areas extends downstream of V2 (Conway et al. 2007). Several of these areas are nestled between others that represent faces and objects (Lafer-Sousa & Conway 2013). Some carry top-down signals related to behavioral task demands (Koida & Komatsu 2007). At the highest levels of the visual cortical hierarchy, neural representations of colorful stimuli appear to be relatively tightly linked to perception (Brouwer & Heeger 2009). These transformations indicate that substantial signal processing occurs in higher cortical areas with respect to color. We should not be surprised, therefore, when words and concepts based on perception fail to map cleanly onto representations in the early visual cortex.

RELATIONSHIP BETWEEN NEURAL ACTIVITY AND PERCEPTION

A central question in visual neurophysiology is how populations of neurons mediate color perception. By analogy with the motor system, different coding schemes may be used in different areas. Some aspects of color are presumably encoded in the collection of active neurons, using either a sparse or a distributed code (Lehky & Sejnowski 1999). For example, the inferotemporal cortex has been shown to contain a sparse code for hue that could be read out using a simple winner-take-all operation (Zaidi & Conway 2019). Whether such a readout is actually used is unclear, as are the brain structures that would implement such a readout and to what end. Stimulation experiments in humans or monkeys, while challenging, could test the winner-take-all hypothesis (Murphey et al. 2008, Nichols & Newsome 2002).

Optical imaging techniques are providing new insight into the architecture of visual representations at a variety of scales, from large functional domains to the dendrites of individual neurons (Lecoq et al. 2019). These techniques hold the promise to revolutionize our understanding of color processing in the early visual cortex, especially in concert with viral tools for circuit dissection and optical methods to manipulate and record neural activity (He & Huang 2018). Theories that are potentially testable with these techniques include the ideas that double-opponent and simple cells are produced via a common wiring scheme, that both simple and double-opponent cells are afferent to complex cells, that color-only cells are inhibited by color-luminance neurons to mitigate the perceptual effects of chromatic aberrations (Vladusich

2007), and that cone-opponent and nonopponent neurons mutually inhibit each other for the computation of brightness and saturation (Gordon & Shapley 2006).

NATURAL IMAGE STATISTICS

The study of natural image statistics has contributed much to our understanding of color (Geisler 2008). The relationship between spectral and intensity gradients in natural images motivates algorithms for shape-from-shading and image segmentation (Kingdom 2003, Kunsberg et al. 2018). Simple and double-opponent cells can be thought of as computing those gradients, and their contributions to shape-from-shading and image segmentation are areas ripe for study.

Independent components analysis (ICA) of natural color images reveals filters that resemble the RFs of double-opponent cells. The fact that these filters are oriented, like simple cell RFs are, was initially viewed with disappointment but turned out to be prescient (Johnson et al. 2004, Tailor et al. 2000). The importance of image preprocessing in ICA serves as a reminder that substantial processing of visual signals occurs between the absorption of light by cones and cortical responses (Kellner & Wachtler 2013).

DEEP NEURAL NETWORKS

ICA is a valuable tool for identifying structure in complex data sets like natural images but, at least in its standard form, is limited to representing images as linear combinations of pixel values, which is qualitatively different from how images are represented in the cortex. Deep neural networks (DNNs) are tools related to ICA for transforming natural images nonlinearly to achieve behaviorally relevant goals, for example, object recognition (Egmont-Petersen et al. 2002). Examination of the inner workings of DNNs may be a useful guide for visual neurophysiology. To be clear, DNNs do not process images identically to the human visual system, but they may reveal general principles of image encoding and foster useful ideas that might not otherwise occur. One observation is that stimulus–response mappings beyond the first layer of units in these networks are difficult to characterize (Zeiler & Fergus 2014). The same is true of many visual cortical neurons. Some of the tools developed to interpret the tuning of DNN units may be useful for characterizing real neurons. Some units have narrow spectral tuning and broad spatial tuning that is neither lowpass nor oriented (Zeiler & Fergus 2014). These properties are reminiscent of the complex-unoriented cells of V2 (Hubel & Livingstone 1985). Some DNN units are particularly sensitive to colors that are diagnostic of a particular object class, for example, green billiard tables or red mushrooms (Rafegas & Vanrell 2018). The spectral tuning of some neurons in the visual cortex may be in the service of object identification or another specialized task.

THE PATH AHEAD

The feedforward approach to understanding vision has been enormously successful in revealing principles of neural signal processing from the photoreceptors through the LGN. It allowed the detailed characterization of cone inputs to RGCs and LGN neurons, a characterization that has had important repercussions on the interpretation of cortical neurophysiological and psychophysical data. The same approach is useful for studying the early visual cortex. The perception-motivated approach—looking for neuronal signals that map cleanly onto perceptual dimensions—has been less fruitful. Similarly, restricting stimulus manipulations on the basis of their perceptual consequences, or mathematical approximations thereof, is artificially limiting. The transformation

of signals that occurs between the LGN and the early visual cortex is likely simpler, and thus easier to understand, than the transformation of signals between the early visual cortex and perception.

The specification of stimuli in terms of cone excitations was useful for cortical neurophysiology, but further progress in this direction is needed. The cones are many synapses away from visual cortical neurons, and the intervening circuitry introduces complexities in cortical responses. For the purposes of studying the cortex, stimuli would ideally be represented in terms of their representation at the level of the LGN. This was a motivation behind the development of the Derrington-Krauskopf-Lennie color space, the axes of which approximate the spectral tuning of LGN neurons to large, static stimuli (Derrington et al. 1984).

The quest to understand signal processing for color in V1 is in large part the quest to understand the convergence of signals from the LGN within V1. To achieve this goal, a more complete characterization of signals in the retina and LGN is needed. Even in these well-studied areas, discoveries continue to be made, and nowhere in the visual system downstream of the cone outer segments is our understanding of stimulus representation complete.

More complete descriptions of cortical stimulus tuning would also be helpful. Nonlinearities and spatiospectral tuning inseparability are formidable but not insurmountable obstacles. New mathematical models of cone signal integration by cortical neurons are needed; without them, spectral tuning cannot be characterized meaningfully (Weller & Horwitz 2018).

The new classes of model should be identifiable, small enough to be interpretable, and large enough to provide useful approximations over a range of conditions. One potentially fruitful way forward is to measure the spectral tuning of individual V1 neurons using a simple stimulus set, perhaps limiting stimulation to the L- and M-cones inside the RF. Once a parametric class of models has been found that describes the data accurately, a stimulus set can be constructed for the efficient characterization of tuning in this reduced stimulus space. Additional aspects of the stimulus can then be manipulated to investigate the changes in tuning that these manipulations produce. As with any model, care must be taken when interpreting the values of fitted parameters lest the model be misspecified (Nasser & Gold 2013). Ultimately, these quantitative models should explain the qualitative taxonomies currently used to describe the responses of single units in the early visual cortex.

The ability to manipulate activity in the major LGN pathways independently would also be useful. Visual stimulation is unlikely to be sufficient to achieve this. An alternative is cell type– or pathway-specific optogenetics (El-Shamayleh et al. 2016). This approach has already proved valuable for isolating the koniocellular pathway to V1 (Klein et al. 2016), although the inability to manipulate neighboring neurons independently in any pathway remains an obstacle. A second alternative is to stimulate RGCs electrically. Multielectrode arrays can be used ex vivo to stimulate and record individual RGCs in nearly complete populations (Jepson et al. 2014). An exciting prospect is to implant such a device in vivo to reveal how spikes in individual RGCs and precisely manipulated RGC populations contribute to the responses of individually recorded cortical neurons.

CONCLUSION

Color is a delightful part of visual experience and a topic of intense scientific investigation. In the early visual cortex, a critical frontier in this investigation, some pieces of the puzzle are in place; we have a good first-order understanding of the afferent signals, the mesoscale anatomy, and the signals carried by individual neurons. A central remaining challenge is to decipher rules by which signals carried by channels segregated in the LGN converge in the cortex. Overcoming this challenge will require developing procedures to control inputs to the visual cortex precisely, to

observe the flow of signals through cortical circuits, and to characterize neuronal stimulus tuning with few measurements.

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

The author thanks Leah Tait, Elise Grover, and Emily Gelfand for excellent animal care and training. He also thanks Lisa McConnell, Paul Horwitz, John Tuthill, and David Brainard for comments on the manuscript.

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Annual Review of Vision Science

Volume 6, 2020

Contents

Errata

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