Progress in Brain Research,
Vol. 144. ISSN 0079-6123

CHAPTER 10

Color contrast: a contributory mechanism to color constancy

Anya Hurlbert* and Kit Wolf

Henry Wellcome Building for Neuroecology, School of Biology, Framlington Place, Newcastle upon Tyne, NE2 4HH, UK

Abstract: Color constancy by which objects tend to appear the same color under changes in illumination is most likely achieved by several mechanisms, operating at different levels in the visual system. One powerful contributory mechanism is simultaneous spatial color contrast. Under changes in natural illumination the spatial ratios of within-type cone excitations between natural surfaces tend to be preserved (Foster and Nascimento, 1994); therefore, the neural encoding of colors as spatial contrasts tends to achieve constancy. Several factors are known to influence the strength of chromatic contrast induction between surfaces, including their relative luminance, spatial scale, spatial configuration and context (Ware and Cowan, 1982; Zaidi et al., 1991). Here we test the hypothesis that color contrast is weakened by differences between surfaces which indicate that they may be under distinct illuminants. We summarize psychophysical measurements of the effects of relative motion, relative depth and texture differences on chromatic contrast induction. Of these factors, only texture differences between surfaces weaken chromatic contrast induction. We also consider neurophysiological and neuropsychological evidence and conclude that the mechanisms which mediate local chromatic contrast effects are sited at low levels in the visual system, in primary visual cortex (VI) or below, prior to image segmentation mechanisms which require computation of relative depth or motion. V1 and lower areas may therefore play a larger role in color constancy than previously thought.

Introduction

Color constancy is a fundamental perceptual phenomenon, by which objects tend to appear the same color regardless of the illumination upon them. Color constancy is a property of surfaces in the context of other surfaces, not of lights in the void. Although it obviously requires interactions between distinct light signals from distinct spatial locations in the image, no single specific physiological mechanism at a particular locus has been identified as responsible for color constancy. In fact, the evidence suggests that color constancy is achieved by a heterogeneous group of mechanisms, operating at different levels in the visual system. For example, chromatic adaptation in the retina must contribute to constancy although its effects are so fundamental that they are difficult to tease apart from the mechanisms into which they feed but cortical mechanisms are also essential, as lesion studies demonstrate (Ruttiger et al.. 1999).

Theoretical arguments also suggest that color constancy may he carried out by different mechanisms, and a number of distinct computational models have been proposed that each achieve constancy with some degree of success, under particular conditions (Hurlbert, 1998). It is useful to group these mechanisms in the following framework, which distinguishes between the type of computational mechanism and the neural level on which it would most likely function:

- *Sensory.* Models at this level require only simple linear transformations of the photoreceptor

---

*Corresponding author. Tel.: +44-191-222-7638; Fax: +44-191-222-5622: E-mail: anya.hurlbert@nncl.ac.uk

DOI: 10.1016 50079-6123(03)14401-0

responses, one example being scaling of the individual receptors by their individual mean activities over the image, or, in other words, DC chromatic adaptation (Von Kries, 1906: Finlayson et al., 1993).

- *Perceptual.* Models at this level require some parsing or segmenting of the image into distinct reflection or surface components, an example being chromaticity convergence algorithms which estimate the illumination spectrum from specular highlights or mutual reflections (Lee, 1986; Funt et al., 1991).
- *Cognitive.* Models at this level require recognition of objects and/or color memory for identified objects, an example being the adjustment of memory color of familiar objects proposed by Beck (1972).

Here, we focus on one contributory mechanism to color constancy, color contrast, and argue from psychophysical, neurophysiological, and neuropsychological evidence that it operates at the sensory level.

Color contrast and its link with color constancy

Color contrast occurs when a surface of one color induces its opponent color in an adjacent surface. Typically, the inducing surface is large and entirely surrounds the target surface: for example, a small grey disk acquires a pinkish tinge when surrounded by a large green annulus. Although it is a labile phenomenon, which occurs only under particular conditions, it is nonetheless powerful when it does occur. Under optimal conditions, color contrast is instantaneous, cannot consciously be 'turned off, and almost entirely determines the color appearance of a surface. For example, in a simple image, the color appearance of a small desaturated disk can largely be predicted by the spatial cone-contrast (the within-type spatial ratio of cone excitations) between it and its background (Shepherd, 1997; Hurlbert et al.. 1998).

The contribution of color contrast to constancy comes about through this dependence of color appearance on spatial cone-contrasts. Under changes in natural illumination (such as daylight) the spatial cone-contrasts between natural surfaces tend to be preserved (Foster and Nascimento, 1994). Thus, the encoding of color appearance by cone ratios between surfaces may help to preserve color appearance under natural illumination changes.

While it is clear that the local cone-contrast between a surface and its immediate background has a strong influence on color appearance, it is not clear to what extent the contrast from more distant surfaces may contribute. The distinction is often made between 'local' and 'global' contrast (see Kraft and Brainard. 1999), but it is perhaps more accurate to distinguish between surfaces which share edges with the target surface (local' contrast) and those which do not ('remote' contrast). Where this distinction is made, the contribution of remote contrast to color appearance has been quantified as much smaller than local contrast (for example, remote fields up to 10 distant from a target surface contribute less than 10% of the induction from its immediate background: Wachtler et al., 2001; Wolf and Hurlbert, 2003). By another estimate, remote surfaces contribute significantly to color constancy, even when they contradict the color specified by immediate local contrast (Kraft and Brainard. 1999). Furthermore, not only the mean chromatic contrast. but also its variance, contributes to color appearance (Brown and MacLeod. 1997), although whether this effect is local or instantaneous is unclear.

Another important distinction is that between simultaneous spatial contrast and temporal adaptation. Ideally, spatial contrast is an instantaneous phenomenon that depends only on spatial interactions between image regions observed within one fixation. Temporal adaptation requires time for nearby and distant regions to influence each other, as neural response gains are adjusted according to signals sampled over several eye movements and via more slowly propagating lateral interactions. Empirically, it is difficult to tease apart the two phenomena: the color appearance of a small target against a large chromatic background, viewed for seconds or longer, will be influenced in the same way by temporal adaptation to the mean chromaticity and luminance of the dominant background as by the instantaneous spatial cone-contrast at the edges between them. When properly teased apart, instantaneous contrast effects may contribute up to 60% of the chromatic induction effects of a large uniform background, and do so within the first 25 ms of the background's initial display (Rinner and Gegenfurtner, 2000). According to Rinner and Gegenfurtner (2000), the remaining induction effects are perpetrated by two adaptational mechanisms, one fast (half-life 40–70 ms), the other slow (half-life 20–30 s). The time scale and spatial characteristics of the former are consistent with fast, local receptoral adaptation mediated by micro-saccades (Shady and MacLeod, 2002).

Qualitatively, therefore, there seem to be at least three distinct sensory mechanisms that interact to determine color appearance: chromatic adaptation to the mean, which occurs over relatively large spatial and temporal scales, alters the neutral point, and requires at least 1 min to complete after a transition in mean chromaticity (Rinner and Gegenfurtner, 2000: Werner et al., 2000); chromatic adaptation to the variance (Webster. 1996) which scales sensitivity to cone-contrasts around the neutral point, and requires probably minutes to complete; and spatial contrast between image regions of distinct cone excitations, which occurs 'instantaneously' (Rinner and Gegenfurtner. 2000). These mechanisms further interact with color filling-in processes, so that color appearance seems to be determined by contrasts spreading away from edges, across regions (Hurlbert and Poggio, 1989: Broerse et al., 1999; Rudd and Arrington. 2001).

Here we focus on near-instantaneous spatial cone-contrast effects between a target surface and its immediate background. The effects we measure are dominated by local contrast, although we cannot exclude a contribution from fast, predominantly local receptoral adaptation.

Psychophysical investigations of simultaneous chromatic contrast

In a series of psychophysical experiments, we have measured the effect of distinct factors on color contrast, in order to help pinpoint its locus and mode of operation in the visual system. One might argue that since we are focussing on 'local' color contrast, we have already defined the locus to be low level. But we now know that 'global' effects may occur in V I - for example, as contextual modulation of classical receptive field responses (Albright and Stoner, 2002) — as well as in the thalamus, via feedback from higher areas, and conversely, that 'local' effects may dominate neuronal responses in higher visual areas (Allman et al., 1985).

Factors already known to influence the strength of color contrast include their relative luminance, spatial scale, spatial configuration and context (Ware and Cowan, 1982: Zaidi et al., 1991). In selecting factors that might influence color contrast, our guiding hypothesis has been that color contrast serves color constancy, and that therefore, reasoning from a 'neuroecological' viewpoint, color contrast should be weakened between surfaces likely to be under different illuminants. Detachable surfaces are more likely to be under different illuminants than attached surfaces. We therefore have considered factors likely to influence the apparent 'detachability' of two surfaces, such as differences in depth, motion, and surface texture (large differences in texture scale are consistent with the surfaces being at different distances from the observer, or made from distinct materials).

In phrasing our motivation in this way, we do not mean to imply that chromatic contrast induction is necessarily preceded by the subconscious analysis or conscious perception of the 'attachedness' of the surfaces involved. Rather, we argue that if chromatic contrast induction evolved to serve the purpose of discounting the chromatic effects of a common illuminant, its success in serving its purpose would depend on its being applied in the appropriate circumstances, and therefore, it might co-evolve with mechanisms that signal the likelihood of a common illuminant. One might expect. therefore, that chromatic contrast mechanisms would segregate from mechanisms that signal distinct illuminants.

On the other hand. because color contrast enhances material differences between surfaces by factoring out the common illuminant, we could argue that surface 'detachability' is necessary to signal the usefulness of color contrast. For the purposes of behavior, it would be more important to distinguish detachable surfaces from each other, so that they may be picked apart for example. red fruit against a background of green leaves. Enhancing the contrast between same-surface color patches may have less behavioral significance, because the patches would not ordinarily need to be picked apart (although representing accurately the colors of a multicolored surface would be important for recognition).

We might therefore expect that contrast operates best within a certain range: for surfaces that are detachable from each other, but not so detached as to appear under distinct illuminants. Other factors that influence whether two surfaces appear to be under the same illuminant or not then become crucial, but we would expect these to operate at a cognitive level, beyond elementary image analysis. Our list of factors is designed to help pinpoint the locus of chromatic contrast within the earlier stages of image processing, if it does indeed occur there.

Experimental paradigm

The experiments employ one of two basic types of color appearance judgment task. The first is a two-interval, forced-choice color discrimination task, in which observers compare the color appearance of two central targets, presented in rapid temporal succession against uniform or articulated backgrounds, based on the paradigm of Wachtler et al. (2001). The first (reference) target and background are neutral in chromaticity (but slightly different in luminance, to insure target visibility); the second (test) background is shifted in chromaticity with respect to the reference, in the direction of increasing L-cone excitation, while the test target is shifted in the same direction but to a different, variable degree (see Fig. 1). The two successive presentations thus simulate a temporal change in a spatially uniform, global illumination and the observer's task is to report whether the color of the central target becomes redder or greener under the change. The cone-contrast (with respect to the neutral reference) required for the test target to appear neutral is our measure of the strength of contrast induction.

The second basic task (described in more detail below) requires the observer to null apparent color changes of a central target against a background whose chromaticity is temporally or spatially modulated along the (L—M) cone-contrast axis. The observer adjusts the extent of temporal modulation of the central square's chromaticity along the same axis, and the strength of contrast induction is measured as the amount of modulation necessary to

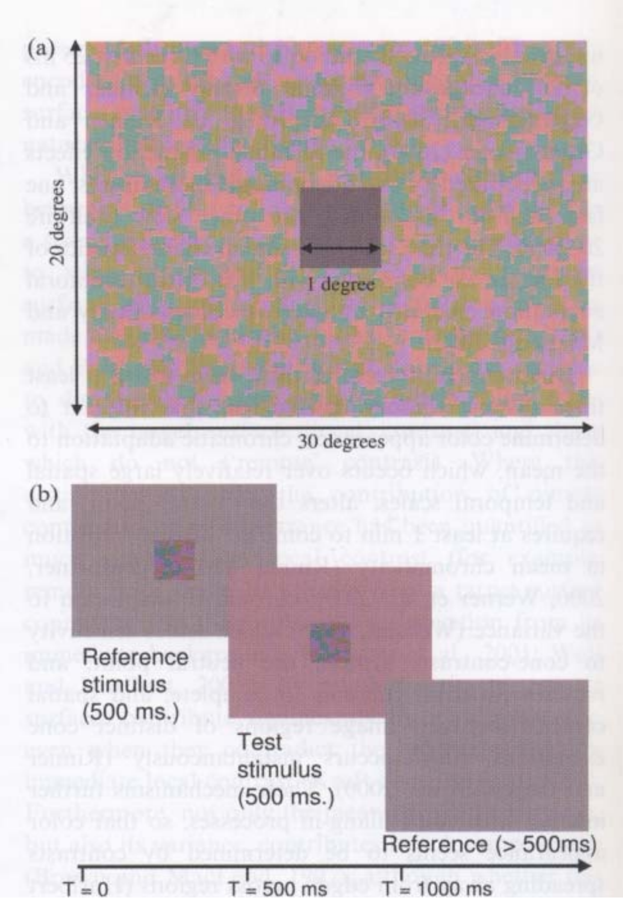


Fig. 1. (a) and (b) Stimulus parameters and protocol for the basic 2AFC task. The basic stimulus (Ia) consists of a `*target* square presented centrally against a rectangular background. To insure its visibility, its luminance is set 8% dimmer than the background level of 15 $cd/m^2$. The background in this example contains a cartoon of the `Mondrian' texture that we used (not to scale). Fig. (I b) shows the time-course of a single trial. During the first stage, presented for 500 ms, the observer memorizes the colour of a neutrally colored target (Reference), set against a neutrally coloured background. The background colour is then shifted is then shifted isoluminantly along the LM-axis by a fixed amount, and a concomitant variable color shift is introduced to the target (Test). The experimental task is to decide, during the 500 ms for which this stimulus is presented, whether the new target viewed against the shifted background appears reddish or greenish. Observers indicate their responses using a game-pad, during a period of top-up adaptation when they view the full-screen neutral reference background.

stabilize the color appearance of the target square at neutral chromaticity.

In each task, there is no opportunity for long-term DC adaptation to the nonneutral inducing back-ground (although the temporal changes in both tasks may influence AC adaptation (Webster, 1996); see discussion below). The brief presentation of the test (inducing) background is immediately followed by a period of readaptation to the neutral back-ground (enforced to a minimum of 1 s); under these conditions, the mean adaptational state remains near-neutral as confirmed in separate control experiments. (The achromatic setting under this rapid-change paradigm deviates by at most 5% from the achromatic setting under steady-state adaptation to the neutral background.)

The test square against the test background is displayed for 500 ms only, long enough for instantaneous spatial contrast effects and fast, local receptoral adaptation (which, aided by micro-saccades, may propagate over several degrees in that time; Shady et al., 2002) to reach completion, but well before completion of the slow chromatic adaptation mechanisms that dominate steady-state color appearance (half-life 20—30 s; Fairchild and Reniff, 1995; Rinner and Gegenfurtner, 2000). The tasks therefore differ from others used to quantify contrast and constancy which involve simultaneous comparisons between distinct stimuli under prolonged viewing. The experimental methods are described in full in Hurlbert and Wolf (2002) and Wolf and Hurlbert (2002a,b), and briefly summarized in the Methods appendix.

Texture segmentation

Differences in the spatial and spectral characteristics of surface texture may signal that two surfaces are made from different materials, or that they are located at different distances from the viewer. Texture differences are powerful cues for image segmentation (see Nothdurft, 1994), and in the achromatic domain, have been shown to disrupt lightness contrast induction when they occur between target and background (Laurinen et al., 1997).

Using the basic 2AFC task with an + L—M background-shift between the reference and test stimuli (see Methods), we investigated whether the strength of contrast induction depends on surface texture properties of the target and background. We compared three texture-difference conditions with one control condition:

(1) Chromatic texture in the central target; spatially uniform background.
(2) Spatially uniform central target; chromatic texture in the background.
(3) Identical chromatic texture in both central target and background.
(4) Spatially uniform central target and background (the control condition).

The chromatic texture resembled a fine-grained `Mondrian', and was created by scattering rectangles between 1 x 1 and 3 x 3 pixels in size (at 32 pixels per degree) at random across a square grid covering the target and/or background (see Fig. 1). Each rectangle was assigned one of five distinct isoluminant colors distributed evenly around the reference chromaticity along one axis of cone-contrast space. The method insured that proportions of pixels of each color did not differ by more than 1%. To change the mean chromaticity of the texture, for example to produce an + L—M shifted background, the reference chromaticity was redefined, but the distribution of the five colors around the reference remained constant in the cone-contrast space that we used. Thus the space-averaged chromaticity and luminance of the chromatic textures remained identical to those of the spatially uniform controls.

For condition 1, we also performed separate experiments using textures defined by different characteristics: for example, chromatic textures of differing spatial scale and regularity, and differing chromatic distributions, and luminance textures of different spatial scales. Qualitatively, the results were the same for all textures, although they differed quantitatively (see discussion below).

The observer's task was as usual to report whether the central target became redder or greener between the reference and test presentations on each trial. Even for the multicolored target with chromatic texture, this task was entirely straight-forward for all observers, in that reddish or greenish shifts in the average color of the texture were clearly discernible.

The results, summarized in Fig. 2, demonstrate that chromatic texture differences do disrupt chromatic contrast induction. But the effect is asymmetric: in condition 1, chromatic texture in the central target almost completely blocks contrast induction from the uniform background, for all 4 observers. In condition 2, chromatic texture in the background weakens contrast induction on a uniform central target, but not as strongly as in condition 1.

Nonetheless, when we add chromatic texture to both background and target, contrast induction is restored to approximately the same level as condition 2 for most observers. This result is notable, as one explanation for the lack of induction of the uniform background on the textured target might be the known inability of contrast induction to propagate across chromatic borders (Zaidi et al., 1992). Yet the total number of chromatic borders in condition 3 (with textured target and background) is larger than in condition I (textured target against a uniform background), and induction is stronger. Thus the number of edges is unlikely to be the crucial factor in blocking induction.

In separate experiments, we varied the intrinsic contrast of the textures, by varying the range of constituent colors around the neutral (or shifted-neutral) point. Even for textures with just-noticeable chromatic contrast, the effect of target-background texture-differences remained powerful, substantially reducing chromatic contrast induction. To determine whether the reduction in contrast-induction might be due to differences in the strength of induction between the individual constituent colors, we measured induction strength for each color individually in the spatially uniform control condition. As Fig. 2 illustrates, each of the constituent colors (from the

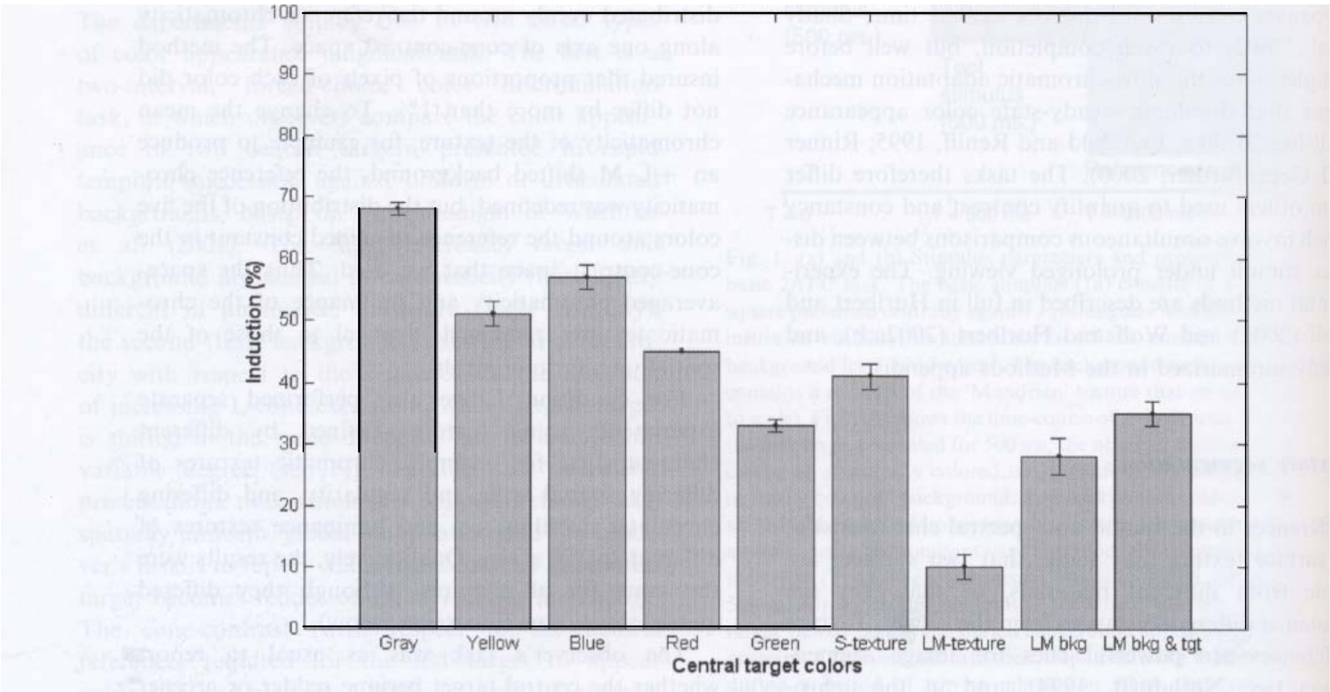


Fig. 2. The strength of contrast induction (see Methods in Appendix) under different stimulus configurations for a single observer (KW). Induction is strongest for a uniform gray target viewed against a uniform background. It is weaker for yellow, blue, red or green targets, but in each case still stronger than when the same individual colors are combined to make a blue and yellow texture (S-texture condition) or a red and green texture (LM-texture condition) for which induction is weakened substantially. The bar labeled LM bkg shows that induction is intermediate in strength for a uniform neutral target against a textured background. The rightmost bar (target + background texture) shows that when both background and target have the same LM-texture, the induction strength is greater than for the target-only texture conditions.

highest-contrast supra-threshold chromatic texture) undergoes substantially greater contrast induction from the + L—M shifted uniform background than does the chromatic-textured target made up of these same colors.

The results also suggest that, while chromatic contrast along any direction in cone-contrast space blocks induction to some extent, as does luminance contrast, the blocking effect is strongest when the chromatic texture varies along the same direction as the background chromaticity shift. As Fig. 2 illustrates, when the background chromaticity shift is in the direction of increasing L-cone excitation, chromatic texture varying along the (L—M) axis blocks induction significantly more strongly than chromatic texture along the S axis. In fact, the induction-blocking effect appears to be tuned to the cardinal axes: chromatic texture which varies along an intermediate axis between the S and (L—M) directions, and therefore contains components of both, significantly weakens induction from backgrounds chromaticity-shifted along any direction in cone-contrast space.

Depth segmentation, via binocular disparity

Previous studies on the effects of depth differences on simultaneous contrast have focussed almost exclusively on achromatic lightness or brightness contrast, with conflicting results. There is no doubt that under certain conditions depth perception strongly influences lightness perception. Using occlusion cues as the sole cues to depth under monocular viewing, Gilchrist (1977) demonstrated that the perceived lightnesses of paper squares changed dramatically when the apparent depth plane to which they belonged changed. Earlier studies in which binocular disparity was manipulated as the primary cue to depth (Gogel and Mershon, 1969; Mershon, 1972) also concluded that the perceived depth separation between a test target and its inducing background strongly influenced brightness (and whiteness) contrast between them. On the other hand, using simpler stimuli, Gibbs and Lawson (1973) found no effect of binocular disparity on brightness contrast, and concluded that previous effects may have been mediated by apparent size changes with depth. More recent studies have reported that depth differences do influence achromatic lightness and brightness contrast (Schirillo and Shevell, 1993) and chromatic contrast (Shevell and Miller, 1996), but the effects described are very small.

Using the nulling task described above, we investigated whether depth-differences defined by binocular disparity may disrupt chromatic contrast. In this task, the central target was again a small square, set against a large inducing background (see Methods) presented as separate left- and right-eye views through a modified Wheatstone stereoscope. To provide sufficient form cues for binocular fusion, we added fine-scale luminance texture to the otherwise uniform background, taking into account the slight weakening in chromatic contrast this background texture introduces. By displacing the central target laterally in opposite directions for each eye, we moved it between three planes across trials, one of which was coplanar with the background, the second in front of the background, and the third behind, as if viewed through a window. On each trial, the background chromaticity was modulated sinusoidally along the (L—M) axis between red and green, and the observer nulled the induced color change of the target using a computer keyboard.

We found that chromatic contrast induction was equally strong for all three depth configurations, for all observers. This finding contradicts earlier reports for brightness contrast (Gogel and Mershon, 1969) but is consistent with others (Gibbs and Lawson, 1973). Many factors may explain the apparent discrepancies. In general, strong effects of depth differences on perceived lightness or color are found with more complex stimuli; ours employ the simplest possible center-surround configuration. The effects in some earlier studies (e.g. Mershon, 1972) may have been confounded by the presence of black borders separating the test and inducing fields, which themselves are known to inhibit simultaneous contrast. Gilchrist (1977) argued explicitly that target lightness depends on perceived depth only if the perceived lighting framework to which the target belongs also depends on perceived depth; the target must be perceived to move from a brightly lit to a dimly lit framework to change in perceived lightness. The presence of multiple, obvious lighting frameworks may therefore be the crucial difference between

Gilchrist (1977) and previous experiments. But other differences may also be important; for example whether actual changes in depth are used or cues such as occlusion or disparity are used to manipulate depth perception.

Our stimuli contain only a single lighting framework, so we cannot exclude the possibility that there are interactions between the perception of lighting frameworks within a scene and the neural mechanisms responsible for simultaneous chromatic contrast. But we do show conclusively that depth segmentation cues alone are not sufficiently strong to disrupt the illusion, unlike the presence of a black border, or texture cues. By keeping our stimuli very simple, we deliberately hoped to avoid contamination of our results by higher mechanisms influencing color perception, which may or may not be independent of those responsible for simultaneous contrast.

Motion segmentation

Relative motion is also a powerful cue to image segmentation (Moller and Hurlbert, 1996), and obviously signals detachability between surfaces. As surfaces move from one location to another, they may move from one illumination framework into another. Using two variants of the color appearance nulling task, we investigated whether motion differences between the inducing background and target may also inhibit contrast induction.

In the first paradigm, the target square moves sinusoidally and vertically against a stationary background with a vertical gradient in chromaticity, varying along the (L–M) axis from neutral in the center to red at the top and green at the bottom of the display. In the second paradigm, the target square remains stationary in the center of the display. and the luminance-textured background moves continuously and sinusoidally, either translating or rotating, while simultaneously oscillating in color between red and green along the (L–M) axis.

In both paradigms, the chromaticity of the target square is modulated along the (L–M) axis in phase with the background modulation. The observer's task is to adjust the amplitude of the target's modulation so that it no longer changes color over the course of its or the background's motion. We measure the strength of the induced contrast as the amplitude of modulation required to null the apparent change in color of the target.

We found that chromatic contrast induction was strong for both paradigms and all motion-difference conditions, for all speeds and frequencies tested, despite the fact that the target and background were clearly disjoint. Thus, motion segmentation does not disrupt simultaneous contrast induction.

Summary and discussion of psychophysical results

Neither motion nor depth differences (conveyed by binocular disparity) disrupt simultaneous chromatic contrast induction, but texture differences do. These results suggest that the mechanisms underlying chromatic contrast are sited early in visual processing, at a monocular level prior to image segmentation based on the computation of relative depth or motion. The effects of texture-differences are also consistent with a low-level locus, since they are tuned to cardinal axes whose physiological instantiation has not been proved beyond primary visual cortex. Furthermore, the blocking effect of texture-differences is very local: we have shown in other experiments that a small (1/3-) textured annulus surrounding the target is as effective as a full-screen textured background in reducing contrast induction (Hurlbert and Wolf, 2002). Thus, the texture-difference effect most probably reflects an intrinsic dependence of the low-level spatial contrast mechanism on local chromatic variance.

We argue that the induction effects we measure are dominated by local rather than global spatial chromatic contrast for several reasons: (1) earlier experiments using a similar rapid-change paradigm conclude that change in remote fields up to 10 distant from the central target have only a small effect on the induced contrast (Wachtler et al., 2001; Wolf and Hurlbert, 2003). (2) Control experiments in which only a very small annulus surrounding the central target undergoes the shift in chromaticity between the reference and test presentations. while the remaining background remains neutral, yield similar induction effects. (3) The strength of contrast induction is similar for the different measurement

■

techniques and conditions we used, despite their temporal differences (Fig. 3).

We further argue that these effects are dominated by instantaneous spatial contrast, rather than temporal adaptation, because the very brief exposures to the inducing background do not permit steady-state chromatic adaptation to the same background. Furthermore, in independent measurements, we determined that a 2 min exposure to the textured inducing background did yield near-complete chromatic adaptation (i.e. the central target required almost the same shift in chromaticity as the background to appear neutral). Therefore, the small amount (10–l5%) of contrast induced by the 500-ms exposure to the textured background provides an upper limit to the amount of adaptation that could occur within this brief duration, although even this small amount is probably primarily due to spatial contrast rather than temporal adaptation.

Other studies support the conclusion that local chromatic induction is monocular in origin (Shepherd, 1997), while there is some evidence that remote induction effects occur beyond the retina at a binocular locus (Shevell and Wei, 1998) and that spatial cone excitation ratios may be computed binocularly (Nascimento and Foster, 2001). In other experiments, we found that the contrast induction effects of remote surfaces presented to one eye only may be cancelled by a stimulus presented to the other eye, and conclude therefore that remote effects are likely to occur at a binocular site (Wolf and Hurlbert, 2003).

Given the evidence suggesting that perceived depth differences inhibit contrast induction, particularly in the achromatic domain, why did we fail to find any such effect of binocular-disparity differences on chromatic contrast induction? Differently from other studies, we used a nulling technique in order to

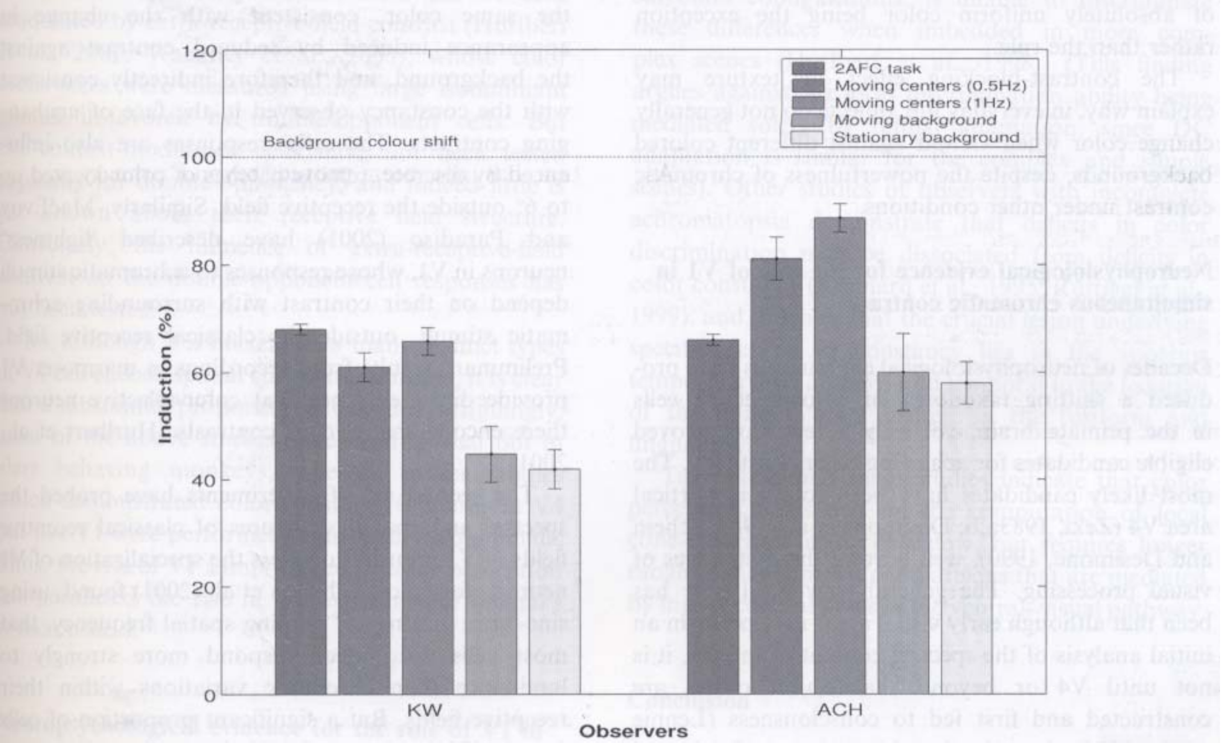


Fig. 3. A comparison of the strength of contrast induction as measured by a variety of techniques. A value of 100% would indicate that the target square must always have the same chromaticity as its immediate background in order to appear neutral. A value of 50% indicates that the target appears neutral when its chromaticity is halfway between that of the immediate background and the neutral point. The strength of induction is comparable in our basic 2AFC experiment and in the `moving-center' experiments. It is weaker for the moving-background experiments, perhaps because of the luminance-texture we used to define the background position. But there are no significant differences between the strength of induction for moving versus stationary backgrounds.

maintain DC adaptation at a fixed neutral point while allowing temporal modulation of background chromaticity. This temporal chromatic modulation may induce AC adaptation. We would therefore expect decreased sensitivity to color deviations from neutral along the (L—M) axis: reds would look less red and greens less green (Webster, 1996). But the DC shift in neutral chromaticity, which is what we measure here, would not be affected. The more likely explanation for the discrepancy lies in the simplicity of our stimuli compared with earlier studies. In fact, our results are in agreement with those of Gibbs and Lawson (1973) for achromatic contrast, whose stimuli are most similar to ours.

Interestingly, the strong dependence on texture of spatial chromatic contrast, despite its low-level mechanism, may be very effective in weakening its operation between detachable surfaces in the natural world, since most natural surfaces are textured, areas of absolutely uniform color being the exception rather than the rule.

The contrast-blocking effect of texture may explain why, in everyday life, objects do not generally change color when viewed against different colored backgrounds, despite the powerfulness of chromatic contrast under other conditions.

Neurophysiological evidence for the role of V1 in simultaneous chromatic contrast

Decades of neurophysiological experiments have produced a shifting taxonomy of color-selective cells in the primate brain, yet only a few have proved eligible candidates for achieving color constancy. The most likely candidates have been found in cortical area V4 (Zeki, 1983a,b; Desimone et al., 1985; Schein and Desimone, 1990), well beyond the first stages of visual processing. The general view until now has been that although early visual areas may perform an initial analysis of the spectral content of images, it is not until V4 or beyond that object colors are constructed and first fed to consciousness (Lennie et al., 1990). In a landmark statement, Crick and Koch (1995) specifically argued against primary visual cortex (V1) as the site for consciousness, because neurons there do not display the properties necessary for color constancy and color constancy is a bedrock of our conscious experience.

In the past few years, the argument has begun to swing the other way: new studies of neurones in V I now suggest that it is a critical site for color constancy. These studies fall broadly into two classes: those that examine contextual modulation and those that examine spatial receptive field properties. The first type stem from the increasing recognition of the large role that nonclassical-receptive-field context plays in modulating the activity of V1 neurons in response to stimuli within the classically defined receptive fields. Context modulates the response to texture or direction-of-motion (Albright and Stoner, 2002); therefore, it should not be surprising if context did the same for color.

Motivated by this reasoning, Wachtler et al. (2003) found that the chromatic tuning of V1 neurons is indeed influenced by their nearby and distant chromatic surroundings. The cells' responses to preferred colors are suppressed by a background of the same color, consistent with the change in appearance induced by reduced contrast against the background, and therefore indirectly consistent with the constancy observed in the face of unchanging contrasts. The cells' responses are also influenced by discrete, remote patches of color located up to 6° outside the receptive field. Similarly, MacEvoy and Paradiso (2001) have described `lightness' neurons in V1, whose responses to achromatic stimuli depend on their contrast with surrounding achromatic stimuli, outside the classical receptive field. Preliminary results from recordings in marmoset V1 provide direct evidence that color-selective neurons there encode spatial cone-contrasts (Hurlbert et al., 2001).

The second set of experiments have probed the spectral and spatial structures of classical receptive fields in V1 in order to assess the specialization of V1 neurons for color. Johnson et al. (2001) found, using sine-wave gratings of varying spatial frequency, that most cells did indeed respond more strongly to luminance than chromatic variations within their receptive fields. But a significant proportion of cells (nearly 40%) either preferred chromatic variations at very low spatial frequencies, or responded equally well to modulations of luminance or color (at the same spatial frequency) when total cone-contrast was equated for the two types of stimuli. Many of these latter `color-luminance' cells share key characteristics with the double-opponent cell newly rediscovered by Conway (2001), in that the L and M cone responses are out of phase with each other across the receptive field. Conway (2001) demonstrated that approximately 10% of neurons in V I satisfy the criteria for true double-opponency, having cone-opponency in the center (e.g. excited by + L contrast, suppressed by + M contrast; + L—M) and the opposite opponency in the surround (i.e. + M—L). Other recent studies report that V1 neurons are more highly specialised for color processing than previously acknowledged (Hanazawa et al., 2000).

Double-opponent cells are ideal candidates for the computation of local cone-contrast, in that they explicitly compare within-type cone excitations across space. But they compute very local contrast only, between the center and surround of receptive fields extending little more than 1—2° in total. They are therefore probably distinct from the V1 cells modulated by extra-receptive-field contrast (Hurlbert et al., 2001; Wachtler et al., 2003), whose color preferences were measured using large isoluminant stimuli ill-favored by double-opponent cells. But the context-modulated cells have not been tested explicitly for double-opponency, and indeed little is yet known about their receptive field structure. Conversely, the influence of extra-receptive-field contrast on the double-opponent cell responses has not been tested.

So, although it is unclear how many distinct types of V1 cell encode spatial chromatic contrast, it is clear that a substantial proportion of cells do. Intriguingly, most of the above studies have been carried out in alert behaving monkeys, whereas earlier studies which demonstrated color-constant responses in V4 but not V1 were performed in anaesthetised animals. Thus, the rise of V Vl's importance to color perception has paralleled the rise in the experimental animal's consciousness.

Neuropsychological evidence for the role of VI in chromatic contrast

Natural lesion studies also suggest that chromatic contrast mechanisms may be mediated at the level of V1 or below. Studies of the cerebrally achromatopsic observer, MS, indicate that he is capable of discriminating small differences in spatial cone-contrasts despite being perceptually unaware of colors (Hurlbert et al., 1998; Kentridge et al., 2003). Similarly, the color names chosen by another cerebrally achromatopsic observer, JPC, show strong dependence on the background against which the colored surfaces are displayed, under otherwise relatively constant viewing conditions (D'zmura et al., 1998). Both observers suffer damage to the ventral and temporo-occipital cortical regions, including the human `color center' localized to the lingual and fusiform gyri (controversially labeled as V8 or V4, and probably corresponding to area TEO in macaque monkey; Hadjikhani et al., 1998) yet both observers retain residual sensitivity to spatial chromatic contrast.

Observer MS, despite being able to discriminate differences in spatial cone-contrasts in simple center-surround configurations, is unable to discriminate these differences when imbedded in more complex scenes (Hurlbert et al., 1998). (This finding argues against his local discrimination ability being mediated solely by retinal adaptation, since DC adaptation is similar for the complex and simple scenes). Other studies of observers with incomplete achromatopsia demonstrate that deficits in color discrimination may be dissociated from deficits in color constancy (Kennard et al., 1995; Ruttiger et al., 1999), and, further, that the crucial lesion underlying specific deficits in constancy lies in the superior temporal gyrus, anterior and temporal to the location of the human `color center' in the fusiform and lingual gyri.

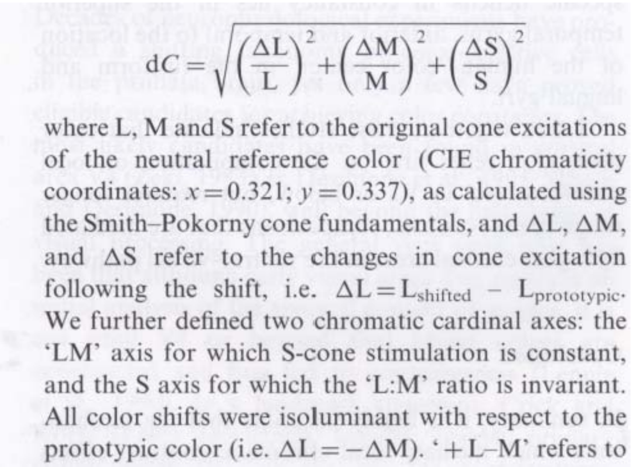
Taken together, these studies indicate that color perception relies first on the computation of local cone-contrasts in V1 or below, but requires longer range spatial contrast comparisons that are mediated by higher cortical areas in the ventral—visual pathway.

Conclusion

In summary, it is highly plausible that the mechanisms which mediate local chromatic contrast effects are sited at low levels in the visual system, in primary visual cortex or below, prior to image segmentation mechanisms which require computation of relative depth or motion. To the extent that color contrast contributes to color constancy (and by some accounts, local color contrast is the major contributor) V 1 and lower areas therefore mediate color constancy. This conclusion might seem counter to the Crick–Koch hypothesis that activity in V 1 cannot rise to awareness; is it possible that the activity in V1 may reach consciousness only if the animal is in fact conscious? Crick and Koch (1995) argue not: "... if neurons in both V 1 and V4 in the alert monkey did turn out to show [color constancy] this would not, by itself, disprove our hypothesis". Instead, the neural activity in V 1 might serve simply to trigger the awareness-related activity in V4 and beyond. It might be that double-opponent cells carry out the essential local contrast calculations (and segment the image in the bargain), while V4 cells stabilize and adjust colors according to global contrast. Both mechanisms would be aided and abetted by chromatic adaptation in the retina, which may propagate far enough and early enough, to show up as long-range contextual effects for all color cells in V1. The fact that color contrast may be perceived without color consciousness further argues that global mechanisms beyond V I are needed for consciousness of color constancy.

Appendix: Methods

Cone-contrast space. Total cone-contrast (dC) was defined as:



$$dC = \sqrt{\left(\frac{\Delta L}{L}\right)^2 + \left(\frac{\Delta M}{M}\right)^2 + \left(\frac{\Delta S}{S}\right)^2}$$

where L, M and S refer to the original cone excitations of the neutral reference color (CIE chromaticity coordinates: $x = 0.321$; $y = 0.337$), as calculated using the Smith–Pokorny cone fundamentals, and ΔL, ΔM, and ΔS refer to the changes in cone excitation following the shift, i.e. $\Delta L = L_{shifted} - L_{prototypic}$. We further defined two chromatic cardinal axes: the 'LM' axis for which S-cone stimulation is constant, and the S axis for which the 'L:M' ratio is invariant. All color shifts were isoluminant with respect to the prototypic color (i.e. $\Delta L = -\Delta M$). '+L–M' refers to increasing L-cone-contrast along the (LM) axis. The results reported here are for induction along the LM axis, with the exception of those relating to the chromatic tuning of the texture-blocking effect.

Stimuli. Our prototypic stimulus, as shown in Fig. 1(a), consisted of an achromatic central square set against a uniform or textured background (with a neutral space-averaged chromaticity and luminance). Except when otherwise stated, the central target was 1 square; the background dimensions were 30' x 20'. For the 2AFC task, the target and background luminances were, respectively 13.8 and 15 cd/m2'; for the nulling experiments (disparity and motion), the values were 28 and 30 cd/m^2.

Stimuli were generated as truecolor bitmaps using Matlab on a PC and displayed on a 20-in. SGI CRT monitor, calibrated and checked for spatial chromatic homogeneity with a Minolta CS-100 chromameter. Observers viewed the stimuli in complete darkness from a distance of 63 cm, through a black-lined viewing box, with a chinrest to limit head movement. Observers were instructed to maintain fixation on the target square throughout each trial. To enforce pre-adaptation, no responses were collected for the first 2 min of each experimental session. Four observers participated in the experiment, all with normal color vision as verified with the Farnsworth–Munsell 100-hue test.

2AFC task. On each trial the following sequence was presented: prototypic stimulus (500 ms); test stimulus (500 ms); neutral background (minimum *500* ms). The test stimulus was identical to the reference in its spatial configuration; only the colors differed. The background colors were uniformly translated along the (L–M) axis in the isoluminant plane relative to their prototypic colors, always with a constant total cone-contrast shift of 0.1. The total cone-contrast of the central square was varied between trials, its value taken at random from a set of constant increments along the isoluminant (L–M) axis relative to the prototypic square color. The observer's task was to indicate by a button-press whether the test square appeared `redder' or `greener' than the prototypic square. Responses were taken during the top-up adaptation period (minimum 500 ms) between trials. Stimulus presentation and response collection was performed under the software package 'Presentation' *(Neurobehavioral Systems, http://www.neurobehavioralsystems.com).*

We quantified the chromatic induction for each condition as the total cone-contrast of the central test square (relative to the prototypic square's neutral color) which, when viewed against the + L—M shifted background, appeared neither redder nor greener than the prototypic square, expressed as a percentage of the total cone-contrast of the + L—M-shifted background. This value was calculated as the 50% point of the best-fitting Weibull function for the psychometric data relating percentage 'redder' responses to total cone-contrast of the test square (see Fig. 2).

Binocular disparity and motion experiments. The backgrounds in our nulling experiments were modulated at 0.5 Hz, with a cone-contrast (dC) amplitude of 0.15. The 'moving-target' experiment was tested at one additional speed of 1 Hz. For the 'moving-background' experiment, the background moved laterally with an amplitude of either 0° or 8°. For the disparity experiment, the background size was reduced to 15' x 20- to fit the screen. In the 'moving-target' experiment, the background was locally uniform, the only chromatic variation being the vertical chromatic gradient applied to it. In the 'moving-background' and disparity experiments, we defined the background position using a low-contrast (± 10% luminance) salt-and-pepper texture, that we had previously shown to have little effect on chromatic induction. We investigated disparities of 0 and ± 0.5^{-}, i.e. with the target in the same plane as its background, in front or behind.

These experiments were programmed as Matlab mex functions, written in 'C' using the NVIDIA openGL library. The computer used was a GNU/Linux PC equipped with an NVIDIA GeForce2 MX/MX4 64Mb graphics card with 'Digital Vibrance' disabled. The monitor refresh rate was 100 Hz.

References

Albright, T.D. and Stoner, G.R. (2002) Contextual influences on visual processing. Ann. Rev. Neurosci., 25: 339-379.

Allman, J.M., Miezin, F.M. and McGuiness, E. (1985) Direction and velocity specific surrounds in area MT of the owl monkey. Perception, 14: 105-126.

Beck, J. (1972) Surface Color Perception. Cornell University Press, London, pp. 145-151.

Broerse, J., Vludsich, T. and O'Shea, R.P. (1999) Colour at edges and colour spreading in McCullough effects. Vision Res., 39: 1305-1320.

Brown, R.O. and MacLeod, D.I.A. (1997) Color appearance depends on the variance *of* surround colors. Curr. Biol., 7: 844-849.

Conway, B. (2001) Spatial structure of cone inputs to color cells in alert macaque primary visual cortex (V-T). J. Neurosci., 21: 2768-2783.

Crick, F. and Koch, C. (1995) Are we aware of neural activity in primary visual cortex? Nature, 375: 121-123.

Desimone, R., Schein, S.J., Moran, J. and Ungerleider, L.G. (1985) Contour, color and shape analysis beyond the striate cortex. Vision Res., 25: 441-452.

D'Zmura, M., Knoblauch, K., Henaff, A-M. and Michel, F. (1998) Dependence *of* color on context in a case of cortical color vision deficiency. Vision Res., 38: 3455-3459.

Fairchild, M.D. and Reniff, L. (1995) Time course *of* chromatic adaptation for color-appearance judgements. J. Opt. Soc. Am. A, 12: 824-833.

Finlayson, G., Drew, M. and Funt, B.V. (1993) Color constancy: diagonal transforms suffice. CSSI/LCCR TR93-02. SFU, Centre for Systems Science, Burnaby, B.C., Canada.

Foster, D.H. and Nascimento, S.M.C. (1994) Relational color constancy from invariant cone-excitation ratios. Proc. Roy. Soc. London B, 257: 115-121.

Funt, B.V., Drew, M. and Ho, J. (1991) Color constant color indexing. Int. J. Comput. Vision, 6: 5-24.

Gibbs, T. and Lawson, R.B. (1973) Simultaneous brightness contrast in stereoscopic space. Vision Res., 14: 983-987.

Gilchrist, A. (1977) Perceived lightness depends on perceived spatial arrangement. Science, 95: 185-187.

Gogel, W.C. and Mershon, D.H. (1969) Depth adjacency in simultaneous contrast. Percept. Psychophys., 5(1): 13-17.

Hadjikhani, N., Liu, A.K., Dale, A.M., Cavanagh, P. and Tootell, R.B.H. (1998) Retinotopy and color sensitivity in human visual cortical area V8. Nat. Neurosci., 1: 235-241.

Hanazawa, A., Komatsu, H. and Murakami, I. (2000) Neural selectivity for hue and saturation *of* colour in the primary visual cortex of the monkey. Fur. J. Neurosci., 12: 1753-1763.

Hurlbert, A.C. (1998) Computational models of colour constancy. In: Walsh V. and Kulikowski J. (Eds.), Perceptual Constancy: Why things look as they do. Cambridge University Press, Cambridge, pp. 283-321.

Hurlbert, A.C. and Poggio, T. (1989) A network for image segmentation using color. In: Touretzky D. (Ed.), Neural Information Processing Systems I. Morgan Kaufman Publishers, California, pp. 297-303.

Hurlbert A. and Wolf K. (2002) The contribution of local and global cone-contrasts to colour appearance: a Retinex-like model. In B.E. Rogowitz and T.N. Pappas (Eds.), Human Vision and Electronic Imaging VII. Proceedings of SPIE 4662, pp. 286-297.

Hurlbert, A.C., Bramwell, D.T., Heywood, C. and Cowey, A. (1998) Discrimination *of* cone contrast changes as evidence for colour constancy in cerebral achromatopsia. Exp. Brain Res., 123: 136-144.

Hurlbert, A.C., Gigg, J., Golledge, H. and Tovee, M. (2001) Neurons are selective for local cone-contrast in Marmoset VI. Soc. Neurosci. Abs.

Johnson, E.N., Hawken, M.J. and Shapley, R. (2001) The spatial transformation of color in the primary visual cortex of the macaque monkey. Nature Neurosci., 4: 409 416.

Kennard, C., Lawden, M., Morland, A.B. and Ruddock, K.H. (1995) Colour identification and constancy are impaired in a patient with incomplete achromatopsia asocial with prestriate cortical lesions. Proc. Roy. Soc. London B. 260: 169-175.

Kentridge, R.W., Cole, G. G. and Heywood, C.A. (2003) The primacy of chromatic edge processing in normal and cerebrally achromatopsic subjects. Prog. Brain Res., 144.

Kraft, J.M. and Brainard, D.H. (1999) Mechanisms of color constancy under nearly natural viewing. Proc. Natl. Acad. Sci. USA, 96: 307-312.

Laurinen, P.I., Olzak, L.A. and Peromaa, T.L. (1997) Early cortical influences in object segregation and the perception of surface lightness. Psycho]. Sci., 8: 386-390.

Lennie, P., Krauskopf, J. and Sclar, G (1990) Chromatic mechanisms in striate cortex of macaque. J. Neurosci., 10: 649-669.

Lee, H.C. (1986) Method for computing the scene-illuminant chromaticity from specular highlights. J. Opt. Soc. Am. A, 3: 1694-1699.

MacEvoy, S.P. and Paradiso, M.A. (2001) Lightness constancy in primary visual cortex. Proc. Natl. Acad. Sci. USA, 98: 8827-8831.

Mershon, D.H. (1972) Relative contributions of depth and directional adjacency to simultaneous whiteness contrast. Vision Res., 12: 969 979.

Moller, P. and Hurlbert, A.C. (1996) Psychophysical evidence for fast region-based segmentation processes in motion and color. Proc. Natl. Acad. Sci. USA, 93: 7421-7426.

Nascimento, S.M.C. and Foster, D.H. (2001) Detecting changes of spatial cone-excitation ratios in dichoptic viewing. Vision Res., 41: 2601-2606.

Nothdurft, H.-C. (1994) Common properties of visual segmentation. In: Morgan M.J. (Ed.), Higher-order Processing in the Visual System. Ciba Foundation Symposium 184. Wiley, Chichester, UK, pp. 245 268.

Rinner, O. and Gegenfurtner, K.R. (2000) Time course of chromatic adaptation for color appearance and discrimination. Vision Res., 40: 1813-1826.

Ruettiger, L., Braun, D.I., Gegenfurtner, K.R., Petersen, D., Schoenle, P. and Sharpe, L.T. (1999) Selective color constancy deficits after circumscribed unilateral brain lesions. J. Neurosci., 19: 3094-3106.

Rudd. M.E. and Arrington, K.F. (2001) Darkness filling-in: a neural model of darkness induction. Vision Res., 41: 3469-3662.

Schein, M.J. and Desimone, R. (1990) Spectral properties of V4 neurons in the Macaque. J. Neurosci., 10: 3369-3389.

Schirillo, J.A. and Shevell, S.K. (1993) Lightness and brightness judgements of coplanar retinally noncontiguous surfaces. J. Opt. Soc. Am. A, 10(12): 2442- 2452.

Shady, S. and MacLeod, D.I.A. (2002) Color from invisible patterns. *Nat. New-acct.,* 5(8):729-730.

Shepherd, A.J. (1997) A vector model of colour contrast in a cone-excitation colour space. Perception, 26: 455-470.

Shevell, S.K. and Miller, P.R. (1996) Color perception with test and adapting lights perceived in different depth planes. Vision Res., 36(7): 949-954.

Shevell, S.K. and Wei, J. (1998) Chromatic induction: border contrast or adaptation to surrounding light'? Vision Res., 38: 1561-1566.

Von Kries, J. (1906) Chromatic adaptation. In: MacAdam D.L. (Ed.), Sources of Color Science. MIT Press, Cambridge, MA, pp. 109-119.

Wachtler. T., Albright, T.D. and Sejnowski, T.J. (2001) Nonlocal interactions in color perception: nonlinear processing of chromatic signals from remote inducers. Vision Res., 41: 1535-1546.

Wachtler, T., Sejnowski, T.J. and Albright, T.D. (2003) Representation of color stimuli in awake macaque primary visual cortex. Neuron, 37: 681-691.

Ware, C. and Cowan, W.B. (1982) Changes in perceived color due to chromatic interactions. Vision Res., 22: 1353- 1362.

Webster, M.A. (1996) Human colour perception and its adaptation. Network: Comput. Neural Sys., 7: 587-624.

Werner, A., Sharpe, L.T. and Zrenner, E. (2000) Asymmetries in the time-course of chromatic adaptation and the significance of contrast. Vision Res., 40: 1 101 1113.

Wolf, K. and Hurlbert, A.C. (2002a) Chromatic texture influences chromatic contrast induction. In: *ARVO* Annual Meeting Abstr. Fort Lauderdale.

Wolf, K. and Hurlbert, A.C. (20026) Influences of chromatic texture on contrast induction. In: VSS Annual Meeting Abstr. Sarasota.

Wolf, K. and Hurlbert, A. C. (2003) The effect of global contrast distribution on colour appearance. In: Mollon J. D., Pokorny J. and Kurblanch K. (Eds.), Normal and Defective Color Vision. Cambridge University Press, Cambridge, pp. 239-247.

Zaidi, Q., Yoshimi, B. and Flannigan. J. (1991) Influence of shape and perimeter length on induced color contrast. J. Opt. Soc. Am. A, 8: 1810-1817.

Zaidi, Q., Yoshimi, B., Flannigan, J. and Canova, A. (1992) Lateral interactions within color mechanisms in simultaneous induced contrast. Vision Res., 32: 1695-1707.

Zeki. S. (1983a) Colour coding in the cerebral cortex: The reaction of cells in monkey visual cortex to wavelengths and colours. Neurosci., 9: 741-765.

Zeki, S. (1983b) Colour coding in the cerebral cortex: The responses of wavelength-selective and colour-coded cells in monkey visual cortex to changes in wavelength Composition. Neurosci., 9: 767-781.