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# Colour at edges and colour spreading in McCollough effects

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**Abstract**

Broerse and O'Shea [(1995) *Vision Research*, *35*, 207–226] proposed that the subjective colours in McCollough effects (MEs) consist of two components: *edge colours* appearing along the edges of contours, and *spread colours* radiating from edge colours into adjacent uncontoured regions of test patterns. This proposal was examined in five experiments. First, we demonstrated that fine coloured lines located immediately adjacent to the edges of otherwise achromatic square-wave gratings (i.e. colour-fringed gratings) are sufficient to induce MEs comparable in strength to MEs induced with desaturated versions of traditional uniformly-coloured gratings (Experiments 1 & 2). We then quantified edge and spread colours while varying light/dark duty cycles (white-bar width) in gratings with colour-fringed edges (Experiment 3), uniformly-coloured gratings (Experiment 4), and in achromatic gratings tinged with ME colours after adaptation to colour-fringed gratings (Experiment 5). Whereas the perceived magnitude of edge colours remained constant in all cases, spread colours remained constant only for uniformly-coloured gratings. For both MEs and gratings with colour-fringed edges, spread colours decreased as a function of increasing duty cycle, confirming that conventional MEs may be simulated by gratings with colour-fringed edges. We propose that edge colours arise as a consequence of neural operations correcting for the eye's chromatic aberration, while spread colours reveal a neural filling-in process operating to achieve colour constancy. In seeking to implement these suggestions, we present a putative framework based on the receptive-field properties of single cells described in contemporary neurophysiological investigations of colour. © 1999 Elsevier Science Ltd. All rights reserved.

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## 1. Introduction

Although much recent research has been concerned with the modularity of visual processing (e.g. Livingstone & Hubel, 1988), less attention has been paid to the question of how modules such as form and colour combine to allow perception of integrated coloured forms. Broerse and O'Shea (1995) have suggested that spatially-contingent coloured aftereffects (CAEs) such as the McCollough effect (McCollough, 1965) should help unravel the nature of such form/colour integration (see also Broerse, Shaw, Dodwell & Muir, 1994; Dodwell & Humphrey, 1990).

To experience McCollough effects (MEs) an observer views a pattern in which a particular colour is paired with a set of uniformly-oriented contours. This induction protocol usually lasts about ten minutes, and also often involves alternating sets of orthogonally-oriented contours paired with complementary colours (e.g. red vertical and green horizontal gratings). On subsequently viewing achromatic versions of these contours, most observers report that these test contours appear to be tinged with a colour complementary to that with which it was paired during induction (i.e. vertical gratings now appear greenish, and horizontal gratings appear pink).

One of the problems in using the properties of MEs to explore form-colour interactions has been the general lack of agreement about the fundamental nature of these illusory colours (e.g. Allan & Siegel, 1993; Dodwell & Humphrey, 1993). On the one hand, McCollough herself reported that after induction with orthogonal sets of contours paired with complementary

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colours, CAEs contingent on particular orientations reverse as the viewer's head is rotated by 90 degrees, showing that it is the retinal orientation of the contour that is important (more recently, see Bedford & Reinke, 1993). It has also been shown that under conditions of fixation, a particular contour can elicit MEs that are complementary to the MEs elicited by adjacent contours of the same orientation, suggesting that under these induction conditions, strict retinotopy of the effect is possible (e.g. Broerse & Grimbeek, 1994; Foreit & Ambler, 1978; Stromeyer & Dawson, 1978). Such evidence is consistent with a general class of explanations, beginning with McCollough's own suggestions, in which MEs are considered to be largely stimulus bound, occurring as a consequence of neural adaptation at relatively early stages of processing in visual cortex (e.g. edge/orientation sensitive mechanisms; see Stromeyer, 1978)

On the other hand, there has been a steady accumulation of evidence that the neural modification underlying MEs is less constrained than that involving edge/orientation mechanisms. Partly based on the historical roots of MEs (see below), and partly based on the construal of MEs as associations between colour and spatial features (e.g. oriented edges), there were many early suggestions that the formation of such associations occur as a result of simple contingency learning (e.g. classical conditioning; Murch, 1976; see Skowbo, 1984). As with neural adaptation, however, the mechanisms underlying contingency in these alternative accounts were also largely stimulus bound, mostly because they shared with neural adaptation the same restricted sets of spatial properties (Crassini, Broerse & O'Shea, 1979; Dodwell & Humphrey, 1990). In more recent associative-learning accounts, however, the notion of contingency has been broadened to encompass global stimulus dimensions, such as the set of relationships between local features (e.g. a pattern) rather than the features per se (Siegel, Allan & Eissenberg, 1992, 1994 and see Broerse & Grimbeek, 1994).

Suggestions that MEs exhibit global pattern qualities are not new. For example, Jenkins and Ross (1977) showed that McCollough-effect colours disappear when the perceived organization of a set of concentric squares changes spontaneously to a set of adjacent triangular wedges (see also Uhlarik, Pringle & Brigell, 1977). This evidence suggests that MEs may be influenced by higher-order levels of processing, such as those commonly assumed to determine perceived organization and figure-ground segregation (for an alternative perspective, see Broerse & Crassini, 1984, 1986).

Additional evidence of MEs as pattern—rather than edge—contingent phenomena has been provided in a series of investigations by Dodwell and his colleagues (see Dodwell & Humphrey, 1990). While in recently re-evaluating some of this evidence, Broerse and O'Shea (1995) reported that most of their findings favoured local (i.e. edge-contingent) rather than global interpretations of MEs. One exception was a previous report by Dodwell and O'Shea (1987) that effects induced with globally-organized orientation/edge components were significantly stronger than those induced with less globally-organized components (see also Sharpe & Tees, 1978; Crassini, Broerse & O'Shea, 1979). Rather than account for these differences in terms of the complex spatiotopic constructs advocated by Dodwell and his colleagues, Broerse and O'Shea (1995) proposed instead that MEs involve two spatial components: One directly bound to the activity of local, edge-specific/retinotopic mechanisms (edge colours), and another whereby colour generated by these local mechanisms spreads from edges to fill in the uncontoured regions of the pattern configuration (spread colours). In support of this proposal, Broerse and O'Shea (1995) measured edge and spread colours of MEs separately, and found that only spread colours, and not edge colours, were influenced by the global pattern organization of induction and test stimuli.

We suppose that edge colours arise from a mechanism that *normally* functions to correct chromatic aberration generated by the optics of the eye. Indeed, it was McCollough's original intention to link MEs to the aftereffects of chromatic aberration reported in experimental investigations requiring observers to wear optical prisms and lenses (e.g. Gibson, 1933; Hay, Pick & Rosser, 1963; Held, 1980; Kohler, 1951, 1962; see also Stromeyer, 1978). The dispersion of light passing through a base-left wedge prism (relative to viewer), for example, produces bluish fringes on white–black edges of objects (i.e. at *luminance* edges), and yellowish fringes on black–white edges. These fringes are visible on first looking through the prism, but tend to disappear when the prisms are worn for any extended period of time, presumably due to some form of corrective neural adaptation. When the prisms are removed, complementary CAEs appear at luminance edges (i.e. edge colours), revealing the action of the correction mechanism. Complementary CAEs, like the original colour fringes, are specific to the *polarity* of luminance edges (i.e. yellowish fringes on white-black edges and blueish fringes on black–white edges). According to the error-correcting view, conventional McCollough-effect induction stimuli would simulate differences in the wavelength composition of chromatic aberration at different edge *orientations*, due to slight irregularities in lens curvature (i.e. astigmatism; see Hohmann & von der Malsburg, 1978; see also Section 5).

Once generated in the visual system, edge colours/fringes are treated as signifying the presence of real colour in a pattern or surface, and may subsequently involve filling-in processes to create what has been assumed to be the characteristic uniformly-coloured appearance of conventional MEs. We conjecture that filling-in is mediated by processes similar to those underlying colour spreading from small coloured lines in the neon colour spreading illusion (van Tuijl, 1975; van Tuijl & de Weert, 1979). Not unlike the McCollough effect, neon colour spreading is a phenomenon that is sensitive to the structural characteristics of the stimuli (Ejima, Redies, Takahashi & Akita, 1984; Redies, Spillmann & Kunz, 1984), and extant accounts of colour spreading therefore provide various conceptual frameworks for understanding the nature of MEs. Among such frameworks, for example, perhaps the most prominent and comprehensive is the neural network model of preattentive Form-And-Colour-And-DEpth (FACADE) vision developed by Grossberg and his colleagues over a number of years (Grossberg, 1987a,b, 1994; Grossberg & Mingolla, 1985a,b, 1987; Grossberg & Todorovic, 1988).

To summarize, we propose that there are two components of MEs, namely, edge colours that are located at contours, and spread colours that spread away from edge colours into uncontoured regions of the test pattern. We consider edge colours to be retinotopic and to serve as the local generators of spread colours, and spread colours to be spatiotopic and capable of being influenced by the overall organization of the pattern in which they occur (Broerse & O'Shea, 1995). For the purposes of the present discussion it suffices to point out that such global influences might occur as a consequence of a neural filling-in process which normally operates to achieve *colour constancy* (Grossberg & Mingolla, 1985a; Grossberg & Todorovic, 1988; see Section 5).

Several past observations have hinted at the distinction between edge and spread colours in MEs. In their investigation of CAEs induced and tested with gratings having sawtooth luminance profiles, for example, Stromeyer, Lange, and Ganz (1973) reported that the saturation of effects at low test frequencies "was concentrated near the edges and *faded* off *gradually* away from edges" (p. 2352, italics in the original), suggesting that this type of asymmetrical display may have allowed direct observation of the *edge* component of MEs (see also Uhlarik & Osgood, 1974, for gratings with rectangular luminance profiles). Variants of *colour spreading* also may have been anticipated in at least three studies: Murch (1974) demonstrated that MEs spread from the portions of test patterns coinciding with adapted retinal locations, to portions located in unadapted regions. Sharpe and Tees (1978) reported that colours spread preferentially along continuous contours, despite being induced with discontinuous contours (see also Broerse & O'Shea, 1995; Dodwell & O'Shea, 1987). Broerse and Crassini (1986) reported that MEs spread only as far as an illusory form boundary.

To provide more explicit evidence for our proposal, we undertook five experiments testing the conjecture that the distribution of colour evident in ME test patterns may be due to some form of spreading process (cf. neon colour spreading). However, since (neon) colour spreading is usually induced with small, coloured lines, rather than with colour-tinted, or colour-fringed edges, we first undertook to demonstrate that colour spreading could be induced with such edges. Accordingly, we simulated colour fringes by drawing a single, fine, coloured line along the white/black edges of a square-wave grating. We found not only that this single line of colour was difficult to resolve, appearing as a colour fringe and simulating what we have called edge colours, but also that desaturated colour was evident at some distance from the edge, corresponding to what we have termed spread colour.

The reader can appreciate these phenomena at different viewing distances by inspecting Fig. 1, which shows a $3 \times 3$ matrix of square-wave gratings. In the middle column of the top row, fine red lines have been added to both sides of the dark bars to simulate colour fringes. When viewed from about three times picture height, these lines are almost invisible, but the overall appearance of this grating is that it is suffused with a desaturated red colour that is somewhat more intense at edges. Readers who have experienced MEs will find the appearance of this grating to be remarkably similar to that of an achromatic test grating after McCollough-effect induction. In the left and right columns of the middle row of Fig. 1, fine blue and green lines have been added, respectively. Likewise, the middle column of the bottom row contains yellow coloured-lines, imparting a yellowish tint to the whole grating. The top left, centre and bottom right gratings have no added coloured lines, and appear achromatic. The top right grating has red lines on black/white edges and green lines on white/black edges (from bottom to top), and the bottom left grating has yellow lines on black–white edges and blue lines on white–black edges. In both cases, these complementary-coloured lines appear to neutralize each other, and little overall spread colour is evident.

Fig. 1 thus shows that fine coloured lines applied to the edges of contours can induce the perception of desaturated colours that spread into uncontoured regions. As far as we are aware, this is a new phenomenon, albeit one which may be related to neon colour spreading, or possibly colour assimilation effects (Hurvich, 1981). In Fig. 2 we illustrate the possibility of inducing counterparts to chromatic edge and spread effects in the achromatic domain. These effects are not unlike the brightness spreading observed in variations of the Craik–Cornsweet–O'Brien illusion (see Grossberg & Todorovic, 1988; Moulden & Kingdom, 1990); and within the context of our suggestions about MEs,

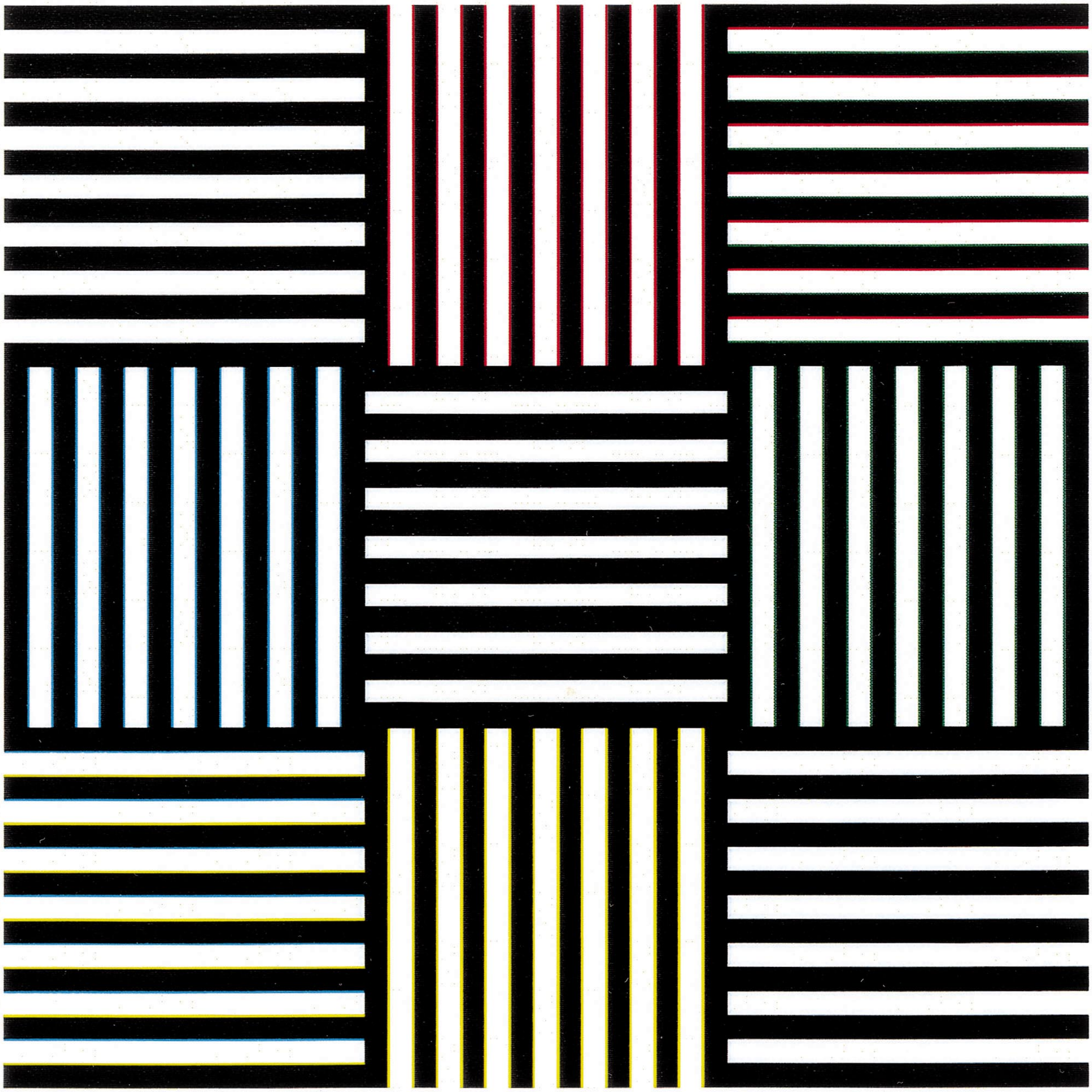

Fig. 1. A demonstration that fine coloured lines at edges can induce McCollough effect-like, uniform, desaturated colours in uncontoured regions. When viewed from about three times picture height, some gratings should appear to have subtle tints of desaturated red, green, blue or yellow. When viewed from close, these uniform tints disappear, and the fine coloured lines applied to the edges of the grating bars can be seen. See text for details.

edges, and spreading, are consistent with early observations of orientation-contingent brightness aftereffects (Over, Broerse, Crassini & Lovegrove, 1974; Stromeyer, 1978).

The major point of the demonstrations in Figs. 1 and 2 is that if MEs originate with illusory fringes (edge colour/brightness) these could indeed spread out to give the uniform colour appearance usually identified with MEs, and measured when the effects are quantified. Before leaving Figs. 1 and 2, it is worth noting that the effects of (colour/brightness) spreading, as in classical MEs, appear in both the light and dark bars of patterns. Thus in Fig. 1 the stimulus perceived as reddish consists of light pink (white) bars, and dark red, or even brown, (black) bars. This bi-directionality is most apparent in the achromatic versions of spreading shown in the lower panels of Fig. 2. However, as McCollough-effect colours that are usually reported/measured are

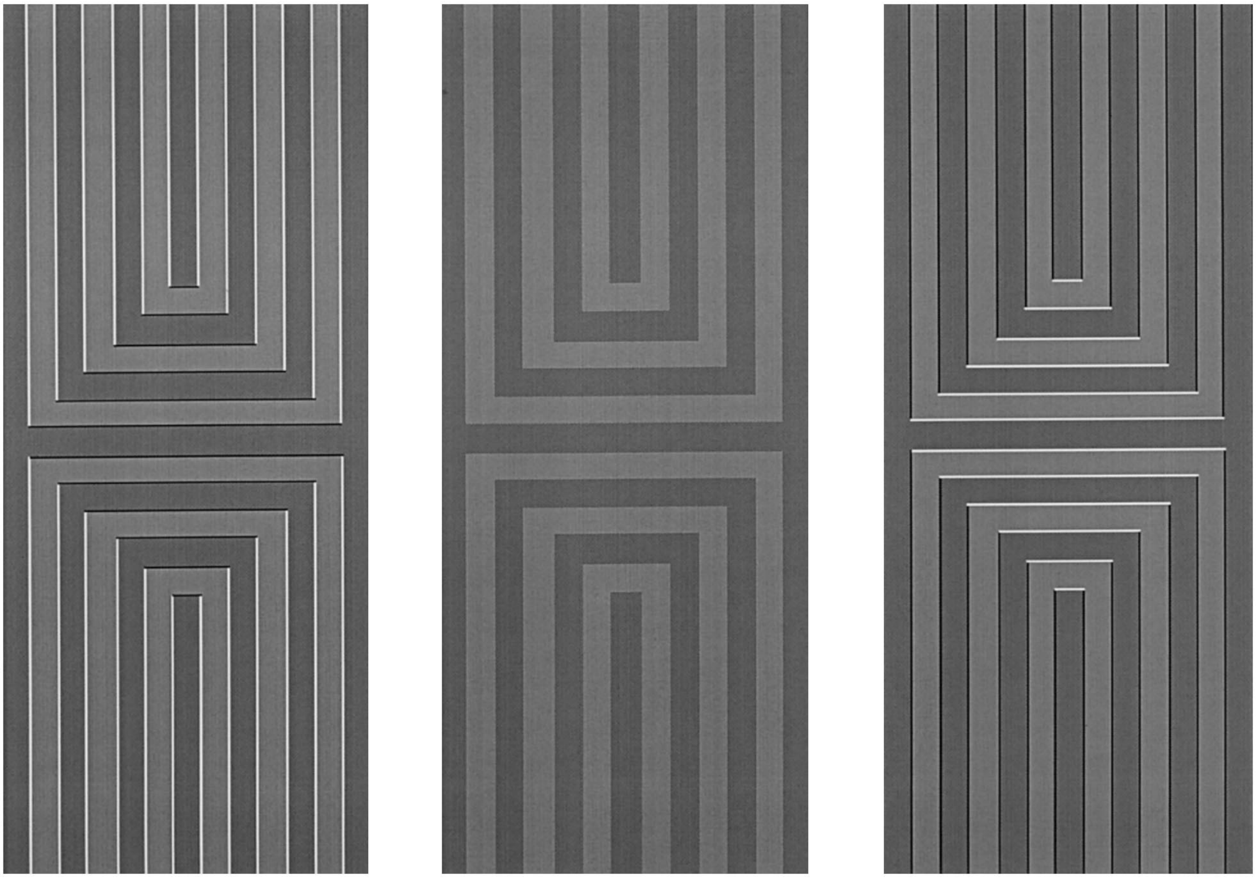

Fig. 2. Achromatic versions (brightness spreading) of the colour spreading effects demonstrated in Fig. 1, generated by superimposing fine light or dark lines on the dark/light edges of bars, and illustrating the relationship between spreading and Craik–Cornsweet–O'Brien edges (left and right panels); a comparison figure in which dark/light edges of bars remain unmodified (middle panel). The figures are variations of test patterns used by Uhlarik, Pringle and Brigell (1977) to demonstrate the influence of perceived organization on complementary (red/green) MEs induced (respectively) with vertical and horizontal contours: MEs were observed when the pattern was perceived as a diamond-shaped area of horizontal bars superimposed on a larger area of vertical bars, but disappeared when the pattern was perceived as a set of concentric upright and inverted Us (see text).

the colours perceived in the light bars, that is where we made the quantifications we report in all our experiments.

As discussed above, in her original demonstration of MEs, McCollough (1965) was attempting to generalize from a phenomenon in which optically-induced coloured fringes on opposite-polarity, but same-orientation, edges were adapted to, and produced aftereffects (e.g. Kohler, 1951, 1962). This was done by using orthogonally-oriented black lines presented on complementary, uniform coloured backgrounds (i.e. same colour on left and right edges/polarities of a particular line/orientation). In Experiment 1, we examined whether uniform colours are necessary to produce aftereffects, and attempted to induce MEs with a simulation of coloured fringes used for the purposes of illustration in Fig. 1. In Experiment 2, we compared the saturation of fringe-induced MEs with those induced by uniform, desaturated colours.

In Experiments 3–5, we used the techniques described in Broerse and O'Shea (1995) to quantify the saturation of edge and spread colours separately. The rationale underlying these experiments is based on observations that the saturation of neon colours decreases with increases in spatial extent (e.g. van Tuijl & de Weert, 1979), and the theoretical hypothesis that colour filling-in is a spatial-averaging process (e.g. Grossberg & Mingolla, 1985a). Specifically, we measured edge and spread colours as a function of duty cycle (i.e. increasing white-bar width) in gratings containing real coloured fringes (simulated with fine, coloured lines; Experiment 3), gratings containing real, uniform, desaturated colours (Experiment 4), and achromatic gratings exhibiting McCollough-effect colours (Experiment 5).

## 2. Experiment 1

As foreshadowed earlier, McCollough (1965) originally supposed that the edge-contingent CAEs induced by inspecting coloured patterns of vertical and horizontal lines, and the colour fringes induced by optical prisms, involve adaptation of the same neural mechanisms. Thus polarity-specific CAEs provided evidence that these edge-detecting mechanisms were sensitive to *luminance-edge polarity*, and orientation-contingent CAEs provided evidence that these mechanisms were sensitive to *orientation* in the fronto-parallel plane. If this is correct, and these two sorts of aftereffects involve the same neural mechanisms, then it should be possible to induce MEs with coloured fringes. That is, the mechanisms which adapt to coloured fringes on opposite-polarity edges in Kohler's experiments (i.e. producing polarity-specific CAEs) should also adapt to coloured fringes when edge orientation is the induction variable (i.e. producing orientation-contingent CAEs). We used the technique illustrated in Fig. 1 to simulate colour fringes with fine coloured lines applied to both sides of the dark bars of square-wave gratings.

## 2.1. Method

### 2.1.1. Subjects

Four volunteers with normal or corrected-to-normal visual acuity and normal colour vision were recruited from the students and staff of the Department of Psychology at the University of Queensland to act as observers. Only one observer (J.B.) was aware of the rationale of the study.

### 2.1.2. Apparatus

All stimuli were displayed on an Apple high-resolution colour monitor driven by customised software implemented on a Macintosh II, using the Hue Saturation Value (HSV) colour space (Apple Computer Inc., 1988). Emitted light characteristics of the monitor were measured with a Minolta Chromameter (CL-100). Corresponding CIE reference coordinates were white (0, 0, 100; $\text{CIE}_{Yxy}$ $Y = 38.8$, $x = 0.254$, $y = 0.286$), green (120, 100, 100; $\text{CIE}_{Yxy}$ $Y = 26.2$, $x = 0.293$, $y = 0.595$) and red/magenta (329, 100, 100; $\text{CIE}_{Yxy}$ $Y = 12.1$, $x = 0.345$, $y = 0.186$; see also Broerse & O'Shea, 1995). All stimuli were viewed binocularly. Induction stimuli were vertical and horizontal square wave gratings of 4 cpd displayed in a rectangular aperture subtending $8 \times 6°$ at a viewing distance of 916 mm. The gratings consisted of black bars (HSV: 0, 0, 0) on a white background (HSV: 0, 0, 100). Along each edge of the dark bars of the gratings, a fine coloured line (0.78 min) was drawn. These lines were either green (HSV: 120, 100, 100) or magenta (HSV: 329, 100, 100).

The test stimuli consisted of square-wave gratings spatially identical to the induction stimuli, but with the coloured lines removed. These were presented as a bipartite field with the left half containing one orientation and the right half the other orientation (i.e. vertical/left, horizontal/right, V/H; and vice versa: H/V). Two homogeneous (uncontoured) colour-matching discs subtending 1.85° were placed 2° below each half of the split-field test patterns. The saturation of each colour matching disc could be varied independently in the directions of the two induction colours by depressing separate pairs of keys. One key in each pair increased the saturation in the direction of the red induction stimulus and reduced saturation in the direction of the green induction stimulus through objective white (i.e. 0% saturation). The other key increased the saturation in the direction of the green induction stimulus and reduced saturation in the direction of the red induction stimulus through objective white.

### 2.1.3. Procedure

Observers were randomly and equally allocated to one of two groups, viewing either vertical gratings with magenta fringes and horizontal gratings with green fringes during induction, or the opposite arrangement of colours and orientations. Prior to induction, observers were given standard instructions and practice at using the colour-matching keys.

After the instructions were given, observers were asked to place their chins on a chin rest, and a series of 4 V/H and 4 H/V pre-test measures were obtained in a random order. They were required to first adjust the colour of the left matching spot, then of the right matching spot, to match the appearance of the light bars of the grating immediately above it.

Immediately after providing pre-test judgements, observers viewed the inducing stimuli alternating every 10 s for a total of 15 min. After induction, observers were allowed to move their heads freely during a 3 min rest period with the lights turned on. This was done to allow any spurious coloured afterimages to dissipate. Observers then placed their heads in the chin rest again and post-test colour judgements were obtained. The procedures used to obtain post-test judgements were identical to those used during pre-test except that a new random order of test stimuli was used.

## 2.2. Results

Saturation measures for each orientation were averaged over the eight trials for both pre-test and post-test phases. Means and standard errors are plotted for each observer in Fig. 3. The results show that each observer showed no difference in colour matches for the two orientations in the pre-test, but differences in the expected direction in the post-test. That is, gratings appeared achromatic in the pre-test, yet were tinted with McCollough-effect colours in the post-test.

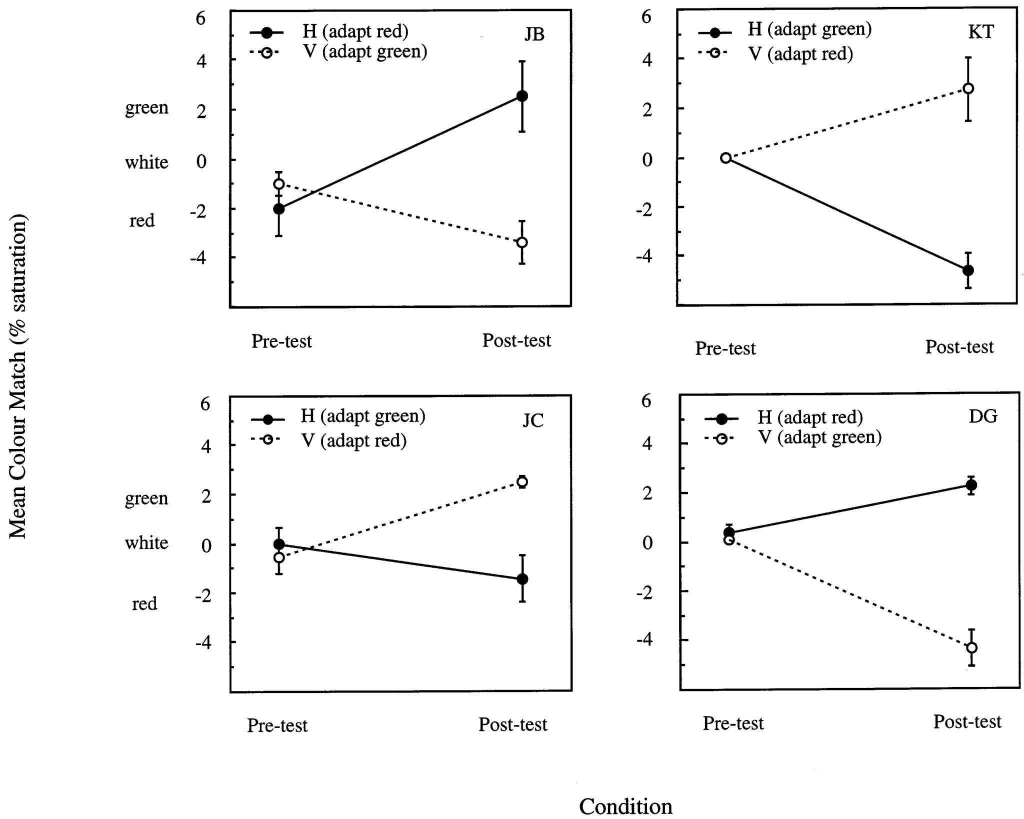


Fig. 3. Mean matched saturation's following induction with simulated colour fringes for four observers. Vertical bars show $\pm 1$ S.E.M.

### 2.3. Discussion

The results show that uniform colour is *not* necessary for inducing MEs. Critically, they show that it is possible to induce MEs with stimuli that are coloured only with fine lines along their edges. This supports our supposition that the McCollough effect occurs through the action of a mechanism correcting chromatic aberration. It also links the classical McCollough effect, induced with uniform colours and opposite orientations, to the phenomenon that inspired McCollough—adaptation to optically-induced coloured fringes on opposite-polarity but same-orientation edges (e.g. Kohler, 1951, 1962).

## 3. Experiment 2

In Experiment 2, we essentially repeated Experiment 1, with the following changes: There were three new naive observers and one observer aware of the experiment's rationale. Instead of using coloured fringes, the white space between the dark bars of the induction gratings was uniformly modified with desaturated versions of the red and green colours used in the fringes of Experiment 1. We desaturated the colours by dividing the saturation of the coloured lines used in Experiment 1 by the number of lines required to fill the space between adjacent bars of the gratings (12% saturation).

### 3.1. Results

Data were treated in the same way as in Experiment 1, and means and standard errors are shown in Fig. 4. It is clear that the pattern of results is largely similar to that of Experiment 1, with essentially no colours reported in the pre-test phase, and classical McCollough-effect colours reported in the post-test phase. To compare results from Experiments 1 and 2, we combined the observers' means in a 2 (type of induction colour: fringes vs uniform) $\times$ 2 (induction colour/orientation pairing: vertical (V)-green (G) and horizontal (H)-magenta (R) vs VR/HG) $\times$ 2 (test phase: pre-test vs post-test) $\times$ 2 (test orientation: V vs H) analysis of variance (ANOVA) with repeated measures on the last two factors.

The analysis revealed a significant two-way interaction between induction colour pairing and test orientation ($F_{(1,4)} = 30.6$, $P < 0.01$), and a significant three-way interaction between these factors and pre-test versus post-test ($F_{(1,4)} = 48.7$, $P < 0.01$). The form of both interactions are consistent with appropriate MEs. Critically, no interactions involving the fringes versus uniform colour condition were significant, although as a

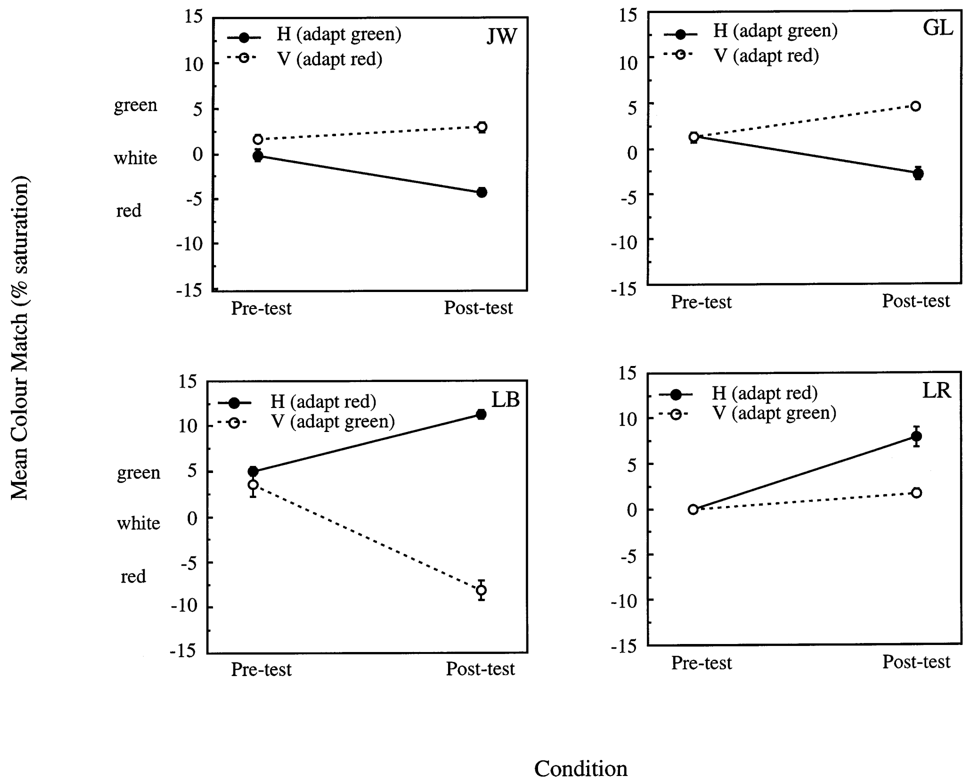


Fig. 4. Mean matched saturation's following induction with desaturated uniform colours for four observers. Vertical bars show $\pm 1$ S.E.M.

main effect the overall mean for fringes ($-0.5$) was less than the mean for uniform colour (1.5; $F_{(1,4)} = 16.5$, $P < 0.05$). By the scoring conventions used, these overall means would be zero if MEs induced with opposite colour/orientation pairings were symmetrical. This main effect therefore reveals an asymmetry, which is not unusual with MEs obtained from small numbers of observers (e.g. in Experiment 2 JW & LB favoured horizontal over vertical MEs irrespective of colour-orientation pairing; see Broerse & Crassini, 1984). In summary, the results of Experiments 1 and 2 indicate that the magnitude of MEs induced by fringes is essentially the same as that induced by uniform, desaturated colours.

### 3.2. Discussion

Taken by themselves, the results of Experiment 2 confirm that MEs can be generated with desaturated colours, a finding first reported by Webster, Day and Willenberg (1988). Taken together with the results of Experiments 1, however, they show that coloured fringes can be used to induce MEs that are of comparable magnitude to those observed following induction with uniformly coloured (desaturated) gratings. This links MEs to aftereffects that arise from optically-induced coloured fringes on same-orientation, opposite-edge-polarity contours, and is consistent with our supposition that MEs are laboratory-induced manifestations of a mechanism that corrects chromatic aberration.

The results of Experiments 1 and 2 address the role of coloured fringes in *induction* of MEs. What we have not addressed so far is whether when conventional MEs are *tested*, the colours have the appearance we predict; namely, edge and spread colour components. Since Broerse and O'Shea (1995) indicated that observers could indeed discriminate between edge and spread colours, Experiments 3–5 were undertaken to quantify the spatial properties of these two components while varying duty cycle.

Uhlarik and Osgood (1974) assessed McCollough-effect colours as a function of the duty cycle of square-wave gratings and reported that the magnitude of the effects decreased as the visual angle of the white space between dark bars increased. Taken in conjunction with early reports that CAEs are difficult to generate with low spatial-frequency stimuli (e.g. Lovegrove & Over, 1972), Uhlarik and Osgood suggested that these decreases reflect size tuning, and may be mediated by the receptive-field properties of mechanisms sensitive to black-bar width (a point also made by Stromeyer, 1978).

We would explain the McCollough effect's dependence on duty cycle as follows: Each edge of the stimulus exhibits a constant amount of edge colour, but the further the colour has to spread, the weaker the spread component (i.e. due to spatial-averaging, or filling-in). To reassure ourselves that this explanation is consistent with what we might expect from spreading of real colours, we first asked subjects to quantify edge and spread colours as a function of duty cycle in gratings containing fine coloured lines (Experiment 3), and in gratings containing uniform desaturated colours (Experiment 4). Finally, we assessed edge and spread colours in achromatic gratings exhibiting McCollough-effect colours (Experiment 5).

## 4. Experiment 3

### 4.1. Method

#### 4.1.1. Subjects

Three volunteers with normal or corrected-to-normal visual acuity and normal colour vision were recruited from students of the Department of Psychology at the University of Queensland. One observer (A.B.) was aware of the experiment's rationale, one had taken part in Experiment 1 (K.T.) but was otherwise naive about MEs, and the final subject (L.E) was new.

#### 4.1.2. Apparatus

The apparatus was the same as in Experiment 1. The stimuli, however, were gratings with rectangular luminance profiles varying in duty cycle over four approximately-equal logarithmic steps between a black:white ratio of 1.0:0.5 through equal width black/white bars (1.0:1.0; square wave) to 1.0:4.0 (see Table 1). These gratings had fine lines of colour added to the edges of the black bars, in the same way as for the induction stimuli of Experiment 1.

#### 4.1.3. Procedure

Stimuli were arranged into 16 possible patterns resembling those of the test stimuli in Experiment 1, such that the duty cycle of each grating in the upper quadrants was equal. These patterns represent the full crossing of three factors: duty cycle (four values), orientation arrangement (H/V vs V/H), and colour/orientation (VG/HR vs VR/HG).

Each observer participated in baseline edge and spread colour matching sessions (achromatic gratings), followed by four experimental colour matching sessions ($2 \times$ edge; $2 \times$ spread). In each session all the test patterns were presented in a random order. Spread colour matches were the same as those described in Experiment 1. For edge colour matches observers were instructed to look at the edges of the black bars, and to match this with the saturation of a variable coloured disk. Subjects were free to move their eyes to fixate either edges or uncontoured regions when required, and were allowed to look back and forth between the test gratings and colour-matching spot as many times as was necessary to make a satisfactory match. Order of making edge and spread colour matches on each test stimulus was random.

### 4.2. Results and discussion

We scored saturation slightly differently from Experiment 1 and 2. Instead of a scale between fully-saturated green (+100%) through white (0%) to fully-saturated magenta (−100%), we used a scale from fully-saturated for both colours (100%) to white (0%). Responses were scored positive if they were of the correct colour (i.e. of the same hue as in the real coloured fringe) and negative if they were not. The results are plotted for each observer in Fig. 5(a).

In inspecting Fig. 5(a), note that our scoring of saturation has changed. Responses now run from 0 to 100%, and responses to individual colours have been averaged. We used linear regression (of mean saturation on the logarithm of duty cycle) to compute the two trend lines for edge and spread colours that have been plotted on the three panels. For each subject, saturation of responses to edge colours is essentially the same at all duty cycles. Note also that the overall level of saturation reported for edge colours is much less than the fully-saturated lines that are physically present in the stimuli, suggesting that subjects could not resolve these fine lines, and that their colour judgement has been integrated over some area.

For spread colours, on the other hand, each subject shows a highly-significant relationship between saturation and duty cycle. With the narrowest white bars, the saturation of spread colours is actually greater than for edge colours. As the width of the white bars increases, saturation of spread colours declines.

The results of Experiment 3 serve as a baseline against which we can compare the results of Experiment 5, in which the colours are not physically present, but are McCollough-effect colours. They are of interest

Table 1
Summary of parameters of black:white widths for test stimuli used in Experiments 3–5

| Black:white | Cycle width (deg) | cpd | White bar width (deg) |
|---|---|---|---|
| 1:0.25 | 0.16 | 6.3 | 0.035 |
| 1:0.50 | 0.19 | 5.3 | 0.065* |
| 1:1.00 | 0.25 | 4.0 | 0.125* |
| 1:1.50 | 0.31 | 3.2 | 0.185 |
| 1:2.00 | 0.38 | 2.7 | 0.255* |
| 1:2.50 | 0.44 | 2.3 | 0.315 |
| 1:3.00 | 0.50 | 2.0 | 0.375 |
| 1:4.00 | 0.63 | 1.6 | 0.505* |
| 1:8.00 | 1.13 | 0.9 | 1.005 |

* All subjects responded to this value.

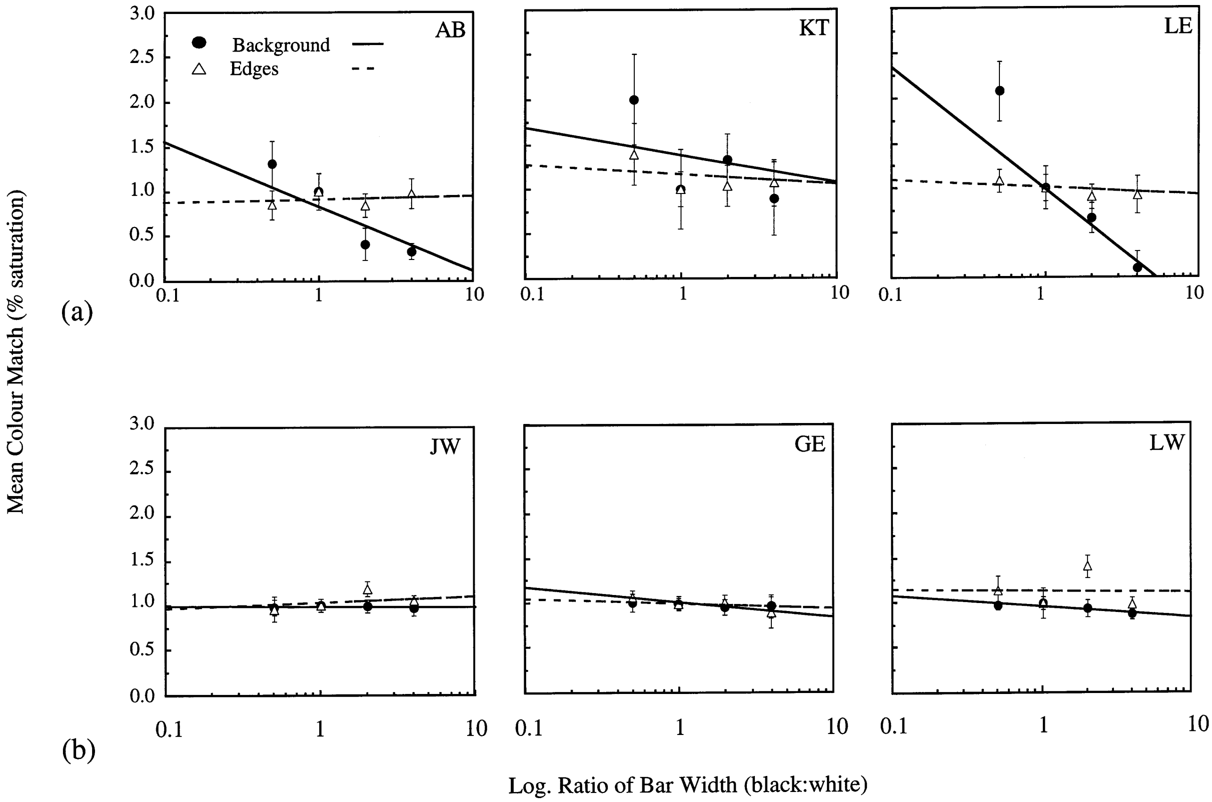


Fig. 5. Mean matched saturation of edge colours (triangles) and spread colours (circles) plotted against the logarithm of black:white bar widths. Vertical bars show $\pm 1$ S.E.M. The lines have been fitted by linear regression. (a) For these three observers, the stimuli had fine, real, coloured fringes added to the margins of the black bars (Experiment 3). (b) For these three observers, the light bars were filled with desaturated, uniform, real colours (Experiment 4).

in themselves because they establish that real colour fringes do spread to produce measurable illusory colour in white parts of stimuli, thereby quantifying what is evident in the demonstration of Fig. 1. The results of Experiment 3 may also be compared with the results of the next experiment, Experiment 4, in which subjects were instructed to observe the saturation of edge and spread colours, in uniformly coloured gratings displayed at various duty cycles.

## 5. Experiment 4

The method of this experiment was similar to that of Experiment 3, except that three new observers were used. Also, instead of coloured lines, uniform, desaturated colours, of the sort used in Experiment 2, filled all of the white bars. The results are shown in Fig. 5(b). These results are simple to interpret: colour at edges and colour away from edges behave in an identical fashion. In other words, subjects' matches were very similar to the physically-presented, uniform colour. This result may be compared with the results of Experiment 5 in which edge and spread McCollough-effect colours are quantified.

## 6. Experiment 5

### 6.1. Method

There were four observers, of whom two were aware of the experimental rationale (J.B. & J.W.). The apparatus was the same as for Experiment 1. The procedure was similar to that of Experiment 1, in that there were pre-test, McCollough-effect induction, and post-test phases. The major difference is that each subject was induced with the two possible combinations of orientation and colour (VR/HG and VG/HR) in separate sessions. Induction stimuli were identical to those of Experiment 1 (i.e. colour-fringed square-wave gratings with a duty cycle of 1.00). Test stimuli were similar to those of Experiment 3, except that all gratings were achromatic, and duty cycle ranged from 0.25 to 8.0. The number of intermediate values ranged from three to seven according to the subject's tenacity.

### 6.2. Results

Subjects' data were analysed in the same way as described for Experiment 3. Means, standard errors, and regression lines are presented in Fig. 6. The results

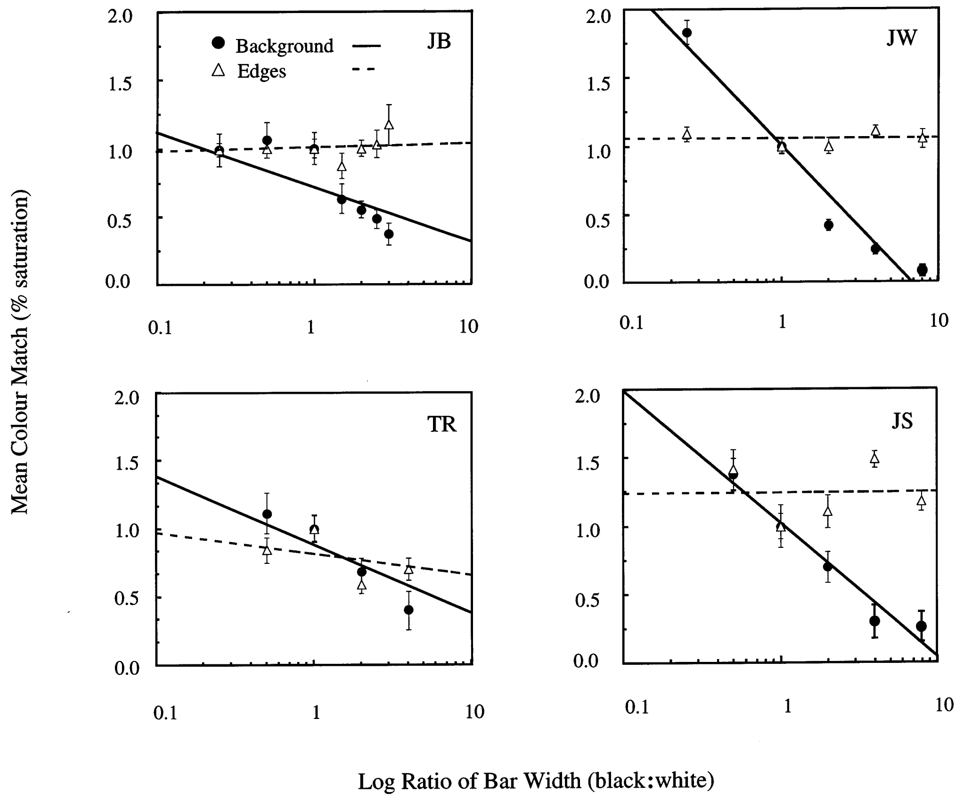


Fig. 6. Mean matched saturation of edge colours (triangles) and spread colours (circles) plotted against the logarithm of white:black bar widths for four observers. Vertical bars show ±1 S.E.M. The lines have been fitted by linear regression. All stimuli were achromatic, the edge and spread colour reports arising from McCollough-effect induction.

are remarkably similar to those of Experiment 3 in which real coloured fringes were presented (see Fig. 5a). A direct statistical comparison was not performed since only a few duty cycle values of Experiment 3 overlapped with those of Experiment 5. Nevertheless, what is clear from Figs. 5 and 6 is that edge colours remain invariant with respect to duty cycle under all conditions tested, whereas spread colours decline with duty cycle under the conditions of Experiments 3 and 5.

### *6.3. Discussion*

The results of Experiment 5 clarify Stromeyer's (1978) study in which he found a relationship between the McCollough effect and duty cycle. What we have called edge colours are essentially the same irrespective of duty cycle. What we have called spread colours, however, decline with increasing duty cycle, as these colours need to spread over more and more white space. In concert with the results of Experiment 3, we see that this sort of colour spreading is essentially the same whether the edge colours are real coloured lines (Experiment 3) or illusory colours from McCollough-effect induction (Experiment 5). Comparing these results with those of Experiment 4 suggests that spread colour is indeed elicited at edges, since the colours seen in uniformly-coloured gratings display no relationship with duty cycle. Taken together, these results support the hypothesis, introduced in Broerse and O'Shea (1995), that MEs are generated at edges and spread away from them to produce the characteristic appearance of achromatic test gratings.

## 7. General discussion

In Experiments 1 and 2 it was shown that fine colour fringes applied to the edges of otherwise achromatic square-wave gratings (Fig. 1) are sufficient to induce MEs comparable in strength to those induced with (desaturated) uniformly-coloured gratings. The MEs induced with colour-fringed gratings in Experiment 1 may be compared with the CAEs arising as a consequence of adaptation to colour fringes (chromatic aberration) reported in studies requiring subjects to wear prismatic lenses (e.g. Kohler, 1951, 1962; see Section 1). In Kohler's study, chromatic aberration produced fringes of complementary colour on opposite-polarity luminance edges, giving rise to polarity-specific complementary CAEs. In the present study, chromatic aberration was simulated by painting fringes of complementary colour on edges of orthogonal orientations (independent of polarity), giving rise to orientation-contingent CAEs.

The results of Experiments 3–5 confirm the conjecture, originally raised in Broerse and O'Shea (1995), that MEs may consist of two spatial components. One component is the induction of illusory colour at the local luminance discontinuities in the test grating (edge colour). The other is the spreading of these induced colours away from the edges into uncontoured regions of the surface (spread colour). The essence of this proposal is illustrated by inspection of Fig. 1, which shows how colour localized at the edges of otherwise achromatic gratings results in the perception of surface colour which is slightly more concentrated at edges than in the uncontoured regions. In Experiment 3, the locus and distribution of colour evident in Fig. 1 was quantified at various duty cycles. The saturation of edge colours was found to stay essentially the same at all duty cycles, while spread colours were found to decline in saturation as duty cycle increased. Similar properties were obtained for the edge- and spread-colour components of MEs (in achromatic test gratings) after induction with colour-fringed gratings (Experiment 5).

As foreshadowed previously, the spreading of colour away from luminance edges in ME test patterns may arise through the implementation of a filling-in process, such as the one proposed to account for neon colour spreading (Grossberg & Mingolla, 1985a; Grossberg, 1987a). Tacit in this proposal is the potential to link MEs and the problem/phenomenon of object *colour constancy* (Land, 1977)—the issue of how the visual system discounts properties of light stimuli (illumination intensity, spectral composition) not intrinsic to the object itself. One solution involves extracting invariant information at object edges (wavelength, luminance), and subsequently filling-in properties of the entire object surface (hue, saturation, brightness). Solutions of this nature have been implemented in the neural network models described by Grossberg and his co-workers (Grossberg & Mingolla, 1985a; Grossberg & Todorovic, 1988). According to this perspective, colour spreading in MEs may be understood to reveal a routine process whereby the visual system achieves colour constancy.

While the spreading of colour away from edge colours in the ME is consistent with extant accounts of colour filling-in (Grossberg, 1987b), it remains to be understood how edge colours are themselves produced. Our focus in this regard turns to the nature and purpose of mechanisms underlying the phantom fringes of colour described in studies involving adaptation to prism-induced chromatic aberration (Gibson, 1933; Hay, Pick & Rosser, 1963; Held, 1980; Kohler, 1951, 1962; see also McCollough, 1965). These phantom colour fringes are thought to reveal the process whereby the visual brain learns to apply appropriate correction factors to cancel the colour fringes associated with *natural* chromatic aberrations of the eye. As discussed in the early work of Kohler (1962), the corrective process must take into account not only the ocular distortion itself (i.e. colour fringes), but also the immediate context in which the distortion occurs (i.e. the orientation and polarity of luminance edges). Luminance discontinuities in a pattern or object may thus afford local contextual cues enabling the identification of a colour fringe *as a colour fringe* and not some property of objects in the environment. Upon learning the relevant correlations occurring between colour fringes and luminance edges (e.g. vertical edge paired with a red fringe), correction factors may then be applied to cancel the appropriate colour fringes (i.e. subtract *X* amount of red from vertical edges).

The suggestions provided by our consideration of chromatic aberration and edge-colour inducers have led us to modify the Grossberg (1987b) model of colour processing and McCollough effects (Vladusich & Broerse, 1997). This modified framework explores the functional significance of opponent-processing mechanisms; namely, the receptive field properties (e.g. Type 1 cells & double-opponent cells) of single cells described in contemporary neurophysiological investigations of colour (Livingstone & Hubel, 1984; Michael, 1978a,b; Zeki, 1983a,b; see also Daw, 1984).

According to our putative framework, colour processing occurs within two (2) parallel streams (Fig. 7). One stream, which we have called the Chromatic Processing Stream (CPS), employs several processing stages to achieve colour constancy (see Fig. 7a). Type 2 cells encode stimulus wavelength/purity, and provide inputs to double-opponent cells. The role of double-opponent processing is to enhance information about colour contrasts (i.e. discount the illuminant; see Daw, 1984). In the simplest scenario, the outputs of double-opponent cells are then used to fill-in the surface properties of hue and saturation within spatial regions defined by the activity of a boundary-detection mechanism, such as the outputs of opponent-colour simple cells (cf. interactions between Grossberg's Boundary & Feature Contour Systems). The filling-in process is suggested to occur within cortical area V4, and may give rise to the properties of colour-coding cells reported by Zeki (1983a, 1983b).

In relation to chromatic aberration, and the edge-colour induction of MEs, it is significant to note that colour filling-in within the CPS may be triggered by *either* the colour contrasts defining object surfaces *or* the colour fringes associated with chromatic aberration (cf. Fig. 1, where colour fringes induce spreading into the entire pattern surface). In order to counteract the potential for chromatic aberration to distort colour perception, some form of compensatory mechanism

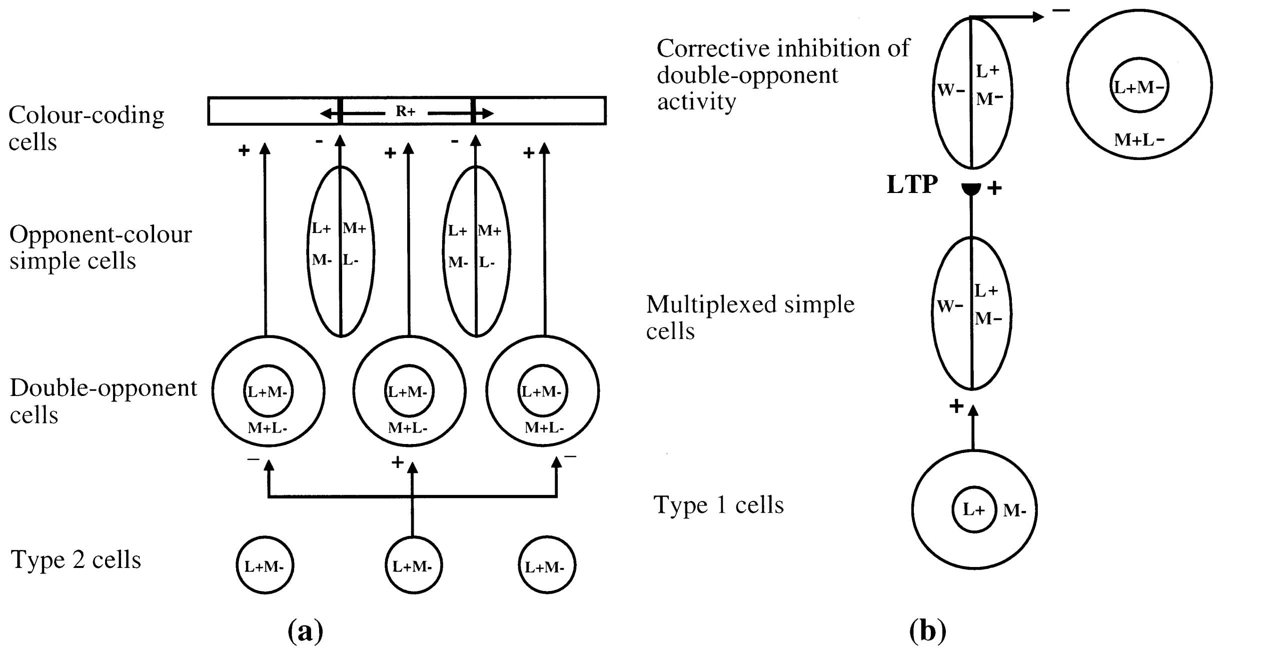


Fig. 7. Putative streams in the processing of colour. (a) Chromatic Processing Stream (CPS). So-called Type 2 cells and double-opponent cells discount the illuminant, and provide parallel inputs to a boundary-detection process (opponent-colour simple cells) and a filling-in process (colour-coding cells). Filling-in is controlled by the boundary-detection mechanism which inhibits the spreading of colour past object edges. Putative colour-coding cells may be compared with the properties of cells residing in cortical area V4 (Zeki, 1983a,b). Colour-coding cells can be activated by either coloured-object edges or the colour fringes associated with chromatic aberration. (b) Multiplexed Processing Stream (MPS). The MPS selectively encodes information about chromatic aberration (Type 1 cells) and learns the relationships between colour fringes and luminance-edge parameters. Learning (adaptation) occurs within simple-type cells which combine sensitivity to luminance-contrast and wavelength information (multiplexed simple cells). Learning is instantiated as a process of long-term potentiation (LTP: increase of synaptic efficacy). Once significant adaptation has occurred in these pathways, outputs from multiplexed simple cells operate as a gate which controls the flow of colour information within the CPS. Simple cells learn that a particular coloured fringe (e.g. a red fringe) is consistently paired with a luminance edge of given orientation and polarity, and apply inhibition to spectrally-opponent cells sensitive to the same wavelengths (e.g. red-sensitive double-opponent cells) at visual locations corresponding to the appropriate luminance edges. Inhibition closes the gate from double-opponent cells to colour-coding cells, thus preventing the filling-in of optically-induced coloured fringes. Edge-contingent CAEs are suggested to probe the dynamics of the corrective mechanism (see text).

needs to be in place. Within the current framework, this mechanism takes the form of a neural system which works in parallel with the CPS (see Fig. 7b). This system, which we term the Multiplexed Processing Stream (MPS), is designed to encode *only* colour-fringe information and to inhibit CPS double-opponent cells, thereby precluding the filling-in of false colour due to chromatic aberration.

The first MPS stage contains Type 1 cells which perform a filtering operation to selectively process information about chromatic aberration. The receptive fields of Type 1 cells exhibit a small excitatory region (e.g. L + centre) enveloped in a much broader inhibitory-surround region sensitive to the opponent wavelength (e.g. M − surround). While it is sometimes assumed that Type 1 cells function solely as colour-processing units (e.g. Livingstone & Hubel, 1984), these cells actually provide information about both luminance-contrast and wavelength (Ingling & Martinez, 1983). The property of combining or *multiplexing* information about luminance-contrast and wavelength makes Type 1 cells ideal for detecting the colour fringes which arise at luminance edges due to the eye's optical limitations. Conversely, Type 1 cells are poorly (if at all) activated by the colour contrasts which arise in natural scenes, such as those formed by a red object on a green background. In other words, Type 1 cells of the MPS are maximally activated by optically-generated colour information but are relatively insensitive to colour information indicative of what's out there in the environment. Perhaps the best way to understand this concept is to compare the receptive field properties of Type 1 cells with those of CPS double-opponent colour cells. Double-opponent cells are maximally excited by precisely the stimulus arrangements to which Type 1 cells are least sensitive (e.g. red-on-green). The CPS and MPS are therefore sensitive to *complementary* sets of stimulus features (see Grossberg, 1994, for a discussion of complementarity in visual processing). A psychophysical corollary of Type 1 cell filtering operations is the finding that MEs are extremely difficult to induce with isoluminant colour contrasts (see Stromeyer, 1978).

The filtered outputs of Type 1 cells provide inputs to putative simple cells within the MPS. These simple cells manifest conjoint (multiplexed) sensitivity to a number of stimulus variables, such as retinotopic position, wavelength, ocularity, orientation, and the polarity of luminance edges. Simple cells are able to learn (LTP of simple cells; see Fig. 7b) the natural correlations which arise as a consequence of the interactions between chromatic aberration and other ecological-optical factors. For instance, due to astigmatism (i.e. irregular curvature) of the eye's lens, luminance edges of a vertical orientation are paired consistently with (say) green fringes and horizontal edges are paired consistently with red fringes (Hohmann & von der Malsburg, 1978). Due to the relationship between colour fringes and edge orientation, MPS simple cells must apply separate inhibitory correction factors to CPS double-opponent cells (coding for *opponent*-colours but the *same* retinotopic locations) when vertical and horizontal luminance edges are being viewed (see Fig. 7b).

The discussion provided above leads to an understanding of why ME-induction procedures involving orthogonal orientations paired with complementary colours can induce strong aftereffects (i.e. why little or no cancellation occurs; see McCollough, 1965). Moreover, the notion that correction factors are applied to spatially-localized regions of the visual field (i.e. regions the size of MPS simple cells' receptive fields) provides a natural explanation of data showing that CAEs are contingent on the *local* properties of edge orientation, polarity and position (Bedford & Reinke, 1993; Broerse & Grimbeek, 1994; Broerse & O'Shea, 1995; McCollough, 1965; Stromeyer, 1978; Stromeyer & Dawson, 1978). This view runs contrary to the proposal that ME induction is sensitive to the global (pattern) properties of stimuli (e.g. Dodwell & Humphrey, 1990), and provides a rationale against such arguments.

Particularly relevant to the present discussion is the set of results showing that MEs are contingent on the spectral composition of light reaching observers' eyes, rather than the (perceived) colour of induction gratings (Thompson & Latchford, 1986; see also Webster, Day & Willenberg, 1988). These results indicate that the adaptation process which gives rise to the ME is not subject to the same neural procedures which operate to accomplish colour constancy, and are consistent with predictions of the CPS–MPS framework. Specifically, the neural system whose adaptation mechanisms give rise to the ME (i.e. MPS) actually operates in parallel with the system whose mechanisms operate to achieve colour constancy (i.e. CPS). Consequently, ME-induction occurs in response to the spectral composition of reflected light independent of surface colour.

With respect to the current set of results, we propose that edge- and spread-colours arise as a consequence of *normal though inappropriate* CPS–MPS dynamics. For instance, MPS simple cells would adapt to red colour fringes (Experiment 1), or the red edges of uniformly-coloured gratings manifesting sufficient luminance discontinuities (Experiment 2). On the basis of this adaptation, MPS simple cells apply inhibition to red-centre double-opponent cells, and preclude the filling-in of red colour from localized chromatic edges. A perceptual corollary of such corrective dynamics is that, given sufficient time, colour fringes seen at luminance edges (e.g. Fig. 1) would eventually disappear (cf. Kohler's study where adaptation led to the disappearance of fringes).

We suggest that, upon removal of the inducing stimulus and presentation of the test stimulus, the MPS continues to apply inhibition to double-opponent cells. This is because Type 1 cells can be activated by luminance edges alone (Ingling & Martinez, 1983), and can therefore continue to activate MPS simple cells which, in turn, continue to apply inhibition to double-opponent cells. If we now assume that double-opponent cells are at least partially activated by the black/white *edges* of a test grating, then the continued application of inhibition by the MPS will generate an imbalance in the activity of double-opponent cells tuned to the inducing colour (red) relative to the activity of cells tuned to its non-induced complement (green), with green-sensitive cells now exhibiting higher activity *at grating edges*. This asymmetry in the activity of double-opponent cells is then propagated through to *both* the boundary-detection and filling-in stages of the CPS (Fig. 7a). The boundary-detection mechanism attempts to trap or restrict colour at edges within filling-in networks, giving rise to edge colours, but cannot do so completely since boundary signals are relatively weak (i.e. double-opponent cells, and hence opponent-colour simple cells, are only partially activated by luminance edges). Consequently, colour leaks away from grating edges and appears to suffuse the entire pattern surface, giving rise to spread colours. The saturation of spread colour declines as duty cycle increases since filling-in occurs over progressively greater spatial regions (i.e. spatial averaging of colour). In contrast, edge-colour saturation stays essentially constant at all duty cycles because the same amount of colour is trapped at luminance edges by the boundary-detection mechanism.

The considerations entertained above reveal the detailed relationship between chromatic aberration, colour at edges and colour spreading in the ME, and the phenomenon of colour constancy. These suggestions are embodied within a putative framework based on receptive-field properties identified in neurophysiological investigations of colour. Our framework signals a paradigm shift away from traditional analytical methods in the investigation of MEs (e.g. fatigue of edge detectors & associative-learning accounts), and instead turns our attention towards questions regarding the functional significance of MEs within the broader theoretical context of form-colour perception (Broerse & O'Shea, 1995; Broerse, Shaw, Dodwell & Muir, 1994; Dodwell & Humphrey, 1990).

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