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Chromatic edges, surfaces and constancies in cerebral achromatopsia

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Abstract

We tested achromatopsic observer, *MS*, on a number of tasks to establish the extent to which he can process chromatic contour. Stimuli, specified in terms of cone-contrast, were presented in a three-choice oddity paradigm. First we show that *MS* is able to discriminate the magnitude of chromatic and luminance contrast, but performance is inferior to that of normal observers. Moreover, *MS* can discriminate isoluminant borders of different chromatic composition. These abilities are not the result of unintended luminance differences and are abolished when chromatic borders are masked by sharp luminance change. In simple displays, local cone-contrast signals can make a significant contribution to surface colour appearance in normal observers. In more complex displays, the perception of a surface's colour becomes largely independent of the local contrast to its background, via processes presumed to be similar to the edge integration and anchoring stages of Land's Retinex algorithm. We show that in simple displays the percepts of both *MS* and normal observers are dominated by local chromatic-contrast. But, although the percepts of normal observers change in line with the predictions of retinex theory in more complex displays, those of *MS* do not, remaining dominated by local contrast signals. We conclude that *MS* has lost the ability to perform edge integration and that this loss is closely related to his absence of colour experience.

Keywords: Vision; Colour; Cortical colour blindness; Colour constancy

1. Introduction

The colour of a surface depends on the wavelength composition of light reaching the eye from the surface and its surroundings. Yet the latter depends on both the propensity of a surface to reflect any particular wavelength and the spectral content of the light that illuminates it. One task of the visual system in primates is to disentangle these two and so assign a constant colour to a surface on the basis of its spectral reflectance. In short, colour constancy must be achieved where colours of objects remain unchanging despite variation in the composition of the illuminant.

Neural signals that remain invariant under illumination changes are likely to form the basis of computations that result in colour constancy. When a visual scene undergoes a change in illuminant, the relative activity within each class of retinal cones elicited by differently coloured adjacent surfaces shows such invariance (Foster & Nascimento, 1994). These local cone-contrasts are important contributors to colour constancy and can indeed determine colour appearance under many circumstances.

Ideal candidates for the neural basis of extracting local cone-contrast are cells with a receptive field (RF) organisation in which sensitivities to the same wavelength are placed in spatial opposition. Such cells respond vigorously when the RF centre and surround are stimulated by lights of wavelengths that differ in the effectiveness with which they stimulate different cone-types but are silenced when uniformly bathed in lights equally effective in stimulating different cone-types. Cells with such properties have been sporadically reported in primary visual cortex (V1) of primates (Michael, 1978; Ts'o & Gilbert, 1988). These so-called 'double-opponent' cells have a RF centre that produces an opponent response to a pair of wavelengths, with the opposite opponency in the RF surround. It has generally been thought that such cells are unresponsive to luminance, lack an orientation preference and their very existence has remained controversial. Recently, it has been confirmed that many neurons in V1 are double-opponent and that some are sensitive to both colour *and* luminance and have oriented RFs (Conway, 2001; Conway, Hubel, & Livingstone, 2002; Johnson, Hawken, & Shapley, 2001). Double-opponent cells are a likely contender for an early stage in the maintenance

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of colour constancy. Moreover, they are well-suited to segmenting the visual scene on the basis of colour variation.

The distinction between wavelength processing for the assignment of surface colour and for segmenting chromatic boundaries is not apparent in the normal observer, i.e. the chromatic contrast thresholds for detecting chromatic contour and detecting colour variation are identical. However, these wavelength-based processes are neatly dissociated in cases of cerebral achromatopsia. Cerebral achromatopsia results from damage to ventromedial areas of cortex in the vicinity of the fusiform and lingual gyri. The damage invariably includes a region dubbed the 'colour centre', identified by neuroimaging normal observers viewing chromatic scenes. Such patients inaccurately and inconsistently fail to name, sort or discriminate coloured samples (Meadows, 1974). Nevertheless, the absence of phenomenal experience of colour does not necessarily impair the *detection* of isoluminant chromatic contour (Barbur, Harlow, & Plant, 1994; Heywood, Cowey, & Newcombe, 1991). Some achromatopsic observers can readily discern a coloured figure displayed against an isoluminant, but differently coloured, background when foreground and background colours are otherwise indistinguishable.

Here we assess, in an extensively studied case of complete cerebral achromatopsia, patient *MS*, the nature of the local chromatic contrast signals that can be accessed and discriminated by the visual system independently of their role in the perception of constant surface colour. The results clarify the stage of wavelength processing at which the construction of colour as a property of objects (and a phenomenal experience) diverges from other uses of wavelength, such as segmentation of objects from their backgrounds.

2. Method

2.1. Subjects

MS, an achromatopsic observer, was tested along with 22 undergraduates of the University of Durham who participated in Experiments 1(C) and (D). The latter observers had normal trichromatic vision and wore lenses to correct any refractive errors.

2.2. Case history

Patient *MS* has been extensively reported elsewhere (Heywood et al., 1991; Heywood, Cowey, & Newcombe, 1994; Newcombe & Ratcliff, 1975) and will be only briefly summarised here. *MS* suffered idiopathic herpes encephalitis in 1970 resulting in a left homonymous hemianopia with macular sparing, complete achromatopsia, prosopagnosia and visual object agnosia. There are no aphasic, agraphic or alexic disturbances. Snellen acuity is normal in both eyes and he retains three functional cone mechanisms (Mollon, Newcombe, Polden, & Ratcliff, 1980). He responds randomly on a task of isoluminant colour ordering, (the Farnsworth–Munsell 100-Hue Test), and can neither match, name nor discriminate colours. His ability to read Ishihara plates at a distance of 2 m, but not at normal reading distance, has been accounted for by his effortless ability to detect isoluminant chromatic boundaries composed of colours which he nonetheless fails to tell apart. The Ishihara plates are composed of coloured dots, which define a numeral, embedded in similar dots of varying lightness. When viewed at normal reading distance, the chromatic border of the numeral is masked by the luminance contour of individual dots. When the plate is optically blurred, or placed at a distance where individual dots can no longer be resolved, *MS* detects the now dominant chromatic boundary and reports the concealed numeral. While broad-band cells in the *M*-channel of the primate visual system will signal such borders, *MS* shows evidence for a preserved colour-opponent P-channel and/or K-channel. For example, his ability to detect isoluminant chromatic borders is unaffected when rapid temporal and spatial luminance variation is introduced into displays (Heywood et al., 1994). Under such circumstances, the *M*-channel is unable to signal the difference between chromatic and luminance contrast suggesting that detection is mediated by colour-opponent processes. Moreover, measurements of spectral sensitivity (Heywood et al., 1991) and chromatic contrast sensitivity (Heywood, Nicholas, & Cowey, 1996) provide further evidence for preserved colour-opponent mechanisms.

Structural MRI (Heywood et al., 1991) revealed that *MS* had sustained extensive bilateral lesions to ventromedial occipito-temporal cortex. There is damage to the second, third, fourth, and fifth temporal gyri in the right hemisphere as well as damage to the right temporal pole. The right striate cortex is destroyed, accounting for a left field hemianopia. In the left hemisphere there is damage to the left temporal lobe, largely confined to the temporal pole, the fourth temporal gyrus, and the hippocampal gyrus. Consistent with the location of damage in other cases of achromatopsia (Meadows, 1974), *MS* has bilateral ventral-occipital damage to the lingual and fusiform gyri.

2.3. Apparatus

Visual stimuli were presented on a γ corrected display monitor (Eizo F-784T), at a refresh-rate of 100 Hz and a resolution of 1024x768 pixels, driven by a VSG 2/3 graphic card (Cambridge Research Systems) providing 15 bit resolution per colour channel.

2.4. Procedure

In all experiments, *MS* was seated 57 cm away from the monitor and asked to indicate whether the top or bottom of three vertically aligned discs was the odd one out. The discs were 1.0° diameter and their centres were 1.5° to the right of a 0.6° grey fixation cross and were centred on, and 4.5°

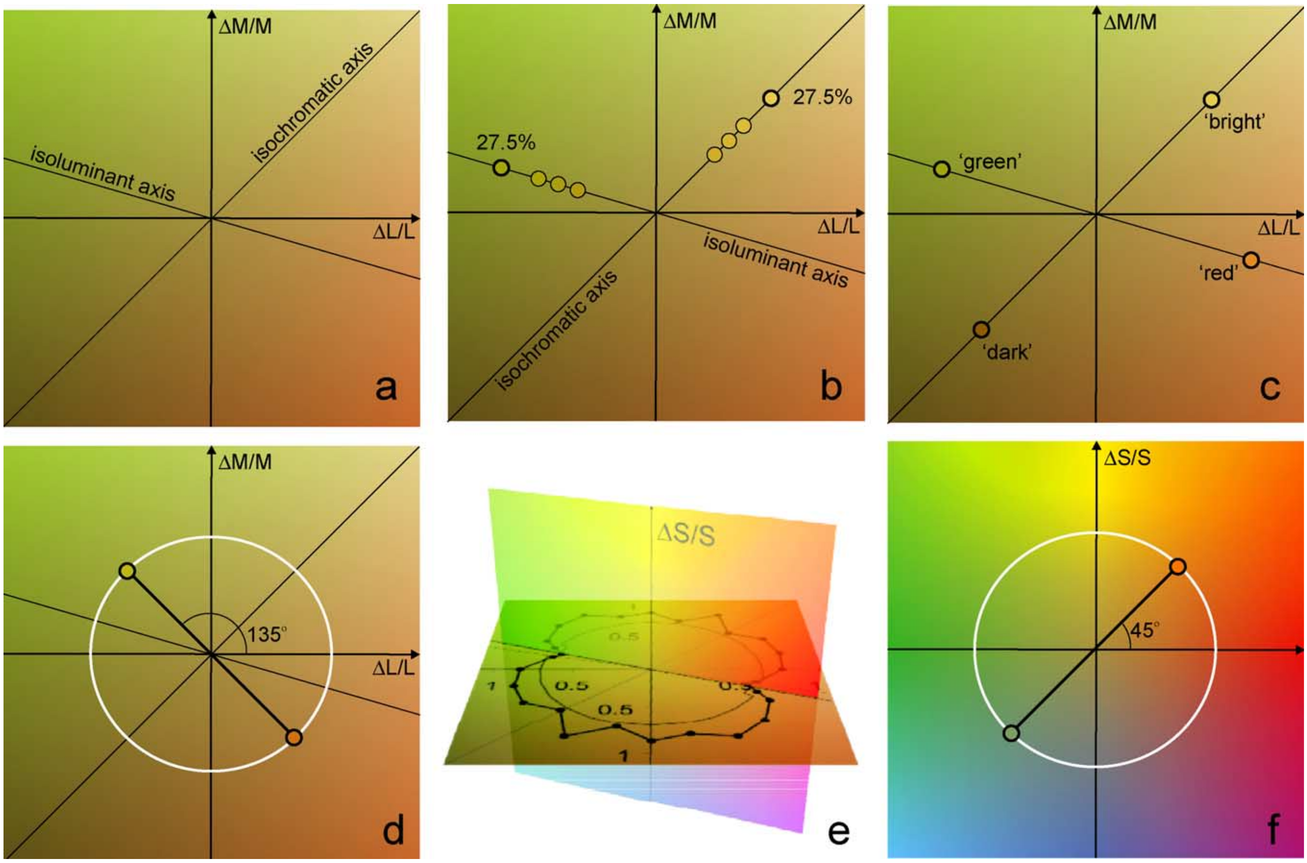

Fig. 1. (a) Cone-contrast space. This is a space in which colours are defined in terms of the proportion of modulation they produce in cone-absorption relative to a background (or adapting) colour. In the example here the background colour, the colour seen at the origin, is a low-intensity yellow. Increasing *M*-cone activation corresponds to colours simultaneously brighter and greener than the background. Colours simultaneously brighter and redder than the background increase *L* cone activation. Colours that produce equal proportionate changes in *L* and *M* cone activation are isochromatic with the background and lie upon a 45° diagonal in cone-contrast space. Colours isoluminant to the background produce equal but opposite magnitude changes in *L* and *M* cone activation. The slope of this axis in a contrast space where distance is defined as changes proportionate to background activation depends upon the relative strength of *L* and *M* background activation. The example axis shown corresponds approximately to that for the background used in the experiments reported here. (b) The bold circle represents a contrast magnitude of 27.5% with lighter circles representing 3/4, 5/8 or 1/2 of that contrast, used to test sensitivity to differences in contrast magnitude. Examples of such stimuli, falling on the isochromatic and isoluminant axis, are shown in Fig. 2a and b, respectively. (c) The figure illustrates stimuli of equal but opposite cone-contrast along the isochromatic axis (Fig. 2c) and isoluminant (Fig. 2d) axis. (d) To establish the isoluminant balance of *L* and *M* activation for *MS*, 8 discriminations between equal but opposite magnitude colours were made around a constant cone-contrast circle. An example of the two colours produced at an angle of 135° is shown. (e) The figure illustrates the isoluminant axis for *MS* in the $\Delta L/L$, $\Delta M/M$ plane. An isoluminant colour plane, produced by modulation of *S*-cones, extends orthogonally from this axis. The performance mapping shown in the $\Delta L/L$, $\Delta M/M$ plane is from Fig. 4a. (f) The figure shows the isoluminant plane used to test discriminability of direction of colour-contrast using a series of comparisons between equal but opposite magnitude colours around a constant cone-contrast circle. An example of the two colours produced at an angle of 45° is shown (Fig. 2g).

above and below, the horizontal midline. The fixation cross was present throughout, although *MS* was free to move his eyes. On each trial the stimuli remained present on the screen until *MS* responded. Testing was conducted in blocks of 48 trials with the odd items and location (always top or bottom) being counterbalanced and randomised within blocks. Stimuli were characterised in terms of cone-contrast to their immediate background using Smith-Pokorny fundamentals (see Fig. 1a). The luminance of the screen background was $19.5\,\mathrm{cd\,m^{-2}}$ and the maximum deviation between computed and measured luminances of discs and background was $0.2\,\mathrm{cd\,m^{-2}}$.

Identical procedures were adopted in testing normal observers.

3. Experiment 1

(A) *Discrimination of chromatic and achromatic contrast magnitude in the constant-S plane*: First we assessed the ability of *MS* to discriminate chromatic and achromatic contrast magnitude. Stimuli were specified in cone-contrast space so that changes in cone-activation

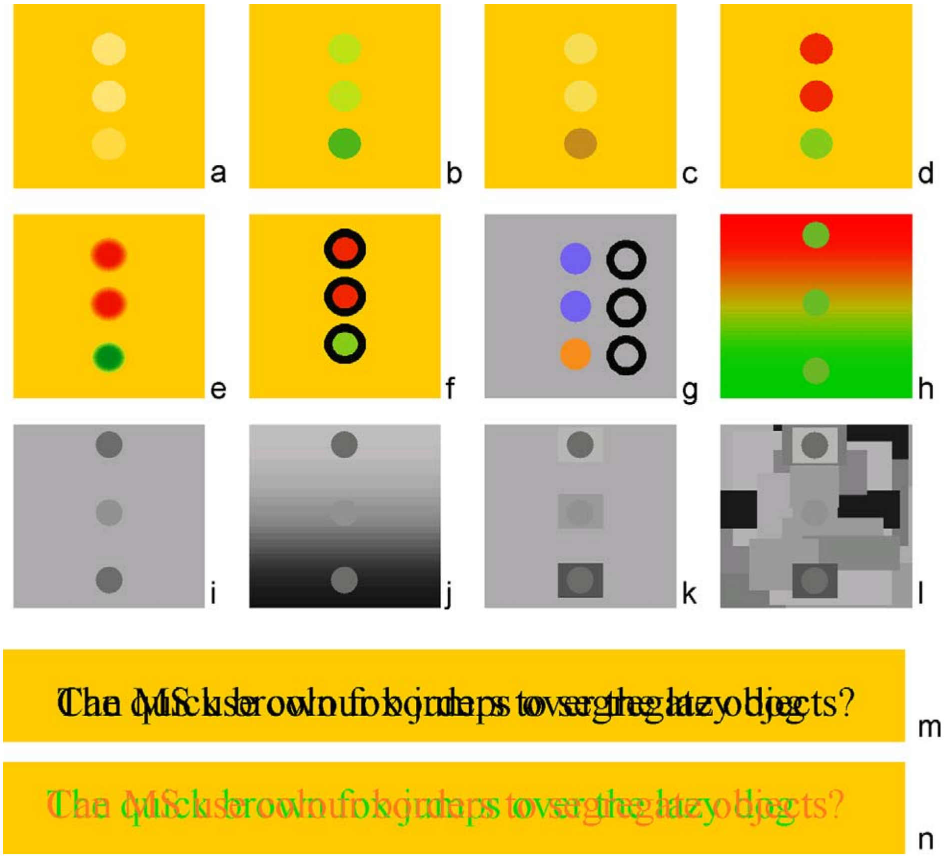

Fig. 2. The displays (a–l) are composed of three discs against different backgrounds. Chromatic and luminance displays are isoluminant and isochrominant with their background, respectively. (a) Luminance contrast magnitude. The isochrominant discs have positive luminance contrast, but the contrast of the bottom one is less than that of the other two. (b) Chrominance contrast magnitude. The discs have positive chromatic contrast in the $-\Delta L + \Delta M$ (i.e. green) direction along the isoluminant axis. The contrast of the bottom one is greater than that of the other two. (c) Luminance contrast direction. The discs have the same magnitude of luminance contrast, but the contrast of the bottom one is negative while that of the other two is positive. (d) Chrominance contrast direction. The discs have the same magnitude of chromatic contrast, but the contrast of the bottom one is in the $-\Delta L + \Delta M$ (i.e. green) direction along the isoluminant axis while that of the other two is in the $+\Delta L - \Delta M$ (i.e. red) direction. (e) Blur (0.5° standard deviation half-Gaussian blur between the colour of the discs and the background) applied to the previous example (the blur reproduced in the illustrative figure is not as gradual as that seen in the display itself). (f) Concentric black annuli applied to the same example. (g) The displaced annuli control applied to an example where three isoluminant discs differ in colour direction near the *S*-cone axis in the cone-isoluminant plane. (h) Chromatic graded background. The background and discs are coloured so that the spectral content of top and bottom discs is identical while the contrast, relative to their immediate backgrounds, of the central and bottom discs is identical. The contrast of the bottom disc is equal in magnitude, but opposite in direction to that of the other two discs. Normal observers perceive the disc with odd-contrast as odd rather than the disc which reflects a different spectrum of light. The effect is stronger with a VDU display than a small printed illustration. (i) An example of three discs in which the luminance of the top and bottom discs is identical. These same discs, presented against different backgrounds, are used in the following three panels (j–l). (j) Luminance graded background. As in panel h, the background is constructed so that the central and lowermost discs have the same contrast relative to their background, while the top disc has contrast of equal magnitude but opposite sign. (k) Isolated patches of background. As (i) but now the immediate background is provided by isolated patches embedded in a uniform field. (l) Isolated patched embedded in a complex background. (m) Superimposed text, where the two sentences are both defined in black 48-point font. (n) As above, where the two sentences are displayed by modulating the *L* and *M*-cones, respectively, at a cone-contrast of 27.5%. The sentences are isoluminant with each other, and the background. One sentence (in red) is written over the other (in green).

relative to the background colour were equivalent, whether a stimulus differed from its background in colour or luminance. The CIE co-ordinates of the yellow background were $x = 0.45$, $y = 0.45$.

On any trial two of the discs were identical and either brighter or greener than their background (Fig. 2a and b) with a cone-contrast of 27.5%. The third disc had a cone-contrast increment of either 75, 62.5 or 50% of that reference contrast (Fig. 1b). We randomly interspersed these three levels of task difficulty for both the luminance and chrominance conditions and *MS* performed 48 trials for each condition.

(B) *Discrimination of chromatic composition of edges of equal contrast in the constant-S plane*: It is conventionally thought that colour is conveyed to the cortex *via* the colour-opponent P- and K-channels, which can be contrasted to the achromatic *M*-channel of visual processing. Since *MS* retains colour-opponent signals (Heywood et al., 1991, 1994), either these, or residual signals arising from the achromatic *M*-channel which will respond to chromatic contour without signalling colour composition, might allow *MS* to discriminate chromatic contrast. We therefore determined whether *MS* can additionally discriminate the chromatic composition of colour edges.

Again, *MS* was asked to identify the odd-one-out in a triplet of discs which now all had the same magnitude of cone-contrast (27.5%) but in which one differed from the other two in the sign of contrast (Fig. 1c). Along an isochrominant axis in cone-contrast space this corresponds to discrimination among targets that are lighter or darker than the background (Fig. 2c). Along an isoluminant axis, where only long- (*L*) and middle-wavelength (*M*) cones are modulated, this entails discriminating among targets which are redder or greener than the background (Fig. 2d). Ninety-six trials were presented in each condition. We initially conducted the experiment using photometrically determined axes. That is, the isoluminant and isochrominant directions were calculated on the basis of the properties of the average human spectral response function, V_λ. To establish whether local-contrast signals at the border between targets and backgrounds could serve as the basis for discrimination, we included 48 trials in which local border contrast was obscured by black annuli surrounding the target discs. The annulus extended 1.0° from the edges of the discs (Fig. 2f). Furthermore, to control for spurious luminance signals as a result of chromatic aberration, we included 48 trials of a control condition in which sufficient Gaussian blur was added to the edges of the discs to render aberration cues unusable (Fig. 2e). In this condition, 0.5° standard deviation half-Gaussian blur between the colour of the disc and the background was added to the edges of the discs in order to eliminate over 95% of the spatial power above 1 cycle per degree.

(C) *Determination of the isoluminant axis*: In the previous experiment, isoluminance was defined photometrically, i.e. for the hypothetical young average observer. If the isoluminant point in *MS* departs from this, it is possible that performance was based on unintended luminance differences. If this were the case, there should nevertheless be a direction in cone-contrast space that represents an isoluminant axis. We therefore presented *MS* with oddity tests in which stimuli, all with ±15% root-mean-square (rms) cone-contrast, were drawn from axes distributed around the constant *S*-cone activation cone-contrast plane (Fig. 1d). We concentrated on axes close to photometric isoluminance and used a lower contrast magnitude than in the previous experiment in order to maximise the chance of finding an *L*:*M* ratio axis that was isoluminant for *MS*. Twenty-four trials were presented at each of eleven polar angles separated by 15° increments in cone-contrast space. In *MS*, 48 trials were presented at each of four additional angles separated by 5° increments about the photometric isoluminant.

Identical procedures were used to test twelve normal observers, with the exception that stimuli with ±1.5% rms cone-contrast were used and 40 trials were presented at each of the 11 polar angles.

(D) *Discrimination of chromatic contrast resulting from S-, M- and L-cone modulation*: Having established the isoluminance axis for *MS* in the *L*:*M* cone-contrast plane we can extend *S*-cone modulations orthogonally from this axis to produce an isoluminant colour-circle in cone-contrast space for *MS* (Fig. 1e). We can then test whether his ability to access local chromatic contrast signals is restricted to the *L*:*M* plane or extends to stimuli composed of mixtures of *L*-, *M*- and *S*-cone modulations. We tested eight axes spaced at 22.5° intervals around the colour circle (Fig. 1f) in the oddity task with 32 trials *per* discrimination. The cone-contrast of two stimuli was 25% and the third was of equal and opposite contrast. The CIE co-ordinates of the background were $x = 0.33$, $y = 0.33$. We also assessed the effect of obscuring stimulus borders with 1° black annuli. We also wanted to rule out the possibility that the mere presence of high contrast luminance borders in the display might interfere with the ability of *MS* to make discriminations. We accordingly included a condition in which the annuli were not concentric with the three stimulus discs but rather were displaced just to the right of them (Fig. 2g). Identical procedures were used to test ten normal observers, with the exception that stimuli with 2.5% rms cone-contrast were used and 40 trials were presented *per* condition.

(E) *Image segmentation*: To establish whether *MS* could use chromatic signals in image segmentation, he was presented with two sentences of superimposed, 48-point font, text against an isoluminant yellow background (CIE $x = 0.45$, $y = 0.45$). One sentence, displayed in red, isolated long-wavelength cones. The second, displayed in isoluminant green, isolated middle-wavelength cones. Each of the pair of sentences were displayed at a cone-contrast of 27.5% (Fig. 2n). The same pair of superimposed sentences was also presented in black (Fig. 2m).

4. Results

(A) *Discrimination of chromatic and achromatic contrast magnitude in the constant-S plane*: As illustrated in Fig. 3, *MS* could discriminate the magnitude of chromatic-contrast boundaries although his performance becomes poorer as contrast difference decreased. Although his performance exceeded chance for the two easier discriminations ($41/48 = 0.85$, binomial $P < 0.001$; $32/48 = 0.67$, binomial $P < 0.05$) his performance was clearly abnormal—all three levels of difficulty were faultlessly discriminated by the experimenters and other normal observers. Surprisingly, *MS* showed a comparable performance in the cone-contrast matched luminance and chrominance conditions. If his deficit were exclusively one of colour vision we would have expected much better performance for luminance discriminations.

(B) *Discrimination of chromatic composition of edges of equal contrast in the constant-S plane*: As illustrated in Fig. 3, *MS* discriminated luminance oddity almost perfectly with plain discs (93/96 correct) and marginally worse with blurred discs (88/96 correct). His discrimination of chrominance oddity with the plain discs was also much better than would be expected by chance (80/96, binomial $P < 0.0001$) and, as his performance was virtually unaffected by blur (41/48, binomial $P < 0.0001$), this ability could not be attributed to a chromatic aberration. However, his performance fell to chance when borders were obscured by black annuli for both luminance (26/48, binomial n.s.) and chrominance (30/48, binomial n.s.) discrimination. This is consistent with the hypothesis that *MS* retains the ability to extract local chromatic

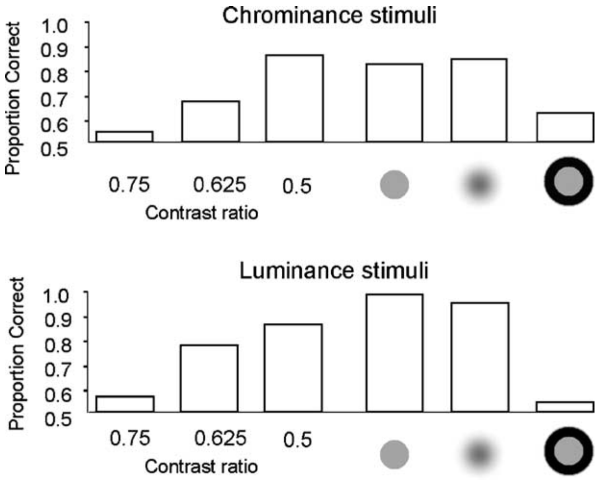

Fig. 3. The upper and lower panels show proportion correct when *MS* performed oddity discriminations for chrominance and luminance, respectively. From the left, the first three histograms show discrimination of contrast magnitude. The remaining three histograms show oddity performance for discrimination of ±27.5% of contrast, along with control conditions where stimuli were either blurred or surrounded by black annuli.

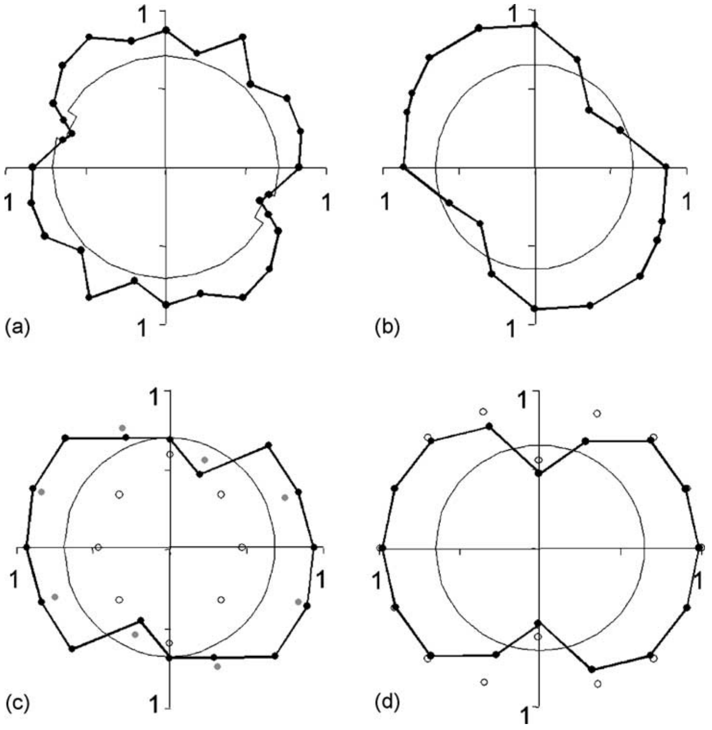

Fig. 4. Polar plots of oddity discrimination performance. In each panel eccentricity represents the proportion of correct oddity discrimination while direction represents the direction of the axis in cone-contrast space from which the positive and negative contrast stimuli were drawn (so discrimination becomes better as distance from the origin increases—the opposite to the convention in polar plots of detection thresholds which readers may have encountered). The fine-lined circle represents the level of performance required to meet a binomial probability level of 0.05. Black-filled markers represent performance when stimuli were plain discs, grey-filled markers represent performance when discs were accompanied by displaced annuli and empty-markers represent performance when discs were presented in concentric annuli. (a) Performance of MS in the $\Delta L/L$, $\Delta M/M$ plane with 15% rms cone-contrast stimuli. (b) Performance of normal subjects in the $\Delta L/L$, $\Delta M/M$ plane with 1.5% rms cone-contrast stimuli. (c) Performance of MS in his cone-isoluminant colour-plane with 25% rms cone-contrast stimuli. *LM*: cone modulation is horizontal, *S*: cone-modulation is vertical. (d) Performance of normal subjects in the cone-isoluminant colour-plane with 2.5% rms cone-contrast stimuli.

contrast signals from a stimulus, although he appears unable to use this information any further in the process of surface colour perception. *MS* may also be relying on local contrast information, rather than comparisons between remote areas of a scene, to perceive luminance.

(C) *Determination of the isoluminant axis*: Fig. 4b shows the mean performance of 12 normal observers performing oddity discrimination around the constant *S*-cone activation cone-contrast plane. For discriminations along the *isochromatic* axis, performance fell below that expected on the basis of chance responding, reflecting the poorer sensitivity to luminance contrast compared with equivalent chromatic cone-contrast in normal observers. As shown in Fig. 4a, *MS* performed most poorly on an axis near but not identical to the photometric *isoluminant*. While his performance did not exceed that of chance along this axis, when retested using stimuli of the original 25% contrast his performance improved (67/96, binomial $P < 0.0001$). So, although it is likely that isoluminance for *MS* differs from the human average, a luminance artefact based on this deviation cannot explain his ability to discriminate the chromatic composition of stimuli using local contrast information.

(D) *Discrimination of chromatic contrast resulting from S-, M- and L-cone modulation*: Fig. 4c and d shows performance of *MS* and normal observers, respectively, for oddity discriminations for complementary colours around an isoluminant colour circle in cone-contrast space. Without annuli *MS* discriminated chromatic oddity above chance levels along all axes apart from two, at and adjacent to the direction corresponding to pure *S*-cone modulation. His ability was unaffected by displaced annuli but was reduced to chance in all directions by concentric annuli which obscured the border between discs and their background (Fig. 4c). Like *MS*, normal observers were poorer at discriminating chromatic oddity along the *S*-axis but their performance was unaffected by concentric annuli indicating that they could make comparisons between non-adjacent areas in the course of making discriminations.

(E) *Image segmentation*: The results of a simple test indicate that *MS* can use chromatic information in image segmentation. When presented with two sentences of superimposed text, the upper one displayed in an *L*-cone stimulating red and the other in an equal contrast magnitude *M*-cone stimulating green, he effortlessly read the uppermost text. Moreover, when asked, he was adept at reading the underlying text. To succeed at either task, without access to the difference in chromatic properties of the borders, would be as hard as segregating the two texts if they were both written in the same colour (see Fig. 1n). Both normal observers and *MS* failed to do so under this condition.

5. Discussion

MS is able to tell apart chromatic borders which have different magnitudes of chromatic contrast or different chromatic compositions albeit that his performance is impaired relative to that of normal observers. In addition, as with normal observers, his performance at discriminating differences in *S*-cone modulation is less proficient than modulation of the other two cone types.

A visual system in which the processing of wavelength is restricted to extracting local-chromatic contrast could not show ‘wavelength based vision’ (i.e. a condition in which the perceived colour of a surface is solely dependent upon the wavelength of light reflected from that surface) because it would not respond equivalently to spectrally identical surfaces if they abutted areas of differing spectral content. Instead, the appearance of a surface would be determined by its local background. It would lack higher-order mechanisms such as integration across boundaries or anchoring which are used to produce background-invariant perception of surfaces in addition to illumination invariance. In Lands’s retinex scheme (Land & McCann, 1971) the ability to make background-invariant comparisons between remote patches in a display is achieved by integrating all of the local border contrasts above a minimum threshold contrast along a path joining the patches. This mechanism fails in normal observers when there is a *gradual* transition in the spectral composition of the background with no supra-threshold borders between the two patches. Thus, when two spectrally identical patches are placed against such a background their colour appearance will be determined by local contrast. The introduction of contrast borders into the background allows for comparison of the two distal patches *via* edge integration and the patches now appear identical. This is illustrated in Fig. 2i–l. We therefore tested whether *MS* still relied on local contrast when he was required to make such judgements by varying both the properties of the discs and their immediate backgrounds in our oddity task.

6. Experiment 2

6.1. Method

6.1.1. Subjects

MS and six undergraduates of the University of Durham were tested in the oddity tasks.

6.2. Apparatus

The apparatus was identical to that used in Experiment 1.

6.3. Procedure

We produced a display in which the background colour made a gradual linear transition, for example from red to yellow, vertically down the screen. We then computed compositions for the three discs such that all three had the same magnitude of contrast relative to their immediate background whereas two of the discs had positive local contrast (e.g. they were both greener) and one negative contrast (e.g. it was redder). It is possible to construct a set of cone-activations that satisfy these conditions where the odd-contrast disc and one of the other discs have exactly the same spectral composition and the third disc has a different composition (Fig. 2h). There are therefore two competing candidates for ‘odd one out’ in this display, a disc with odd contrast and a different disc with odd spectral content. When shown this display normal observers generally select the odd-contrast item. Discs were presented at locations 1/4, 1/2 and 3/4 of vertical screen extent with their centres 1.5° to the right of fixation.

We produced two further versions of such displays. In both displays rectangles surrounded each of the three discs, producing local contrasts identical to those in the original graded-background displays. In one display the discs and their surrounding rectangles were presented against a uniform background. In the second the discs and rectangles were embedded in a ‘Mondrian’ of random patches. In the Mondrian condition the discs and patches were presented against a background filled randomly with rectangles whose colour was randomly selected from the gamut of the original graduated backgrounds. Monochrome examples of these two displays are presented in Fig. 2k and l, respectively.

The presence of intervening local contrast borders in these latter two displays should support background-invariant constancy. We produced all three types of display using discs and backgrounds that varied along the *LM* plane isoluminant axis, the *LM* plane isochrominant axis and, with higher contrast, along the *S*-axis. Sixty-four trials were presented in the oddity paradigm, under each of the nine conditions.

7. Results

As there were only slight minimal differences between responses to *LM* isoluminant, isochrominant and *S*-axis stimuli for each type of background, we pooled results across stimulus types. It is, however, important to note that *MS* was as consistent in his oddity selection using the *S*-axis displays as he was with the other types, indicating that he can, indeed, make *S*-axis local contrast discriminations with high contrast stimuli. As expected the normal subjects selected the odd-contrast item most often (81%) with the graded background display (Fig. 2h). *MS* did not differ significantly from them ($\chi^2(2) = 0.53$ with expected frequencies based on the performance of normal subjects) in his pattern of responses to odd-contrast (79%), spectrally-odd (13%) and non-odd items (8%). In this case the percepts of *MS* and the normal subjects are based on local contrast cues. Our prediction that normal subjects would switch to selecting the spectrally-odd items against more complex backgrounds (Fig. 2k and l) was also borne out. They selected spectral oddity on 54%, contrast oddity on 28% and the other alternative on the remaining 18% of trials. *MS*, however, persisted in choosing the *local-contrast* item most often (57%) even with these other displays, suggesting that he was unable to make use of edge integration to achieve background-invariant colour constancy. He selected spectral oddity on 27%, and the other option on 16% of trials. Statistically the difference between the responses of *MS* and of normal observers with complex backgrounds is almost impossible to attribute to chance ($\chi^2(2) = 160.76$, $P < 10^{-34}$).

8. Discussion

MS retains an ability to process chromatic stimuli based on local-contrast at chromatic boundaries. He can use these local contrast cues to segment a complex stimulus. Access to these cues is, however, disrupted by coincident luminance contours. Mechanisms that integrate series of these local contrast boundaries across space in order to produce background-invariant colour constancy appear to be lost in *MS*. What is the likely physiological and anatomical basis for these abilities? What is the relationship between these abilities and the phenomenal experience of colour which *MS* has lost?

The ability to discriminate local chromatic contrast might arise out of Von Kries type adaptation in which the sensitivity of each cone-system is scaled in inverse proportion to that system’s average intensity of stimulation. Hurlbert, Bramwell, Heywood, and Cowey (1998) have shown that *MS* can match dichoptically presented surfaces under differing simulated illuminants after adaptation to the illuminant (although other findings in that study cannot be explained by adaptation). Our current finding that he matches discs according to their local border contrasts in free viewing with a series of relatively rapidly changing displays clearly depends upon processes beyond simple adaptation.

Our results are consistent with *MS* having access to the output of double-opponent cells similar to those recently reported in macaque striate cortex (Conway, 2001; Conway et al., 2002; Johnson et al., 2001). Sensitivity to chromatic edges requires a receptive field organisation in which sensitivities to the same wavelength are put into spatial opposition. Having the centre field and surround fields of such cells stimulated by lights of different wavelength can produce a response whereas bathing both the centre and surround of the field in the same wavelength leaves such cells more or less silent. If the luminance sensitivities of the centre and surround balance then the cell will respond exclusively to the chromatic contrast of a border. If, however, the luminance sensitivities of centre and surround differ, then the cell will respond to both chromatic and luminance borders. Receptive fields of both types have recently been identified in macaque striate cortex (Conway et al., 2002; Johnson et al., 2001). It has been suggested (Conway et al., 2002) that cells with mixed colour-luminance opponency are good candidates for the mediation of the perception of form from colour; if so they may underlie much of the residual ability of *MS* to extract form from colour. In principle both types of cells respond to luminance or chrominance borders (with certain provisos, e.g. unadapted colour-only cells only respond to luminance modulations of unbalanced colours in which *M* and *L* activations differ). Without an understanding of the manner in which the outputs of double-opponent cells are subsequently combined it is impossible to say whether either type plays a special role in hue perception. It is, however, the case that *MS* showed distinctly different patterns of responses to balanced *LM* isoluminant modulations and to pure *S* modulations in comparison to those of other cone-mixtures. This is at least suggestive of a special role for cone-space cardinal axes in discrimination of chromatic borders and perhaps their later use in hue perception.

In Land's retinex algorithms, two important processes must follow local contrast computation. These are edge integration, which allows remote patches to be compared, and anchoring, in which an absolute surface colour (e.g. a white point) is estimated from the visual scene. The second study reported here suggests that *MS* does not retain the ability to perform edge-integration. One might, therefore, hypothesise that edge-integration is a necessary concomitant of colour-experience.

It is difficult to assess whether anchoring and edge integration processes can exist independently. D'Zmura, Knoblauch, Henaff, and Michel (1998) describe a patient with cortical damage, JPC, who does not report subjective colour experience, but might be considered dyschromatopsic as he refers to reddish lights as being 'teinté' (tinted, hued). When asked to name paper colours presented against a uniform background he responds mostly black ('noir') or white ('blanc') (but occasionally 'marron' or 'teinté') but these responses depend strongly upon the lightness of the background. In such a simple display there is no demand for edge integration so D'Zmura et al. (1998) interpret the pattern of response as a failure of anchoring and an over-reliance on local (luminance) contrast signals. We do not know whether this patient retains edge integration. It may be the case that both edge-integration and anchoring are necessary concomitants of hue perception. However, Zeki, Aglioti, McKeefry, and Berlucchi (1999) report results that might also be interpreted as a failure of anchoring without loss of subjective colour experience. They studied PB, a patient who has lost the ability to perceive form and is described as virtually blind, yet still experiences phenomenal colour. PB was presented with a large test patch embedded in a surround of four different patches. When illuminated with white light PB and normal observers reported the large patch as having the same colour. When the spectral composition of the illuminant light was varied, PB, unlike the normal subjects, reported changes according to the dominant wavelength of reflected light. Zeki et al. therefore describe PB's colour vision as being wavelength based. The ratio of cone-excitations at the borders between the large test patch and the surrounding patches should be nearly invariant under changes in the illuminant, so, PB's wavelength based colour vision is clearly unlike that of *MS* who responded on the basis of local contrast signals.

PB's extremely poor spatial vision must make identifying an anchor nearly impossible. If a specific surface cannot be identified as a white point and used as an anchor and instead some constant arbitrary surface is used, the consequence is much the same as would be expected for wavelength based vision. Zeki et al. (1999) base their suggestion that he is responding to wavelength on an earlier electrophysiological finding that some cells could be found in striate cortex that are tuned to wavelength as opposed to colour appearance (Zeki, 1983). Recent findings on modulation of wavelength responses by remote changes in background (Wachtler, Sejnowski, & Albright, 1999) suggest that this conclusion may have depended crucially upon the size of stimuli used. If it is indeed the case that PB has intact double-opponent cells in striate cortex then an explanation of his wavelength based responses in terms of anchoring failure becomes tenable. As a result, it would suggest that the subjective experience of hue is most closely entwined with the process of edge integration rather than that of anchoring.

The locus of *MS*'s brain damage (Heywood et al., 1991) suggests that the edge-integration processes that give rise to background-invariant colour constancy are mediated by occipital ventro-medial cortex. These processes and these structures, presumably including the human 'colour-centre', are also necessary for the phenomenal experience of hue. A world without background-invariant colour constancy for *MS* is not one of ever-changing unstable colour, it is one in which colour is absent and meaningless. This is not to say, however, that discrimination of local contrast is unconscious. For all but the most difficult discriminations *MS* either deliberated at length over his decisions or made them unhesitatingly. Only on very rare occasions did he need to be prompted to simply make a guess. The neural response to local chromatic contrast therefore produces a percept which is acted upon consciously. The most likely source of this neural response is in double-opponent cells in V1; certainly much of the later (so-called higher-order) parts of the visual system for colour are destroyed in *MS*. The implication is that activity in V1 in this experiment correlates with a conscious experience, a conclusion at odds with Crick and Koch's (1998) hypothesis that only activity in areas making direct projections to frontal lobes may correlate with conscious experience. In *MS* the route is most likely to be indirect, for example from V1 to dorsal parietal cortex and only then onwards to prefrontal cortex.

The conclusion that a cortically colour blind observer perceives chromatic local-contrast signals seems at first to fly in the face of well-accepted findings. However, experimental tests of colour discrimination in *MS* always appear to have been carried out against backgrounds that differed in luminance from their targets even when the targets were isoluminant with one another, in which case local chromatic border signals might be masked by coincident luminance contrast signals. Finally, it should be noted that the hallmark of achromatopsia is poor performance on the Farnsworth–Munsell 100-Hue test. The coloured chips in this test are embedded in, and surrounded by, black casings which resemble the stimuli surrounded by black annuli (Fig. 2f) which we used in the present experiment to demonstrate the importance of local contrast under circumstances where *MS* performs chromatic discriminations.

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