

C.A. Heywood · R.W. Kentridge · A. Cowey

Form and motion from colour in cerebral achromatopsia

Abstract Patients with cerebral achromatopsia, resulting from damage to ventromedial occipital cortex, cannot chromatically order, or discriminate, hue. Nevertheless, their chromatic contrast sensitivity can be indistinguishable from that of normal observers. A possible contributor to the detectability of chromatic gratings is the subadditive nature of certain colour combination such that mixtures of, for example, red and green (yielding yellow) appear dimmer than expected from the simple addition of luminances. This subadditivity is believed to reflect colour-opponent interactions between the outputs of long- and medium-wavelength cones. We performed a first-order compensation for such subadditivity in chromatic gratings and demonstrated that their detection was still not abolished in an achromatopsic patient. In addition, we used a two-alternative forced-choice procedure with an achromatopsic patient, who was required to judge the apparent relative velocity of two drifting gratings with different degrees of compensation for subadditivity. It is well known that isoluminant gratings, constructed by adding a red and green sinusoidal grating of identical peak luminances in antiphase, appear to drift substantially slower than an achromatic grating with the same velocity. Adding $2f$ luminance compensation to an isoluminant grating of spatial frequency f , resulted in an identical minimum of perceived velocity at a compensation contrast of 5% in both achromatopsics and normal observers. Furthermore, while compensation for subadditivity did not substantially compromise *grating* detection at low contrasts, such correction severely affected *motion* detection. Saccadic eye movement accuracy and latency were also measured to uncompensated chromatic, compensated chromatic and achromatic targets. We conclude first that subadditivity, resulting from colour-opponent P-

channel processes, influences motion judgements. The ability to extract motion from chromatic differences alone is little, if at all, different in achromatopsic and normal vision. Second, the paradoxical detection of sinusoidally modulated chromatic gratings in achromatopsic patients is not merely a result of subadditivity. Third, saccadic latency, but not accuracy, to chromatic targets is affected by luminance compensation. Finally, and more generally, wavelength processing continues to contribute to several aspects of visual processing even when colour is not perceived.

Key words Achromatopsia · Chromatic contrast sensitivity · Motion vision · Subadditivity

Introduction

Ventromedial occipital brain damage can result in the complete loss of colour vision, a condition known as cerebral achromatopsia. Such a patient is quite unable to tell apart hues that are appropriately matched for luminance (for reviews see Meadows 1974; Zeki 1990a). However, and surprisingly, they can retain the ability to discern form defined by such isoluminant chromatic differences, which is reflected in their essentially normal sensitivity to chromatic contrast (Victor et al. 1989; Heywood et al. 1996).

Sensitivity is conventionally measured by determining the threshold contrast required for the detection of sinusoidally modulated red/green gratings, constructed by the addition of a red and a green luminance grating in spatial antiphase to produce a pattern that can be distinguished solely on the basis of colour differences. The definition of luminance derives from photometric measurements on many normal observers, where the relative luminous efficiencies of lights of different wavelengths, known as $V(\lambda)$, is established from heterochromatic flicker photometry by rapidly alternating two colours and adjusting their respective luminances until perceived flicker is minimal. Luminance is then defined as the integral over wave-

C.A. Heywood (✉) · R.W. Kentridge
Department of Psychology, Science Laboratories, South Road,
Durham DH1 3LE, UK
Tel.: +44-191374624, Fax: +44-1913747474

A. Cowey
Department of Experimental Psychology, South Parks Road,
Oxford OX1 3UD, UK

length of the radiance of the source, weighted by the spectral luminous efficiency $V(\lambda)$, i.e.

$$\text{Luminance} = K_{\max} \int_{\lambda} L_{e\lambda} V(\lambda) d\lambda$$

where K_{\max} is the maximum luminous efficiency. This definition implies that luminance is additive, as enshrined in Abney's Law (Abney 1913). However, luminous efficiencies are quite different under sustained viewing, as is the case in heterochromatic direct brightness matching of unchanging samples, where the function is broader than that derived from flicker photometry (Wagner and Boynton 1972). Moreover, flicker photometry obeys Abney's Law such that the addition of two colours results in a hue with a luminance equal to their sum (Guth et al. 1969). Additivity fails under conditions of heterochromatic brightness matching, in that when two opponent colours, red and green, are mixed, hue cancellation occurs and the outputs of chromatic channels are at a minimum. The outcome is a colour mixture that is perceptually dimmer than predicted by Abney's Law. Thus the output of the chromatic channel contributes to brightness.

The division of labour between the analyses of colour and motion is commonly and respectively assigned to the colour-opponent, P, and broad-band, M, processing channels (Livingstone and Hubel 1987a, b; Zeki 1990b). An early view that cerebral achromatopsia is the simple result of destruction of the P-channel is no longer tenable (Covey and Heywood 1995). In a case of complete achromatopsia the patient, M.S., showed both a spectral sensitivity and subadditive brightness perception of colour mixture consistent with residual P-channel processes (Heywood et al. 1994). This raises the question of whether sinusoidally modulated red/green gratings contain unintended brightness differences as a consequence of subadditivity that could account for M.S.'s striking and paradoxical sensitivity to chromatic gratings. We now report the results of presenting chromatic gratings to M.S. where the amplitude of a compensatory grating, with the same chromatic content, was modulated to compensate for the subadditivity present in conventional red/green sinusoidal gratings. If chromatic contrast sensitivity in achromatopsia arises solely from the subadditive nature of red/green mixtures, then with appropriate adjustment it should be abolished or substantially reduced.

A prominent characteristic of isoluminant chromatic gratings is that they display "motion slowing". The perceived velocity of a drifting chromatic grating is substantially reduced compared with that of a grating modulated in luminance and drifting at the same speed (Cavanagh et al. 1984). Thus an isoluminant, saturated red/green grating appears to move at a speed of some 40% less than a 10% luminance grating drifting at the same speed (Cavanagh et al. 1984). Contrary to the view that motion and colour processing are mediated by separate neural pathways, it is now apparent that motion of an isoluminant stimulus is mediated by a colour-opponent mechanism (Hawken et al. 1994; Cropper and Derrington 1996;

Gegenfurtner and Hawken 1996). The phenomenon of motion slowing occurs only at low temporal frequencies and is mediated by a "slow" colour-opponent channel of processing that is highly sensitive to chromatic contrast, but velocity coding is contrast-dependent and not veridical. Grating detection and motion identification of luminance-modulated gratings are subserved by a separate system. At high temporal frequencies, velocity is coded veridically for both luminance-defined and isoluminant chromatic gratings. The "fast channel" is highly sensitive to achromatic contrast and while it does not signal colour itself, it treats chromatic and low-contrast luminance modulation in a similar fashion. We therefore examined the sensitivity of an achromatopsic patient to chromatic motion using conventionally constructed chromatic gratings, in addition to those where additional, and varying, levels of luminance modulation were introduced to compensate for the effects of subadditivity.

Sharp chromatic edges remain visible to the M-channel regardless of the relative luminance of the wavelengths of which they are composed. However, such chromatically generated contour is also visible to M.S. (Heywood et al. 1994) and other achromatopsic patients (Barbur et al. 1994), even in the presence of random luminance masking that renders the M-channel ineffective. This implies a further role of the P-channel in the chromatic vision of M.S., again in the absence of perception of the surface property of colour. We therefore measured saccadic eye movements to peripheral targets to ascertain whether latency and accuracy were influenced by subadditive effects. We also examined the ability of M.S. to make saccades to chromatic and achromatic discs.

Materials and methods

Case history

Patient M.S. has been reported in detail elsewhere (Newcombe and Ratcliffe 1975; Ratcliff and Newcombe 1982; Heywood et al. 1991, 1994, 1996) and will be only briefly described here. While a police cadet in 1970, he contracted presumed herpes encephalitis. His initially severe visual disturbances resolved within a year, leaving him with a left homonymous hemianopia with macular sparing and normal Snellen acuity. He remains, however, severely agnostic for objects and faces but has no alexia, agraphia or aphasia. His total achromatopsia has remained unchanged and is reflected in a random performance on a task requiring the chromatic ordering of isoluminant chromatic chips (Farnsworth-Munsell 100 Hue test: score 1245). He is unable to discriminate large hue differences in an oddity task (Heywood et al. 1991) but retains a normal retinal three-cone mechanism (Mollon et al. 1980) and a spectral sensitivity function that indicates the presence of colour-opponent processing (Heywood et al. 1991). His dense colour blindness coexists with essentially normal sensitivity to chromatic contrast and cortically elicited visual evoked potentials to chromatic gratings (Heywood et al. 1996).

Magnetic resonance imaging revealed ventromedial damage in both hemispheres involving the lingual and fusiform gyri (Heywood et al. 1991). The second, third and fourth temporal gyri and pole of the temporal lobe are destroyed in his right hemisphere. There is additional damage to the parahippocampal gyrus and occipital lobe, sparing the caudal tip of the calcarine sulcus, which presumably accounts for macular sparing. In the left hemisphere, the fourth temporal and parahippocampal gyri, the pole of the temporal lobe and the

area of the mesial occipitotemporal junction are destroyed. The dorsal aspects of both hemispheres show relatively little damage, which is confined to the white matter under the inferior half of the inferior parietal lobe in the right hemisphere.

Control subjects

Ten control subjects participated in the judgements of motion slowing. Eye movement recordings were taken from a naive observer, U.S.

Apparatus

Visual stimuli were presented on a gamma corrected display monitor (either a 14-inch Taxan 885LR; CIE phosphor coordinates Red: $x=0.610$, $y=0.342$; Green: $x=0.298$, $y=0.588$, or a 20-inch Eizo F-784T CIE phosphor coordinates Red: $x=0.625$, $y=0.340$; Green: $x=0.285$, $y=0.605$) driven by a VSG 2/2 graphics card (Cambridge Research Systems), providing 13-bit resolution on each gun. Display luminance was measured with a Minolta LS-110 photometer. Eye movements were measured using a Fourward Technologies Dual Purkinje Eye-Tracker (Crane and Steele 1985).

Motion slowing

Visual stimuli were presented on a 14-inch display monitor. Mean display luminance was 5 Cd m^{-2} . Subjects were seated 57 cm from, and directly facing, the display screen, in a darkened room, with their head in chin and forehead rests. Visual stimuli were sinusoidally modulated gratings, subtending $24^\circ \times 16^\circ$, with a spatial frequency f of $0.125 \text{ cycles deg}^{-1}$, at 100% chromatic contrast, and drifting from left to right at 0.82 Hz. Fifteen gratings contained incremental or decremental luminance compensation of frequency $2f$, the amplitude of which could be varied to yield eight gratings of luminance contrast between 0 and 15.2% (0, 2.5%, 5.0%, 7.2%, 9.3%, 11.4%, 13.3% and 15.2%) and seven containing luminance decrements, in a similar fashion (2.6%, 5.4%, 8.3%, 11.4%, 14.7%, 18.2% and 21.8%). The gratings were constructed as follows. Given a pair of counterphase gratings defined by:

$$\text{Red}(X) = \text{RedIntensity} + \text{RedIntensity} \cdot \sin(X)$$

$$\text{Green}(X) = \text{GreenIntensity} + \text{GreenIntensity} \cdot \sin(X + \pi)$$

The colour-matched luminance compensation intensity is given by:

$$\text{Compensation}(X) = \text{Compensation} + \text{Compensation} \cdot \sin(2X + \pi/2)$$

To ensure that the chromaticity of the original grating remains constant, the compensatory grating must be composed of:

$$\begin{aligned} \text{RedCompensation}(X) &= \text{Compensation}(X) \\ &\cdot \text{Red}(X) / (2 \cdot \text{RedIntensity}) \end{aligned}$$

$$\begin{aligned} \text{GreenCompensation}(X) &= \text{Compensation}(X) \\ &\cdot \text{Green}(X) / (2 \cdot \text{GreenIntensity}) \end{aligned}$$

At each level of compensation, the mean luminance of the grating was maintained at 5 Cd m^{-2} . Examples of gratings and their construction are illustrated in Fig. 1.

A two alternative temporal forced-choice (2AFC) procedure was used. In the first interval a single drifting grating appeared followed by a blank screen of the same mean luminance and chromaticity. In the second interval a second grating was displayed, followed by a blank screen. The grating was exposed for 1.22 s (during which it moved one cycle), the intervening blank screen for 0.28 s and the intertrial interval was terminated by the subject's response. The subject was required to indicate, by a key press, the interval during which the grating appeared to be moving more rapidly. Each of the 15 gratings was paired with every other grating, producing a to-

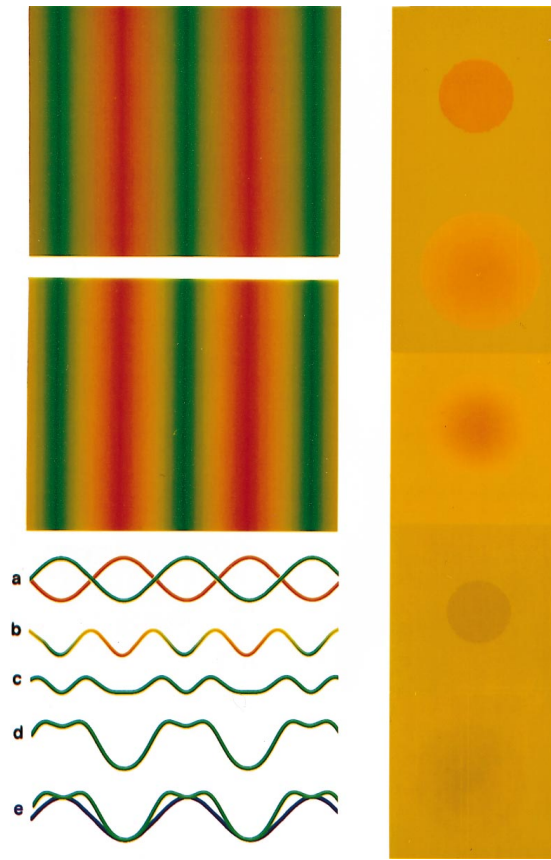


Fig. 1 *Left* A conventional chromatic grating of spatial frequency f , below which is one where $2f$ luminance modulation has been added to compensate for the effects of subadditivity. The waveforms represent: (a) the modulation of the red and green guns of the conventional grating, (b) the chromatic content of the $2f$ luminance modulation alone, achieved by modulating the red and green guns as shown in (c), (d) the green modulation of the compensated grating, which is compared in (e) with the conventional modulation. For (c), (d) and (e) the red modulation is identical, but in spatial antiphase. *Right* The targets displayed during eye movement recordings are shown. Chromatic discs and sinusoids are shown above their achromatic counterparts. A compensated target is displayed centrally

tal of 210 trials. Subject M.S. and 10 normal observers performed the task.

Motion detection

The subject was seated, and gratings were produced as described above, using seven different contrasts: 25%, 20%, 17.5%, 15%, 12.5%, 10% and 5%. They were either uncompensated, or compensated by the addition of $2f$ luminance contrast, of a magnitude of 5% of the chromatic contrast of the carrier grating (the value derived from the results of judgements of motion slowing), yielding 14 gratings. Each grating was presented in blocks of 20 trials in a task requiring motion detection, in a 2AFC paradigm. The grating appeared in each of the two 2.96-s intervals, separated by 0.74 s. In one interval the grating was stationary; in the other it drifted to the left or right, randomly determined, at a speed of 0.82 Hz. M.S. had to indicate whether the moving grating appeared in the first or second interval, which it did with equal probability, by making the response on one of two keys. The intertrial interval was 1 s. M.S. performed two blocks of each grating type in a counterbalanced design.

Saccadic eye movements

Displays on a 20-inch monitor were viewed binocularly and two-dimensional recordings were made of the right eye. Eye position was sampled at 200 Hz. Each block of 50 trials was preceded by a calibration where subjects saccaded in a fixed sequence to each target in a 3×3 uniform array of crosses, separated by 6°, that were sequentially presented in the nine locations, column by column. Because of the hemianopic field of M.S., stimuli were presented exclusively in the right hemifield. The display consisted of 1° targets presented in one of seven possible locations that formed a semicircle at 4° eccentricity and a 1.56° separation between target centres. The target location was randomly selected from trial to trial. The targets were either chromatic or achromatic discs, with luminances of 13.1 and 11.3 Cd m⁻², respectively, and equivalent cone contrast of 13.14%, or they consisted of $\pi/2$ of a 0.5 cycles deg⁻¹ rotated sinusoidal grating. The latter targets were either achromatic, or compensated and uncompensated chromatic (red/yellow). Examples are displayed in Fig. 1. The subject was seated in a darkened room, 57 cm from the display screen, with head motion minimized by a chin and two forehead rests, and instructed to view a fixation cross. A trial consisted of the disappearance of the cross and the simultaneous presentation of a target, to which the subject was required to saccade. The target remained for 1 s and the subject was then required to re-fixate. The intertrial interval was 2 s. The five different target types were confined to different 50-trial blocks and two blocks were presented in a counterbalanced design. Practice trials were delivered prior to data collection.

Results

Motion slowing

Pairs of gratings, with different degrees of first-order compensation, were compared for their apparent speed of motion in 10 naive observers and patient M.S. M.S. responded as rapidly as normal observers and informal observation suggested that no level of compensation appeared any less conspicuous to him than any other.

If the attenuated brightness of the colour mixture, resulting from subadditivity, did not influence perceived velocity then the uncompensated grating would be gauged as moving more slowly than any of its partners. However, Fig. 2 illustrates that a grating with the addition of 5% frequency-doubled luminance contrast was judged to be moving more slowly, when paired with each of the remaining 14 gratings in the stimulus set. This was true for both normal observers and patient M.S., where the peak of the curve is displaced to the right in an identical fashion. A 2*f* luminance modulation of 5% was therefore used in further tasks (reported below) to counter subadditive effects.

To confirm that subadditivity was not a substantial contributor to the ability of M.S. to detect isoluminant gratings, he was asked to perform an orientation discrimination task and a presence/absence judgement of gratings of different contrasts and levels of compensation. Stationary gratings, which were otherwise identical to those used above, of 100% chromatic contrast and containing 2.5%, 5% or 10% 2*f* luminance contrast, were briefly presented in blocks of 20. The gratings were randomly presented horizontally or vertically, and M.S. had to report their orientation. The procedure was repeated for presentation

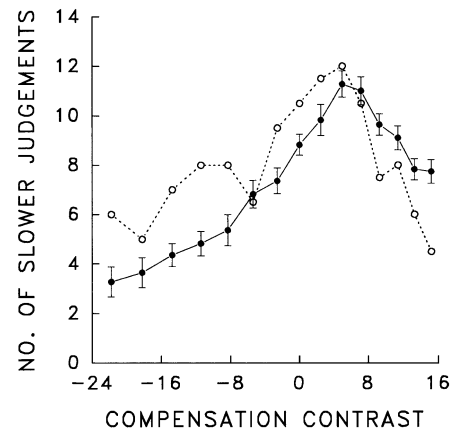


Fig. 2 For normal observers (*filled circles, continuous line*) and M.S. (*open circles, dotted line*) the percentage of presentations where gratings of each compensation contrast were judged to be moving more slowly when paired with those of every other compensation contrast in a two-alternative forced choice (2AFC) task. Standard error bars are shown. Note that the maxima are displaced to the right of the abscissa representing the grating, constructed in the conventional manner, which lacks added 2*f* luminance

times of 85 ms and 170 ms. M.S. performed confidently and without error. Time constraints did not permit grating detection to be carried out in a 2AFC paradigm. Nevertheless, in a presence/absence task where M.S. was required to detect drifting uncompensated gratings (0.125 cycles deg⁻¹, 0.82 Hz) presented for 1.22 s, he produced a contrast threshold of 2.5%, corresponding to a sensitivity of 40, which is close to the published figure at low spatial frequencies (Heywood et al. 1996). Revealingly, this threshold remained unaltered with the addition of 2*f* luminance compensation.

Motion detection

Figure 3 shows the performance of M.S. for the detection of motion of sinusoidally modulated chromatic gratings. Performance was significantly poorer when the gratings were compensated for the effects of subadditivity (Walsh test; $p < 0.047$, two-tailed). As contrast was reduced, he found it increasingly difficult to detect the motion of the grating. Adding luminance compensation decreased motion detectability for all contrasts except the lowest, the effect being equivalent to an approximately 2.5% reduction in chromatic contrast of the uncompensated grating.

Saccadic eye movements

Data were analysed off line by a procedure that detected the first of two successive samples with a velocity > 25 s⁻¹. Saccade latency, the time taken from display onset to the initiation of the first saccade, and landing position were recorded. Landing positions were recorded for saccade direction. A few trials, where saccades were of a la-

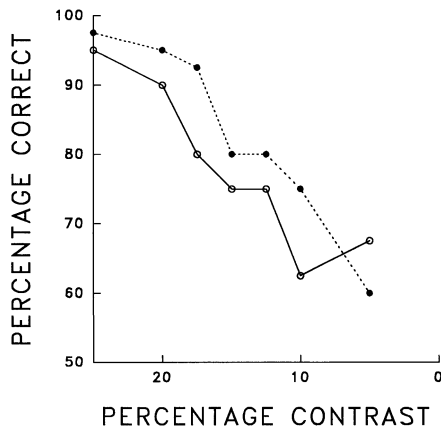


Fig. 3 For M.S. the percentage correct in a 2AFC task of motion detection is plotted against the percentage chromatic contrast of the grating, with (continuous line) and without (dotted line) additional luminance compensation to correct for the perceptual consequences of subadditivity

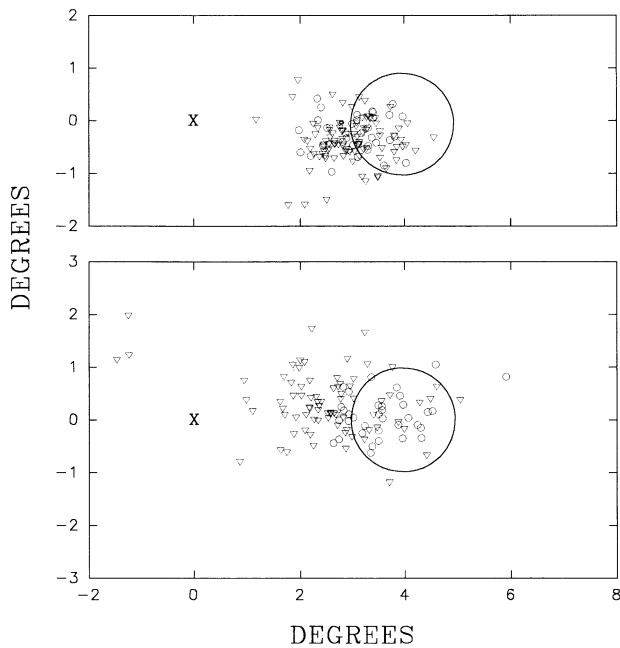


Fig. 4 Points represent the amplitudes of saccades made from the fixation point (cross) to the circular target area that contained chromatic discs (open circles) or sinusoids (triangles). Data for compensated and uncompensated sinusoidal targets did not differ in their distribution and are pooled. The upper and lower portions of the figure show data for the control subject and M.S., respectively

tency less than 180 ms or an amplitude smaller than 1° , were discarded. Saccadic eye movements to chromatic targets are displayed in Fig. 4 for a normal observer and M.S.

The accuracy with which M.S. was able to saccade to square-wave chromatic or achromatic disc targets was similar to that of a normal observer U.S. (means: chromatic, M.S. 3.63° , U.S. 3.11° ; achromatic, M.S. 3.10° , U.S. 3.38°). Saccades of both observers fell short of the

target centre at 4° , which is a characteristic of saccades elicited by such targets. For sinusoidally modulated targets the distribution of landing positions for the normal observers (means: chromatic, 3.03° ; achromatic, 3.14°) was identical to that of disc targets ($t=0.96$, df 128, $p>0.05$; $t=1.09$, df 73, $p>0.05$, for chromatic and achromatic targets, respectively). However, M.S. showed a wider distribution of landing positions and made significantly smaller saccades to sinusoidally modulated targets (means: chromatic, 2.68° , achromatic, 2.55°) than to discs ($t=5.78$, df 115, $p<0.01$; $t=3.78$, df 44, $p<0.01$, for chromatic and achromatic targets, respectively). Introducing a luminance correction for the effects of subadditivity did not influence target accuracy for either subject (M.S. 2.69° , U.S. 3.17°).

However, analysis of variance of saccade latencies using Accuracy (saccades on-target vs off-target, i.e. $<14^\circ$ or $>14^\circ$ of angular error) and Compensation (compensated or uncompensated) as factors revealed further differences. M.S. made significantly slower saccades overall to compensated targets than to uncompensated targets ($F=5.09$, df 1,124, $p<0.05$) and was quicker to on- than off-target saccades ($F=21.8$, df 1,124, $p>0.001$). However, the interaction of Accuracy \times Compensation was not significant ($F=0.81$, df 1,124, $p>0.05$). Thus for saccades on-target, mean latencies were 383 ms and 355 ms, for compensated and uncompensated targets, respectively. For inaccurate, off-target saccades mean latencies were 498 ms and 432 ms, for compensated and uncompensated targets, respectively. In short, M.S. showed slower, but no less accurate, saccades to compensated compared with uncompensated targets. But for the normal observer there was no effect on saccadic latency to chromatic sinusoids of Accuracy ($F=3.51$, df 1,124, $p>0.05$), Compensation ($F=2.27$, df 1,124, $p>0.05$) or their interaction ($F=0.25$, df 1,124, $p>0.05$). Thus for saccades on-target, mean latencies were 230 ms and 251 ms, for compensated and uncompensated targets, respectively. For inaccurate, off-target saccades mean latencies were 254 ms and 264 ms, for compensated and uncompensated targets, respectively.

Both M.S. and U.S. were overall quicker to make saccades to discs than to sinusoids (M.S.: $F=27.27$, df 1,157, $p<0.001$; U.S.: $F=18.97$, df 1,201, $p<0.001$). However, while M.S. was also slower with either type of chromatic target compared with their achromatic counterparts ($F=6.42$, df 1,157, $p<0.05$), this was not true for the normal observer ($F=1.41$, df 1,201, $p>0.05$). Additionally, M.S. showed a significant interaction ($F=8.34$, df 1,157, $p<0.005$) whereby saccadic latencies were substantially slower to chromatic sinusoids (mean 379 ms) than to the three other target types. This was not found with U.S. ($F=0.25$, df 1,201, $p>0.05$).

Discussion

A grating that varies in both wavelength and luminance will stimulate both chromatic (P) and broad-band (M) cells. They are preferentially sensitive to slow and fast ve-

locities, respectively. An isoluminant chromatic grating will minimally excite M cells, causing it to be perceived as moving slower than an achromatic grating. This is motion slowing. If M.S. has no useful P-channel and therefore detects motion only with his M cells he should not show motion slowing and should not perceive slow velocities well. Neither is true, confirming that he does process chromatic information despite being colour blind.

We chose low spatial frequency gratings to avoid the introduction of luminance artefacts by chromatic aberration. While the relative luminances of the red and green guns were selected by flicker photometry to be indiscriminable to M.S., we could not be sure that they were isoluminant for our normal observers. Slight deviations are tolerable because the point of interest was judgements of motion slowing and not the detection of gratings per se. An alternative means of ensuring isoluminance is described by Mullen (1985), where the spatial and temporal frequency maxima or minima are determined in contrast sensitivity functions to gratings and where the mean luminance of the component colours is varied. It is not immediately apparent whether this procedure creates subadditive colour mixture. The interested reader is referred to the Appendix below, which shows that our method of correction compensates for subadditivity in the subjective brightness function while Mullen's compensates for changes in the relative subjective brightness of red and green without providing fortuitous subadditivity compensation.

The chief findings can be summarized as follows. Compensation for subadditivity, an effect resulting from colour-opponent processes, conspicuously influenced judgements of chromatic grating velocity and motion detection. A minimum apparent velocity of drifting gratings was achieved by the addition of $2f$ luminance modulation at a contrast of 5% in both M.S. and control subjects. Subadditive correction neither accounted for preserved threshold sensitivity to chromatic contrast in an achromatopsic patient, at least at the low spatial frequency tested, nor impaired the ability to determine the orientation of a suprathreshold grating. Failure to perform coarse isoluminant hue discriminations is therefore accompanied by a striking sensitivity to chromatic contrast that cannot be explained by additivity failures providing unintended luminance differences. M.S. was able to make accurate saccades to chromatic and achromatic disc targets but had greater difficulty in locating sinusoidal targets. Saccadic latencies increased significantly for all chromatic, compared with luminance, targets but were faster to chromatic discs than to sinusoids. Introducing subadditive compensation further decreased saccadic latency.

Detection of an isoluminant red/green chromatic grating is subserved by an opponent mechanism, the RG hue system, which performs a differencing on the outputs of L and M cones. The chromatic mechanism is distinct from, and approximately 7 times more sensitive than, the L+M luminance mechanism (Stromeyer et al. 1995). We assume, given the method by which luminance is defined, that an isoluminant chromatic grating produces little or

no modulation of activity in the broad-band M-channel. Modulation of activity in the P-channel signals the variation in wavelength across the stimulus. However, activity of the channel is at a minimum for a red/green mixture which results in a nulling of opponent responses and a reduction of perceived brightness. We attempted to compensate for subadditivity by adding a luminance modulation that corresponded (as a first-order approximation) to the pattern of subadditivity produced by a stimulus. This luminance variation should produce modulation of activity in the M-channel, albeit negligibly at detection threshold. However, if the luminance variation increases the quantum catch by an equivalent amount in the P-channel, then the L-M chromatic signal will remain unaltered. Compensation should therefore have no effect on chromatic detection thresholds of static gratings. M.S.'s detection threshold for a low spatial frequency grating was unaffected by the addition of luminance compensation. For suprathreshold gratings of 100% chromatic contrast, 5% frequency-doubled luminance compensation did not render the grating any less visible to him, implying again that the visibility of the uncompensated grating was not determined by subadditive effects. However, it is clear that while compensation may attenuate the perceptual effects of subadditivity, it will introduce an L+M signal that may be detected by the luminance mechanism. The utility of such a signal will depend on colour/luminance interactions that are not straightforwardly predictable from their independent properties. For example, colour is more effective at masking luminance than the converse (Switkes and De Valois 1983), perhaps as a result of the multiplexing of these properties by the same cells early in the visual pathway.

While different compensation contrasts failed to affect detection, they had reliable effects on the perception of motion. Thresholds for perceiving slow chromatic motion are determined by a spectrally opponent mechanism (Stromeyer et al. 1995). At suprathreshold levels, adding a $2f$ luminance profile resulted in additional motion slowing in M.S. and normal observers, and affected motion detectability in the former. This implies that slow-motion chromatic mechanisms are intact in M.S. for gratings constructed with wavelength mixtures that he cannot tell apart. Detailed consideration of why luminance addition compromises the opponent motion pathway cannot be dealt with adequately here. It is clear that there is considerable interaction between the luminance and opponent motion pathways (Cavanagh and Anstis 1991). We can no longer assume that the output of P cells is solely determined by a colour-opponent mechanism. In addition, there is some summation of centre and surround activation as a result of phase shifts between L and M responses. As a consequence, compensation will influence the P-channel (to an extent not readily quantifiable) because, although the output of the colour-opponent mechanism is not changed by additional luminance, luminance will produce changes of output through the centre-surround additive mechanism even at the point of colour balance. This provides a route through which luminance compensation

can affect P-channel processes. The addition of compensation decreases the rate at which P-channel colour signals (i.e. separate red-on and green-on activations) vary across the stimulus, and also reduces the overall (i.e. summed red-on and green-on) variation in P-channel activation across the stimulus. Hence, we should expect compensation to affect motion discrimination but not detection thresholds. Further support for the notion that the P-channel alone can signal slow luminance motion stems from the demonstration that detection of such motion is unaffected by lesions to magnocellular geniculate layers of the monkey (Schiller et al. 1990).

The results of the eye movement recordings confirmed previous findings in normal observers, where the distribution of saccadic reaction times is the same both for chromatic targets, with a range of colour contrast including isoluminance, and for low-contrast achromatic targets (Weber et al. 1991). While M.S. made saccades that, on average, fell short of the sinusoidal targets, compared with those of the control subject, he showed a wider distribution of landing positions. However, the most conspicuous difference was in saccadic latencies which were longer to sinusoidal targets than to disc targets, and were further lengthened with the introduction of subadditive compensation. In the monkey, the superior colliculus, implicated in eye movements, receives a direct projection from retinal M cells as well as P and M inputs from layer V of striate cortex (Tootell et al. 1988). While their relative contributions to the programming of saccades is not known, it is clear that the speed and accuracy of eye movements to chromatic sinusoidal targets are reduced in achromatopsia and are further compromised by compensating for perceived brightness differences resulting from subadditivity.

In conclusion, while the mechanisms responsible for discerning differences in hue are absent in a patient with total cerebral achromatopsia, wavelength processes signalling other visual attributes are not compromised. Notably, the mechanisms for detecting spatial and temporal variation of hue, subserved by chromatically opponent mechanisms, are essentially normal. In contrast, compensation for perceived brightness differences affects eye movements to stationary targets in an achromatopsic patient in a manner not apparent in the normal observer.

Appendix

Other authors have measured the extent to which subjective brightness deviates from expected luminance when colours are added in relatively low temporal frequency stimuli. The most widely cited approach was described by Mullen (1985). We can, however, show that the method we have described and that of Mullen correct for different types of deviation from ideal luminance additivity. Our method involves the addition of a $2f$ isochromatic luminance correction while Mullen's depends on changing the ratio of the mean luminances of the red and green components of a grating while maintaining their individual chromatic contrasts. Compensation using our method produces a stimulus with a $2f$ luminance modulation while Mullen's method produces a $1f$ modulation. Intuitively it would appear that our method corrects for subadditivity (which produces

brightness variation with a frequency of $2f$ – one cycle falling between each “yellow” band of the stimulus), while Mullen's corrects for changes in the relative brightness of red and green. It is not, however, intuitively obvious whether the changes in chromaticity (in particular the spatial distribution of colour) that occur as a result of Mullen's procedure serendipitously compensate for subadditivity. This hypothesis can be tested by fitting subjective brightness functions:

$$B(r, g) = k_r r + k_g g + k_{rg} r g$$

to stimuli corrected using each method. The fit must minimise variation of subjective brightness across the stimulus [measured as the coefficient of variation: $C_v(B) = \sigma(B)/\bar{B}$] at some amount of correction that does not trivially leave the stimulus isoluminant.

Our correction is governed by a single parameter, c_k , which determines the relative amplitudes of the underlying isoluminant grating and the $2f$ luminance compensation. We can express the luminance of the red component of the stimulus at each position x as:

$$K_r(x, c_k) = \sin(x) + c_k \sin(2x + \Pi/2) \sin(x)$$

and the green component as:

$$K_g(x, c_k) = \sin(x + \Pi) + c_k \sin(2x + \Pi/2) \sin(x + \Pi)$$

Mullen's correction is also governed by a single parameter, c_m , which expresses the relative mean luminances of the red and green components [e.g. $c_m = r/(r+g)$ where r and g are the mean luminances of the red and green components]. We can express the variation of luminance with position as:

$$M_r(x, c_m) = [1/(1 + 1/c_m)] + \sin(x)$$

for red, and

$$M_g(x, c_m) = [1/(1 + c_m)] + \sin(x + \Pi)$$

for green.

Our aim is therefore to find a function $B_k(r, g)$ that minimises

$$C_v[B_k(K_r(x, c_k), K_g(x, c_k))]$$

with the constraint that:

$$C_v[B_k(K_r(x, c_k), K_g(x, c_k))] < C_v[B_k(K_r(x, c_k + \delta), K_g(x, c_k + \delta))] \\ < C_v[B_k(K_r(x, c_k - \delta), K_g(x, c_k - \delta))]$$

for some $c_k \neq 0$ and similarly to find another function $B_m(r, g)$ that minimises

$$C_v[B_m(M_r(x, c_m), M_g(x, c_m))]$$

with the constraint that:

$$C_v[B_m(M_r(x, c_m), M_g(x, c_m))] \\ < C_v[B_m(M_r(x, c_m + \delta), M_g(x, c_m + \delta))] \\ < C_v[B_m(M_r(x, c_m - \delta), M_g(x, c_m - \delta))]$$

for some $c_m \neq 1/2$. In both cases the constraints involving variation of the correction parameter by a small amount δ ensures that the solutions found are true minima of subjective brightness variation with respect to the control parameter.

Computational method and results

We computed these optimisations using Newton's method with quadratic estimates for a number of values of c_k and c_m with the following results:

Four our function with $c_k=0.2$ and $\delta=0.05$ we obtained $B_k=1.30 r+1.31 g-0.38 r g$ with coefficients of variation for c_k , $c_k+\delta$ and $c_k-\delta$ of 0.0071, 0.0126 and 0.0150 respectively (Fig. A1). For $c_k=0.4$ and $\delta=0.05$ we obtained $B_k=1.17 r+1.18 g-0.51 r g$ with coefficients of variation for c_k , $c_k+\delta$ and $c_k-\delta$ of 0.0204, 0.0223 and 0.0214 respectively.

Fig. A1 Optimisation of a subjective brightness function for our compensation function. In each panel the *continuous line* represent the output of the subjective brightness function and the two *dashed lines* represent the compensated red and green components of the stimulus. The *first panel* shows results for the optimised compensation; the *other panels* show results for this value $\pm\delta$

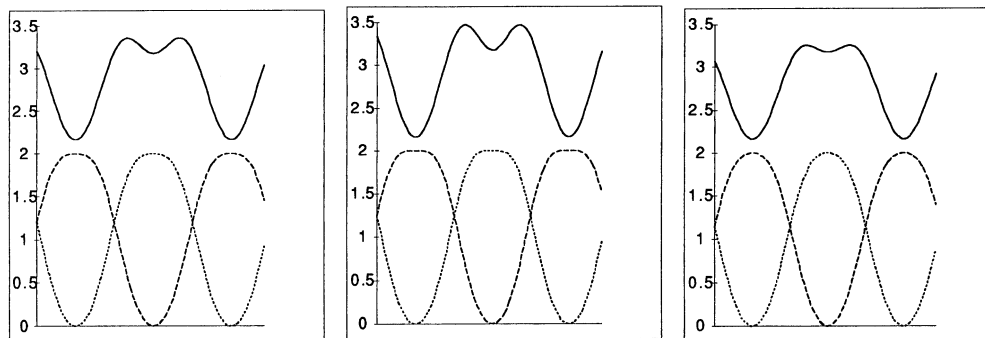
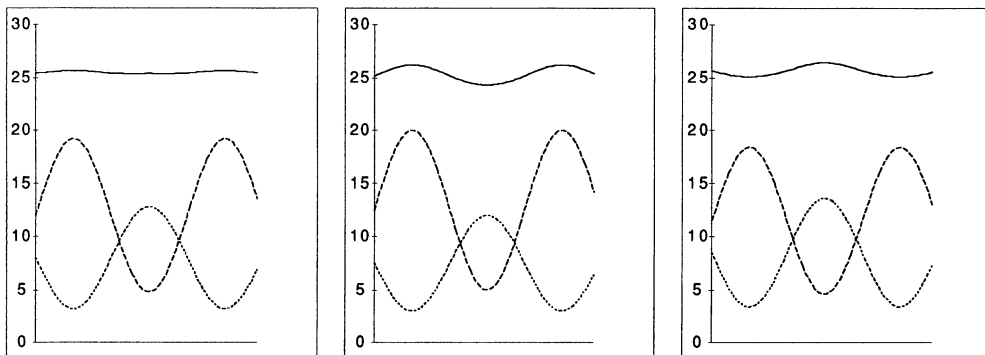


Fig. A2 Optimisation of a subjective brightness function for Mullen's compensation function. In each panel the *continuous line* represent the output of the subjective brightness function and the two *dashed lines* represent the compensated red and green components of the stimulus. The *first panel* shows results for the optimised compensation; the *other panels* show results for this value $\pm\delta$



For Mullen's function with $c_m=0.6$ and $\delta=0.025$ we obtained $B_m=1.08 r+1.59 g-0.0028 rg$ with coefficients of variation for c_m , $c_m+\delta$ and $c_m-\delta$ of 0.0035, 0.0258 and 0.0182 respectively (Fig. A2). For $c_m=0.7$ and $\delta=0.025$ we obtained $B_m=1.11 r+2.60 g-0.0130 rg$ with coefficients of variation for c_m , $c_m+\delta$ and $c_m-\delta$ of 0.0043, 0.0241 and 0.0241 respectively.

Conclusions

It is clear from these results that variation in the control parameter of our function leads to changes in the optimal value of the rg factor while leaving the ratio of r to g factors near unity. Variation of the control parameter of Mullen's function, however, leads to changes in the optimal ratio of the r and g factors while leaving the rg factor very small. We can therefore conclude that our method of correction compensates for subadditivity in the subjective brightness function while Mullen's compensates for changes in the relative subjective brightness of red and green without providing fortuitous subadditivity compensation.

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