



Attentional capture by colour and motion in cerebral achromatopsia

Geoff G. Cole^{a,*}, Charles Heywood^a, Robert Kentridge^a, Ian Fairholm^a, Alan Cowey^b

^a Department of Psychology, University of Durham, South Road, Durham DH1 3LE, UK

^b Department of Psychology, University of Oxford, Oxford, UK

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Abstract

Cerebral achromatopsia is a rare condition in which damage to the ventromedial occipital area of the cortex results in the loss of colour experience. Nevertheless, cortically colour-blind patients can still use wavelength variation to perceive form and motion. In a series of six experiments we examined whether colour could also direct exogenous attention in an achromatopsic observer. We employed the colour singleton paradigm, the phi motion effect, and the correspondence process to assess attentional modulation. Although colour singletons failed to capture attention, a motion signal, based solely on chromatic information, was able to direct attention in the patient. We then show that the effect is abolished when the chromatic contours of stimuli are masked with simultaneous luminance contrast. We argue that the motion effect is dependent on chromatic contrast mediated via intact colour-opponent mechanisms. The results are taken as further evidence for the processing of wavelength variation in achromatopsia despite the absence of colour experience.

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1. General introduction

Colour vision is ubiquitous in our perceptual and mnemonic processing of the visual environment. It can be used to segment the visual scene, disambiguate a moving object from a background of moving shadows and assist in the rapid detection of visually presented objects. Colour aids object identification, and enhances memory storage and retrieval for subsequent recognition (Gegenfurtner & Rieger, 2000). Colour also facilitates detection of objects more effectively than either shape or brightness differences (Williams, 1966).

Cortical colour blindness, or cerebral achromatopsia, is a rare condition in which damage to the ventromedial occipital area of the cortex in the vicinity of the lingual and posterior fusiform gyri results in the loss of colour vision. Patients with achromatopsia usually have no difficulty seeing movement, depth, or fine detail but report that their visual world has become either pale, washed out, drab, brownish, or appears in shades of grey (Cowey & Heywood, 1997; Heywood & Cowey, 1999). Formal diagnosis of the condition is typically defined by poor performance on the Farnsworth-Munsell 100-hue test in which a number of isoluminant coloured discs have to be ordered on the basis of

their chromaticity. By contrast, such a patient can arrange a series of achromatic grey discs on the basis of their lightness (Heywood, Wilson, & Cowey, 1987). Achromatopsia is commonly associated with other visual deficits such as agnosia, prosopagnosia, and upper field scotomata. This probably reflects the proximity of cortical areas involved in the processing of these attributes. Increased brain activity in normal observers, whilst viewing chromatic displays during neuroimaging, has further implicated the ventromedial occipital region as being the cortical “colour centre” (Zeki, 1990).

The loss of colour vision however, does not invariably result in a concomitant loss of all of the products of processing wavelength variation. For example, the absence of the phenomenal experience of colour in achromatopsic observers does not necessarily preclude the processing of wavelength differences to extract form (Barbur, Harlow, & Plant, 1994; Heywood, Cowey, & Newcombe, 1991), perceive motion in moving gratings (Cavanagh et al., 1998; Heywood, Kentridge, & Cowey, 1998), or to perceive a colour-specific motion aftereffect (Mollon, Newcombe, Polden, & Ratcliffe, 1980). For one well-studied achromatopsic observer, patient M.S., when two isolated hues cannot be discriminated, the chromatic border created when they abut is nevertheless visible. Additionally, when presented with two rows of abutting isoluminant coloured patches he can discriminate a chromatically ordered array from one in which the constituent patches are in random

* Corresponding author.

E-mail address: g.g.cole@durham.ac.uk (G.G. Cole).

chromatic order (Heywood et al., 1991). Presumably, the jumbled and ordered arrays are distinguished on the basis of the relative salience of adjacent boundaries, i.e. adjacent isoluminant hues in an ordered array have less chromatic contrast which renders them less conspicuous. Moreover, M.S. shows unimpaired threshold sensitivity to chromatic contrast (Heywood, Nicholas, & Cowey, 1996). Indeed, we have recently shown that M.S. is relatively proficient in the discrimination of the magnitude and direction of chromatic contrast, enabling him to discriminate between borders composed of different colours presented against identical isoluminant backgrounds. In an oddity task where two identical coloured discs are presented against an isoluminant background, along with a third of a different colour, M.S. can determine the odd-one-out. When the discs are presented against a black background, the prominent luminance borders between discs and the background mask any differences in border contrast caused by wavelength alone and the odd-one-out is no longer identifiable.

M.S. therefore can make perceptual judgements when chromatic borders defining the stimuli are present. However, these judgements are effortful and slow. He can take many seconds to identify an odd-one-out where normal observers take less than half a second. In striking contrast, there are circumstances where he can respond rapidly to the sign of chromatic contrast. If an isoluminant grating is presented such that the phase of the grating is shifted by 90° from moment to moment, pairs of successive changes result in the replacement of borders with one sign (e.g. red/green) with those of opposite sign (e.g. green/red). The direction of motion should thus be ambiguous to a colour-blind observer. M.S. however has no difficulty in reporting the 'correct' direction of apparent movement, even though he is unable to tell apart the constituent colours of the grating (Heywood, Cowey, & Newcombe, 1994).

Given previous reports that an achromatopsic patient can use wavelength to discriminate form and direction of motion the aim of the present work was to examine whether wavelength could also modulate exogenous attention. To examine this issue we employed the 'colour singleton' paradigm (Jonides & Yantis, 1988; Turatto & Galfano, 2001), the 'phi motion' effect (Kolers, 1972), and the 'correspondence process' (Green, 1986, 1989; Green & Odmon, 1986; Ullman, 1979) to index attentional modulation. Data from normal observers in each of these paradigms have already provided evidence that colour guides attention.

1.1. A single case study

Patient M.S. is a 55-year-old male who sustained brain damage as a result of contracting idiopathic herpes encephalitis when aged 22 years. The condition has since left him with agnosia, mild amnesia, and cortical colour blindness and has been reported in detail elsewhere (Heywood et al., 1991). M.S. has normal visual acuity, is able to read and write, and has a verbal IQ score of 101. Magnetic res-

onance imaging (Heywood et al., 1991) revealed that M.S. has damage to the second, third, fourth, and fifth temporal gyri in the right hemisphere as well as damage to the right temporal pole. Damage is less extensive in the left temporal lobe, being largely confined to the temporal pole, the fourth temporal gyrus, and the hippocampal gyrus. The striate cortex in the right hemisphere is destroyed resulting in left hemianopia but V1 remains intact in the left hemisphere. Crucial to his colour deficit, M.S. has bilateral ventral-occipital damage to the lingual and fusiform gyri, consistent with the location of damage in other cases of achromatopsia (Meadows, 1974). Neuropsychological assessment has shown that M.S. scores at chance (1245) on the Farnsworth-Munsell 100-Hue test and that he cannot read the numbers presented on the Ishihara plates when viewed at normal reading distance.

2. Experiment 1

In our first experiment, we used the 'colour singleton' paradigm (Jonides & Yantis, 1988) to assess the issue of attentional modulation by colour in achromatopsia. In this task participants are required to search a display of letters for a target, as in any standard search experiment. One of the letters happens to be associated with a different colour from the others, a so-called 'colour singleton'. For example, one green letter might appear amongst an array of red letters. Importantly, the odd coloured letter is no more likely to be the target letter than it is any of the distractors. In other words, letter colour is task irrelevant. This ensures that there is no advantage in the participant directing endogenous attention to the odd colour. Hence, stimulus-driven (i.e. automatic or exogenous) attentional capture by colour is said to have occurred if a processing advantage is observed for targets presented at a colour singleton location. Although initial evidence suggested that colour does not facilitate reaction time (RT, e.g. Jonides & Yantis, 1988) later research has shown that colour singletons can automatically capture attention (Horstmann, 2002; Turatto & Galfano, 2001). In Experiment 1 we therefore used the colour singleton procedure to assess whether colour would automatically capture attention in M.S. On each trial four isoluminant squares were presented, one of which was a colour singleton. At 150 ms stimulus onset asynchrony (SOA) single letters then appeared inside the squares. M.S.'s task was to respond as quickly as possible to the onset of one of two target letters. If colour can direct attention in M.S., his RT to detect a target should be reduced when the target coincides with the singleton location.

2.1. Method

2.1.1. Stimuli and apparatus

All stimuli were presented in the right visual field as M.S. is a left-heminope. The four squares were all located at an eccentricity of 2.9° from the centre of each square to

the fixation point. The squares measured 0.8° along each side and were presented at 30° , 60° , 120° , and 150° from the vertical meridian. Either a single red square was presented amongst three green squares or a single green square was presented amongst 3 red squares, always against a yellow background. The squares were isoluminant with respect to the background with a luminance of 44 cd/m^2 . For set size 4, a single letter appeared in each of the four squares whereas for set size 2 letters appeared in the squares located either at the 30° and 120° positions or at 60° and 150° positions. The experiment was carried out in a dimly lit room and was driven by a Pentium PC running an Eizo F55 colour monitor at a refresh-rate of 60 Hz. M.S. was seated approximately 80 cms from the display and responded by pressing one of two keys on a standard keyboard.

2.1.2. Design and procedure

A 2×2 factorial design was employed with location of the target (at a singleton or non-singleton location) and set size (2 or 4) as factors. The trial sequence is shown in Fig. 1. Each trial began with the presentation of a fixation point for 1000 ms before the appearance of the four squares. After a further 150 ms the letters then appeared inside the squares. This display remained until a response was made. M.S. was instructed to respond as quickly as possible to the onset of one of two possible target letters. The beginning of a trial was initiated by a response on the previous trial. He was asked to press a left hand key if an 'L' occurred or a right hand key if an 'H' appeared. For set size 4 the target appeared at the singleton location once in every four trials whereas for set size 2 this probability was once in every two trials. Ls and Hs occurred with equally frequency, as did red and green singletons. Thirty-six practice trials were given following a demonstration trial. Six blocks of 96 trials were then presented in the experiment proper. Hence, a total of 576 experimental trials were presented.

2.2. Results and discussion

In all experiments reported here, outliers were omitted from analysis. The criterion for an outlier was an RT lying 2 standard deviations outside the mean for a block. This resulted in the omission of no more than 8% of data from any one experiment. For the set size 2 condition, mean RT for targets located at the colour singleton position was 861 ms and for targets located at the non-singleton position RT was 884 ms. For the set size 4 condition, the respective RTs were 1183 and 1178 ms. The data were entered into 2×2 analysis of variance (ANOVA) with the correspondence of the target and singleton (at the same location or a different location) and set size (2 or 4) as factors. As expected, a main effect of set size was observed, $F(1, 532) = 68.7$, $P < 0.001$. Neither the main effect of target/singleton correspondence nor its interaction with set size was significant (both $F < 1$).

The data from the first experiment therefore show that RT to detect a target letter was not facilitated when the target was presented inside the colour singleton. This suggests that residual colour processing did not automatically capture M.S.'s attention. Given that M.S. has previously demonstrated residual wavelength processing the issue remains as to why this does not manifest itself in terms of attentional capture, at least using the singleton paradigm. An important distinction between previous demonstrations of chromatic processing and the present attempt is that previously M.S. showed residual effects when no time limit was imposed on the task. That is, RT was not the dependent measure. For instance, although he can select an isoluminant colour singleton he does require 3 or 4 s to detect the odd disc. This contrasts with normal observers where task relevant colour singletons 'pop-out' (Treisman & Gelade, 1980). The present experiment however required M.S. to select a target letter as quickly as possible.

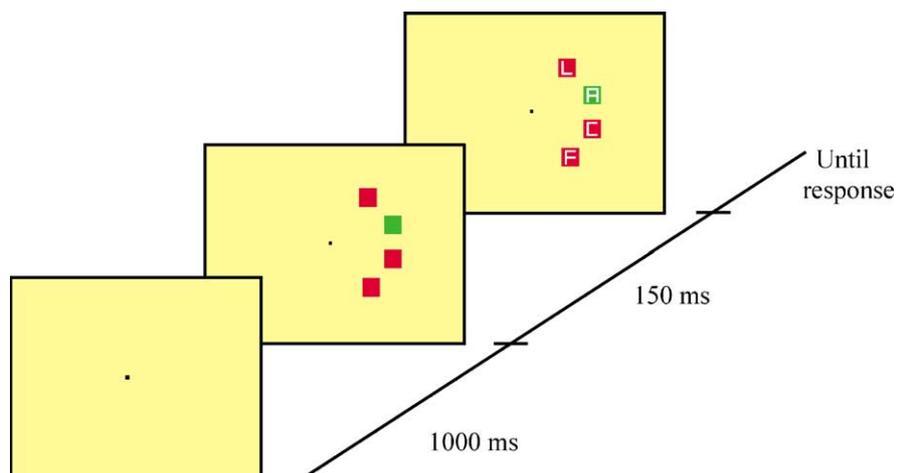


Fig. 1. Trial procedure in the colour singleton paradigm. The participants task is to detect a target letter amongst distractors. One of the letters is associated with uniqueness in colour. Here, the letter A is presented inside a green singleton. The figure shows the display used in Experiment 1 for set size 4. Because M.S. is a left-hemiope stimuli were presented in his right field in all experiments.

Research on the colour singleton task has also not yet been able to establish the variables that give rise to consistent automatic capture by colour oddity. Indeed, evidence for automatic capture has been somewhat mixed. Gibson and Jiang (1998) suggest that colour may, in principle, be able to summon stimulus-driven attention, but participants could habituate to the repeated appearance of colour singletons that they know are task irrelevant. They reasoned that capture might occur for the initial (unexpected) presentation of a singleton but fails to do so after a repeated number of presentations. Furthermore, Kentridge, Cole, and Heywood (in press) have shown that colour singletons defined by chromatic contrast captured attention, but those defined by spectral composition did not. Thus, the subtleties of how a singleton is generated even within the same attribute (i.e. colour) can influence capture. Finally, to argue, on the basis of Experiment 1, that residual colour processing does not guide attention in M.S. is to conclude from the null hypothesis. Therefore, the aim of Experiment 2 was to investigate further whether colour could capture exogenous attention in an achromatopsic patient.

3. Experiment 2

Experiment 2 assessed whether M.S.'s attention could be directed by a motion signal. We used a variation of a classic phi motion display whereby the inducing stimuli were based solely on colour. A coloured disc appeared briefly at fixation before the onset of a same coloured disc in one of the two quadrants to the right of the display. For normal observers this induces the perception of apparent motion of a coloured disc from fixation to either the upper or lower right. A target letter then appeared either inside the right hand disc or at the corresponding location in the other quadrant. RT to detect the target letter was measured. If the apparent motion directs M.S.'s attention then RT will be reduced when the target appears at the location corresponding to the apparent motion.

3.1. Method

3.1.1. Stimuli and apparatus

The two discs used to induce apparent motion were circles measuring 1° in diameter. One appeared at fixation whilst the second appeared successively at an eccentricity of 7.7° on the right of the display at either 45° or 135° from the vertical meridian, i.e. either the upper or lower right quadrant. In each trial both discs would either be red or green presented against an isoluminant (23.5 cd/m^2) yellow background. The CIE co-ordinates of the red, green and yellow were (0.543, 0.374), (0.309, 0.566) and (0.450, 0.450), respectively. These colours were chosen so that the cone-contrasts between the yellow background and the red and the green were of equal root mean square magnitude but opposite direction in $\Delta L/L$, $\Delta M/M$ cone-contrast colour-space. A letter 'L' or 'R' of 0.8° height would appear either inside the peripheral disc

or in the other quadrant, that is, either presented in spatial correspondence with the apparent motion or presented at a non-motion location. The experiment was carried out in a dimly lit room and was driven by a Cambridge Research Systems VSG 2/3 driving an Eizo F784T colour monitor at a 100 Hz refresh-rate. M.S. was seated approximately 57 cm from the display and responded by pressing one of two buttons on a Cambridge Research Systems CB2 response box.

3.1.2. Design and procedure

A 2×4 factorial design was employed with location of the target with respect to the phi motion (motion location or non-motion location) and SOA (75, 150, 225, and 300 ms) as factors. We introduced a varying temporal interval between the onset of the second disc and the appearance of the target in order to examine whether any effect of phi motion varied over time. Each trial began with a set of four black dots moving in from the corners of the screen to the fixation point followed by a visual countdown positioned at fixation descending from 4 to 1. The aim of these procedures was simply to ensure that M.S. began each trial by making an appropriate fixation. A disc then appeared at fixation for 1500 ms before being replaced by a peripheral disc. At one of the four SOAs following appearance of the peripheral disc one of the two target letters then appeared. This display remained until a response was made. As with Experiment 1 M.S. was instructed to respond as quickly as possible to the onset of one of two possible target letters. He was instructed to press a left hand key if an 'L' occurred or a right hand key if an 'R' occurred. Ls appeared on 80% of trials and Rs on 20%. Thus, the presentation of Rs effectively acted as 'catch' trials. A target occurred at a motion location on 50% of trials and at a non-motion location on the remaining 50%. Direction of phi motion towards the upper and lower quadrant and the presentation of red and green inducing circles occurred with equal frequency. A block of 128 practice trials was given following a demonstration trial. Six blocks of 128 trials were then presented in the experiment. Hence, a total, of 768 trials were presented.

3.2. Results and discussion

Across all SOAs, mean RT for targets presented at a motion location was 589 ms compared with 771 ms for targets presented at a non-motion location. Indeed, M.S. reported the perceptual experience of the phi motion. Table 1 shows these means disseminated for each of the four SOAs. The figure clearly shows an RT advantage at all SOAs for targets appearing at a motion location. The data were entered into a 2×4 ANOVA with the position of the target with respect to the direction of motion (motion location or non-motion location) and SOA (75, 150, 225, and 300 ms) as factors. The main effect of target/motion correspondence proved to be significant, $F(1, 727) = 199$, $P < 0.001$, as did the main effect of SOA, $F(3, 727) = 6.4$, $P < 0.001$. The interaction was also significant, $F(3, 727) = 3.27$, $P < 0.05$.

Table 1

RT for targets presented at a spatial location corresponding to the apparent motion and for targets presented at a non-motion location in Experiments 2, 4, and 5

	Targets presented at a motion location	Targets presented at a non-motion location
Experiment 2		
75 ms SOA	646	771
150 ms SOA	622	787
225 ms SOA	550	783
300 ms SOA	539	742
Experiment 4		
75 ms SOA	624	767
150 ms SOA	541	724
225 ms SOA	514	742
300 ms SOA	480	695
Experiment 5		
75 ms SOA	849	880
150 ms SOA	825	865
225 ms SOA	789	808
300 ms SOA	728	783

RTs are given for each SOA.

The interaction and means show that the strength of the facilitatory effect at the motion location was weakest in the 75 SOA condition and strongest in the 225 SOA condition. Indeed, the RT advantage was almost double in the 225 ms condition. This concurs with an abundance of research investigating the effects of introducing a varying temporal delay between the ‘arrival’ of attention at a location and the onset of a target. For instance, in the precueing paradigm (Posner, 1980; see the present Experiment 4) the weakest facilitatory effect is usually observed at shorter SOAs before an optimal effect at approximately 200 ms SOA.

The crucial analysis however concerns the main effect of target/motion correspondence. When a target letter was presented in a location corresponding with apparent movement RT to detect the target was shorter than when the target appeared at a different position. This suggests that M.S.’s attention moved in the direction of the phi motion even though the movement was dependent solely on wavelength differences. These results therefore provide further evidence of residual colour processing in an achromatopsic patient. The aim of Experiment 3 was to assess whether the motion effect observed in the present experiment is sensitive to whether the inducing discs are matched for colour.

4. Experiment 3

Apparent motion is likely to be mediated by activity of cells in middle temporal cortex (area MT). Cells in MT respond to image borders defined by chromatic contrast without signalling the colours that make up those borders. Nevertheless, when motion is otherwise ambiguous they can utilise the sign of chromatic contrast to detect direction of motion (Dobkins & Albright, 1994). One means of deter-

mining whether the chromatic nature of the border, as opposed to the resulting motion signal, is modulating attention in M.S. is to examine whether changes in the composition of the stimuli used to induce apparent motion influences the strength of attentional capture. Thus, presenting two differently coloured discs may reduce the strength of the phi effect and the effect it has on RT to subsequently presented stimuli. Given that M.S. has been shown to discriminate borders with different wavelength composition (Heywood et al., 1991) Experiment 3 investigated whether the facilitated RT at the phi location observed in Experiment 2 is influenced by the correspondence of colour. In one condition we replicated the procedure from Experiment 2 whereby the two inducing discs shared the same colour (the ‘congruent-colour’ condition) and compared this with a second condition in which their colours differed (the ‘incongruent-colour’ condition).

4.1. Method

All aspects of the method were as described for Experiment 2 with the exception that on half the trials the two discs differed in colour (the central one being red and the peripheral one green, or vice versa). Given the extra condition the experiment also had twice as many (1536) trials and was run in 12 blocks of 128 trials.

4.2. Results and discussion

Overall mean RT for targets presented at a motion location (across both congruency conditions) was 526 ms compared with 689 ms for targets presented at a non-motion location. This broadly replicates the effect reported in Experiment 2. However, the crucial analysis concerns RTs in the congruent- and incongruent-colour conditions. Means for these two conditions were 528 and 526 ms, respectively. Data from these two congruency conditions were entered into a 2×4 ANOVA with SOA as a second factor. The main effect of SOA proved to be significant, $F(3, 746) = 29.1$, $P < 0.001$, but the main effect of colour congruency did not, $F(1, 746) < 1$.

The results have therefore shown that manipulating colour congruency of the inducing discs did not influence RT. This suggests that the phi motion was induced regardless of whether the discs were matched for colour. Although we will go on to show that wavelength processing nevertheless plays a role in M.S.’s perception of phi, an alternative explanation is that the appearance of the second disc might simply act as a peripheral cue that captured exogenous attention. Experiment 4 was designed to investigate this possibility.

5. Experiment 4

Although Experiments 2 and 3 have shown that residual wavelength processing can influence response selection in a cortically colour-blind patient, the experiments have not

shown that this effect was due to a motion signal. The differential RT observed need not necessarily have relied on motion but may have been due to the attentional capturing effect associated with abrupt onset. The fact that the incongruent-coloured discs condition of Experiment 3 did not influence the motion effect further supports this.

An abundance of evidence suggests that the onset of a new object is particularly effective in eliciting bottom-up capture of attention (Gellatly & Cole, 2000; Jonides, 1981; Jonides & Yantis, 1988; Theeuwes, 1994; Yantis & Johnson, 1990; Yantis & Jonides, 1984). Indeed, object onset may be the most effective stimulus property in attentional capture (Cole, Kentridge, & Heywood, *in press*; Cole, Kentridge, Gellatly, & Heywood, 2003; Yantis, 1993). Perhaps the most familiar demonstration of attentional capture by abrupt onset is observed in a variation of the precueing paradigm of Posner and colleagues (e.g. Posner & Cohen, 1984). RT to detect the presence of a target is reduced if the target is preceded by the onset of a cue that occurs in close spatial proximity to the target (Steinman, Steinman, & Lehmkuhle, 1995). When the cue and target are presented in different locations RTs are relatively longer. Although rarely remarked upon, these cues can be considered new object onsets and treated as such by the visual system (Cole, Gellatly, & Blurton, 2001). Furthermore, the facilitation associated with object onset relies neither on the luminance change that normally accompanies onset (Gellatly & Cole, 2000), nor on the chrominance change, nor on the object being the only visual transient in the display (Gellatly, Cole, & Blurton, 1999). Although such attributes may not be a necessary condition of attentional capture they may be sufficient. For instance, Snowden (2002) has demonstrated that a colour transient in the absence of luminance change can effectively capture attention. This is also apparent when one considers the ease with which a colour change is detected in the ‘change blindness’ paradigm (e.g. Simons, 2000) in the absence of the global transient, or ‘flicker’, employed to induce such blindness.

In order to tease apart the effects of phi motion from the effects of exogenous cueing, Experiment 4 replicated the procedure used in Experiment 2 with the sole exception that the initial central disc was not presented. Thus, a single isoluminant disc appeared in either the upper or lower right hand quadrant. As with Experiment 2 a target then appeared either inside the disc or in the other quadrant. Rather than phi motion being induced trial displays were now equivalent to ‘valid’ or ‘invalid’ cue trials (Posner, 1980). If the effect observed in Experiment 2 was due to the peripheral disc capturing attention, rather than being due to phi motion, then the same pattern of results should again be observed.

5.1. Method

Every aspect of the method was as described for Experiment 2 with the exception that the central disc was no longer presented.

5.2. Results and discussion

Collapsing across SOA, mean RT for targets presented at valid locations was 540 ms compared with 732 ms for targets presented at invalid locations. Table 1 shows mean RT for both validity conditions for each of the four SOAs. The data were entered into a 2×4 ANOVA with validity and SOA as factors. The main effect of validity was significant, $F(1, 734) = 239, P < 0.001$, as was the main effect of SOA, $F(3, 734) = 12.9, P < 0.001$. The interaction however narrowly failed to reach conventional statistical significance, $F(3, 734) = 2.37, P < 0.07$.

The crucial aspect of this analysis concerns the facilitatory effect of valid cues. RT was reduced when the target appeared in the same spatial location as the peripheral disc. Therefore, results from the current experiment suggest that the effect reported in Experiments 2 and 3 could have been due to the second disc acting as an attention capturing cue, or visual transient, rather than due to a motion signal directing attention. However, the cueing effect induced in Experiments 2–4 may have been too strong to reveal any RT differences due to wavelength (assessed in Experiment 3). Put another way, our procedure may not have been sensitive enough to index any wavelength-based RT variation. The aim of Experiment 5 was therefore to further test the motion and abrupt-onset hypotheses using the ‘correspondence’ or ‘matching’ process paradigm. The experiment was designed to provide a more sensitive assessment of whether the RT facilitation observed in Experiments 2–4 was based on a motion signal.

6. Experiment 5

The failure to find evidence for an effect of colour congruency in Experiment 3 is very likely to be a ceiling effect. In this design a strong motion cue will always be induced between the contours of the two discs regardless of their colour (it has been shown that cells in MT respond to colour borders regardless of the sign of those borders; (Saito, Tanaka, Isono, Yasuda, & Mikami, 1989). Any weak effect of match or mismatch of borders between inducers must compete with the fact that there is always a strong motion signal to one location. In the present experiment, we attempt to reduce, if not eliminate, this competition.

For an observer to perceive continuity of object identity during motion the visual system must match certain attributes belonging to the object at time t_1 with the same attributes at time t_2 . This is particularly the case when many objects are moving in the visual scene some of which may briefly occlude and be occluded by other objects. The process by which the visual system makes this attribution is often referred to as the ‘correspondence problem’ or the ‘matching process’ (Green, 1986, 1989; Green & Odmon, 1986; Ullman, 1979). One of the aims of the research concerned with this issue is to identify the properties of objects,

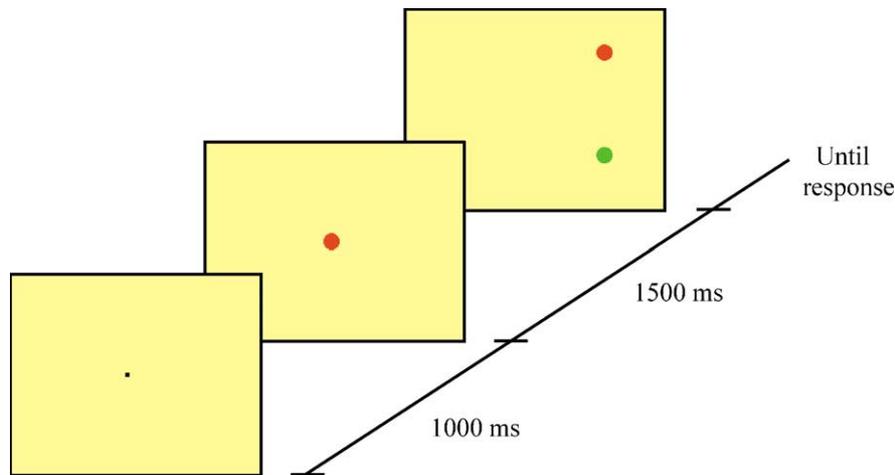


Fig. 2. Trial procedure for the colour correspondence paradigm. Normal observers perceive a bias in apparent motion from the central disc to the peripheral disc that shares the same colour. The procedure, a variant of Green (1989) and Ramachandran et al. (1983), was employed in Experiments 5 and 6.

or ‘correspondence tokens’, which are used to match across time and space.

A common experimental paradigm used to assess this issue presents observers with an object or objects that undergo ambiguous or ‘split motion’. For instance, in frame one a red square appears at fixation. In the second frame, the square is now extinguished and replaced by two squares, one either side of fixation. One of the squares is red the other green. If colour is used as an object property to solve the correspondence problem the motion should be biased from the initial red square to the matching red square presented in the second frame. This procedure can also be used to directly pit one attribute against another in order to assess which of the two dominates as a correspondence token. For example, Ramachandran, Ginsburg, and Anstis (1983) showed that perceived motion was biased towards an object that possessed the same spatial frequency compared with an object that shared the same orientation of object edge. In other words, spatial frequency appears to provide a greater input to apparent motion than edge orientation (see Fig. 2).

Using variants of the split motion paradigm, Cavanagh, Boeglin, and Favreau (1985) and Green (1989) showed that the perceived direction of motion can indeed be resolved solely on the basis of chromatic identity. Movement would be perceived between pairs of stimuli that shared the same hue. In Experiment 5, we used this effect to assess whether M.S.’s attention to the direction of split phi motion would bias towards a disc that shares the same colour. The procedure was identical to that of Experiment 2 with the exception that two discs were presented in the second frame, one in the upper right quadrant the other in the lower. One of the discs shared the same colour as the central disc the other differed. The advantage of this design is that any RT differences observed between targets presented at congruent and incongruent discs have to be based solely on differences

in wavelength. The problem of attentional cueing by abrupt onset is circumvented because an onset appears at both congruent and incongruent locations.

6.1. Method

All aspects of the method were identical to that described for Experiment 2 with the sole exception that two discs appeared in the periphery, one was the same colour as the central disc the other was a different colour.

6.2. Results and discussion

RT for targets presented at congruent-colour locations was 797 ms compared with 834 ms for targets presented colour-incongruent locations. Table 1 shows these means broken down for each SOA. The figure reveals that RT for congruent-colour targets was shorter than RT for incongruent-colour targets at all SOAs. The data were entered into a 2×4 ANOVA with colour congruency and SOA as factors. The main effect of colour congruency proved to be significant, $F(1, 735) = 5.7$, $P < 0.01$, as did the main effect of SOA, $F(3, 735) = 10.16$, $P < 0.001$. The interaction however was not significant, $F(3, 735) < 1$.

The results showed that M.S. produced shorter RTs to targets presented inside the disc that shared the same chromatic identity as the disc presented in the first frame. M.S.’s visual system does therefore appear to use wavelength information to produce the same orienting of attention (driven by a motion signal) seen in normal observers using the (colour) correspondence paradigm (Cavanagh, Boeglin, & Favreau, 1985; Green, 1989) This occurred despite M.S. not being able to consciously perceive a bias in motion towards the congruent disc. This is perhaps not so surprising given that many attentional phenomena can result in facilitatory

effects of less than 30–40 ms, below the threshold of conscious awareness of the facilitation.

We carried out a further test to assess whether the data could reflect a matching process whereby M.S. rapidly matched the central disc with the peripheral disc that shared the same colour. Put another way, we tested whether the effect may have been the result of a top-down memory process rather than a bottom-up motion process driven by wavelength. M.S. performed a task in which he viewed trials identical to the procedure of Experiment 5¹ but now attempted to match the central disc with one of the two peripheral discs. When given no time limit for each trial he was able to score 96 out of 128 (binomial, $P < 0.0001$). This above chance responding was unsurprising given that M.S. is able to perform the analogous task of selecting an odd coloured disc from a set of three isoluminant stimuli, on the basis of the different cone-contrasts induced by the targets and distractors. However, as stated previously this task is not effortless, taking 3 or 4 s to select the singleton. Similarly, the present matching task was also performed with difficulty. It is therefore improbable that the effect was due to a top-down matching process. In order to confirm this we repeated this procedure with the exception that the initial disc was presented for 150 ms only, i.e. an exposure duration too short for M.S. to be able to match. He now performed at chance scoring 72 out of 128 (binomial, $P < 0.1$).

7. Experiment 6

Although the present series of experiments has shown that M.S. can use wavelength to direct behaviour the data have not allowed us to identify the mechanism responsible for these effects. As reviewed in the general introduction M.S. is able to perceive form, motion, and oddity based on his ability to discriminate local chromatic contrast. In Experiment 6, we tested the hypothesis that the colour congruency effect reported in Experiment 5 was also based on this mechanism. This chromatic contrast hypothesis is supported by as yet unpublished work from our lab showing that M.S.'s ability to select a colour singleton from three discs is abolished when the discs' edges are obscured with black annuli. If local chromatic contrast is indeed the mechanism by which the colour correspondence effect occurred in Experiment 5 presenting the stimuli against a black background should also abolish the effect.

7.1. Method

All aspects of the method were identical to that of Experiment 5 with the sole exception that all the stimuli were presented against a black background.

¹ The procedure was identical with the exception that no letters were presented.

7.2. Results and discussion

Collapsing cross SOA, mean RT for colour-congruent targets was 955 ms compared with 960 ms for colour-incongruent targets. The data were entered into a 2×4 ANOVA with validity and SOA as factors. The main effect of validity did not prove to be significant, $F(1, 730) < 1$, whereas the main effect of SOA was, $F(3, 730) = 10.8$, $P < 0.001$. The interaction also failed to reach significance, $F(3, 730) < 1$. Overall, these results show that unlike Experiment 5 targets presented at colour-congruent peripheral locations no longer accrued an RT advantage. Hence, the colour correspondence effect observed in Experiment 5 is eliminated when the inducing discs are presented against a black background. As hypothesised, the correspondence effect does appear to be based on local chromatic contrast.

8. General discussion

In a series of 6 experiments we examined the issue of whether colour can guide attention in an achromatopsic observer, patient M.S. More specifically, we have investigated attentional modulation by colour singletons, colour transients, and motion from colour. This was partially motivated by previous reports of achromatopsic patients who show preserved ability for the recognition of form (Heywood et al., 1991) and motion (Cavanagh et al., 1998; Heywood et al., 1998) that depend on wavelength processing, despite the absence of colour experience.

In Experiment 1, M.S. performed a search task in which the target and distractors were presented inside squares, one of which was a colour singleton. Contrary to some previous reports of automatic capture by such singletons (Horstmann, 2002; Turatto & Galfano, 2001) results did not show a reduction in RT when the target occurred at the singleton location. In Experiment 2, a classic phi motion display was presented using stimuli defined solely on the basis of colour. Results showed that targets presented at locations corresponding to the phi motion were subject to an RT reduction compared with targets presented at non-motion locations. Experiment 3 examined whether this effect was sensitive to the colour correspondence of the inducing discs. Results showed that presenting different coloured discs did not reduce the RT and hence apparent motion effect. Experiment 4 assessed the hypothesis that the effect observed in Experiments 2 and 3 was in fact due to, or at least influenced by, the peripheral disc acting as an attentional capturing onset. Results showed that targets presented at (colour defined) onset transient locations were also subject to an RT advantage. The design of Experiment 5 eliminated the effect of onset transient by presenting two peripheral onsets one of which matched the central disc for colour the other did not. Results showed that targets presented at the peripheral disc location that matched the central disc for colour was subject to an RT reduction. Experiment 6 showed that this effect was eliminated when the

stimuli were presented against a black background. Hence, chromatic contrast appears to mediate the motion effect. Overall these findings support the idea that attention, via a motion signal, can be directed in an achromatopsic observer by stimuli that are defined solely on the basis of wavelength information.

It is the elimination of the cueing advantage when presented against a black background (Experiment 6) that provides the best clue as to the mechanism responsible for the effect. These results are consistent with other accounts showing how the masking of chromatic edges interrupts performance in M.S. For instance, M.S.'s ability to discriminate between a chromatically ordered row of isoluminant colours from a random row is also abolished when a narrow grey strip occurs between each of the coloured patches that comprise the rows (Heywood et al., 1991). Analysis of the role of two primary visual pathways in the cortical and sub-cortical regions reveals how chromatic contrast could have mediated the present results.

The parvocellular (P) and magnocellular (M) channels originate in the ganglion cells of the retina and remain semi-independent up to primary and secondary visual areas via the lateral geniculate nucleus. The response properties of cells in the P and M channels reveal their role in visual processing. Principally, P cells are colour-opponent and are therefore usually associated with wavelength processing whereas M cells show little evidence for wavelength selectivity but do so for motion. Furthermore, the M channel projects to cortical area MT, or V5, a region specialised for motion processing. Saito, Tanaka, Isono, Yasuda, and Mikami (1989) have shown that M cells respond to a chromatic border presented in their receptive field without providing any information about the spectral composition of the colours creating the border. They also showed that the normally colour unselective cells of MT will however signal direction when presented with chromatically defined motion. Therefore, one possible explanation of the present results is that the P channel is compromised, leaving the M channel to convey information about colour contrast. This information is no longer available when swamped by the 100% luminance contrast created by a black background.

Although the above hypothesis is possible other evidence suggests that M.S. has access to information other than that conveyed by the M channel. Heywood, Cowey, and Newcombe (1991) recorded spectral sensitivity functions for the detection of light at different wavelengths. Results showed detection thresholds and a three peaked sensitivity curve indicative of colour-opponent mechanisms. Heywood, Kentridge, and Cowey (1998) demonstrated that wavelength-based motion perception in M.S. is mediated by these colour-opponent P-channel mechanisms rather than those of the M channel in which signals from the three different cone types are simply summed. Although it is not possible to silence all M-channel cells even when using stimuli that minimise luminance responses psychophys-

ically, the colour-opponent system should, nevertheless, respond in a characteristic fashion to stimuli with a spectral distribution in which the wavelengths put into opponency are in balance. A stimulus in which wavelengths producing excitation and inhibition balance will produce less response than one in which net excitation can be elicited in at least some cells. This subadditive response can be corrected by increasing the intensity of the stimulus. The colour input to motion is unlike the luminance input in that the speed of perceived motion depends not only upon the speed of a stimulus, but also its perceived contrast. Correcting subadditivity can therefore slow the perceived speed of a moving chromatic stimulus. The same correction was needed to minimise perceived speed both to M.S. and to normal subjects, implying that at least the early stages of the colour-opponent P channel were intact in M.S. It would seem therefore that intact cortical chromatic opponent processes explain the presently observed wavelength observed motion effect.

Initially colour and motion were assumed to be processed independently by the early cortical visual areas following the discovery of the M and P channels (Livingston & Hubel, 1987; Zeki, 1978). This suggests that motion areas respond to luminance information only and that chromatic information makes no contribution to the perception of motion (Ramachandran & Gregory, 1978). However, this sharp segregation is not supported by later findings showing that, although compromised, motion is still observed for isoluminant stimuli, i.e. stimuli defined by chrominance alone (Cavanagh et al., 1985; Moreland, 1982). Cavanagh and Anstis (1991) assessed the contribution that colour-opponent mechanisms make to motion perception in normal and colour deficient observers by measuring the 'motion-nulling' of two superimposed colour and luminance gratings moving in opposite directions. With both normal and colour deficient observers Cavanagh and Anstis were able to show that residual information conveyed via the luminance pathway could not account for the contribution colour makes to motion. The authors argued that this contribution occurred via colour-opponent mechanisms. It is our contention that the present results are also due to mediation via colour opponency.

Finally, our results also shed light upon the correspondence of colour in apparent motion. Cavanagh, Boeglin, and Favreau (1985) and Green (1989) showed that motion can be perceived solely on the basis of chromatic identity. However, both these studies confounded the effects of chromatic identity per se and the effects of chromatic contrast. The results from Experiment 5 by contrast cannot be due to the correspondence of chromatic identity since M.S. has lost all information concerning spectral composition. This suggests that direction in colour-space of chromatic contrast alone is sufficient to solve the correspondence problem. In summary, our data provide further evidence of how an achromatopsic observer can use wavelength to guide behaviour despite the lack of colour experience.

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