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Cortical colour blindness spares colour input to motion perception

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Abstract

Two patients with central achromatopsia showed normal motion responses to chromatic stimuli even though they could not see colour, indicating that the contribution of colour to motion follows pathways undamaged by their cortical lesions. Both patients had severe loss of colour perception but could distinguish the borders between adjacent colours, possibly due to a residual response of non-opponent pathways to chromatic borders. A chromatic stimulus moving in steps of 90° eliminated the possible contribution of these borders and revealed a strong, colour-specific response. These results indicate that for normals, as well as for these patients, the motion of equiluminous colour stimuli can be signaled by low-level motion detectors and does not require highlevel tracking of the colour patterns.

Losses of specific visual functions have been used as evidence for modular processing of information in vision and as an aid to understanding the hierarchy of information flow in the cortex. Two classic examples are the loss of colour information while retaining black and white spatial vision (achromatopsia) [1–9] and the loss of motion perception while retaining the perception of static patterns (akinetopsia) [10]. In achromatopsia, patients have lost the sensation of colour and they often report that the world appears solely in shades of grey, as in a black and white movie. Clearly pattern analysis based on colour is degraded. Nevertheless, we now report that achromatic patients also present an example of loss of pattern information (for colour) while preserving a response to the motion of these same colour patterns. We have been careful to isolate the colour-specific responses to our stimuli independently of an achromatic response to colour borders that exists in these patients and in normals.

The two patients with central achromatopsia were similar in that they had bilateral lesions, made errors on the Ishihara and made many errors on the Farnsworth–Munsell test. They both had visual agnosia, prosopagnosia and upper field loss. The spectral sensitivity of both showed only a single peak (T. Troscianko, personal communication), implying a loss of opponent-colour mechanisms at the level of pattern detection. Normals and some achromatic observers [3,5] show a three-peaked

function indicating functioning opponent-colour mechanisms, at least at the level of detection. JPC was 43, a former florist, and his bilateral lesions on the ventral surface of the temporal lobes were the result of a mugging. WM was 74, a former electrician and his lesions followed a series of transient ischemic attacks which left large, bilateral occipito-temporal lesions. Achromatic contrast sensitivity was normal for JPC [7] whereas the visual acuity for WM was somewhat reduced (OS 0.3, OD 0.5) [8]. WM reports no conscious sensations of colour, but JPC occasionally notices reds although he would also often accept a grey as a match to a red.

Pattern vision for colour-defined shapes is not totally lost in these and other cases of central achromatopsia. If two colours are placed side by side and their relative brightness adjusted, it is possible to find a setting where the two colours appear identical but, nevertheless, a border is perceived between them [3,5–7]. We can find a likely candidate for this border response in the physiology of the visual system. In

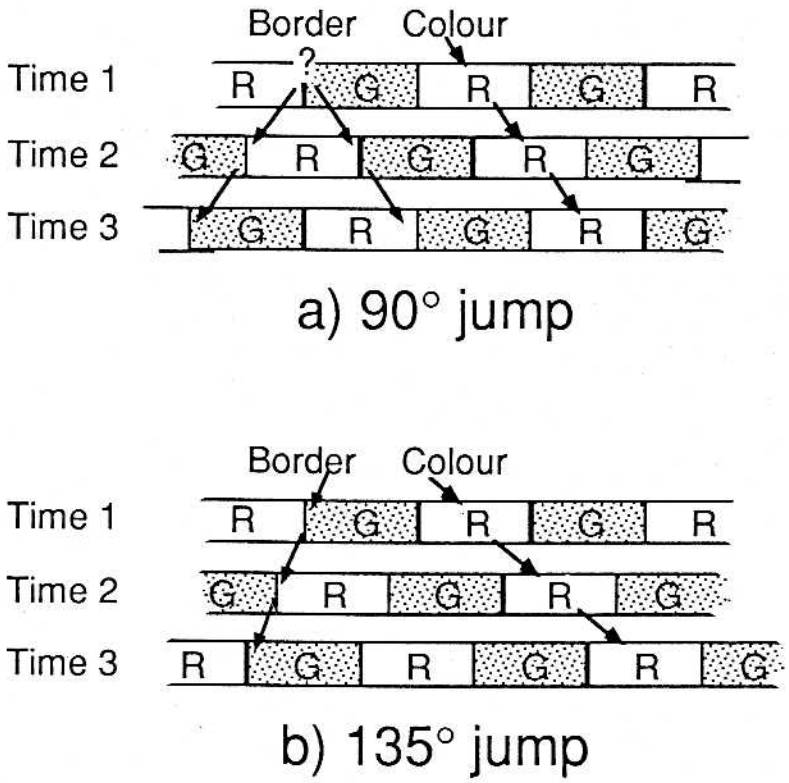

Fig. 1. The contribution to motion of coloured bars and of their borders can be isolated by using discretely jumping stimuli. Matching the colour-specific regions across frames would require an opponent-colour input to motion detectors; matching the chromatic borders in a non-specific manner across frames can be mediated by non-opponent input to motion detectors. In (a), the coloured regions jump to the right by 90° on each frame. On the other hand, the motion of the borders is ambiguous; it is an equal distance from a border in one frame to the adjacent border to the left or the right in the subsequent frame. Only colour-based motion is available for this stimulus. In (b), the coloured regions are again moving to the right, now by 135° per frame. The borders also have a consistent nearest match but it is to the left! Colour-based and border-based motions should therefore be in opposite directions for this stimulus.

primates, the parvocellular or colour-opponent pathway carries colour-specific information in early stages of visual processing whereas the magnocellular, or non-opponent, pathway is non-specific (response is determined by the luminance of the light, irrespective of its colour) [11]. Although it does not show colour-specific responses, the magnocellular pathway nevertheless responds to colour transitions [12,13]. The division of information between chromatic and achromatic pathways once they reach the cortex may differ from that seen for the earlier parvo/magno division [14,15] but it is likely that the achromatic colour-border response originating in the magnocellular stream is passed on to higher analyses of achromatic information. In an achromatic observer, then, the outlines of chromatically defined regions could be retained due to the response to the colour borders even though the colours themselves were indistinguishable. We have developed specific tests to examine the pattern and motion responses to chromatic information and, independently, to the chromatic borders in these patients.

In an earlier paper, Mollon et al. [3] also examined the motion responses of central achromats to moving colour stimuli. The achromatic observer adapted to a slowly moving disk covered with a red texture. When tested with a similar stationary red disk, the duration of the aftereffect was almost twice that found when tested on an otherwise similar, stationary green disk. Although this result implies a colour-specific input to adaptable motion detectors, caution is required because the authors did not test the reverse contingency (adapt to green, test on red and green) so the observed colour specificity may have been a bias towards longer motion aftereffect durations with red tests, irrespective of the adapting colour. This would not require input of opponent-colour information to motion detectors.

In our experiments, we used three conditions to test the perception of motion. In the first, red/green sinusoidal gratings moved smoothly (within the limitations imposed by the 66 Hz raster rate). In this condition, both the colour information and the borders between the colours moved in the same direction. In the second condition, jumps of 90° generated consistent colour motion but ambiguous border motion (see Fig. 1a). Finally, displacements of 135° generated opposite directions of motion for the colour and border patterns (Fig. 1b). Previous tests have shown that normals do see motion mediated by colour for 90° and 135° steps of sinusoidal red/green gratings [16,17]. Motion mediated by the chromatic borders can be seen by normal observers but this does not become apparent until the grating jump is at least 150° [17].

Our stimulus was a rotating wheel of eight colour spokes, varying sinusoidally between red and green (Fig. 2a). The wheel rotated with three different step sizes where the rate was fixed at 2 Hz in all cases (0.25 revolutions/s). We measured not only the direction of the perceived motion for these colour stimuli but also for the smooth and 90° conditions, we measured the colour-based motion strength in terms of its "equivalent luminance contrast" [16]. For the 135° condition, we recorded only the perceived direction of motion because it was too weak to provide reliable strength judgements.

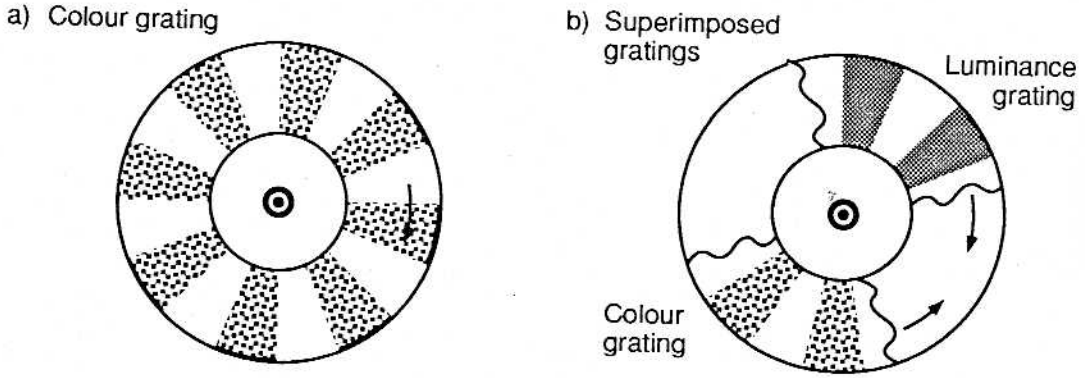

Fig. 2. (a) Observers made judgements of motion direction for the colour grating alone when the motion jump was 135°. The radial gratings had an outer diameter of 10° and an inner diameter of 2.2°. Mean luminance was 45 cd/m^2. The red and green were modulated sinusoidally in opposite directions and the colour contrast was set at the maximum available between the red and green phosphors. Approximate equiluminance was determined with a minimum motion technique [18]. Radial gratings were used to avoid tracking eye movements. (b) For the smooth and the 90° jumps, a sinusoidal, equiluminous, colour grating (red/green) and a sinusoidal, luminance grating (light and dark yellow) were superimposed, moving in opposite directions. In a forced-choice procedure, while fixating the bull's-eye, the observers reported the direction of the global motion seen in the combined stimulus. The contrast of the luminance grating varied from trial to trial and the value that produced a motion null (equal motion reports in both directions) was taken as the "equivalent luminance contrast" of the colour grating [16]. We also conducted these tests for at least two (and as many as seven) additional luminance contrasts between the red and green of the colour grating, spaced typically by 5% around the predetermined equiluminance point. In every instance, the minimum equivalent luminance contrast occurred at the predetermined equiluminance setting.

Several other factors could contribute to motion perception for the colour grating. Chromatic aberration produces significant luminance artifacts at spatial frequencies greater than 1.0 cycle per degree [16] but the highest spatial frequency in our display was 0.6 cycles per degree. Monitor misalignment and non-uniformity can also produce a luminance response within regions of our stimulus. To control for all these factors, we ran several congenitally colourblind observers on the same tasks. These observers have anomalous or missing classes of photoreceptor pigments and see little or no colour pattern for red/green stimuli but can respond to luminance artifacts which are present. Finally, five colour-normal observers were also tested to estimate the range of normal responses.

The normal observers required between 15 and 25% luminance to null the motion of the equiluminous colour grating whether it moved smoothly or in 90° jumps (Fig. 3 shows average values). The congenitally colour blind observers showed motion strengths in the 2–4% range for smooth or 90° jump stimuli indicating that the sum of their weak colour response and all monitor and optical artifacts was less than 4%. This places an upper bound on luminance artifacts from monitor and optical sources for all the observers. For the 135° stimulus, normals reported mostly motion in the

colour direction (occasional reports of no motion) whereas no congenitally colour blind observer reported any consistent motion.

The results for the two achromatic observers show equivalent luminance contrasts of 20 and 15% for the smoothly moving (10° steps) red/green gratings. These values are within the range of values seen for normals. Most important, both show a robust response (15 and 17%) for the gratings which jumped by 90°. These responses can

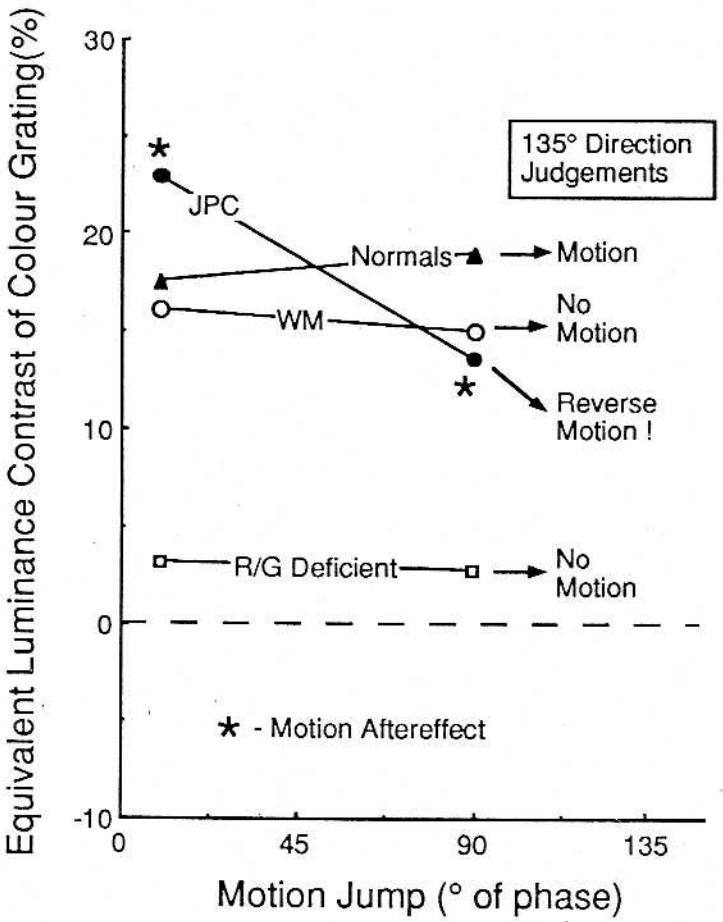

Fig. 3. Equivalent luminance contrasts for colour gratings moving in 10° and 90° jumps (left-hand ordinate) and judged motion direction (right-hand column) for colour gratings moving in 135° jumps. Data are shown individually for two achromatic patients, WM (open circles) and JPC (closed circles). Group averages are shown for four congenitally colourblind observers (open squares) and the range of normal values (four observers) is shown as a gray band (not yet!). Motion aftereffects were also measured for JPC. While fixating on the central bull's-eye, he adapted to the rotating colour grating described in Fig. 2a. A luminance grating of 15% contrast was then presented briefly. This grating's contrast reversed in place at 2 Hz and the patient reported the direction of apparent movement. The adaptation then continued and tests were repeated every 15 s for ten trials or until five consistent responses were obtained. The asterisks beside the datum points at 10° and 90° for JPC indicate that he showed a motion aftereffect to rotating equiluminous colour gratings at these two jump sizes but not to the 135° stimulus. The same pattern held for normal observers. WM was not tested for a motion aftereffect. Congenitally colourblind observers do not show a consistent motion aftereffect to any of the colour stimuli.

only be mediated by colour-specific motion analysis because the red/green borders produced ambiguous motion signals in this stimulus. The equivalent luminance contrasts found for the two patients also demonstrate that they have normal retinal cone function [16] as any retinal deficit results in very low equivalent luminance contrasts.

Finally for the 135° steps, WM reported no motion (a common response for normals as well) whereas JPC reported reverse motion (never reported by normals). For at least one patient then, the colour borders are sufficiently visible to mediate a motion response for a 135° jump whereas, for normals, the jump size must be over 150° to produce motion in the direction of the borders [17]. When asked to point to the features which were moving in the stimulus, JPC pointed immediately to the thin yellow borders lying between the red and green bars and followed them with his finger. Normals are generally incapable of performing this tracking task.

This observation for JPC supports the previous reports of the perception of chromatic borders in patients who cannot distinguish the colours adjacent to the borders [3,5–7,9]. This border response could not have mediated the motion percept in the 90° condition, so even this patient retains a robust opponent-colour contribution to motion analysis. It is possible, however, that the border percept did contribute to the strength of motion perceived in the smoothly moving stimulus for this patient. His motion strength for this condition (where borders and colour are both moving in the same direction) was larger than for the 90° condition, a difference that did not occur for WM or for the normals.

These results indicate that opponent-colour information contributes to low-level motion processes. Previous studies have demonstrated that there are two independent motion processes: one which is "low-level" or automatic in that it signals motion even in the absence of attention to the stimulus; the other, high-level process is mediated by attention to visible features [9]. Some authors [20,21] have claimed that coloured stimuli do not contribute to low-level motion processes. Several studies show that colour does produce impressions of motion [16,22–25] but these studies do not resolve whether these responses are mediated by low-level detectors or by attentive tracking. Our data show that when tracking is difficult or impossible, colour still produces a robust response, implicating by default a low-level response. Specifically, the two achromatic patients tested here should be unable to track colour gratings especially when they are displaced by 90°. Indeed, in a test of tracking the bars in the rotating stimulus, JPC performed very poorly.

It is nevertheless possible that some residual cues might differentiate the red and the green of the gratings for the achromatic patients and allow them to track individual grating bars with either attention or with eye movements. However, these strategies (which the two patients did not report) are unlikely to produce equivalent luminance contrasts in the normal range seen here. On the other hand, JPC does report some residual "red" sensations (red appears tinted "some sort of brown"), and so all the tests were repeated with magenta/green gratings modulated in a direction near the tritan confusion line for both WM and JPC. They again showed the same results as normals. Nevertheless, to be sure of our conclusion of a colour contribution to low-

level detectors, we also tested whether the rotating colour gratings produced any motion aftereffects with the patient JPC. He had a normal motion aftereffect for the 10° step stimulus and, most important, for the 90° step stimulus over a range of luminance ratios between the red and green that included the predetermined equiluminance point. He had no consistent aftereffect for the 135° stimulus. Normals show the same aftereffect pattern whereas congenitally colourblind subjects show no aftereffect for any of the stimuli. These results support the conclusion that opponent-colour information contributes to adaptable, low-level detectors. Earlier tests on normals had demonstrated motion aftereffects for chromatic gratings [26–28] but these experiments did not test the critical 90° step condition which rules out the potential non-opponent response to the chromatic borders.

In summary, we conclude that colour information takes a direct path to cortical motion detectors and does not rely on higher-level attentive tracking (Fig. 4). This high-level motion pathway relies on visible patterns and this cue is unavailable for the opponent-colour information in the two achromatic patients. We also find evidence in patient JPC for the visibility of the borders between adjacent colours. This border response, probably originating in the magnocellular projecting units of the retina [12], was not present in the other patient so that its presence in normals may be similarly variable. Other reports of implicit processing of chromatic information in central achromatopsia have depended either on this non-opponent response to chro-

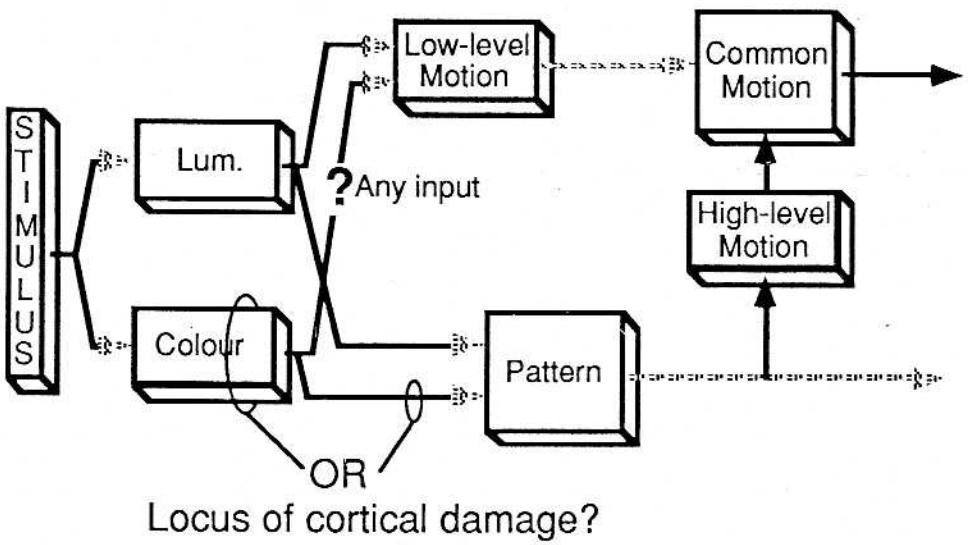

Fig. 4. Contribution of colour to low-level and high-level motion and the possible functional site of cortical damage in achromatopsia. The contribution of colour to motion is preserved in the achromatic patients so some cortical processing of colour is spared in achromatopsia. The site of damage must therefore be in the colour-specific analyses of pattern or in the transfer of colour information to pattern analysis. Since we assume that high-level motion is based on the tracking of visible patterns, this route cannot mediate the perception of moving colour stimuli for the achromatic patients. Their motion perception, especially in the case of the 90° jump stimuli, must be mediated by a contribution of opponent-colour information to low-level motion processes. The same pathway must, of course, be present in normal observers.

matic borders [3,6,7] or on residual opponent-colour information as indicated by a three-peaked spectral sensitivity curve [3,5]. Neither of these hold in this study because we have controlled for the chromatic border response and the patients have only a single-peaked spectral sensitivity function.

The results with the patients indicate that the contribution of colour to motion must follow pathways unaffected by their cortical damage. Physiological recordings in area MT of monkeys, an area specialized for motion analysis, have shown responses to equiluminous chromatic gratings [29,30] and, using a 90° stimulus like that used here, Dobkins and Albright have shown that this response can be based on opponent-colour information, not just on the chromatic borders [30]. According to these authors, however, this response is quite weak, with an equivalent luminance contrast of only 2.5%. This is within the range seen for congenitally colour blind observers and therefore attributable to distortions in the monitor, the eye or the non-opponent pathway. If MT is not the site of the robust low-level response to opponent-colour stimuli that we report here, then we suggest that another site, perhaps even V4 where a fair percentage of cells are directionally selective [15], mediates the robust low-level motion response to colour.

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