

Color in Complex Scenes

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Abstract

The appearance of an object or surface depends strongly on the light from other objects and surfaces in view. This review focuses on color in complex scenes, which have regions of different colors in view simultaneously and/or successively, as in natural viewing. Two fundamental properties distinguish the chromatic representation evoked by a complex scene from the representation for an isolated patch of light. First, in complex scenes, the color of an object is not fully determined by the light from that object reaching the eye. Second, the chromatic representation of a complex scene contributes not only to hue, saturation, and brightness, but also to other percepts such as shape, texture, and object segmentation. These two properties are cornerstones of this review, which examines color perception with context that varies over space or time, including color constancy, and chromatic contributions to such percepts as orientation, contour, depth, and motion.

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INTRODUCTION

Seeing in color has many advantages. Apart from the enrichment of our visual experience,

more information is in a colored than in a black-and-white world. Flowers on a shrub escape notice in a black-and-white image but are seen immediately with color (**Figure 1a**). Objects in colored scenes are more easily detected (Domini & Lucas 2001, Mollon 2000, Sumner & Mollon 2000), more easily identified (Mollon 1989; **Figure 1b**), more easily grouped (**Figure 1c**), and more easily remembered (Gegenfurtner & Rieger 2000) than objects in black-and-white scenes.

In natural viewing, colored objects are seen within a complex surrounding context. Within the eye and brain, the neural representations of color in complex scenes can be influenced by complicated, and sometimes subtle, aspects of the natural viewing environment. These representations allow the chromatic property of an object to be extracted from the light entering the eye, even though this light depends in part on the source of illumination and on shading. These representations also carry information about the spatial and temporal structure of the scene. In this review, we examine how context affects color perception and also how chromatic representations serve other visual percepts such as form, depth, motion, and object segmentation.

Color is Not in Light

The practice of describing light by its hue, for example a “yellow light,” confuses a perceptual phenomenon (the hue yellow) with the physical world (light). True, a particular physical wavelength near 580 nm appears yellow, 540 nm lime green, 600 nm orange, and 660 nm red. But a yellow indistinguishable from 580 nm is seen also with a mixture of only 540 nm and 600 nm; or only 540 nm and 660 nm; or an infinite number of other light mixtures. The identical color percept from all these physically distinct lights is mediated by identical neural responses evoked by the lights. The determination of color by neural responses to light—not apprehension of color within the light rays themselves—is a

foundational and functional property of color vision.

The Significance of Context in Color Perception

The world we see would be chaotic if an object's color were directly determined by the wavelengths from it that enter the eye. An egg that appears white and an eggplant that is seen as purplish at an outdoor market would be, respectively, yellow and a shade of orange in a kitchen illuminated by a common screw-in light bulb. Of course, this does not happen, and the reason is that neural representations for the color of the egg and the eggplant compensate for the change in wavelengths reflected from objects when moving from outdoor to indoor illumination. More generally, neural processes that mediate perception exploit the spectral and spatial distribution of light so we experience objects with a nearly stable color, despite changes in the wavelengths from the objects that reach the eye.

These neural processes cannot operate when the light from an object is seen without context. Consider an isolated piece of paper that normally appears white and another paper printed with an ink that reflects only long wavelengths. In daylight, one paper appears white and the other red, but if the first paper is illuminated by only long wavelengths and the second paper by daylight, then the wavelengths of light that reach the eye are the same from both papers. There is no information to distinguish their appearance, so they must look identical. In natural viewing, light reflected from other objects in view—that is, context—provides the critical information required to perceive the papers as different in color under various typical spectral distributions of illumination.

Classical theories of color vision focus on isolated patches of light unaffected by context (Wright 1946). They reveal fundamental properties of photoreceptors, which trans-

duce physical light into neural responses at the first stage of vision. Context, however, alters responses within the retina, lateral geniculate nucleus, and visual cortex, so it is hardly surprising that light that is nearby or was viewed previously can change the color appearance of a particular fixed physical stimulus. An example of color-appearance changes induced by context is shown in **Figure 2** where the words ANNUAL and REVIEW are printed in the same ink but within different contexts (similarly OF and PSYCHOLOGY share a common ink). In natural viewing, variegation in the retinal image is abundant over space and time. Such complex visual stimuli excite neural mechanisms that underlie color perception of natural scenes but that are not revealed by an isolated patch of light.

The Principle of Trichromacy and Why it Fails to Explain Color in Natural Viewing

Most human observers can match any spectral distribution of light by a mixture of three primary lights. This is the principle of trichromacy, which follows from neural coding: any uniform, isolated patch of light is encoded by exactly three distinct neural responses. Two physically different distributions of light will be indistinguishable if they result in the same three responses. Trichromacy, however, is silent about the colors one perceives; that is, it explains which lights look alike but not what lights look like.

The distinction between the neural responses that determine trichromacy versus neural representations of hue, while critical, is sometimes lost. The three types of photoreceptor that mediate color vision were called at one time the red, green, and blue cones. Just as “yellow light” inappropriately confuses perception with physical light, the term “blue cone” wrongly confuses perception with a type of neuron. The response of this type of cone is neither restricted to those wavelengths that appear bluish (it responds

Spectral distribution of light: a function giving the amount of energy at each wavelength of light

L, M, and S cones:

the three types of photoreceptors in the retina that respond during daylight. Each type of cone responds to a broad range of wavelengths but has a different wavelength of peak sensitivity

also to wavelengths well beyond 500 nm, which in isolation appear yellowish green) nor is essential for the sensation of the hue blue, which can be experienced with a small, sharply focused retinal stimulus that does not fall on any so-called blue cones (Hofer et al. 2005). Modern terminology includes no color percepts in the names of receptors; the cones are labeled L, M, and S (for long-, middle-, and short-wavelength sensitive, respectively) instead of red, green, and blue. Trichromacy follows from responses of the L, M, and S cones irrespective of the hue they evoke.

Trichromacy implies that any isolated patch of light can be matched by a mixture of three primary lights, but the range of colors we see with all possible mixtures of primaries is much smaller than the gamut of colors we commonly experience. The reason is context, which not only alters color perception (**Figure 2**) but also vastly expands the domain of colors we see. A mixture alone never appears brown, maroon, or gray, which are commonly experienced but evoked only when a light is viewed with other light nearby (that is, with context). Trichromacy also implies that two physically different patches of light that look alike in the dark will look alike in any shared context. The two patches evoke the same neural responses at the first stage of vision, so they are substitutable for one another (Grassmann 1853). Context can affect the patches' color appearance but it does so equally; thus, trichromacy cannot reveal what lights look like in a complex scene.

To distinguish light from the percept it evokes, light is described here by its wavelength or spectral distribution. A nonselective spectral distribution, such as equal energy at all wavelengths, is called "broadband." Color names (e.g., brown, red, green, pink, and white) are reserved exclusively for percepts, as is the term "achromatic," which refers to a percept of white, gray, or black. Luminance or radiance is a magnitude of physical light, whereas brightness refers to the perceived level of emitted light.

CONTEXT IN COMPLEX SCENES

Complex Context Cannot be Reduced to Simple Context

The simplest context is a uniform background field, which has been studied extensively for over a century (e.g., Chichilnisky & Wandell 1995, Jameson & Hurvich 1972, Shevell 1982, von Kries 1905, Walraven 1976; for review, see Shevell 2003). The influence of the context in a complex scene might be understood with theories that explain color changes from a uniform background, a possibility called the equivalent-uniform-background hypothesis.

The hypothesis has alternative forms. The strongest form holds that complex context is equivalent to a uniform field at the space-average chromaticity and luminance of the context. In this form, averaging is at the level of physical light and the context is reduced to a trichromatic description of the space-average stimulus. A different form holds that the effect of each region within a complex background can be represented by its effect as a uniform background; the effects from multiple regions are combined to explain the influence of complex context. This implies aggregation at a neural level. A third form posits that some (unspecified) uniform background is equivalent to (that is, completely substitutable for) any complex context.

The equivalent-uniform-background hypothesis provides a first-order account of some studies of color (Bauml 1995, Brainard & Wandell 1992, Valberg & Lange-Malecki 1990), but none of its variants is consistent with color perception in complex scenes. The space-average form is tested explicitly by substituting different inhomogeneous backgrounds that have the same space-average chromaticity and luminance. Such substitutions alter color appearance, even with a locally uniform field surrounding the region judged in color so that edge contrast is fixed (Barnes et al. 1999, Mausfeld & Andres 2002). Also, adding retinal disparity and thus stereoscopic depth to a complex scene changes

the influence of context without altering the space average of light in each eye (Yang & Shevell 2002).

Aggregation of neural influences from each distinct region fails a test of independence. Consider three lights: 540 nm, which appears yellowish green; 660 nm, which appears red; and a broadband light that appears white. Initial measurements can establish the color change caused by a uniform background of only 540 nm, 660 nm, or broadband light; as expected, the broadband background has little effect on color. Next, consider (a) a new background with two separate regions, one composed of 540 nm and one composed of the broadband light; and (b) a second new background with 660 nm in place of 540 nm in one region and the same broadband region as in (a). Identical broadband regions should have the same influence, whether paired with 540 nm or 660 nm; moreover, that influence should be weak because of the minimal influence of the broadband background alone.

Measurements, however, show a substantial change in color perception when the broadband region is introduced within either a 540 nm or 660 nm background. Furthermore, the direction of color change evoked by adding the broadband region to 540 nm [background (a)] is opposite in direction to the change due to adding the broadband region to 660 nm [background (b)]. This implies that even minimally complex backgrounds composed of only two chromaticities fail the independence condition implicit in this form of the equivalent-uniform-background hypothesis (Wesner & Shevell 1992). Independence is inconsistent also with the color induced by chromatic patterns, each one at a single spatial frequency, in comparison with a compound pattern with both frequencies. The compound pattern reveals nonlinear spatial interactions (Zaidi et al. 1992).

The form that posits the existence of some uniform background equivalent to any complex context fails to account for color-appearance shifts caused specifically by chromatic variegation within a scene (Brenner &

Cornelissen 2002, Ekroll et al. 2004, Shevell & Wei 2000, Singer & D'Zmura 1994). For example, different chromatic lights perceived as green, red, blue, or yellow (rectangles, *upper panel* of **Figure 3**) lose most of their color when viewed against a background pattern containing strong chromatic contrast (*lower panel* of **Figure 3**; from Brown & MacLeod 1997). This gamut compression with high-contrast context occurs even with thin gray "grout" between the elements of the background mosaic, a result that excludes local contrast at the edge of the rectangles as the cause of the color differences in the two panels of **Figure 3**. Gamut compression is separable for color and brightness (Brown & MacLeod 1997).

Color Perception with Context that Varies Over Space or Time

Background context that varies in space or time may influence separate processes at distinct levels of the visual system. Background light at spatial frequencies above 4 cycles per degree alters the number of photons absorbed by receptors in nearby regions due to imperfections in the eye's optics, which cause spread light (Smith et al. 2001). Spread light varies with the specific wavelengths in the stimulus and increases with spatial frequency (Marimont & Wandell 1994).

With complex context, separate neural processes can be influenced by the mean and the variability within a background over time and/or space. For example, a spatially uniform background that oscillates slowly in time (1 Hz) between two chromaticities causes a light at their physical average to have an appearance approaching achromatic; at the same time, the hues of other lights are compressed along the axis of chromatic oscillation (Webster & Mollon 1994, 1995). Consider a range of lights that all appear bluish but are somewhat dissimilar in hue because of modestly different L-, M-, and S-cone stimulation. After viewing a steady uniform background at their mean chromaticity, these

Gamut

compression: the phenomenon in which colors or brightnesses that normally cover a given range appear to cover a smaller range

Spatial-frequency tuning: a function giving relative sensitivity at each spatial frequency of a visual stimulus. Spatial frequency is the number of cycles of a repeating pattern within a given visual angle (for example, the number of cycles within one degree of visual angle)

Equiluminant: constant in luminance (i.e., may vary in only chromaticity)

same lights appear to have a range of different hues around white. These percepts are described fairly well by adaptation-induced rescaling of L-, M-, and S-cone responses. If, however, a temporally oscillating field with the same time-average chromaticity replaces the steady background, then further color shifts occur. The variability of the background light over time causes compression of a separate postreceptoral chromatic neural representation. Furthermore, this compression of the range of perceived color occurs selectively along virtually any direction of chromatic oscillation, which implicates a neural representation of dimensionality exceeding the three of trichromacy, presumably at a cortical locus.

Steady backgrounds with spatial variation (as in **Figure 3**, *lower panel*) rather than temporal variation cause similar compression when chromaticities in a background mosaic are selected randomly from a line in color space. Color-selective compression in any chromatic direction again suggests a nontrichromatic cortical process (Webster et al. 2002).

A central neural mechanism is revealed also by chromatically varying spatial context in one eye, which evokes the same shift in the color of a light presented to either the same eye or fellow eye (Shevell & Wei 2000). A cortical neural process may be inferred also for the perceived color differences in **Figure 2**. The spatial-frequency tuning and chromatic selectivity of the color shifts implicate an S-cone antagonistic center-surround (+S/-S) receptive-field (Shevell & Monnier 2005). No such neuron is found in the retina (Calkins 2001; Dacey 1996, 2000), but physiological studies reveal cortical neurons with S-cone center-surround organization (Conway 2001, Solomon et al. 2004).

Chromatic variation within background context alters perceived chromatic contrast as well as hue. A region with a fixed magnitude of L-cone/M-cone chromatic contrast appears to have less contrast when surrounded by a background of high rather than low L-cone/M-cone variation. Chromatic selectivity

of perceived contrast reduction is substantial though not complete: perceived L-cone/M-cone contrast is more strongly compressed by an equiluminant background that varies stimulation of the L and M cones, compared with a background with only S-cone contrast (**Figure 4**; similarly, perceived S-cone contrast is more strongly reduced by an equiluminant background with S-cone than L-cone/M-cone contrast (Singer & D'Zmura 1994). Compression of perceived chromatic contrast shows interocular transfer (chromatic-contrast background in one eye, test presented to the other eye), which implicates a central neural mechanism.

Context that contains chromatic variation typical of natural scenes points to the functional significance of these neural mechanisms. Chromatically selective compression along any direction of chromatic variation, as discussed above, allows adaptation to the specific color gamut within individual scenes and natural environments. Chromatic compression varies according to (*a*) the colors found in different natural scenes (Webster & Mollon 1997, Webster et al. 2002) and (*b*) the chromatic variation within a single scene, which shifts under different spectral illuminations (Webster & Mollon 1995).

Chromatically selective neural responses within the retina, lateral geniculate, and visual cortex have been studied extensively [reviewed by Gegenfurtner (2003) and Solomon & Lennie (2007)]. A general conclusion is that cortical responses show a greater diversity of chromatic selectivity than responses from subcortical neurons. The multiple levels of chromatic representation imply that a full understanding of color perception in complex scenes requires knowledge of the influence of context at each level.

COLOR CONSTANCY

Most objects we see are visible only when they reflect illumination from a light source, such as a lamp or the sun. The objects cannot be seen when the lights go off or the

sun goes down, which reveals a basic conundrum: The light from an object depends on both the selective spectral reflectance of the object and the spectral composition of the illumination. In normal viewing, however, the color of an object remains quite stable under different illuminants even though only the object's spectral reflectance (irrespective of the illumination) defines the object's chromatic characteristic. Color constancy is the stable perceived color of an object under different light sources, despite the different spectral distributions of light from object to eye. Recall the example of the egg and the eggplant mentioned above.

Perceptual constancy would be a minor issue if changes of illumination caused small differences in the spectral distribution of light entering the eye, but exactly the opposite is true. If the color of an object depended on only the light reflected from it, the shifts would be dramatic. A mosaic of colored objects known as the Macbeth ColorChecker (Munsell Color Laboratory, New Windsor, New York) gives a full range of colors under sunlight (**Figure 5**, *top*). The same mosaic illuminated by an indoor (tungsten) light bulb reflects much less short-wavelength light to the eye; this change of illumination would cause substantial shifts if just the light from each region within the mosaic mediated its perceived color (as simulated in **Figure 5**, *bottom*). In general, the changes in receptor stimulation from a single object due to changes in everyday illumination are comparable to the differences in receptor excitation when one light illuminates separate objects of categorically different hue (Shevell 2003).

Context provides the biologically available information necessary (though not sufficient) to achieve color constancy. Theories of constancy differ in terms of how context contributes to the color appearance of objects.

Color Constancy is Imperfect

Color perception is closer to constancy than to the color percept expected from the wave-

lengths reflected by an object, but constancy is not complete. Estimates of the degree of color constancy vary widely with the viewing context and the task asked of the observer which, in different studies (reviewed by Smithson 2005), requires full color matching of an object under different illuminants, a judgment of the chromaticity that appears colorless ("gray" or "white"), assignment of color names to objects, categorization of the color of a surface as one of a small number of possible hues, or identification of identical surfaces under different illuminants. Color constancy indexes range from zero (no constancy) to 1.0 (perfect constancy). Constancy is found to be nearly perfect when categorizing the hue of a pulsed stimulus seen on a larger field reflecting the illuminant, but it falls by about half if the same stimulus is viewed steadily and the illuminant is in only a remote, spatially separated region (Hansen et al. 2007). Constancy can be high (index >0.8) for the judgment of a colorless percept in a room with real illuminated objects and surfaces but drops substantially if the change of illuminant fails to alter local edge contrast, the spatial average of light in view, or the most intense stimulus (Kraft & Brainard 1999). Constancy index values below 0.7 are common in studies employing various experimental approaches (e.g., Arend et al. 1991, Smithson & Zaidi 2004, Yang & Maloney 2001).

Receptor Responses are Always Ambiguous

The light from an object absorbed by each type of cone L, M, or S, Q_L , Q_M , or Q_S , is

$$\begin{aligned} Q_L &= \int_{\lambda} \{E(\lambda)R(\lambda)\}q_L(\lambda)d\lambda, \\ Q_M &= \int_{\lambda} \{E(\lambda)R(\lambda)\}q_M(\lambda)d\lambda \quad \text{and} \\ Q_S &= \int_{\lambda} \{E(\lambda)R(\lambda)\}q_S(\lambda)d\lambda. \end{aligned}$$

The integration is over the wavelengths λ of visible light from 400 to 700 nm; $E(\lambda)$ is a function with the (unknown) energy level of

Spectral

reflectance: a function giving the fraction of energy reflected from an object or surface at each wavelength of light

Color constancy index: a summary measure of the degree to which perception follows color constancy in a given situation

the illuminating light at each wavelength; $R(\lambda)$ is a function with the (unknown) proportion of incident light reflected from the object at each wavelength; and $q_L(\lambda)$, $q_M(\lambda)$, and $q_S(\lambda)$ are functions with the physiological spectral sensitivity of each type of cone L, M, and S. Only the spectral reflectance at each wavelength, $R(\lambda)$, carries the intrinsic chromatic characteristic of an object; as shown by the equations, however, the biologically available information (Q_L , Q_M , and Q_S) depends on the product $E(\lambda)R(\lambda)$ at each wavelength.

In natural environments, the integrals that give Q_L , Q_M , and Q_S are approximated very closely by summing values at 10 nm intervals (that is, at 400, 410, 420, . . . , 700 nm). In this case, $E(\lambda)$, $R(\lambda)$, $q_L(\lambda)$, $q_M(\lambda)$, and $q_S(\lambda)$ are each vectors with 31 values, and the light absorbed by each cone type is

$$\begin{aligned} Q_L &= \sum_{\lambda} \{E(\lambda)R(\lambda)\}q_L(\lambda), \\ Q_M &= \sum_{\lambda} \{E(\lambda)R(\lambda)\}q_M(\lambda) \quad \text{and} \\ Q_S &= \sum_{\lambda} \{E(\lambda)R(\lambda)\}q_S(\lambda). \end{aligned}$$

This summation form makes clear that adding more objects (i.e., context), each with its own spectral reflectance $R(\lambda)$, does not deterministically solve the constancy problem because each new object adds three biologically available quantities (Q_L , Q_M , and Q_S) as well as an additional unknown spectral reflectance vector $R(\lambda)$ with 31 values [$R(400)$, $R(410)$, . . . , $R(700)$]. The neural responses of receptors, therefore, carry insufficient information to specify the chromatic characteristic of the object. Theories of color constancy must resolve this implicit ambiguity by applying assumptions about the visual system and/or the physical world.

Modeling Illumination and Reflectance

With N objects, each with its own reflectance $R(\lambda)$ and all under a single illuminant with energy distribution $E(\lambda)$, summation at 10 nm intervals requires 31 unknown values for each object's reflectance plus 31 additional

unknowns for the illuminant [thus $31(N+1)$ unknown values in all]. Each object results in three separate receptor quantal absorptions, Q_L , Q_M , and Q_S , so there are $3 \cdot N$ neural responses available to determine $31(N+1)$ unknowns, which, of course, is too little biological information to solve for so many unknown reflectance values. Models of illuminant spectra and reflectance spectra reduce the number of unknowns so the biological information is sufficient to determine the reflectance vectors $R(\lambda)$. For example, the illumination $E(\lambda)$ can be posited to be some weighted sum of three known, fixed spectral energy distributions $e_1(\lambda)$, $e_2(\lambda)$, and $e_3(\lambda)$. Then the 31 unknowns for $E(\lambda)$ are reduced to just three unknowns: the weights a_1 , a_2 , and a_3 that give the illuminant $E(\lambda) = a_1 e_1(\lambda) + a_2 e_2(\lambda) + a_3 e_3(\lambda)$. Similarly, all reflectances can be posited to be a weighted sum of three known, fixed reflectance distributions $r_1(\lambda)$, $r_2(\lambda)$, and $r_3(\lambda)$, so the reflectance of any object depends on just three weights, b_1 , b_2 , and b_3 ; then, an object's reflectance $R(\lambda)$ is given by $b_1 r_1(\lambda) + b_2 r_2(\lambda) + b_3 r_3(\lambda)$. Under these assumptions, and with a reference patch of known (or assumed) reflectance $R_{\text{STANDARD}}(\lambda)$, the $3N$ quantal catches are sufficient to determine the values b_1 , b_2 , and b_3 and thus establish color constancy (Buchsbbaum 1980, Sallstrom 1973).

The assumptions that all illuminants and reflectances can be expressed as a weighted sum of just three spectral distributions are reasonable approximations of the variations of natural illumination that occur with weather and over the course of a day (Judd et al. 1964) and of the spectral reflectances found in natural scenes (Cohen 1964, Dannemiller 1992). Neither assumption is perfect but neither is color constancy. If reflectance is assumed to be a weighted sum of only two distributions, so $R(\lambda) = b_1 r_1(\lambda) + b_2 r_2(\lambda)$, then the $3N$ quantal catches ($N \geq 3$) give constancy without requiring a reflectance standard in view (Maloney & Wandell 1986). Other models of illumination and reflectance invoke alternative assumptions (reviewed by Shevell 2003).

Estimating Illumination

Since Helmholtz (1866/1962), the stable color percept of an object has been attributed to our ability to “eliminate” (volume II, p. 287) differences in spectral illumination. This can be wrongly interpreted to mean that the intrinsic chromatic property of an object [that is, its reflectance $R(\lambda)$] can be determined by directly viewing the illuminant (or inferring an equivalent neural representation) so that the illuminant can be eliminated. The idea may be that receptor stimulations from an object, which depend on the product $E(\lambda)R(\lambda)$, can reveal the reflectance $R(\lambda)$ if there is a neural representation of the illuminant alone. Viewing the illuminant, however, provides only a trichromatic neural representation: the amount of illuminating light absorbed by each type of cone, Q_L , Q_M , and Q_S . This biologically available information is insufficient to determine either the spectral energy distribution of illumination $E(\lambda)$ or the intrinsic chromatic property of an object $R(\lambda)$ (Maloney 1999).

Nonetheless, estimating the illuminant can be an integral component of a theory of color constancy that includes other assumptions, such as a model of illumination and reflectance (discussed above). Simple estimates of illumination can be based on the receptor responses to the average light over the entire scene (“gray world assumption”; Buchsbaum 1980) or to the brightest patch in view (Land & McCann 1971), though these fail to capture many available physical cues to illumination. These cues include specular reflections from surfaces, shadows, mutual inter-reflections among objects, and luminance-chromaticity correlation within a scene (Golz & MacLeod 2002, MacLeod & Golz 2003, Maloney 2002; reviewed by Smithson 2005); some cues require a three-dimensional scene (Maloney 1999). A further complication is multiple sources of light (Yang & Shevell 2003), which are common in natural viewing. Given the availability of multiple cues, which may not be equally informa-

tive about illumination or even be available in some environments, two basic questions are how each cue is selected (or ignored) and how the selected cues are aggregated. This is the cue combination problem (Maloney 2002), which optimally should consider each cue’s reliability as well as its relative value for estimating the illuminant.

Another approach to illuminant estimation exploits features of the natural environment. The spectral characteristics of lights in natural scenes are not random. This property can be used to determine the most likely combination of illumination and object reflectance consistent with the ambiguous receptor responses. For example, the two papers described in the Introduction section that reflect identical long-wavelength light to the eye and thus cannot be distinguished by photoreceptor signals would, on this account, be seen as reddish because an object reflecting only long wavelengths under daylight illumination is more likely in the natural environment than is an object that reflects all wavelengths equally under only long-wavelength illumination. Object color so determined goes beyond the biologically available information from the scene by using prior knowledge about illuminated objects in the natural world. Such estimates of illumination and the consequent color percepts are called Bayesian, after the eighteenth-century mathematician Thomas Bayes, who formulated an approach that incorporates prior knowledge with new information to assess the likelihood of events. A Bayesian illuminant-estimation model can account well for a surface perceived to be colorless (gray or white) when part of a complex (simulated) scene under various different spectral illuminants (Brainard et al. 2006; see Knill & Richards 1996 for other applications of the Bayesian approach to visual perception).

Relational Color Constancy

Color constancy is the stable perceived color of objects under different spectral light

Spectrally unselective representation:

a representation that can be achieved with any wavelength of light. An example is a representation sensitive to only luminance (i.e., the representation gives no information about chromaticity)

sources. This definition, based on color appearance, is akin to a similar problem called relational color constancy (Foster & Nascimento 1994): Is a change in light from a scene perceived as a change in object color or, instead, only spectral illumination? Relational color constancy would provide the functional ability to discriminate a change in a physical object (ripening of fruit) from a change in ambient lighting (long-wavelength light at sunset). Although the color appearance of the object could change with illumination, its inferred chromatic properties would not when the difference in the visual stimulus is attributed entirely to an illumination change.

There is a close relationship between standard and relational color constancy for an ideal visual system viewing surfaces under a single illuminant, though in practice, the two types of constancy are empirically dissociable (Foster et al. 1997). Relational color constancy is tested by asking an observer to judge whether the difference between two separate visual stimuli is due to a change in illumination or a change in object reflectance. Humans make this discrimination accurately and reliably. This ability can be modeled by the relative receptor stimulation across space for each type of cone (L, M, or S), which changes very little with changes in spectral illumination (Foster & Nascimento 1994). In fact, a scene undergoing a (simulated) change in only natural spectral illumination but that causes a modest change in a cone-type's relative excitation across space is often misperceived as a change in object reflectance; furthermore, nearly the same change but with artificial manipulation that preserves relative receptor excitation is judged wrongly as a change in only illumination (Nascimento & Foster 1997).

CHROMATIC REPRESENTATIONS IN SERVICE OF VISUAL PERCEPTS OTHER THAN COLOR

The primary function of color vision is the percepts of hue and saturation. In fact, color

vision is defined as the ability to distinguish two lights regardless of their luminance levels. Chromatic neural representations, however, contribute also to other visual percepts such as shape, texture, and object segmentation. For example, color vision can reveal objects that are camouflaged in a black-and-white image (**Figure 1a**); in this case, a chromatic representation serves object segmentation. As with the perception of hue, context is critical for understanding the role of color vision in the perception of form and motion, which by definition refer to relations within a stimulus across space and/or time. A poignant indicator that hue and form are separate functions of color vision comes from cerebral achromatopic patients, who through brain injury have lost all sensation of hue yet often perceive the form of purely chromatic patterns as well as normal persons do (Heywood et al. 1998).

A number of interrelated questions concern the contributions of chromatic neural responses to form, motion, and other percepts. First, is there evidence that purely chromatic stimuli drive percepts of form or motion? Second, if such evidence indeed exists, is a chromatic neural representation better or worse than a spectrally unselective representation based only on luminance? Third, how do chromatic and spectrally unselective representations combine, if at all, to determine perceived form or motion? Fourth, are there circumstances in which a particular combination of chromatic and spectrally unselective information alters the percept of form or motion? Although the first two of these questions have received considerable attention over the past 20 years (reviewed by Regan 2000 and Gegenfurtner & Kiper 2003), the question of how chromatic and spectrally unselective representations interact for form and motion perception has only recently begun to be addressed. To approach these questions, first consider the relations among chromaticity, luminance, and form in the physical world, and the manner in which these physical features are initially encoded by the visual system.

Correlations Among Cone and Cone-Opponent Responses

Visual information about form and motion is provided by the spatiotemporal pattern of luminance and chromaticity in the image. The advantage provided by color vision depends on at least two neural representations that are not confounded, for if every spatiotemporal change in brightness were accompanied by a comparable change in color, there would be no biologically useful information in the representation of color. In daylight vision, the retinal image captured by the L, M, and S cones (**Figure 6a**) is transformed into three postreceptoral responses (Derrington et al. 1984, DeValois 1965, Krauskopf et al. 1982): a luminance response, which sums the signals from the L and M cones, and two chromatically selective pathways, one of which compares the responses of the L and M cones (the L-M response) and one of which compares the response of the S cones with the summed responses from the L and M cones [the S-(L+M) response]. [These postreceptoral chromatic responses are sometimes—and again inappropriately—labeled “red-green” and “yellow-blue,” respectively. This is a carryover from the misnomers for cones, discussed above. Although each response encodes chromatic information, neither one is mapped to only one pair of hues (Knoblauch & Shevell 2001, Mollon & Cavonius 1987, Wuerger et al. 2005)].

The three postreceptoral responses decorrelate the cone signals; that is, they remove information that is redundant in the signals by virtue of the close overlap in the cones' spectral sensitivities (Buchsbbaum & Gottschalk 1983, Fine et al. 2003, Johnson et al. 2005, Ruderman et al. 1998, Zaidi 1997; but see also Lee et al. 2002). The responses of each cone-type to the image in **Figure 6b** are shown in **Figure 6c**, where cone-response magnitudes are represented by gray level. The Pearson correlation coefficient R between the image pixel values of each pair of cone responses is 0.96 for L and M, 0.78 for M and S, and 0.73

for L and S. These values are typical for natural scenes (Ruderman et al. 1998) and Munsell papers (McIlhagga & Mullen 1997). They show that the L-, M-, and S-cone responses are in most instances highly correlated. The postreceptoral responses formed by combining cone signals are shown in **Figure 6e**. The figure is drawn in black and white to reinforce the point that each response alone cannot signal hue. Hue is only made explicit at a later stage, where the postreceptoral responses (or subsequent recordings of them) are compared to each other (DeValois & DeValois 1993, Wuerger et al. 2005). The correlations among the postreceptoral responses in **Figure 6e** are much smaller than the correlations among the cone signals: 0.17 for L+M with L-M, 0.14 for L+M with S-(L+M), and -0.16 for L-M with S-(L+M). Decorrelation is a fundamental property of sensory systems (Barlow & Foldiak 1989, Field 1994, Simoncelli & Olshausen 2001) and means that the L-M, S-(L+M), and L+M signals are largely independent. There are, however, some consistent correlations among the postreceptoral responses in natural scenes, and these can be important for perception. Correlations between “redness” and “luminance” (L-M with L+M) are exploited for color constancy (Golz & Macleod 2002). The negative correlation between L-M and S-(L+M) in **Figure 6e** is found across scenes (Johnson et al. 2005, Webster & Mollon 1997) and is especially pronounced in scenes with arid landscapes and blue skies (Webster & Mollon 1997), revealing a tendency for colors to fall along a continuum between the hues blue and yellow.

The relative independence of the L-M and S-(L+M) responses highlights that color-defective individuals lack certain types of form information normally provided by chromatic coding. About 8% of the male population is born without normal L- or M-cone photopigment (Smith & Pokorny 2003). A quarter of these, known as dichromats, are missing altogether either functional L or M cones and experience only those color percepts carried by the S-cone pathway. Loss of functional

S cones, resulting in tritanopia, is extremely rare. The information loss experienced by dichromats can be modeled by transforming a natural image into a two-cone, as opposed to the normal three-cone, representation. As dichromats can have no appreciation of the hues experienced by trichromats (and vice versa), any model of dichromatic hues inevitably requires some assumptions (Viénot et al. 1995). Nevertheless, **Figure 7b,c** suggests the reduction of color differences for protanopes and deuteranopes compared with normals: The red flowers are no longer conspicuous against the green foliage. Tritanopes, on the other hand, might be expected to miss violet flowers. The figure emphasizes that what is missing from the visual world of the dichromat is not just the ability to experience and discriminate certain hues, but also the ability to detect certain types of objects.

Correlations Among Higher-Order Representations

The strongest correlations among the three postreceptoral neural representations are found not among pixel intensities but rather among pixel-intensity relations. The relations among points in an image define higher-order structures such as edges, contours, shapes, and textures. In the three postreceptoral representations, the higher-order structures have similar mathematical properties (Parraga et al. 2002, Wachtler et al. 2001) and for a given scene are positively correlated. For example, in **Figure 6e**, the shape of the violet flower is visible in both the S-(L+M) and L+M postreceptoral representations, and the upper edge of the terracotta pot can be seen in all three responses. The edge maps (**Figure 6f**) reinforce the point that the three postreceptoral responses are closely related when image structure is considered (Fine et al. 2003, Johnson et al. 2005).

The reason for higher-order correlations among the postreceptoral responses to everyday scenes is that a change in chromaticity

is accompanied by a change in luminance at most object borders; thus, a change in one postreceptoral response is typically accompanied by a change in another. Given the importance of object boundaries to visual object recognition, neurons in the visual cortex might be expected to be tuned simultaneously to both chromatic and luminance contrasts, and many such neurons are reported (Horwitz et al. 2005, Johnson et al. 2001; reviewed by Solomon & Lennie 2007).

Does it follow, then, that color is made redundant by considering change relations rather than point intensities? The answer is no for illuminated objects, as in natural viewing. Object boundaries typically cause luminance changes together with chromatic changes, but shadows and shading tend to cause luminance changes free of chromatic change (Kingdom et al. 2004, Rubin & Richards 1982). These relations are illustrated in **Figure 8**. Chromatic variations, therefore, are more reliable indicators of material boundaries than are luminance variations (e.g., see also Switkes et al. 1988), particularly in scenes where shadows and shading are prevalent.

Experimental evidence shows that the visual system uses these chromatic-luminance relations in a way that directly influences perception. The luminance grating in **Figure 9a** appears almost flat, yet when combined with the orthogonally oriented chromatic grating in **Figure 9b**, produces a “plaid” (**Figure 9c**) that appears markedly corrugated in depth (an example of shape-from-shading). The changes in luminance are not tied to the changes in chromaticity; this promotes the perceptual interpretation that the plaid in **Figure 9c** is a material surface with differences in shading (just as the luminance but not chromatic change in **Figure 8** is interpreted as shading). This shading is characteristic of a corrugated material illuminated obliquely, which is what is perceived. If, on the other hand, the luminance changes are accompanied by corresponding chromaticity changes, then the percept of shading and thus depth should be lost. This is exactly what

happens. Adding a second chromatic grating in alignment with the luminance grating, as in **Figure 9d**, strongly reduces the impression of corrugated depth. Now, the changes in luminance are perceived to belong to the material rather than to shading of the illuminant. These percepts from chromatic-luminance patterns (Kingdom 2003) reveal that color vision helps segment a retinal image into perceived material and illumination components, which is critical for object perception. The color-as-material assumption can sometimes lead to striking perceptual errors. The building in **Figure 10** appears to be painted two-thirds orange, yet the orange part is in fact sunset illumination shining on a spectrally unselective reflecting surface.

Not only does color affect perceived shape, but perceived shape also affects color perception. Consider a card that is painted magenta on its left half and white on its right half. When folded vertically along the central color boundary, with the fold more distant than the card's edges (like so $>$, viewed from the left), the concave shape causes some light to be reflected from the magenta half onto the white half, resulting in a perceived pinkish glow on the white side. The perceived shape of the card can be inverted with an optical device (a pseudoscope) that reverses binocular disparities so the fold appears to be nearer than the edges (perceived shape like so $<$, viewed from the left), even though the card itself and the physical reflection of light from the magenta half is unchanged. Now the white half of the card appears a deep magenta color (Bloj et al. 1999). The substantial color shift caused by a change in perceived shape implies the visual system uses information about shape to counteract the physical interreflection of light between surfaces. Specifically, the reflected light from the magenta half that falls on the white half tends to be discounted when the geometry is consistent with interreflection between surfaces. On the other hand, when the card is perceived with the center fold forward (like looking at a peaked roof from a helicopter), the geometry does not support interreflection;

in this case, the light reflected from the magenta half is attributed to the surface of the white half, which appears magenta.

The spatial relations between color and luminance are important also for the percept of transparency that we experience when viewing materials we can see through. Spectrally unselective transparencies, such as dark glasses or the simulated transparency in the center of **Figure 11a**, reduce the level of light without altering its chromatic content, akin to how a cast shadow is primarily a change in luminance, not chromaticity (**Figure 8**). In chromatically variegated scenes, a sharp change in luminance unaccompanied by a change in chromaticity is therefore consistent not only with a shadow but also with a spectrally unselective transparency (Kingdom et al. 2004), though a compelling impression of transparency often requires additional cues, such as sharp borders and X-junctions (Kanizsa 1979). Introducing random chromatic changes across the borders of an otherwise compelling spectrally unselective transparency (**Figure 11c**) reduces or eliminates the impression of transparency (Kingdom et al. 2004, Ripamonti & Westland 2003). But this does not mean that continuity of color across the transparency border per se is the prerequisite for the impression of transparency. Provided that the changes in chromaticity across the transparency border are consistent along the length of the border (that is, always toward a particular color—blue in the example in **Figure 11d**), a strong impression of transparency results, but now of a colored transparency such as color-tinted acetate (D'Zmura et al. 1997, Fulvio et al. 2006, Khang & Zaidi 2002, Ripamonti & Westland 2003). It would appear that the critical chromatic requirement for transparency perception is consistency, rather than absence, of chromatic change across the transparency border. Cross-border chromatic consistency is an important factor also in the related phenomenon known as neon-color spreading (**Figure 12**; Anderson 1997, van Tuijl 1975).

X-junction: a feature of a stimulus where four distinct regions meet such that the boundaries between them form an X (for example, when an edge created by a shadow falls perpendicular to an edge of an object)

Isochromatic:

constant in chromaticity (i.e., may vary in only luminance)

Contour:

a continuous line or edge, such as the outline of an object

Low spatial resolution system:

a system that is relatively sensitive to coarse detail (low spatial frequencies) but relatively insensitive to fine detail (high spatial frequencies)

Equiluminance

Despite the importance of the interaction between representations of chromaticity and luminance for perceived form, as discussed above, most studies use equiluminant stimuli to assess the chromatic contribution to form or motion perception. Equiluminant (that is, constant-luminance) stimuli are designed to evoke only chromatic neural representations in order to probe their isolated contributions. They are often employed to answer the question: Are the neural responses that are driven by only chromaticity “better or worse” than the responses to luminance? A difficulty, however, arises in comparing chromaticity and luminance for a given form/motion task because performance usually improves with stimulus contrast, and there is no common metric to equate chromatic contrast and luminance contrast. One approach to this problem is to use a behavioral measure that is independent of how contrast is measured physically. One such measure defines contrast in multiples of the amount of contrast required to detect the stimulus. With contrast defined in this way, form and motion tasks at equiluminance (that is, purely chromatic stimuli) tend to require higher contrast to achieve a given level of performance than do their isochromatic counterparts with luminance contrast (Morgan & Aiba 1985, Mullen & Boulton 1992, Simmons & Kingdom 1994, Webster et al. 1990). The precise reason for this is not clear, but two possible reasons are that chromatic form/motion mechanisms (*a*) have higher internal noise levels and/or (*b*) employ fewer neurons in comparison with the mechanisms involved in chromatic detection (Kingdom & Simmons 2000, Solomon & Lennie 2007).

Recall that equiluminant stimuli have an inherent limitation in that they cannot reveal how chromaticity and luminance jointly contribute to percepts of form or motion. In a given natural scene, for example, chromatic contrast might contribute very little to some types of form or motion because sufficient lu-

minance contrast is present to produce asymptotic performance. On the other hand, certain benefits of color vision might be revealed only when chromatic and luminance variations are both present, as discussed above.

Color and Spatial Resolution

When the L-M and S-(L+M) component images of **Figure 6** are rendered in colors that isolate their respective postreceptoral representations, as shown in **Figure 13b,c**, there is a striking lack of fine detail compared with both the original (**Figure 6b**) and the L+M image (**Figure 13a**). This is due to two possibly related reasons. First, the chromatic content in natural scenes tends to be less densely variegated (that is, more patch-like) than the luminance content. This is due mainly to shading and shadows, which often proliferate in the luminance representation but tend to be free of chromatic differences (as discussed above). Second, color vision is a “low spatial-resolution” system (Granger & Heurtley 1973, Mullen 1985), as can be seen in **Figure 13d** from the desaturation of the regions that appear yellow and blue when viewed from a distance of a few meters. One consequence of color vision’s poor spatial resolution is that pure colored edges are blurred in the neural representation, yet we are unaware of this fact in our everyday visual experience (e.g., **Figure 6b** and plate 7 of Wandell 1995) in spite of our good judgment of blur at equiluminance (Webster et al. 2006, Wuerger et al. 2001). This may be because color tends to spread into areas defined by borders with sharp luminance contrast (Boynton 1978, Mollon 1995, Pinna et al. 2001), a phenomenon exploited by watercolor artists.

Color and Position, Orientation, Contour, and Texture

Contours often delineate the shapes of objects and therefore are important for object recognition (Marr 1982). The orientations

and positions of local parts of contours are first detected in the early stages of vision. After these contour parts are linked to form whole contours, the contour shapes are encoded at higher levels of the visual system. Studies using equiluminant test patterns reveal that color can mediate positional judgments (Krauskopf & Forte 2002, Morgan & Aiba 1985), orientation judgments (Beaudot & Mullen 2005, Clifford et al. 2003, Webster et al. 1990), judgments of blur (Webster et al. 2006, Wuerger et al. 2001), contour linking (McIlhagga & Mullen 1996, Mullen et al. 2000), and contour shape processing (Gheorghiu & Kingdom 2007, Mullen & Beaudot 2002). Contour linking by color has been studied using an innovative stimulus that was originally designed by Field et al. (1993) and is shown in **Figure 14a**. The task is to find the string of elements that are collinearly arranged in the form of a path. Paths constructed from equiluminant elements that appear red and green (**Figure 14a**) are detected as easily as paths constructed from isochromatic elements that vary only in luminance (not shown; McIlhagga & Mullen 1996). When the path elements, however, alternate between equiluminant and isochromatic (**Figure 14b**) or between L-M and S-(L+M), performance declines considerably (McIlhagga & Mullen 1996, Mullen et al. 2000). This shows that contour linking is selective along chromatic and luminance dimensions.

Dense arrays of local orientations produce textures, and the detection of spatial variation in texture is important to vision for segmenting a scene into surfaces and determining their three-dimensional shapes. Equiluminant texture variations are detectable (Cardinal & Kiper 2003, McIlhagga et al. 1990, Pearson & Kingdom 2002) by visual mechanisms broadly tuned for color (Cardinal & Kiper 2003), though, unlike contour linking, not independently from isochromatic texture variations (Pearson & Kingdom 2002). Equiluminant textures can elicit an impression of three-dimensional shape (Troscianko et al. 1991,

Zaidi & Li 2006), which suggests that chromatic signals contribute to neural processes mediating shape-from-texture.

Luminance-defined texture boundaries are camouflaged by random chromatic variations that appear red and green. This can give a rare advantage to individuals with a dichromatic red-green color defect: Such observers can break the camouflage because they do not perceive the chromatic variation (Morgan et al. 1992).

Color and Stereopsis

Small differences in the two eyes' views of a scene provide the basis for stereoscopic depth perception (Howard & Rogers 2002, Julesz 1971). A compelling observation is that a random-dot stereogram that contains a depth-target, which is visible only when viewed stereoscopically, disappears when the display is made equiluminant (de Weert 1979, Gregory 1977, Livingstone 1996, Livingstone & Hubel 1987). This has led some to conclude that color vision is stereoblind (Livingstone 1996, Livingstone & Hubel 1987). Yet stereoscopic depth is perceived at equiluminance with relatively simple stimuli such as bars or grating patches (de Weert & Sazda 1983, Kingdom & Simmons 2000, Scharff & Geisler 1992), so for these stimuli there is evidence for stereo mechanisms sensitive to chromaticity (Simmons & Kingdom 1997, Ts'o et al. 2001). The poor depth quality in equiluminant random-dot stereograms probably results from a specific deficit in integrating many local chromatic depth signals in order to generate a depth-defined surface (Kingdom et al. 1999).

A prerequisite for successful stereopsis is correct matching of the corresponding parts of the scene in each eye's view. Spurious matches tend to occur in scenes containing dense arrays of similar elements lying in multiple depth planes. However, even if the elements have similar luminance contrasts, orientations, and sizes, chromatic differences could reduce the number of false matches

Stereoscopic depth perception:

the ability to perceive the relative depth of objects from the slight difference between the two eyes' views of the world

Random-dot stereogram:

two stimuli, one to each eye, consisting of an identical array of dense dots, except for a subset of the dots in one eye that is slightly offset horizontally relative to this subset in the other eye. When viewed stereoscopically, the subset of dots appears to be in a different depth plane than the other dots

Random-dot

kinematogram: a stimulus consisting of a dense array of dots in which a subset of dots is visually segmented from the other dots only when the subset is in motion

Global motion: the overall perceived direction of motion from an array of objects with different individual motion directions

if the visual system matches corresponding chromatic responses. A number of studies demonstrate that the introduction of chromatic differences to complex stereo displays indeed reduces the number of false matches, to the benefit of stereopsis (den Ouden et al. 2005, Jordan et al. 1990, Julesz 1971).

Color and Motion

Equiluminant objects appear to move more slowly than their luminance counterparts (Cavanagh et al. 1984, Lu et al. 1999, Mullen & Boulton 1992, Troscianko & Fahle 1988), and the target shapes in random-dot kinematograms, which are only visible when the dots are moving (analogous to the random-dot stereograms mentioned above), are difficult or impossible to discern at equiluminance (Livingstone & Hubel 1987, Ramachandran & Gregory 1978). Furthermore, motion of simple stimuli such as equiluminant chromatic L-M grating patches can be masked by the addition of randomly moving luminance “noise” (Yoshizawa et al. 2000). This last result, if taken alone, might be explained by chromatic signals that feed into a common chromatic-luminance motion mechanism; however, the finding that moving chromatic L-M noise fails to mask luminance motion (except at very high contrasts) makes this possibility unlikely (Yoshizawa et al. 2000).

An alternative proposal is that perceived motion of simple L-M chromatic stimuli is mediated by a luminance artifact generated within the visual system, possibly due to a temporal difference in the L- and M-cone signals (Mullen et al. 2003). Although this suggestion runs counter to other evidence for chromatic contributions to simple-stimulus motion, albeit ones that can interact with luminance signals (Cropper & Derrington 1996, Dobkins & Albright 1993, Gegenfurtner & Hawken 1996, Morgan & Ingle 1994; reviewed by Cropper & Wuerger 2005), the chromatic

contribution to motion for simple stimuli is at best very weak.

The consensus is more favorable for a chromatic contribution to motion for more complex objects, such as those defined by variations in chromatic contrast rather than color (Cropper & Derrington 1995, Yoshizawa et al. 2000). Some have argued, however, that for both simple and complex objects, perceived motion at equiluminance is mediated by only a general-purpose, attention-based, high-level mechanism that responds to the movement of any figure-ground relation, whether defined by color, luminance, or texture (Lu et al. 1999). Such a mechanism is implicated by the ability to attentionally track an equiluminant moving object even where the motion percept itself is severely degraded (Cavanagh 1992).

The question of whether there exists a chromatic contribution to motion, as opposed to a general-purpose, attention-based, figure-ground mechanism, emerges also from studies of color in “global motion” (Figure 15). In this type of display, most of the elements—the “distractors”—move in random directions, but a subset—the “targets”—moves coherently in one direction or another. Studies disagree as to whether coherent motion in these displays is perceptible at equiluminance (e.g., against, Bilodeau & Faubert 1999; in favor, Ruppertsberg et al. 2006). In studies using nonequiluminant global motion displays, in which all elements have luminance contrast, the introduction of a color difference between the target and distractor elements reduces the number of target dots needed to identify the direction of motion (Croner & Albright 1997; Figure 15), and this could be taken to imply a chromatic contribution to global motion. If, however, subjects are prevented from selectively attending to the target dots in these displays (Snowden & Edmunds 1999), or if the displays are designed in such a way as to render selective attention useless (Li & Kingdom 2001a), the chromatic-difference advantage disappears. Thus, while

global-motion experiments using nonequiluminant displays implicate color as a useful cue for picking out moving objects that would otherwise be camouflaged, the experiments provide no evidence that the chromatic difference actually contributes to motion. A failure to find evidence for a chromatic contribution to global motion in nonequiluminant displays emerges also from studies in which local motion signals are used to generate an impression of global three-dimensional structure (Li & Kingdom 2001b).

There is a caveat, however, to these conclusions. It was pointed out above that in mixed color-luminance stimuli there are likely to be cases in which color contributes little or nothing to the task because the luminance contrast alone drives asymptotic performance. Thus, it is possible that besides the role of color in attentional cuing, there is a weak chromatic contribution to global motion, but in nonequiluminant displays, it does not manifest itself because it is swamped by the luminance signal. Some support for this idea comes from physiological studies of the chromatic sensitivity of neurons in monkey middle temporal (MT) area, which forms part of the dorsal pathway and is believed to be specialized for global motion processing (reviewed by Gegenfurtner & Kiper 2003). Most studies reveal that MT neurons are sensitive to both L-M (Gegenfurtner et al. 1994; Thiele et al. 1999, 2001) and S-(L+M) chromatic contrast (Barberini et al. 2005), though in general sensitivity to L-M chromatic contrast is low (e.g., Gegenfurtner et al. 1994). Importantly, however, when sufficiently high luminance contrast is present in the stimulus, the chromatic contribution from L-M contrast to MT responses becomes negligible (Thiele et al. 1999). This last finding might be a physiological correlate of the appar-

ently contradictory psychophysical findings described above, namely perceptible global motion at equiluminance (Ruppertsberg et al. 2006) and absence of chromatic contributions to global motion with nonequiluminant stimuli (Li & Kingdom 2001a,b; Snowden & Edmunds 1999).

CONCLUSION

Complex scenes reveal the rich contribution to perception from light varying in spectral composition. Chromatic variation within a scene over space or time alters the hue of a given light; moreover, it allows the intrinsic color of an object to be separated from the light illuminating it despite the ambiguity of receptor responses that vary with the spectral distribution of illumination. Furthermore, chromatic features of a complex scene influence percepts other than color, including orientation, shape, texture, and object segmentation.

The ambiguity implicit in the early encoding of light is resolved by neural processes that often exploit properties of the natural world. This suggests a fundamental limitation of research conducted with equiluminant chromatic patterns, which lack the complexity of natural scenes required to investigate two implicit aspects of normal viewing: (*a*) congruent (or incongruent) changes in chromaticity and luminance and (*b*) the relative importance of chromaticity when both chromatically selective and spectrally unselective neural responses contribute to the same percept. The many levels of chromatic neural representation reinforce the importance of using complex visual stimuli, including ones that vary in both chromaticity and luminance, to advance our understanding of chromatic contributions to vision.

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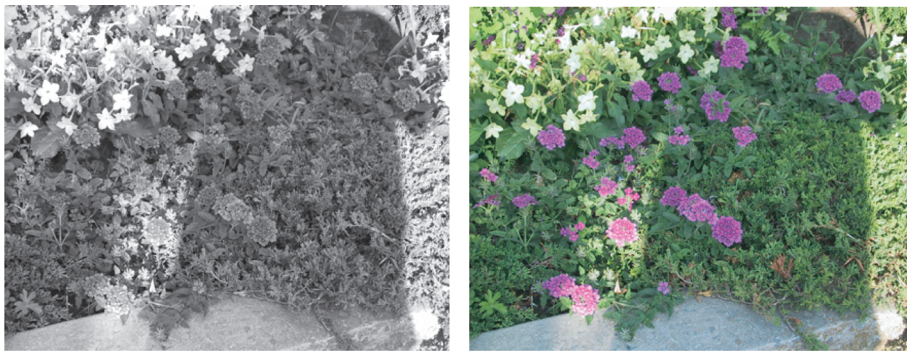
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(a)



(b)



(c)



Figure 1

Some of the many functions of color vision. (a) Color reveals otherwise camouflaged objects. (b) The aptly named Blue Jeans frog (*Dendrobates pumilio*) is easily identified from its coloration (photo courtesy of D. Montero). (c) Color is useful for grouping and identifying fruit (photo courtesy of D.I. Thompson).

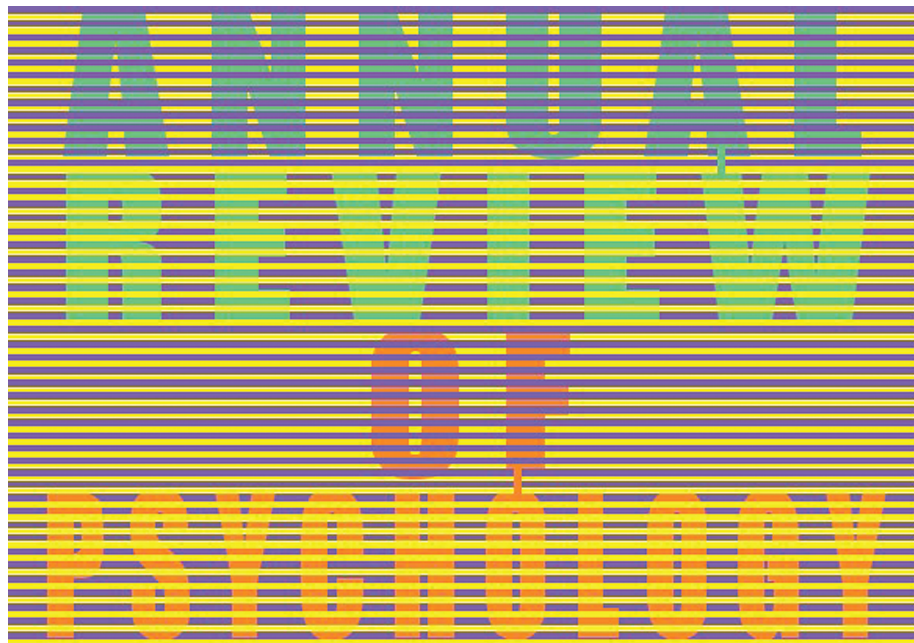


Figure 2

The words ANNUAL and REVIEW are printed in identical ink (check the connector bar above W). They appear different in color because of the patterned context in which they are seen. Similarly, OF and PSYCHOLOGY are in the same ink (check the connector bar below F).

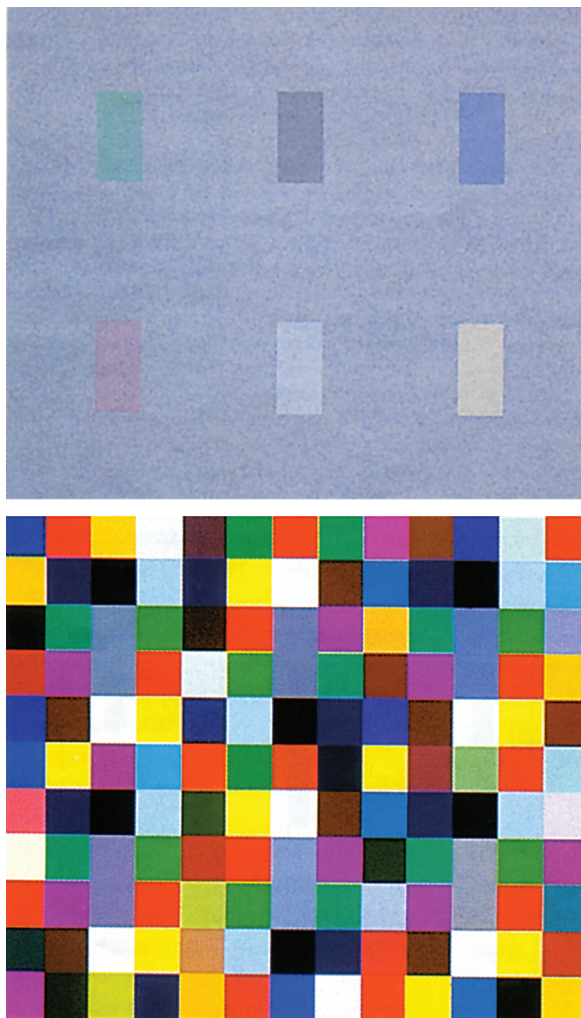


Figure 3

(Upper panel) Six rectangles within a uniform surround. (Lower panel) The same six rectangles are within a surround that has chromatic and luminance contrast. Both surrounds have the same space-average chromaticity and luminance. From Brown & MacLeod 1997 (copyright 1997, reprinted with permission from Elsevier).

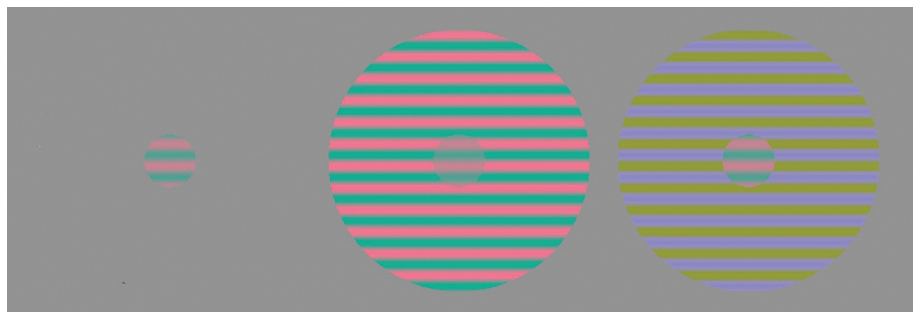


Figure 4

A small circular equiluminant grating with only L-cone/M-cone contrast (*left*) has a greater reduction in perceived contrast when within a surrounding equiluminant grating at the same chromaticities (*center*) compared with an equiluminant grating with only S-cone contrast (*right*). (Limitations of color reproduction and individual observer differences do not allow exact cone isolation.) After D’Zmura & Singer 1999 (images courtesy of M. D’Zmura).



Figure 5

The chromatic surfaces of the Macbeth ColorChecker (Munsell Color Laboratory, New Windsor, New York) as it appears under sunlight (*top*) and as it would appear under tungsten illumination (*bottom*) if color perception followed directly from the wavelengths from each region reaching the eye.

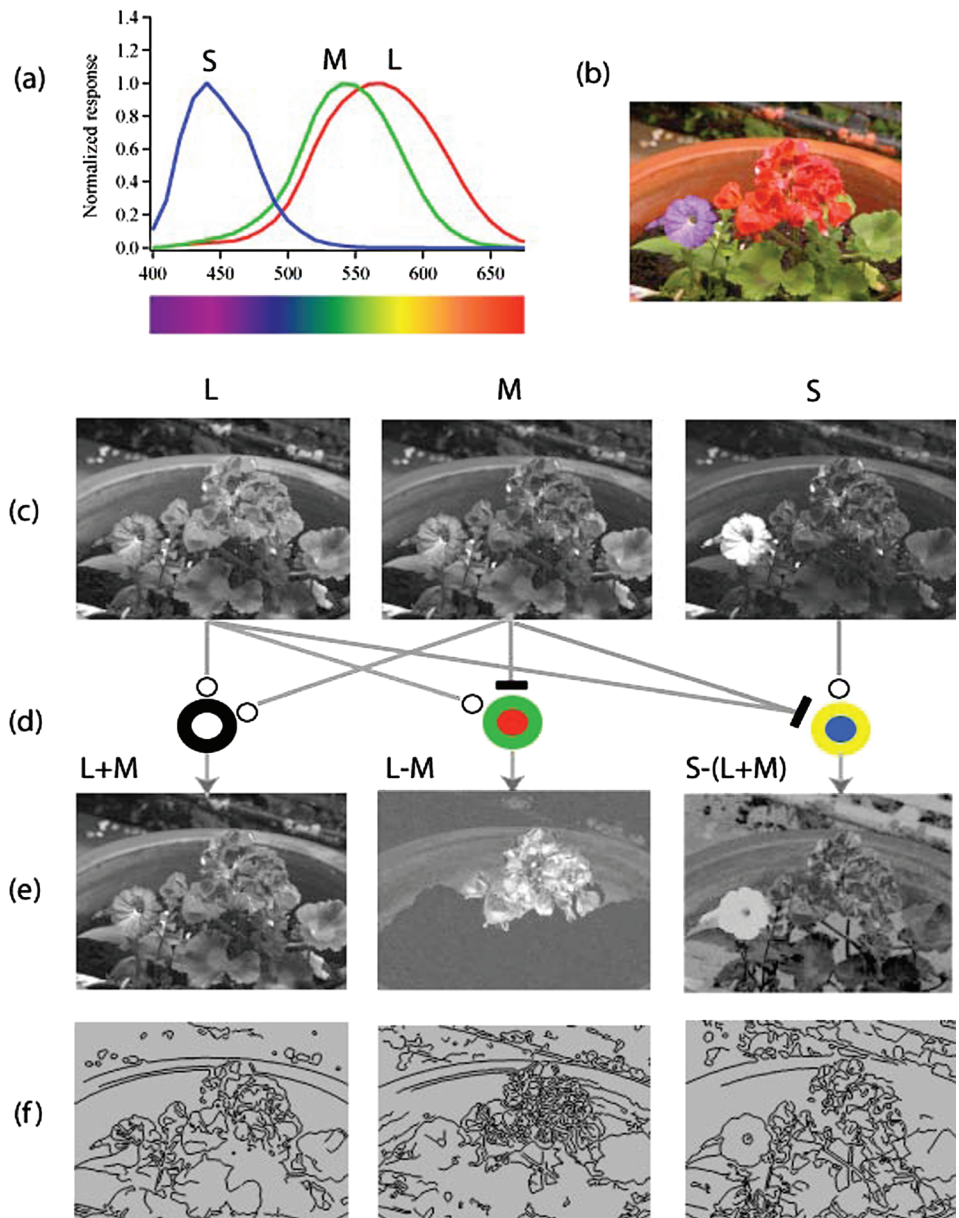


Figure 6

Stages of chromatic neural responses. (a) Spectral sensitivities of the L, M, and S cones. (b) Original image. (c) Responses of the three types of cones to the image. (d) Cone signals combine to give postreceptoral responses. (e) Postreceptoral responses to the image. (f) Edge maps from postreceptoral responses. (Original image from the McGill Calibrated Color Image database: <http://tabby.vision.mcgill.ca>.)

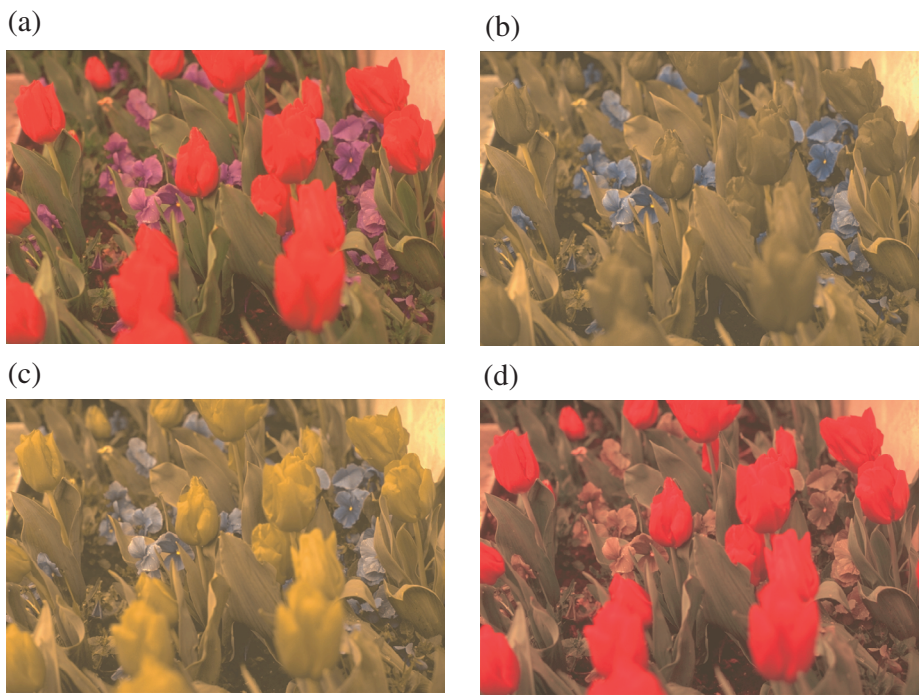


Figure 7

Simulated appearance of flowers as seen by (a) normal trichromats, (b) protanopes, (c) deuteranopes, or (d) tritanopes. After Viénot et al. (1995) (images courtesy of F. Viénot).



Figure 8

Shadow cast across a grass-pavement border. At the grass-pavement border, there is a large change in both color and luminance (and texture); at the shadow border, the change is primarily in luminance with little change in color (no change in texture).

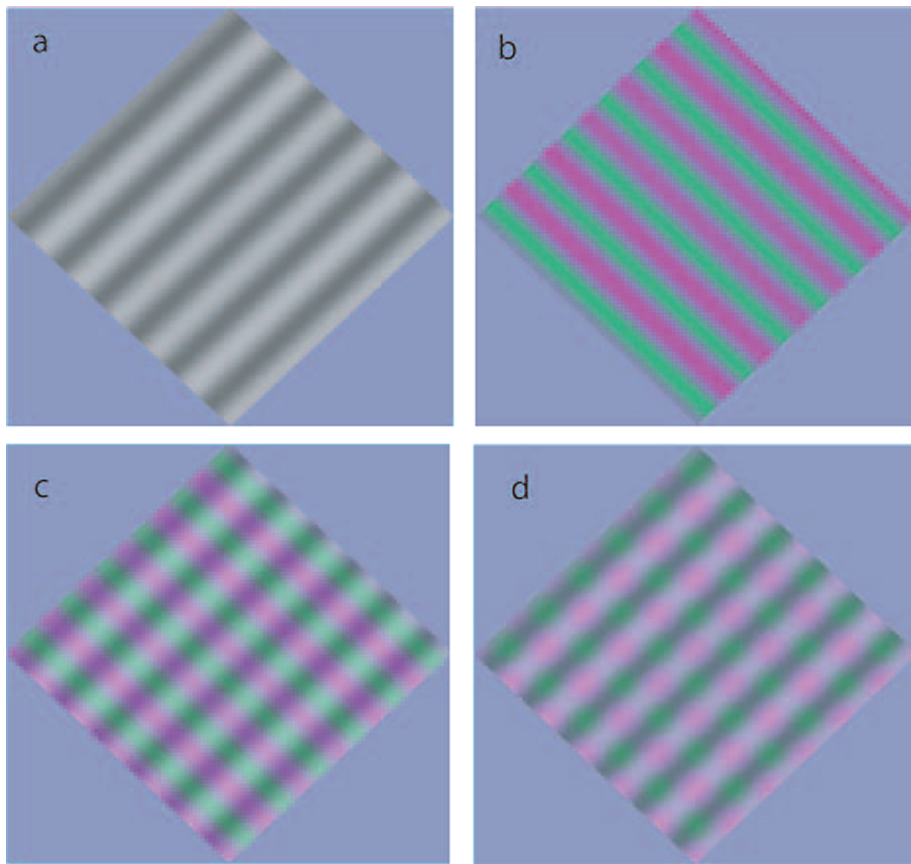


Figure 9

Color can promote or inhibit shape-from-shading. (a) Right oblique luminance grating. (b) Left oblique chromatic grating. (c) Combining (a) and (b) gives the impression of a depth-corrugated surface. (d) Adding a second chromatic grating aligned with the luminance grating in (a) inhibits the impression of depth.



Figure 10

The tall building in sunset illumination appears to many observers as if painted two-thirds orange (photo courtesy of B. Micklethwait).

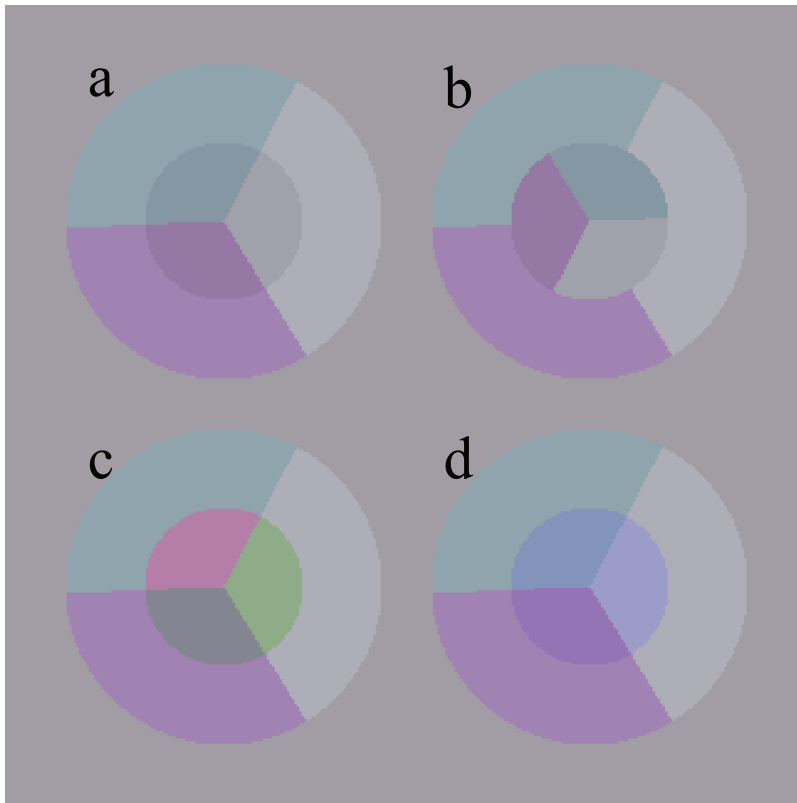


Figure 11

Color and transparency. (a) Simulated spectrally unselective transparency on a chromatically variegated background. (b) Rotating the central region destroys the impression of transparency. (c) Introducing random chromatic changes across the surround's border reduces the impression of transparency. (d) Consistent chromatic changes across the surround's border create the impression of a colored transparency.

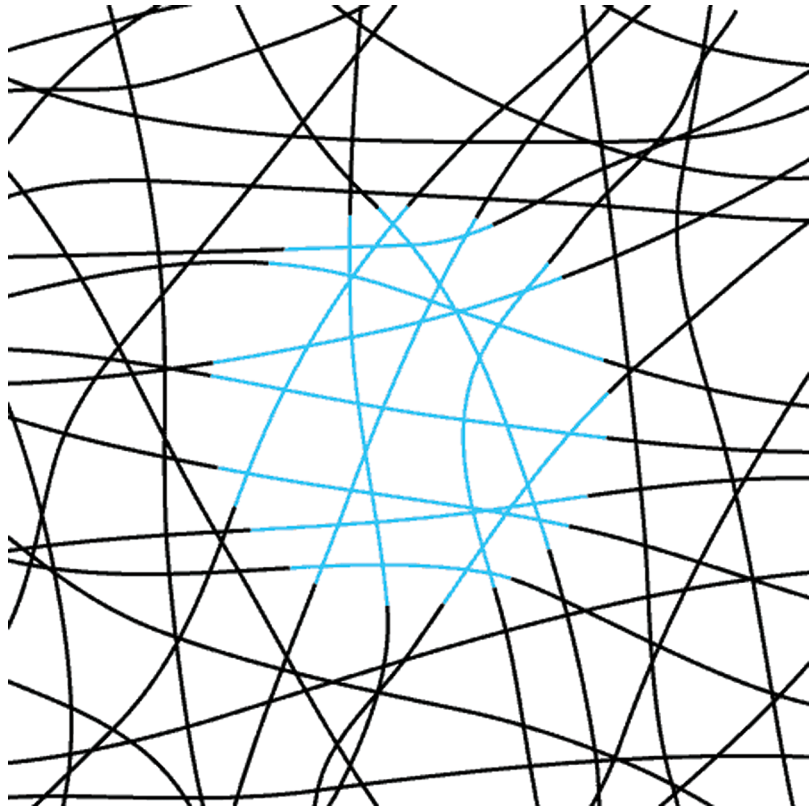


Figure 12

Neon-color spreading. (Image courtesy of Hans Knuchel, www.blelb.ch.)

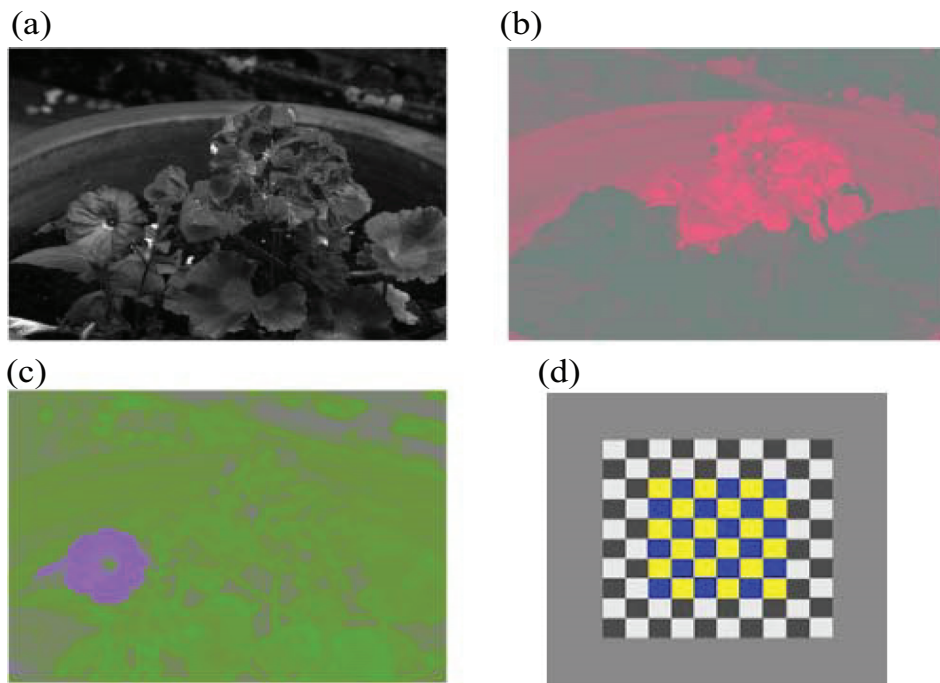


Figure 13

Color and resolution. The three postreceptoral representations of the image in **Figure 6b**: (a) L+M, (b) L-M, and (c) S-(L+M). [The images in (b) and (c) are not exactly equiluminant due to limitations of color reproduction and individual observer differences.] (d) A demonstration of poor chromatic resolution. As one walks away from the image, the blue and yellow checks become increasingly desaturated and eventually appear black and white (after Moulden et al. 1993).

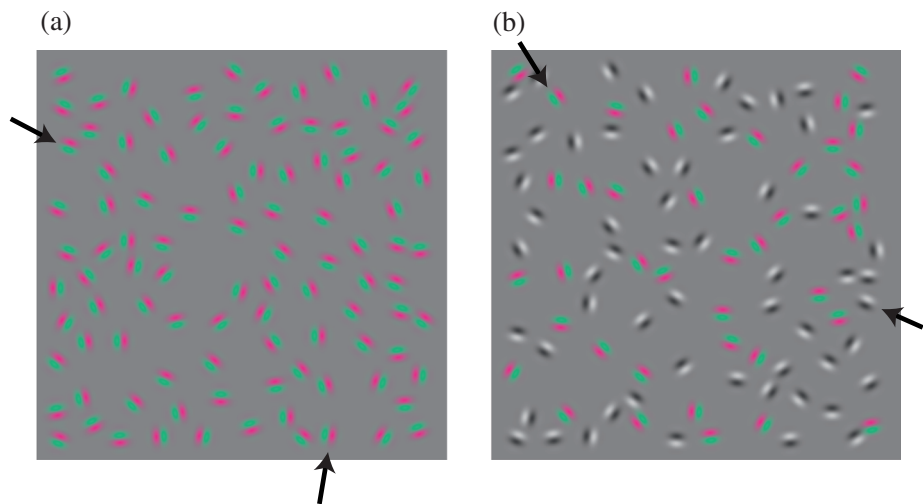


Figure 14

Color and contour linking. (a) The pattern is constructed from red-green equiluminant gabor micropatterns. The arrows show the beginning and end of the target path—a string of orientationally aligned gabor micropatterns that the observer must detect. (b) When the path alternates between equiluminant red-green and isochromatic white-black gabors, it is more difficult to detect. After McIlhagga & Mullen (1996) (images courtesy of K. Mullen).

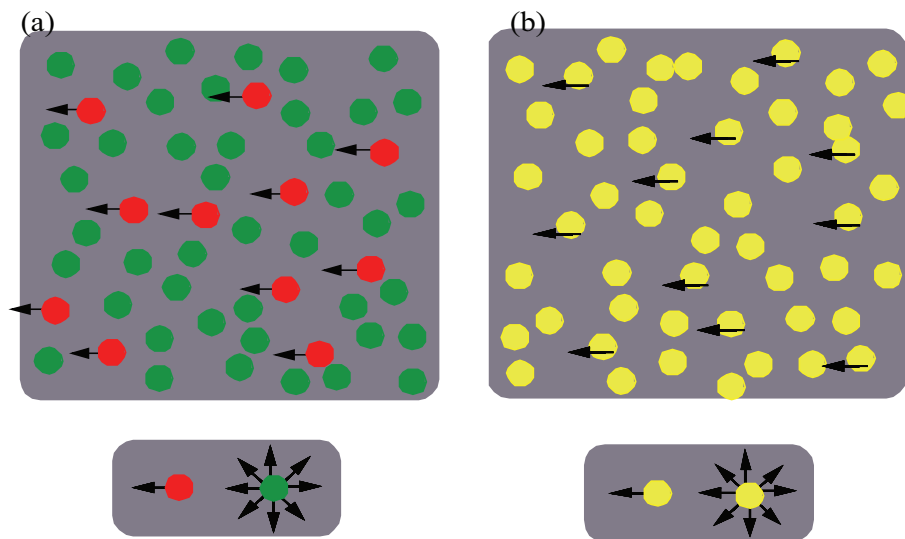


Figure 15

Color and global motion. In (a), the target elements (moving in one direction) and distractor elements (moving in random directions) have different colors, but in (b) they have the same color. Fewer target elements are needed in (a) than in (b) to identify the target's direction of motion. After Croner & Albright (1997).