About the Series

The Springer Series in Vision Research is a comprehensive update and overview of cutting-edge vision research, exploring, in depth, current breakthroughs at a conceptual level. It details the whole visual system, from molecular processes to anatomy, physiology and behaviour and covers both invertebrate and vertebrate organisms from terrestrial and aquatic habitats. Each book in the series is aimed at all individuals with interests in vision including advanced graduate students, postdoctoral researchers, established vision scientists and clinical investigators. The series editors are N. Justin Marshall, Queensland Brain Institute, The University of Queensland, Australia, and Shaun P. Collin, Neuroecology Group within the School of Animal Biology and the Oceans Institute at the University of Western Australia. This volume on Human Colour Vision covers many recent developments in the field and provides descriptions of new methods and emerging hypotheses. Although relatively colour blind, or at least compromised, compared to some other animals, humans are particularly concerned with colour. We fill our world with it and in common with other species use colour for object detection and discrimination of certain features, basing many of our day-to-day judgements on colour differences. We therefore hope that this book will be of interest to anyone with interests in the biology of colour vision, the medical aspects of what happens when it fails, other areas of colour science and within the world of art and design.

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Human Color Vision

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Preface

Color vision is considered to be a visual sensation that is intimately related to emotions. If the world is "colorful," then it is positively full of wonder and surprises. When it is "bleak" or "gray," then the prospects are sad and pessimistic. Red is warm but can mean danger. Blue is cold. Yellow is a color of warning.

Color vision is a marvelous subdiscipline in vision research, embraced by those who study it and sometimes carefully avoided by those for whom it is only of indirect interest.

In the recent years, our understanding of human color vision has been tremendously advanced by many new developments, ideas, and achievements. It has been and still is an exciting time for color vision scientists. We therefore think that it is timely that these new developments are brought together in a book, particularly if it is one in a series on Vision Research. In this book, many new developments have been assembled, covering many different levels from genetics to perception, and studied with state-of-the-art methods such as genetics, morphology, imaging techniques, electrophysiology, psychophysics, and computational neuroscience. The genetics of cone photopigments is discussed in Chap. 1. Further new exiting developments have been obtained in the study of cone mosaics (Chap. 3), in the physiology of color vision in retinal (Chaps. 2 and 4) and cortical circuitries (Chap. 7), and in color psychophysics and perception (Chaps. 5, 6 and 8). Going beyond the questions about the processes leading to visual perception within an individual, the book also considers the latest computational models (Chap. 9), clinical implications and the question how retinal disorders can compromise color vision (Chap. 10), and finally the evolution of color vision (Chap. 11). We hope that the reader will find the chapters inspiring and helpful in defining scientific topics that will be of interest in the future. We think that there will be many interesting challenges. To name but a few, the following topics may emerge: the molecular basis of color vision; the study of single cells and pathways and their visual responses in the living retina; the responses of cells in their intact circuitries; the mathematical description of color processing; the improved use of color vision in diagnosing and monitoring inherited and acquired disorders of the retina; a better understanding of the many perceptual aspects of color vision.

We were supported by world experts who contributed to the book and wrote chapters on the new developments in their field of interest. We encouraged them to seek contact and collaborate with other experts. The result often was an interesting discussion amongst the authors and with the editors. We are extremely glad and proud that all authors have put so much effort in writing their chapters. We asked the authors to keep the text as simple and understandable as they could (without compromising on the scientific content), so that it also would entice and interest nonexpert scientists and students. The result is a book of which we think highly of and we are confident that it brings the latest developments in color vision research for a broader scientific audience. We hope you, as a reader, will agree.

We would like to thank the authors for their brilliant efforts. We appreciate it enormously. The collaboration between the series editors and with Springer was also extremely positive and inspiring.

It remains to thank those who continuously supported us. More particularly:

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Chapter 7
Color in the Cortex

Elizabeth N. Johnson and Kathy T. Mullen

Abstract We begin with a discussion of the role of human color vision, asking what value the possession of color vision adds to the perception of the natural scene, both in terms of our ability to see color differences (contrast) and in color identification. We then consider the psychophysical properties of cortical color vision and what they reveal about its use in determining shape and form. We pit against each other different models accounting for how achromatic (luminance) contrast and color contrast may be linked in the determination of shape, comparing a coloring book model, in which color plays only a subordinate or minor role, an intrinsic images model in which color contrast makes an independent contribution, and an integration model in which color and luminance contrast both provide cue-invariant form information to color–luminance shape detectors. These models are also interpreted in the light of what we know about the physiological basis of color vision through primate single cell recordings, particularly in area V1. Finally, we discuss what has been revealed about human color vision in V1 and extra striate cortex from fMRI studies.

Keywords Color agnosia • Color boundaries • Color contrast • Color identification • Cone-opponent • Contrast sensitivity • Cortex • Double-opponent • Isoluminance • Orientation • Shape processing • Spatial frequency

7.1 Roles of Color Vision

A clear understanding of color vision begins with an appreciation of its goals and functions. To this end, we begin our chapter with an introduction to the roles of human color perception: what does color vision do for us? The roles of color vision

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can be divided into two broad categories: the perception of color differences (contrast) and color identification. The first role relies on the extraction of contrast from the visual scene to enhance visibility, but requires no knowledge or conceptualization of what the different colors are, whereas the second role, color identification, is based on an internal conceptualization of color and does not require the presence of color differences in the visual scene.

7.1.1 *The Role of Color Contrast Perception*

The vision of all sighted animals has the dimension of intensity, providing information about the black and white (achromatic) contrast in the image. Dichromatic mammals possess an additional dimension of contrast, based on the opponent combinations of short wavelength (S) cones with a middle wavelength (M) cone type. This produces a new dimension of contrast, one of color varying from "warm" to "cool," and passing through a neutral point so increasing the differences that can be perceived in the visual scene. In a further evolutionary step, catarrhines (Old World monkeys and apes) evolved into trichromats around 40 million years ago [1–3] and possess an additional dimension of contrast: one based on the combination of long wavelength (L) and M cones into a cone opponent system that enhances the perception of differences in the mid-long wavelength spectral regions. (These two dimensions of color contrast are frequently termed "blue-yellow" and "red-green" although these names used in this context are simply a matter of convenience and do not refer to the perception of unique hues.) Our understanding of the genetic basis of the evolution of the cone types that mediate these color contrast dimensions has developed rapidly over the past 3–4 decades [1, 2, 4–6] and is covered in other chapters of this book (Chaps. 1 and 11).

Given the rarity in the natural world of abutting surfaces of identical luminance (termed "isoluminance" or "equiluminance"), edges and contours with color contrast are likely to have an associated achromatic contrast; a color difference in the visual scene is typically generated from variations in the material properties of objects or surfaces, and so is most likely to have an associated change in luminance. On the other hand, there are many instances in which achromatic contrast may arise in the absence of color contrast; for example, by variations in the illumination of a surface causing shadows and shading, and inherent variations in surface reflectance of objects. Given the good sense that we can make of black and white images, it is self-evident that much information about shape and form is available based only on the achromatic components of the image.

The question is, what does an additional two dimensions of color contrast add to the vision of catarrhines that is so useful? Here we discuss three likely advantages of the enhanced contrast perception that color vision provides, illustrated with pictorial examples.

Fig. 7.1 Illustrations of two example roles of color contrast in natural scenes. *Top panels.* Detection of fruits and berries in achromatic and chromatic images of foliage (Photo courtesy of Martin LaBar). *Lower panels.* Use of color in image segmentation and as a linking feature: achromatic and chromatic images of fall foliage (from The Weather Channel)

7.1.1.1 Perception When "Lightness Is Varying Randomly"

Mollon [7] elegantly describes a fascinating series of historic accounts of color vision deficits, dating from as early as 1688 (by Robert Boyle), and the particular difficulty that ensues with searching for objects in "*dappled or variegated backgrounds where lightness is varying randomly*". As the colored versus black and white photograph pairs shown in Fig. 7.1 illustrate, in the natural environment, particularly amongst foliage or vegetation, the variation in achromatic contrast across the image is very high, creating a very complex scene. Multiple light sources are effectively created as the sun's rays penetrate through foliage or vegetation and the surfaces of the leaves reflect light at all possible angles with multiple occlusions. In this monochrome world, shapes perceived on the basis of boundaries and shading are masked by complex variations in shadows, reflected light, and multiple light

sources. Figure 7.1 (top) shows how the shapes of the berries are all but invisible when viewed in monochrome, particularly at a distance. However, the addition of color contrast, reveals information in the scene that is absent or masked in the achromatic image, breaking the achromatic camouflage and enabling fruits or berries to be clearly detected against their leafy backgrounds. Color contrast enables the detection of objects that are otherwise invisible and is clearly advantageous when searching for objects in foliage, particularly at a distance [8]. This benefit of color vision is presumably also useful for birds, many of which have excellent color vision.

7.1.1.2 Color in Image Segmentation and as a Linking Feature

The visual scene can be segmented into common parts that belong together on the basis of a range of possible visual attributes, including stereoscopic depth, texture, motion or color. Once segmented, spatially distributed parts of the image with a common attribute may be perceptually linked together to extract an overall object, shape or contour. Color has long been recognized as an important basis for image segmentation and as a linking feature [7, 9, 10]. This important capacity of color vision is clearly exploited in the foliage example in Fig. 7.1 (lower). The achromatic image is too noisy for us to be able to extract any meaningful shapes or segregate the image into separate trees and distinct limbs. The addition of color contrast, however, causes the red, autumnal tree to dramatically pop out from the other still green ones, and enables us to link the common parts of the image based on their color. The Ishihara color vision tests also exploit this advantageous ability of color vision, in which circular disks of two contrasting colors, if distinguishable, can be grouped to form a figure against a background. Grouping and linking are by nature global tasks that allow shapes to be determined in the absence of contiguous boundaries or edges. The variable achromatic contrast of the individual elements masks any residual mean brightness differences between the two colors, effectively rendering them isoluminant.

Color contrast presumably combines with other spatial stimulus attributes, such as depth, texture and other higher order variations, to enhance image segmentation (Chap. 8). Segmentation by color and texture variations play a similar role as both are associated with changes in surface and specific object properties. On the other hand, color may also be manipulated to compete with image segmentation based on other visual attributes. Morgan et al. [11] show an example of competition between image segmentation based on texture and color: a small area of elements differently oriented from the others pops out in the achromatic version, but is much harder to see if random color variations are introduced. Image segmentation by color dominates over the conflicting segmentation by texture in this example. They argued that the reduced color vision of dichromats confers a visual advantage in this particular image; however, this conflict is probably uncommon in natural scenes in which texture boundaries and color boundaries are likely to coincide because both typically arise from common material variations. McIlhagga and Mullen [12] have shown that the linking of Gabor elements by common orientation into a winding contour is disrupted if the elements alternate between chromatic and achromatic

contrast. An illustration of McIlhagga and Mullen's effect is shown by Shevell and Kingdom [13] (see their Fig. 14). This is another example of how competing image segmentation by color disrupts the spatial linking by orientation.

7.1.1.3 Color Vision and the Use of Edge Information

As already discussed, in a visual scene populated by surfaces and objects, variations in the material properties of surfaces produce color contrast that is typically associated with some level of achromatic contrast. Figure 7.2 illustrates the achromatic and chromatic (Red/Green (RG) and Blue/Yellow (BY)) edges present in an example image. Inspection shows that the edge plots are similar in each case, and the plots below show a strong correlation in this image between the chromatic and achromatic contrasts at the edges. A similar analysis averaging over multiple images, however, suggested that although most edges combine chromatic and achromatic contrast to varying degrees there is no overall correlation between the magnitudes of the two types of contrast [14]. In other words, achromatic edge contrast

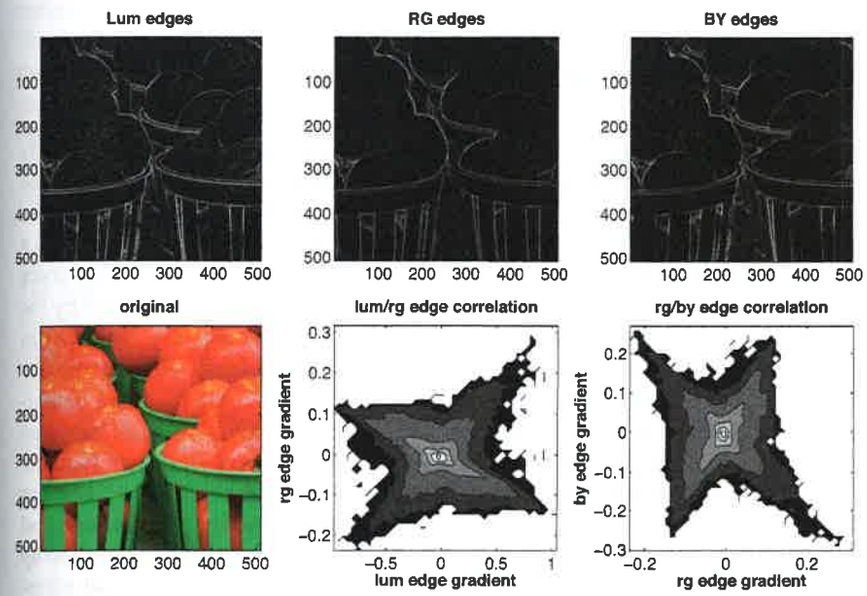

Fig. 7.2 An illustration of the color (red-green, rg, or blue-yellow, by) and achromatic (lum) edges of an image. The edges were computed as smoothed Gaussian derivatives in the x and y directions. The x and y edges were combined to form oriented edges at angles of 0°, 45°, 90°, and 135°. The edge values at each orientation can be positive (dark to light, red to green) or negative (light to dark, green to red). The edge values were divided by the local luminance as a rough normalization. The plot of luminance ("lum") versus chromatic edges in the *middle bottom row* suggests that for this image a combined color–luminance edge detector would be an effective way of encoding the edges (*Courtesy of William McIlhagga*)

does not predict chromatic edge contrast. How edges with both color and achromatic contrast might be encoded, either separately by purely chromatic or achromatic edge detectors or by cue invariant edge detectors that respond to both types of contrast, is discussed later in this chapter.

Shadows and shading in the visual scene produce achromatic edges and contrasts without associated color contrast. Thus, the presence or absence of color contrast in association with achromatic contrast can potentially provide crucial information for the disambiguation of shadows and shading from genuine changes in surface reflectance. Kingdom [15] elegantly demonstrated how simply the presence of color contrast can induce the perception of three-dimensional shape-from-shading from an overlaid achromatic grating. The presence of a chromatic grating, appearing as a continuous, striped colored pattern causes the overlaid orthogonal achromatic grating to appear as three-dimensional relief, giving rise to the perception of a corrugated surface [15, 16]. If a small amount of color contrast is added to the achromatic contrast, the 3D depth effect disappears, presumably because a spatially associated color and luminance variation cannot be interpreted as shading. This effect demonstrates a powerful role of color contrast in defining the continuity of a surface and in disambiguating shape from shading.

7.1.2 *The Role of Color Identification*

If asked to "find something red in the room," you would likely be able to quickly comply. This ability demonstrates "red" as an internalized color concept that can be used to search for and identify objects in the visual scene. Knowing what colors are is not the same as simply seeing colors as different from each other and requires a knowledge or cognition of color in addition to color perception [17]. That color cognition and color perception are distinct processes is clearly demonstrated by the neuropsychological deficit color agnosia. Color agnosic patients say they see "in color" but lack the ability to identify colors [18–21]. Color agnosic (J.T.) studied by one of the authors (KTM), who had acquired color agnosia after a brain hemorrhage, was in no doubt that he could see "in color." Psychophysical tests indicated that he had normal color contrast perception: his color contrast sensitivity function and suprathreshold color contrast discrimination were both normal [18]. He was also able to determine the isoluminant point using a minimum motion task and count the bars of a red-green isoluminant grating, which he reported to be made up of different colors, although he was incapable of identifying them. He had a profound deficit in color identification. He could verbally recite the colors of familiar objects with ease ("grass is green," etc.) suggesting that he did not suffer from color anomia, an aphasic condition in which colors cannot be connected to their names.

Color recognition relies on the existence of a cognitive or semantic color space. The color space is divided into fundamental response categories associated with different color sensations and names. Categories are not hard-edged boundaries but distributions around focal colors, the best examples of their categories. The presence

of categorization means that the cognitive or semantic color space is of lower dimensionality than the perceptual color space. Color naming and categorization has a rich history that cannot be covered in this chapter, and is thought to be present in nonhuman [22] as well as human primates [20, 23–26]. That there is a fundamental distinction between color recognition and perception is also demonstrated by their different developmental trajectories. As reported by Petzold and Sharpe [27], in 1877 Charles Darwin wrote about his concerns that his children were color blind,

> "I attended carefully to the mental development of my young children, and with two or as I believe three of them, soon after they had come to the age when they knew the names of all common objects, I was startled by observing that they seemed quite incapable of affixing the right names to the colors in colored engravings, although I tried repeatedly to teach them. I distinctly remember declaring that they were color blind, but this afterwards proved a groundless fear. On communicating this fact to another person he told me that he had observed a nearly similar case. Therefore, the difficulty which young children experience either in distinguishing, or more probably in naming colors, seems to deserve further investigation".

That young children have difficulty with naming colors, or choosing named colors, has been borne out in many subsequent studies [27–30]. Throughout the twentieth century, the age at which children were reported to develop reliable naming of primary colors has consistently fallen, beginning at the age of 7 years in the early 1900s [29]. The most recent report shows that children rapidly acquire a reliable knowledge of 9 of the 11 basic colors within a 3-month period around the age of 36 months, after which there is a significant lag of 6–9 months before accurate knowledge of the final two colors, brown and gray, is acquired [30]. This delay in the acquisition of color knowledge is not explained by a delay in the development of color perception, which develops much earlier during infancy and in line with achromatic contrast perception [31–34].

The ability to identify color, as opposed to just seeing color differences, provides a huge set of advantages and provides much information about surfaces and objects. The sensation of color is based on the spectral reflectance of a surface and hence encodes a constant property of an object. Since the spectral composition of the light reflected from a surface is a confound of its spectral reflectance and the spectral composition of the illuminant, the effective, reliable use of color identification also requires color constancy, discussed elsewhere in this book (Chap. 6). In Fig. 7.3 we give some illustrated examples, although the list is far from exhaustive:

1. Food identification: Color identification plays an important role in the rapid identification of the type of food (fruit, leaves, etc.), especially at a distance, along with the judgment of its ripeness or off-ness.
2. Toxicity: Color may be used as a warning to signal the toxicity of animals by enhancing identification and so deterring predators.
3. Social signaling: This is used in countless examples of color identification. The socially dominant Gelada illustrated in Fig. 7.3 has vivid red chest markings, linked to testosterone levels (and resembling the markings on a hockey or football jersey). Color is also used to signal sexual availability, fertility, and estrous.
4. Identification of con-specifics and gender.

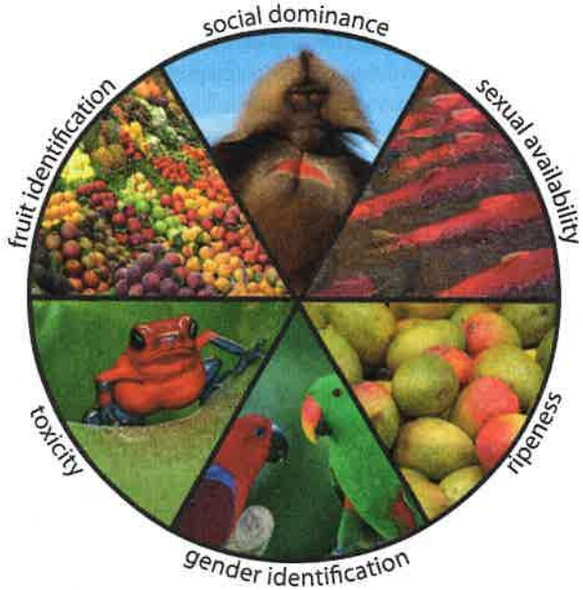

Fig. 7.3 Illustrations of examples roles of color identification in natural scenes. Wikimedia Commons Attributions: *"Fruit on display at La Boqueria market in Barcelona"* released into the public domain by copyright holder, Filip Maljkovic, via Wikimedia Commons. *"Poster frog"* released into the public domain by copyright holder, A. Amarnath, via Wikimedia Commons. *"Eclectus Parrot (Eclectus roratus)—pair"* by Flickr user Shiny Things used under Creative Commons Attribution 2.0 Generic license. Photos of "*Red salmon*" courtesy of Rachel A. Hovel and "*Male gelada*" courtesy of Noah Snyder-Mackler. (*Figure designed by Irem Onay*)

7.2 Color Vision in Form and Shape Perception

Our perception of color and achromatic contrasts are seen through very different but mutually complimentary spatiotemporal passbands, as illustrated in Fig. 7.4. In this figure, contrast sensitivity is compared in cone contrast units based on measurements of contrast detection thresholds. The use of the cone contrast metric to describe the stimuli allows visual sensitivity to two different physical properties, modulations in the spectral composition and the intensity of the stimulus, to be directly compared. From the *Principle of Univariance* we know that variations in the wavelength of light and variations in light intensity both have the same effect on the cones, causing a change in the amount of light absorbed and a consequent change in cone response. Hence, the visual response to color and luminance contrast can be directly compared based on their common effect on the cone photoreceptors response to absorbed light (Chap. 5).

Figure 7.4 (left panel) compares the spatial color and achromatic contrast sensitivity functions, and temporal contrast sensitivity is shown in the right panel. The lowpass shape of the color contrast sensitivity functions shows that we are highly sensitive to gradual changes in color occurring relatively slowly over large areas

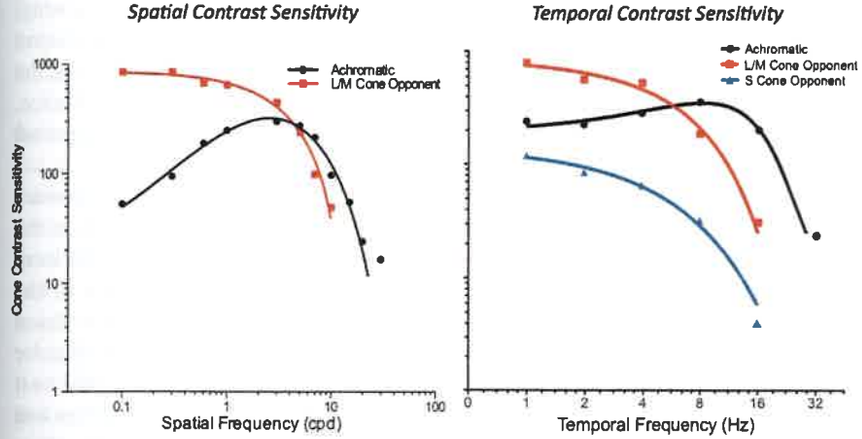

Fig. 7.4 Comparisons of chromatic and achromatic cone contrast sensitivity functions (CSF) for spatial frequency (*left panel*, in cycles per degree (cpd)) and temporal frequency (*right panel*, in Hz). *Red lines* and *data points* show L/M cone opponent responses, *blue* for S cone opponent, and *black* for achromatic. The use of cone contrast sensitivity allows chromatic and achromatic sensitivities to be directly compared. Cone contrast sensitivity for the spatial CSF is measured at 2 Hz and is based on data from Mullen [36], and for the temporal CSF is measured at 0.5 cpd, and is based on data from Mullen et al. [143]

[35–37]. In terms of cone contrast, color sensitivity is extremely high, achieving typical visual detection thresholds of around 0.3 %, and is significantly higher than the optimal achromatic contrast sensitivity, so winning a long-standing competition to answer the question, *what does the eye see best*? [38–40]. It remains unanswered whether color contrast sensitivity remains as high as spatial frequency is lowered to the point at which stimuli effectively become full fields of color. If so, it would reveal an absolute sensitivity to uniform color (dc) in the absence of spatial variation. (Clearly, some form of slow frequency temporal modulation will always remain arising from stimulus onset and offset.) While visual responses to achromatic contrast at low spatial frequencies (and mean luminance) are effectively removed by bandpass spatial filtering, these same attributes in terms of color are seen with the highest contrast sensitivity. The very high sensitivity of color vision to color changes over large areas is advantageous for tasks involving image segmentation and in defining surface colors, which typically operate over large spatial scales. It has also been specifically proposed that the spatial and chromatic properties of human red-green color vision has adapted to the detection of visual scenes of fruit against foliage; scenes that contained reddish objects (such as fruit) on a background of leaves, viewed within reaching distance, have been shown to correspond to the spatial properties of red-green human contrast sensitivity [40, 41].

As spatial frequencies increases above 0.5 cycles per degree (cpd), chromatic contrast sensitivity declines and color vision has poor visual resolution, with cut-off estimates ranging from around 12 cpd with chromatic aberrations optically corrected [36], to 20 cpd if the chromatic grating is created directly on the retina using

laser interferometry to entirely by-pass the eye's optics [37]. Under natural viewing, however, visual resolution in color vision is limited by the chromatic aberration inherent in the eye's optics, which significantly degrades the color contrast of the image above 1–3 cpd and inserts achromatic contrast into the image [42]. Hence, the perception of fine spatial details and good visual resolution are supported entirely by achromatic vision.

During the 1980s the psychophysical study of color contrast at isoluminance became established as a tool for the investigation of color vision [43] and, at the same time, the idea that color vision played very little role in shape and form perception became popular [44, 45]. The lowpass, low-resolution nature of the color contrast sensitivity function initially encouraged the idea that color vision lacked the neural machinery for edge and contour detection. This view of color vision was termed the *coloring book* model by McIlhagga and Mullen [46] as it held that color vision played a subordinate role in shape and form perception and was poor at seeing form by itself, lacking the machinery for edge and contour detection. The main role of color vision was seen as one of filling-in between luminance-defined boundaries and linking areas of a similar color. An opposing model, named with the term *intrinsic images* borrowed from computer vision [46, 47], holds that both color and achromatic contrast can independently extract edges, performing the same computation, but on different data (color versus achromatic contrast). Color and luminance edges that coincide are due to object boundaries and unmatched luminance edges are due to changes in the intensity of the illuminant. A third model, more recently recognized, which we call the *integration* model, proposes that there are common, cue-invariant edge detectors that can respond to either color or achromatic contrast [48, 49]. This model has mainly been proposed on the basis of primate single cell data, particularly in V1, as described in further detail below [49–51]. How does the evidence stack up for these different models? Exploring their predictions reveals some inherent contradictions in the current psychophysical data.

Models 2 (*Intrinsic images*) and 3 (*Integrative*) both propose that color vision can support shape and form processing. Overwhelming support for this property has emerged in the psychophysical literature over the last three decades. Simple shape processing is hierarchical and begins with the encoding of local spatial frequency, edge, and orientation information in the primary visual cortex (V1). In the next stage (sometimes called "global") the distributed features such as local curvature, angles, etc. are integrated over space to extract an overall form, a process thought to occur at the level of cortical areas V2 to V4. At higher stages, in areas in human inferotemporal cortex, shape is encoded independently of its retinal position and spatial scale. Over several decades, the role that color contrast plays in these different hierarchical stages has been investigated, most commonly by comparing psychophysical performance using isoluminant chromatic and achromatic stimuli. The comparison is usually made using chromatic and achromatic stimuli of similar spatial frequency and matched in visibility. Stimuli have typically been matched in visibility by scaling their contrasts in multiples of their respective detection thresholds, which controls for the differences in chromatic and achromatic contrast sensitivity (see Fig. 7.4). Because the differences in contrast sensitivity depend critically on the spatial frequency of the stimulus, this approach may only be used with stimuli that have a limited spatial or temporal frequency range (called spatiotemporally narrow band).

Tasks involving the discrimination or detection of local spatial frequencies, or the local orientation of edges or gratings are considered to be psychophysical tasks that are likely to be limited by neural performance at the level of V1. Accumulated evidence shows that such tasks are performed very similarly for color and achromatic contrast. Noise masking, sinewave masking, and adaptation experiments have revealed the presence of bandpass spatial filtering in color vision with similar bandwidths to achromatic contrast [52–56]. Presumably, the lowpass contrast sensitivity function is the upper envelope of these spatially tuned responses. A recent study using image classification has also indicated the presence of edge detectors in color vision similar to those of achromatic vision [57], supporting the presence of bandpass spatial tuning.

Psychophysical evidence definitively supports the presence of orientation tuning in color vision, based on orientation discrimination [58–60], sinewave masking [61], noise masking [62], adaptation [55, 63], and subthreshold summation experiments [64, 65], and is supported by fMRI results [66, 67]. Orientation discrimination is only slightly poorer in color than in achromatic contrast and orientation tuning has a similar or slightly broader bandwidth for color compared to achromatic contrast [61, 62]. A recent study of orientation tuning in color vision using subthreshold summation, however, found similar orientation bandwidths for color and achromatic contrast at mid spatial frequencies, but at low spatial frequencies orientation tuning dramatically broadened for the chromatic stimuli only, suggesting poor or absent orientation tuning for color [64, 65], as illustrated in Fig. 7.5. This result suggests two different types of orientation mechanisms may exist in color vision; an isotropic (untuned) detector at low spatial frequencies, which would be well-equipped for determining surface color, and orientation-tuned mechanisms at high spatial frequencies, which are configured for edge and contour detection. The presence of both isotropic and orientation tuned mechanisms in color vision is supported by the primate neurophysiological results in V1 discussed later in Sect. 7.3.2.

As color vision has the neural "apparatus" for form and shape coding, Model 2 (*Intrinsic images*), suggesting independent chromatic shape processing, and Model 3 (*Integration*) are both potential candidates to account for the role of color vision in shape perception. There is very little physiological support, however, for an independent, color-only shape processing system at this early cortical level (as proposed by Model 2). As detailed later in Sect. 7.3.2, color-only cells are found in primate V1 or V2 in only a limited number, and they do not typically have good spatial or orientation tuning. A more likely explanation is that neurons sensitive to both color and luminance contrast mediate shape processing in the early cortical stage. Thus circumstantial evidence supports the idea of the *Integration* model, in which edge detection is dependent on cue invariant mechanisms that can respond to either color or achromatic contrast. The presence of color–luminance neurons in significant numbers is well supported in primate V1, as described later in this chapter (Sect. 7.3.2).

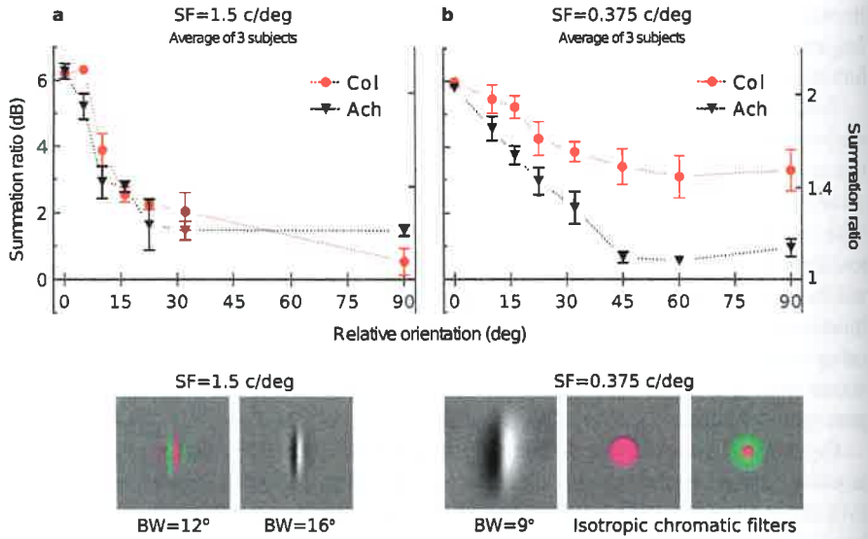

Fig. 7.5 *Top two panels* show orientation tuning curves for red-green (*red circles*) and achromatic (*black triangles*) stimuli at (**a**) 1.5 cpd and (**b**) 0.375 cpd for the average of three subjects (+/-se). The experiment measured the amount of subthreshold summation between two overlaid, cross-oriented gratings and is expressed as a summation ratio relative to the threshold for either grating presented alone, right axis, also expressed in dB, left axis). Summation ratio is plotted as a function of the relative orientation between the two gratings. Note the broad orientation tuning for low spatial frequency chromatic stimuli. Data are fitted with a model (not shown) to determine the orientation tuning of the underlying detection mechanisms. *Lower panels.* Representations of the optimal Log Gabor filters estimated from the model fits. At 1.5 cpd, similar narrow band orientation tuning is found for chromatic and achromatic stimuli. At low spatial frequencies (0.375 cpd), achromatic tuning remains essentially unchanged but chromatic orientation tuning is well fitted by an isotropic detector that may be spatially lowpass (e.g., red 'blob' detector) or bandpass (circularly symmetric color contrast detector). *Modified from Gheiratmand & Mullen* [65]

The abilities of color for form and shape processing typically extend to higher global tasks that depend on the integration of local information across space. The performance of color vision on contour integration [12, 68] and global shape perception using radial frequency patterns [69] and Glass patterns [70, 71] generally reveals relatively minor deficits in comparison to performance using achromatic contrast. These small deficits may arise from the marginally poorer orientation discrimination found at isoluminance [72].

The encoding of shape and form at an early cortical stage by cue-invariant, color–luminance mechanisms leads to the direct prediction that the processing of color and achromatic contrast do not occur independently. On the other hand, many different studies using a range of different approaches have tested for interactions between color and achromatic contrast at detection threshold, and these have mostly found independent mechanisms sensitive to color and achromatic contrast. A quantitatively rigorous approach has been to look for the effects of achromatic noise masking on chromatic detection. In general, when the test stimulus (signal) and

masking noise both have the same contrast type (both achromatic or both chromatic), the energy of the test signal at detection threshold rises in proportion to the spectral density (power) of the noise mask—in other words the test becomes proportionally harder to see. If the test and masking noise are of different contrast types (chromatic vs. achromatic), however, little or no masking effect occurs [56, 73–75] indicating that the detection of the test and mask are mediated by separate color and achromatic neural responses. Interestingly, there is also little cross masking when test stimuli and masking noise have different polarities of response; for example, if the test stimulus is red (+L, −M) and the noise green (+M, −L), or vice versa. This suggests that the cone-opponent responses may be split into separable color poles (red vs. green) via a separation and rectification of the signals, in a similar fashion to the separation of the luminance system into ON and OFF pathways [73, 76].

A second rigorous psychophysical approach used to determine the nature of the responses at threshold is the measurement and modeling of detection threshold contours within a color space, pioneered by Stromeyer et al. [77] and King-Smith [78]. The shape of the threshold contours, particularly in the context of a biologically relevant space such as the cone contrast space, allows the cone contributions to separable post receptoral mechanisms to be determined. A series of studies has shown thresholds are determined by three separable mechanisms at detection threshold; two cone-opponents and one achromatic, each based on the linear combination of cone types [77, 79–82]. The absence of subthreshold summation between these mechanisms supports the presence of independent mechanisms that do not combine linearly at detection threshold [83, 84]. Other studies on overlay masking [85] and cross orientation masking [86] also suggest independent color and achromatic processes determine threshold.

There is a clear conundrum between the evidence pointing to the role of psychophysical cue invariant color–luminance responses in shape processing and the wide-ranging evidence for separable color and achromatic responses at detection threshold. Various explanations exist that might resolve this issue. First, by definition, measurement of simple detection thresholds will only reveal the most sensitive psychophysical mechanisms, a subset of all potential responses. It is quite likely that these most sensitive mechanisms are color-only or color dominated, and color–luminance mechanisms are only recruited when stimuli are presented at suprathreshold contrasts. In support of this, the responses of color-only neurons in V1 are reported to be among the most sensitive to cone contrast [51] (see Sect. 7.3.1). Furthermore, on the basis of one study of single cells in primate V1, around half of the neurons that responded to chromatic stimuli at the monkeys' detection threshold became responsive only to achromatic modulation at high contrast [87], hence switching their selectivity. So far, it is unknown how or where in the visual system detection thresholds are determined, with comparisons of neural sensitivities in V1 an educated guess.

Second, color–luminance responses may be mediated at the cortical level by the nonlinear combinations of cones or post-receptoral mechanisms. Such nonlinear combinations may only be revealed psychophysically under specific conditions. For example, it is well known that the presence of suprathreshold achromatic contrast facilitates chromatic detection, driving color thresholds down to extremely low

levels (as low as 0.1 % cone contrast) [86, 88–91]. The psychophysical mechanism for this is under debate. However, a nonlinear model of single cell responses in V1 based on nonlinear combinations of chromatic and achromatic contrast has been proposed to explain the enhancement of color processing by achromatic contrast, at least for the S cone opponent response [92]. Hence color–luminance interactions at a suprathreshold level are still compatible with the presence of separable color and achromatic mechanisms under other conditions.

Third, color and luminance contrasts interact at suprathreshold levels. There are many wide ranging examples of interactions and cross effects between color and luminance contrast occurring at suprathreshold contrast levels. A full description of these is beyond the scope of this chapter, but some are described in reviews by Shapley and Hawken [49] and Rentzeperis et al. [48]. However, the presence of complex interactions at suprathreshold contrasts is entirely compatible with the existence of separable color and achromatic mechanisms at near-threshold low conditions. This issue remains to be explored further.

7.3 The Physiological Basis for Color Vision in Primate Cortex

Three questions continue to drive neurophysiological research into cortical color processing: Which neurons code color? How are color signals transformed in cortex? And how do these physiological responses impact human color perception?

7.3.1 Which Neurons Code Color?

Much debate has centered on what the requirements are for a neuron to be responsible for color signals. Are cells that contribute to color perception restricted to those that are highly specialized for color detection and highly selective for different colors? That is, are the only cells that contribute to color perception those that respond to color and not to achromatic stimuli? The most comprehensive study of color cortical neurophysiology is from macaque V1, with far fewer studies focusing on the processing of color signals in other cortical areas. Most of the projections from the lateral geniculate nucleus (LGN) to the cerebral cortex terminate in V1. Evidence that color-opponent neurons existed in the primate visual system and were likely homologous to the mechanisms involved in human cortical color processing was first provided by De Valois [93].

Early investigations found that many V1 neurons are tuned for the orientation and spatial frequency of black-and-white patterns, with few strongly selective for color [94, 95]. The small population of strongly color-selective V1 neurons lacked orientation selectivity and were spatially low-pass, which fit with the low-pass human color contrast sensitivity function [36] (see Sect. 7.2). Many subsequent studies have favored

this viewpoint and have screened for color-responsive cells only if they respond best to isoluminant color [96–100]. This has had significant impact on the methods employed to determine the processing of cortical chromatic signals, namely that the localization and strength of cortical color signals are often determined (for example, with fMRI and optical imaging) by differencing the neural responses to isoluminant color stimuli (often full-field or low spatial frequency) and spatially defined black-white achromatic stimuli to determine a color "preference" (see Sect. 7.4).

However, there is growing evidence for the interaction of color and luminance, as described earlier in this chapter, as well as a prominent role for color in form processing (for recent reviews see Shapley et al. [101] and Rentzeperis et al. [48]). This makes it quite likely that neurons that respond to both chromatic and achromatic stimuli carry important information relevant for color perception. Single cell recordings in macaque V1 indicate that approximately 10 % respond exclusively to color (i.e., only to isoluminant color modulations), and these cells lack orientation tuning [50, 51, 96, 102, 103]. However, 40 % of all macaque V1 cells are color-responsive [50, 51, 103], and this percentage rises to 60 % of the cells in the superficial layers (layer 2/3), the main output layers of V1 [50, 51, 102, 103]. This larger fraction responds to both luminance and color contrast, and is selective for the orientation of both chromatic and luminance stimuli [50, 102, 104, 105].

As this chapter addressed above, there is mounting psychophysical evidence to suggest that color-preferring neurons, and neurons that respond to both color and luminance contrast, are likely involved in cortical color processing, perhaps at different contrast levels and in different contexts (for example, at edges versus color surfaces).

7.3.2 How Are Color Signals Transformed in Early Visual Cortex?

Much work has focused on the specific transformations of color signals as they progress from retina to LGN and then V1, and it is clear that color is not passively relayed even to early visual cortex. One very useful tool to examine how signals change from retina to thalamus and cortex is to use color-modulation stimuli that isolate signals from each of the cone types, which provides a direct way to study cone inputs to LGN and cortical neurons [96, 103, 106–108]. Such "cone-isolating" stimuli provide information about each of the cone inputs to a given neuron, the sign and weight of the inputs, and other spatiotemporal receptive field properties of the individual cone inputs when incorporated into tests of spatial frequency, temporal frequency, and subspace reverse correlation techniques (cf. Ringach et al. [109], see also Chap. 2). Studies using such cone-isolating stimuli indicate that the cone inputs to neurons in V1 are broadly distributed [103]. This is consistent with other findings of broad spectral tuning in various cortical areas, including V1, V2, and inferior temporal cortex (IT), when measured with cardinal stimuli derived from a color space based on the isolation of cone-opponent mechanisms (L-M, M-L, S-(M+L), L+M(+S)), often called "DKL space" [110], rather than L-, M-, and S-cone-isolating

stimuli [111–114]. Many of the studies using cardinal stimuli derived from color-opponent mechanisms have suggested that the spectral diversity in V1 and subsequent visual areas is quite different from the narrow distribution in the LGN. However, the coordinate axes of color-opponent mechanisms in DKL space [110], or cardinal axes, are based on responses in the LGN to full-field stimuli. The majority of LGN color-sensitive neurons have receptive fields where the spatial extent of the center mechanism is smaller than that of the surround (Type I parvocellular cells [115]). These cells respond with the weighting L-M to full-field stimuli, but the weighting changes significantly when smaller spots fill just the receptive field center [108]. When spatial patterned stimuli are used, the interpretation of the axes of DKL space as the directions of stimuli that isolate LGN cell classes (often interpreted to be the input to cortex), is not correct because the spatiospectral response functions in the LGN as well as the cortex are not separable. Therefore, the ensemble of color spaces is also wider in the LGN than originally proposed by Derrington et al. [110], and the ensemble will shift for each different spatial pattern. Thus, the finding of a broader distribution of spectral responses in cortical neurons with spatially patterned stimuli is likely not a distinctively cortical transformation, but a by-product of emerging receptive field properties, such as orientation tuning, and thus the more common use of spatially defined stimuli. Cone contrast spaces do not pose the same problems because these axes represent retinal cone activation, not opponent color mechanisms.

There are significant transformations of color signals in early visual cortex. As noted above, many color-responsive V1 neurons are also selective for spatial patterns (orientation and specific spatial frequencies) [51, 105, 112, 116]. Although some V1 cells, like their retinal and LGN counterparts are "single-opponent," responding best to large, uniform areas of color, many more V1 cells are both chromatically and spatially opponent—thus termed "double-opponent" cells [103]. The single-opponent V1 cells are color-preferring. These cells are similar to their LGN counterparts, as they give maximal responses to red-green grating patterns of low spatial frequency, and low-pass spatial frequency responses for color overall. Unlike LGN parvocellular neurons, however, they respond extremely poorly to achromatic patterns of higher spatial frequency. When the receptive fields of V1 single-opponent cells are mapped with cone-isolating stimuli, the receptive fields have nearly equal and opposite inputs from L- and M-cones, with some receiving S-cone input [103], and they are roughly circularly symmetric—consistent with the finding that they have weak to nonexistent orientation selectivity [50, 51, 96, 97].

The double-opponent cells, however, often respond to both red-green grating patterns as well as achromatic patterns, with spatial specificity. Most of these cells are tuned for spatial frequency in the 1–3 cpd range, with similar spatial tuning for both chromatic and achromatic stimuli [51, 117]. When the receptive fields of V1 double-opponent cells are mapped with cone-isolating stimuli, the L- and M-cone inputs demonstrated spatial opponency for each cone and are of opposite sign at each location (as shown in Fig. 7.6). These cells respond poorly to extended areas of color or to color patterns of low spatial frequency, and are also orientation-

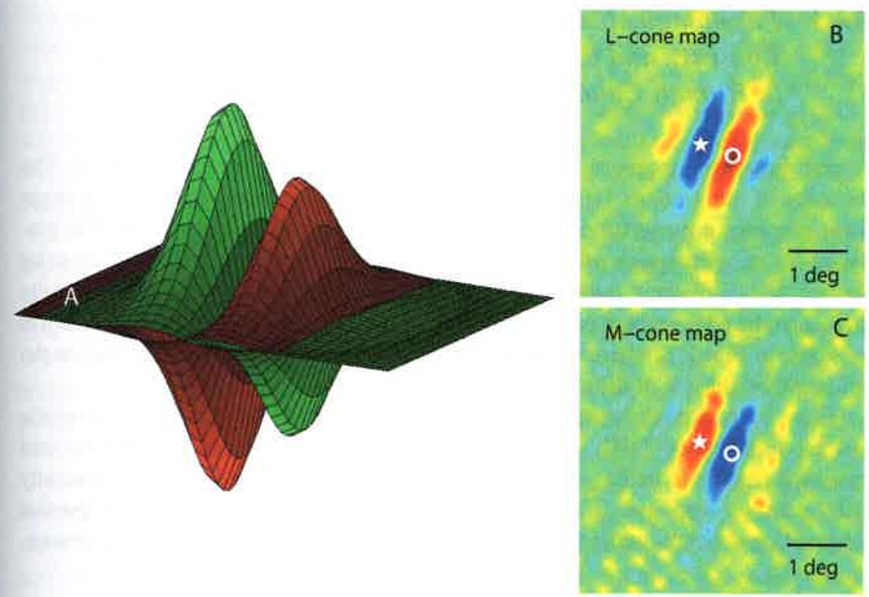

Fig. 7.6 Double-opponent cells in V1 (*from Johnson* et al. [50]). The spatial receptive field organization of an orientation-selective, spatial-frequency-bandpass, double-opponent neuron. (**a**) A schematic receptive field with side-by-side spatially antagonistic regions with opponent cone weights. The weighting above the horizontal plane is ON, where an increment of light will evoke an increase in response; the weighting below the line is OFF, where a decrement will result in a response. (**b**) Two-dimensional spatial map obtained from a neuron in V1 by means of subspace reverse correlation [109] with L-cone isolating grating stimuli. (**c**) Map obtained with M-cone isolating stimuli. At the starred location in **b**, the L-cone map is decrement excitatory. At the same location in (**c**), the M-cone map is increment excitatory, and vice versa for the locations marked by the *open circles*, demonstrating that the cell is indeed spatially and chromatically opponent (double-opponent). The schematic in (**a**) is a three-dimensional representation of the overlay of the two cone maps to give an overall profile. (**a**) is not to scale with respect to (**b**) and (**c**)

selective for both achromatic and chromatic stimuli, although a few double-opponent cells responded weakly to achromatic stimuli [50, 103]. The spatial maps of the receptive fields of the double-opponent cells were often elongated along the axis expected for their orientation preference, and most did not show even (concentric center/surround) symmetry, a departure from the classical double-opponent concept [118]. Since many double-opponent cells respond well to color differences across a border, they could play a crucial role in boundary detection in natural scenes, suggesting that color and form are inextricably bound together from the very earliest stage of cortical processing. Since most edges are defined by both color and luminance contrast with a wide variation in the proportions [14], the sensitivity of most double-opponent cells to both achromatic and isoluminant color boundaries is well-suited to natural image statistics and may be more efficient because they have the capacity of jointly detecting color and luminance-defined boundaries [119].

7.3.3 *Physiological Mechanisms for Color Appearance, Color Contrast, and Color Categorization and the Relevance to Human Color Perception*

A very important property of color appearance is its sensitivity to context. The presence of other colors (including black and white) in a specific spatial arrangement provides a powerful contextual influence on our color perception. The tendency for our perception of a color to change depending on its surrounding color context was discovered many centuries ago [120]. This phenomenon is especially intense at the edges where colors meet. An illustration of this kind of context effect is shown in Fig. 7.7, where a central square changes appearance depending on the color and brightness of the surrounding area.

There is increasing evidence that early visual cortical cells process chromatic context information [102, 113, 121] and that the presence of boundaries and extended regions (whether defined by color, luminance, or both) can significantly alter neuronal responses. These kinds of studies are likely to provide important information about the neurophysiological mechanisms underlying color appearance.

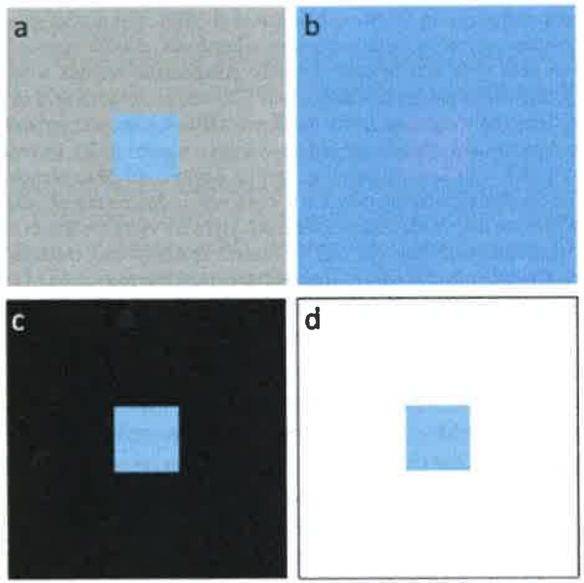

Fig. 7.7 Color contrast, brightness contrast, and color appearance. All four central squares have identical wavelength spectra, yet the color appearance of each central square may be strongly influenced by its surrounding context. (**a**) The central square surrounded by an isoluminant gray results in a saturated blue square. (**b**) The central square surrounded by a slightly different blue surround appears desaturated bluish purple, almost white. (**c**) The blue square on a black background results in a perception of reduced saturation and increased apparent brightness. (**d**) The blue square on a white background appears darker than in the other contexts

There is also a nascent, but growing body of work exploring the physiological interactions between color and luminance signals in V1 and other visual cortical areas, including V4, and inferior temporal cortex (IT) [121–125]. In the psychophysical literature, interactions between color and luminance are found to occur at suprathreshold contrasts and are often complex and nonlinear. Deviations from linearity in cortical neurophysiological responses to luminance and color are also likely, but have not yet been explored systematically.

But where do signals about color contrast emerge? The fact that edges seem to have a substantial influence on color appearance suggests that edge-sensitive color cells are likely important. This could place the neural basis of color contrast perception, which includes color constancy, as early as V1. Explicit tests to determine whether edge-sensitive V1 color cells respond to the color contrast of edges or boundaries are an obvious area for future research. Recent computational models suggest that double-opponent neurons with concentric center-surround receptive fields may contribute to color constancy by coding the external light source color [126, 127], while double-opponent cells with oriented receptive fields and responses to both achromatic and chromatic stimuli may be quite important for detecting salient boundaries in complex color scenes [119]. Nonoriented and spatially low-pass chromatic neurons, like the single-opponent neurons found in V1, could instead play a role in determining surface color and/or color identification.

Of course, color information is also represented in cortex beyond V1. Zeki discovered clusters of color-tuned cells within the macaque superior temporal sulcus in area V4, and proposed this area as a dedicated color center [99, 100]. This has been a source of controversy ever since, as has been its homologue in human cortex. With the mounting evidence for the interaction and mixing of chromatic and luminance signals as early as V1, along with the emergence of spatial specificity in many color-responsive neurons, one might argue that it is unlikely that subtracting responses like luminance, orientation, shape, etc. from pure color responses will give us much insight into the specific brain areas involved with color contrast perception, but these methods might instead provide insight into the areas involved with color identification, color categories, and/or color memory.

As noted in the introduction, discrimination and identification are different aspects of our visual perception, and both are apparent in human color vision. We can discriminate subtle differences in color contrast, and we categorize similar colors into groups, such as "red" and "green." The inferior temporal (IT) cortex is believed to play an important role in the recognition and memory of visual stimuli. Lesioning or inactivating cortical area IT in macaques degrades, but does not abolish their ability to discriminate colors [128, 129], making it likely that areas both within and outside IT cortex contribute to color discrimination. Cells in macaque anterior IT cortex (AITC) respond to hue [130], and response magnitudes in these neurons may depend on whether the behavioral task is discrimination or color categorization [131]. Figure 7.8 shows results for two representative AITC neurons that demonstrate task dependency. This allows for enhancement of the signal differentiating red from green colors during the categorization task and suppression during the discrimination task.

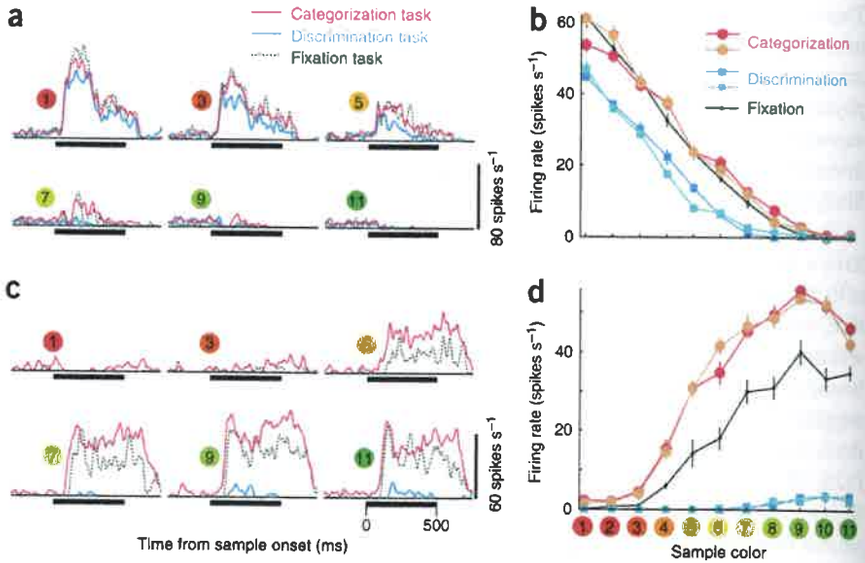

Fig. 7.8 Responses of two color-selective neurons in IT showing task dependency during a color categorization and a color discrimination task (*from Koida and Kamatsu* [131]). (**a** and **b**) Spike density functions showing the responses of each neuron to six sample colors (*filled circles* with *numbers*) during each task (*red line* shows the categorization task; *blue line* shows the discrimination task; *dotted black line* is a fixation task). (**c** and **d**) Color tuning curves of the same neurons as in (**a**) and (**b**) for the entire set of 11 sample colors recorded in separate task blocks (two blocks for each task). *Circles* indicate responses from the categorization task, *squares* are responses from the discrimination task, and *small dots* joined by the *black line* indicate those in a fixation task

Inferior temporal and ventral occipital cortical areas are also highly involved with object-related vision, so responses may be better understood in the future by utilizing stimuli that combine color and form, such as faces, shapes, scenes, etc., rather than simple, large fields of uniform color. That said, these kinds of stimuli are more difficult to control and the responses to them are more difficult to interpret.

7.4 Color Vision in Human Cortex: fMRI Studies

Until several decades ago insight into the physiological basis of color vision relied almost entirely on neurophysiological studies in nonhuman primates. The advent of fMRI, however, has allowed investigation of the visual cortex and LGN in the normal human brain to begin in earnest. fMRI is limited by its spatial and temporal resolution, with voxel size typically in the region of 3 mm^3 of cortex, although with improved processing methods and higher scanner strengths resolutions down to 1 mm^3 are possible. Even at this level, the method remains best at revealing responses in visual brain areas and cortical regions over a relatively large scale, and provides less insight into neural mechanisms or processes.

From an early stage it became clear that human area V1 responds very well to color contrast, at least as well as to achromatic contrast, with color contrast being a very effective driver of BOLD responses [117, 132–140]. Even the human LGN is driven very effectively by red-green color contrast [141]. It is worth noting, however, that the robust color response is typically elicited by using stimuli optimized for color contrast sensitivity (see the cone contrast sensitivity functions in Fig. 7.4) and may diminish relative to the achromatic response for stimuli with higher spatial frequencies, as color sensitivity is lost. As spatial contrast sensitivity functions of the BOLD response have not yet been systematically measured we do not yet know how well the psychophysical and BOLD functions match. In terms of the response to temporal frequency, psychophysical responses and BOLD responses in V1 do not correspond well since the BOLD responses in V1 are maintained with increasing temporal frequency whereas there is a steep decline in psychophysical sensitivity to higher temporal frequencies [142, 143]. In general, BOLD responses to color relative to achromatic contrast are also reduced as stimuli are presented further away from the fovea, particularly for RG stimuli [133], introducing a further source of variation in BOLD signals.

A number of fMRI studies have supported a reduced color response in the dorsal regions V3A and hMT+ of the occipital cortex when compared to early visual areas (V1, V2) and/or more ventral regions including V4 [136, 144, 145], although hMT+ retains some response to color contrast [146]. These studies support a division already well established in nonhuman primates based on single cell recordings and lesion studies.

Much interest has been focused on the role of the ventral pathway in color processing in human vision. The most common approach has been to search for areas that are highly responsive to color, and this has been done with two distinct methods. In one, a *Mondrian color localizer* is used, in which responses to a standard Mondrian stimulus with color and luminance contrast is differenced from the black and white (luminance-only) version [147–150]. In this case, the average luminance contrast is constant between display blocks but chromatic contrast is modulated. This localizer potentially reveals voxels with *any* response to color modulation. Another type of color localizer ("color preference") determines the voxels that show a significantly stronger activation to isoluminant chromatic gratings than to achromatic gratings (presented at the same cone contrast), and hence reveals regions with a color preference [144, 151, 152]. This localizer is more stringent and is likely to reveal fewer color selective regions as it determines voxels with a significant color preference rather than just any response to color. Differences between the two color localizers used may account for some of the variations in the reported color sensitive areas of the ventral visual pathway in human vision. As discussed above, variations in the spatial and temporal stimulus properties as well as their central/peripheral distributions across the visual field will also introduce variability into the determination of visual areas with color "preferences."

While it is clear that a retinotopically mapped area, thought to be human V4, responds well to color contrast, there is accumulating evidence that an area lying adjacent, but more anterior to it in the human brain shows a stronger and more

robust color response. This area has been named variously V4a [147, 148], V8 [138] or VO [144, 152, 153] reflecting its controversial history and disputes over its precise location and naming [137]. The issue is particularly complicated given that there appears to be differences between human and nonhuman primates emerging in the IT cortex [151]. Nevertheless, this region can be retinotopically mapped as distinct from hV4 and probably represents a cluster of retinotopically organized areas (VO-1, VO-2) in human cortex [152, 153]. Taking a different approach, Mullen et al. defined an area in this region, also termed VO, which was localized functionally based on the color preference localizer, in which area VO comprised voxels with significant color preferences that were not part of hV4 [84]. Brewer et al. [152] suggested that stronger color responses are found in VO-1 rather than VO-2, but exactly how the region of color specialization defined by Mullen et al. [144] and the retinotopically mapped regions correspond is not yet well-established, and will be challenging to determine with confidence.

As raised in Sect. 7.3.2, single neurons in nonhuman primate V1 that are responsive to color differ in their color selectivity. Unselective neurons may respond similarly to both color and luminance contrast (called "color–luminance" neurons), whereas selective neurons will have their response dominated or exclusively driven by color contrast ("color-preferring" neurons). Both types will be responsive to color. Thus selectivity and responsivity to color are distinct properties. fMRI adaptation methods can be used to distinguish between these two properties in the human cortex [67, 154, 155]. If a BOLD response to color contrast can be significantly reduced (adapted) by previously viewing the same RG pattern, but is not adapted by viewing an achromatic pattern, it suggests the underlying neural response is selective for color and not driven by achromatic contrast. Conversely, if the BOLD response to color contrast can be significantly reduced by previously viewing both chromatic and achromatic patterns, it suggests an unselective response to both types of contrast. Using this approach Mullen et al. [155] found no sign of selectivity in the early visual areas (e.g., V1, V2), compatible with the dominant presence of color–luminance signals (although see Engel and Furmanski [154] for a different result). However, color selectivity appeared to increase along the ventral pathway with significant color selective adaptation found in area VO. This lends considerable support to a role for area VO in human color processing, although exactly what that role is remains to be determined.

A recent fMRI study on color memory suggests that responses from midlevel visual regions such as area V4 and lateral occipital cortex (LOC) may feed back onto V1 [156]. This finding raises issues with thinking strictly about color, and visual processing in general, as a hierarchical feed-forward process. This common assumption is likely to be as incorrect as classic conceptions of neural mechanisms in terms of single neurons rather than as neural populations working in concert. It is clear that much still remains unknown about cortical color processing, including how memory and sensory areas work together to recognize, discriminate, and remember colors and colored objects in both humans and nonhuman primates.

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