

Optimization of large field tritan stimuli using concentric isoluminant annuli

Neil R. A. Parry

University of Manchester Health Science Research
Centre and Vision Science Centre,
Manchester Royal Eye Hospital, Manchester, UK



Anthony G. Robson

Institute of Ophthalmology, University College London
and Department of Electrophysiology,
Moorfields Eye Hospital, London, UK



Large, nominally isoluminant chromatic gratings containing a short-wavelength component are prone to luminance contrast intrusions due to retinal inhomogeneity, especially as a result of the uneven distribution of macular pigment. Isoluminance is usually determined for a relatively small, central area, but a significantly larger stimulus cannot be isoluminant across the whole field, largely due to macular pigment absorption of short-wavelength light. This confounds attempts to maintain high selectivity, particularly in suprathreshold electrophysiological and brain-imaging studies that require large stimulus fields. Here we introduce the concept of a panisoluminant grating (PIG), which comprises a series of concentric annular regions, each adjusted to location-specific isoluminance for the observer. Gratings were modulated along subject-specific tritanopic confusion lines and the selectivity of responses to the PIG was tested according to both psychophysical and electrophysiological criteria. The psychophysically-determined temporal tuning function obtained using the PIG showed lower sensitivity and lower resolution than with a conventional tritan grating of equal diameter (18°). Chromatic onset visual evoked potentials (VEPs) to the PIG were dominated by a chromatic-specific negative wave and reduced achromatic response components that were prominent in VEPs to the conventional grating. These data demonstrate that a large tritan PIG is capable of eliciting selective responses of the S-cone-driven pathway at threshold and at suprathreshold levels. The PIG stimulus may prove beneficial in investigations that require large fields such as electrophysiological and brain imaging studies of chromatic processing.

Keywords: isoluminance, blue-yellow, koniocellular, macular pigment, VEP, psychophysics

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Introduction

The primate retinostriate visual system may be subdivided into anatomically distinct magnocellular, parvocellular, and koniocellular pathways. Attempts to investigate these selectively have commonly involved the use of achromatic and chromatic gratings. Numerous spatiotemporal and chromatic stimulus parameters have been employed, a major thrust of this work being to optimize visual pathway response selectivity. It is well-established that psychophysically-determined chromatic temporal tuning functions exhibit low temporal resolution and low-pass temporal tuning (DeLange, 1958; Gouras, 1968; Granger & Heurtley, 1973; McKeefry, Murray, & Kulikowski, 2001; Swanson, Ueno, Smith, & Pokorny, 1987), consistent with the slower conduction velocities of color-opponent axons (Dreher, Fukada, & Rodieck, 1976) and the activity of chromatic sustained (tonic) response mech-

anisms of the parvocellular or koniocellular pathways (Gouras, 1968).

Cortical visual evoked potentials (VEPs) may also be used to characterize the activity of these pathways objectively. The onset-offset presentation of low contrast, low spatial frequency isoluminant red/green or tritan gratings elicits waveforms that are dominated by a negative component of opposite polarity to corresponding chromatic reversal or achromatic VEPs (Berninger, Arden, Hogg, & Frumkes, 1989b; Carden, Kulikowski, Murray, & Parry, 1985; Crognale, Page, & Fuhrel, 2001; Kulikowski, Murray, & Parry, 1989; Kulikowski, Murray, & Russell, 1991; Murray, Parry, Carden, & Kulikowski, 1987; Parry et al., 1988; Porciatti & Sartucci, 1999; Rabin, Switkes, Crognale, Schneck, & Adams, 1994; Suttle & Harding, 1999). There is some intersubject variability but the onset negativity is often followed by a positive wave. Conversely, the onset VEP to a coarse achromatic grating is usually characterized by a major early

positive component, flanked by two smaller negative components. With low spatial frequencies, achromatic VEPs have a similar shape to stimulus onset and offset but chromatic VEPs show a marked difference and this has been attributed to the dominant contribution of sustained chromatic responses to stimulus onset (Kulikowski et al., 1989; Kulikowski & Parry, 1987). These psychophysical and electrophysiological characteristics may be used to test response selectivity at threshold and suprathreshold levels (Kulikowski, McKeefry, & Robson 1997).

A major problem with chromatic gratings is that isoluminance varies between individuals and must be optimized for each observer using techniques such as heterochromatic flicker photometry (HFP) or fast-flicker VEPs (Kulikowski et al., 1991; Kulikowski, Robson, & McKeefry, 1996; McKeefry, Russell, Murray, & Kulikowski, 1996). Additionally, nominally isoluminant stimuli are prone to luminance contrast intrusions due to chromatic aberration (Bedford & Wyszecki, 1957; Cavanagh & Anstis, 1991; Charman & Kulikowski, 1991) and filtering by macular pigment (MP); these effects are worse for stimuli containing a short-wavelength component. Chromatic aberration can be minimized (Kulikowski & Walsh, 1991) but the effects of MP may be more problematic (Robson, Holder, Moreland, & Kulikowski, 2006; Robson & Parry, 2008). Both peak MP optical density and the

distribution of MP across the central retina vary between individuals (Pease, Adams, & Nuccio, 1987; Robson, Moreland et al., 2003). One solution is to determine isoluminance for the central, heavily pigmented, macular area using HFP and then to use a similarly small central stimulus. However, this has obvious disadvantages in some psychophysical studies and in paradigms that require suprathreshold testing to elicit robust responses, e.g., cortical visual evoked potentials and functional brain imaging studies.

The aim of the current study was to optimize the chromatic specificity of large tritan stimuli by using a novel panisoluminant grating (PIG) comprising multiple concentric annuli. The key feature of this stimulus is that the luminance ratio within each annulus is adjusted for each individual using HFP, thus compensating for retinal inhomogeneity, particularly that relating to MP. The selectivity of the PIG was compared with that for conventional tritan gratings by measuring psychophysically-determined temporal tuning functions. We also gauged their selectivity by recording VEPs to PIGs and conventional tritan stimuli.

Methods

Stimuli

Grating stimuli were generated using a VSG2/5 (Cambridge Research Systems Ltd, Rochester, UK) card in a PC. The display screen was a 21-inch high-resolution graphics monitor (GDM-F520, Sony Corporation, Tokyo, Japan) with a frame rate of 120Hz. Red, green and blue gun gamma functions were calibrated using an OptiCal photometer head (Cambridge Research Systems Ltd, Rochester, UK), and checked with a PR-650 photospectroradiometer (Photo Research Inc., Chatsworth, CA). Nonlinearities in the OptiCal photometer were corrected using the two-pass technique described by Parry, McKeefry, and Murray (2006). Gratings were oriented vertically and spatial frequency was $2\text{ c}/^\circ$. Chromatic stimuli were created by choosing two points in CIE 1931 color space and modulating sinusoidally between them (see Figure 1). The chromatic vector was rotated to determine subject-specific tritanopic confusion axes according to a minimum distinct border criterion (Robson & Kulikowski, 1998; Tansley & Boynton, 1978). The stimuli were initially modulated along one of two chromatic axes (Figure 1). Vector 1 initially intersected copunctal blue (i.e., $x = 0.175, y = 0$; Smith & Pokorny, 1975) but was then rotated around a yellow point (Porciatti & Sartucci, 1999), halving its length to

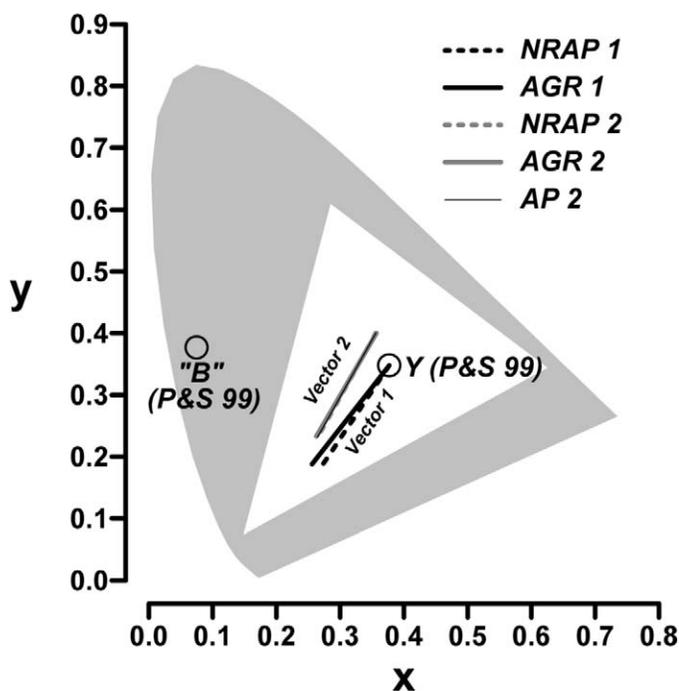


Figure 1. CIE 1931 Chromaticity diagram (gray area), showing the monitor's gamut (white triangle), Porciatti and Sartucci's (1999) quoted blue and yellow loci, and the vectors used here to generate blue-yellow gratings. Note that Porciatti and Sartucci's 'blue' falls outside the gamut of the monitor.

remain within the gamut. Vector 2 was the $90^\circ/270^\circ$ cardinal axis and this was rotated around its midpoint.

The chromaticity coordinates for vector 1 (before rotation) were $x = 0.377$, $y = 0.348$ (yellow) and $x = 0.276$, $y = 0.174$ (blue). The midpoint (i.e., zero contrast) varied slightly depending on the final chosen vector rotation. The chromaticity coordinates for vector 2 (before rotation) were $x = 0.348$, $y = 0.404$ (yellow) and $x = 0.272$, $y = 0.228$ (blue). The midpoint was illuminant ‘C’ ($x = 0.31$, $y = 0.316$). The achromatic version of vector 1 was luminance-modulated yellow while, for vector 2, luminance was modulated around illuminant ‘C’.

Four different stimulus configurations were employed:

- Achromatic grating.* A circular field with a diameter of 18° .
- Small centrally isoluminant grating.* A circular field with a diameter of 3° (vector 1) or 2.7° (vector 2). Subject-specific isoluminance was determined using HFP for the central 1.2° .
- Large centrally isoluminant grating.* A circular field with a diameter of 18° . Subject-specific isoluminance was determined using HFP for the central 1.2° .
- Large panisoluminant grating (PIG).* A 1.2° circular field surrounded by seven contiguous and concentric annuli; 1.8° , 2.7° , 4° , 6° , 9° , 13.5° , and 18° in diameter. The chromaticity and luminance ratio of component wavelengths within the central field and each of the concentric annuli could be adjusted (see Figure 2). The radii of the stimuli were chosen according to a previous study that used narrow

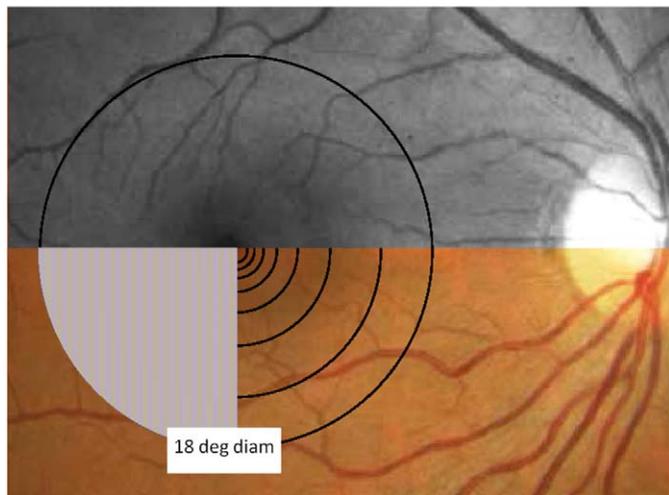


Figure 2. Section of the multiple annular panisoluminant grating showing the grating in one quadrant, and the borders of the annuli in another. These are superimposed on a normal fundus photograph, part of which is shown in grayscale to visualize the macular pigment. Only a quarter of the actual stimulus is shown here for illustrative purpose.

annuli for retinal areas over which MP distribution changes most steeply (Robson & Parry, 2008). The borders between annuli were undetectable.

Mean luminance was 10 cd/m^2 . A small (0.3°) black fixation cross was provided at the center and the stimulus was viewed binocularly at a distance of 70 cm. The unmodulated part of the screen had the same mean luminance and chromaticity as the grating.

Procedure

Vector optimization

Subject-specific tritan stimulation was determined by first establishing the vector rotation that gave a minimally distinct border using a 2° bipartite field with each half containing the color at one or other end of the vector. The stimulus reversed every 2 s to minimize adaptation. Using the mouse scroll-wheel and method of adjustment, the subject rotated the vector in CIE space in increments of 1° , searching for the setting that gave the least distinct percept of a border. The average of five settings was taken. Using this vector, isoluminance was then established using heterochromatic flicker photometry. To construct the PIG stimulus, the central 1.2° field was first presented on an otherwise blank field of the same mean hue and mean luminance. The 2 c/° grating was presented at a rate of 8Hz (16 reversals/s) and the relative luminance of adjacent hues were adjusted reciprocally until the flicker was minimized. Blue-yellow ratio was defined as

$$\text{Ratio} = \frac{L_B}{L_B + L_Y} \quad (1)$$

where L_B and L_Y were the luminances of the blue and yellow ends of the vector. For vector 1 this was changed in steps of 0.1 and for vector 2 the step size was 0.0005. The setting was determined five times and the average used. The procedure was then repeated for each isolated annulus, with center and surround again set to mean hue and luminance. Together the two procedures took about 30 minutes to complete. The panisoluminant grating was composed of the central field and all the individual annuli, each at its own predetermined isoluminance ratio. For the conventional grating the blue-yellow luminance ratio across the whole of the stimulus field was that determined for the central 1.2° area.

Psychophysics

Contrast thresholds were measured for all stimulus configurations. One hundred percent contrast was defined as the maximum vector. Cone contrasts were similar for each unrotated vector. At 100% modulation, they were $L = 0.002$, $M = 0.002$ and $S = 0.574$

(vector 1) and $L = 0.003$, $M = 0.003$, $S = 0.610$ (vector 2). These figures were computed from the spectral radiance of the CRT phosphors and the spectral sensitivity of the cones (Kremers & Meierkord, 1999).

Contrast was set in dB where

$$C_{dB} = -20\log_{10}(C) \quad (2)$$

Thus 100% contrast = 0 dB, and 50% = 6 dB, representing a halving of the vector length. Temporal sensitivity was measured using a reversing $2\text{ c}/^\circ$ grating at frequencies between 0.3 Hz and a maximum of 20 Hz. The temporal envelope was sinusoidal. At each temporal frequency, two thresholds were determined. Following Kulikowski and Tolhurst (1973), subjects were required to determine the contrast at which temporal modulation was just detectable (“movement”), or at which the spatial structure of the grating could be distinguished (“pattern”). Five movement and five pattern thresholds were measured using the method of adjustment and an average taken for each.

Visual evoked potentials

Cortical VEPs were recorded to onset-offset presentation of each stimulus with on and off durations of 260 ms each. The acquisition was triggered by the onset. Signals were recorded from a midline occipital electrode located at Oz (10% of the inion-nasion distance) with linked ear electrodes as reference and a forehead ground electrode. All electrodes were 9 mm Ag/AgCl discs (BioSense Medical Ltd, Chelmsford, UK). The skin was gently abraded using NuPrep paste (Weaver, Aurora, CO). The electrodes were attached to the scalp using Ten20 conductive EEG paste (Weaver, Aurora, CO) and to other areas with adhesive tape and Signagel conductive gel (Parker Laboratories, Fairfield, NJ). Impedance was less than 5 k Ω . The signals were amplified using a Grass Model 15A94 neurophysiological amplifier (Astro-Med Inc., W. Warwick, RI) with bandwidth 0.3 to 100 Hz and gain 20,000x. The amplified signals were averaged using a CED1401plus interface (Cambridge Electronic Design Ltd, Cambridge, UK) running CED’s own software (Signal Version 2.16).

Subjects

The two authors were the main subjects (NRAP, aged 53 and AGR, aged 44); both have extensive experience as observers in psychophysical experiments. For experiments involving vector 2, additional data were collected from a third subject (AP, aged 29), who was an experienced psychophysicist but naïve as to the purpose of the experiment. All subjects had normal color vision (Ishihara, 100-hue, Nagel Model 1

Anomaloscope [Schmidt and Haensch GmbH, Berlin, Germany]) and corrected visual acuity better than 0 (LogMAR). The study was conducted under the tenets of the declaration of Helsinki.

Results

Isoluminance

To achieve a minimally distinct border, vector 1 was rotated clockwise by 3° for subject NRAP and 6° for AGR (see Figure 1). The isoluminant ratio varied with eccentricity and between subjects. The results for vector 1 are summarized in Figure 3. The amount of short wavelength light required to achieve minimum flicker was greatest for the small central circular field. Progressively less was needed for annular gratings with increasing eccentricity, in keeping with the distribution of normal macular pigmentation (Robson & Parry, 2008). From this figure it can be inferred that a large tritan stimulus field cannot be uniformly isoluminant.

Psychophysics

Figure 4 shows temporal tuning functions for the different stimulus configurations. The top row shows overall detection thresholds. In the middle and bottom rows, the thresholds for spatial modulation (“pattern”)

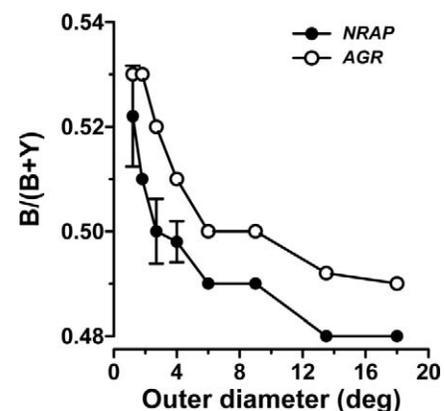


Figure 3. Blue-yellow ratios at isoluminance for vector 1 measured using the individual annular components. These were later combined to form a multiple-annular panisoluminant grating. The x-axis denotes the outer diameter of the stimulus, so that the lowest value was for the central disk, and each subsequent value refers to the outer diameter of each annulus, the inner diameter being the previous value. Data points are joined to illustrate the similarity of shape to typical MP distribution profiles. Each data is the mean of five measurements; 95% confidence limits are shown where they exceed the symbol size.

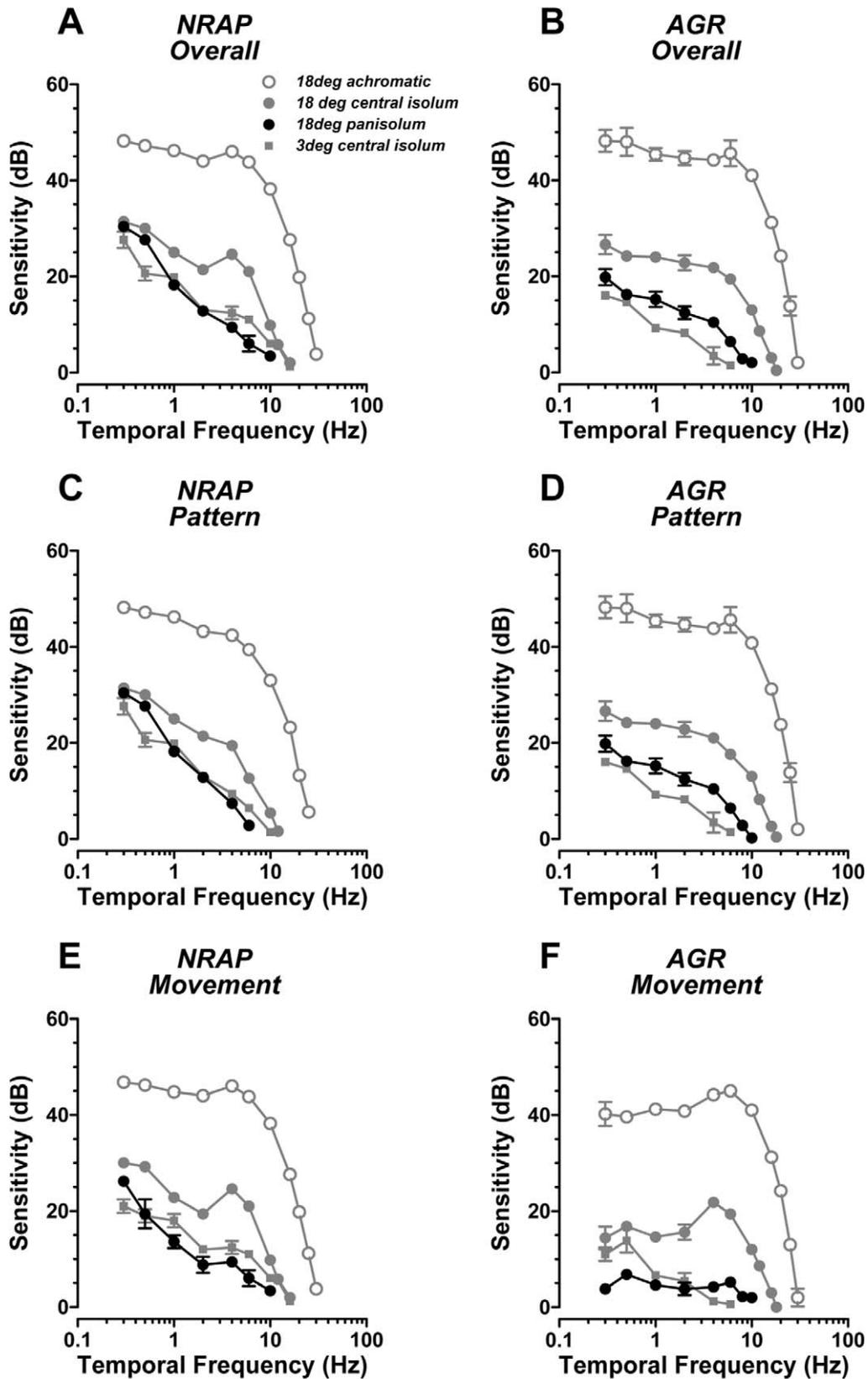


Figure 4. Temporal frequency response curves for the three chromatic gratings modulated along vector 1 and for the large achromatic stimulus. Subjects set separate detection thresholds for spatial modulation (“pattern”) and temporal modulation (“movement”). Each data point is the mean of five determinations. Error bars denote 95% confidence intervals and are not shown if they are smaller than the symbols.

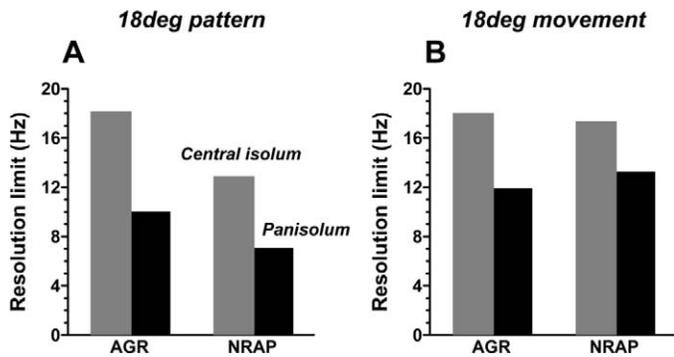


Figure 5. Pattern and movement temporal resolution limits for panisoluminant and centrally isoluminant 18° stimuli. Data were derived by extrapolating to 100% contrast on the last three detectable points on each temporal frequency curve.

and temporal modulation (“movement”) are plotted separately. Figure 5 shows the resolution limits for the 18° conventional grating and for the 18° PIG. When plotted on a linear scale the descending branches of the temporal tuning functions were linear and allowed measurement of temporal resolution by linear regression through the last three data points and extrapolation to 100% contrast (0 dB). All chromatic detection tuning functions showed lower sensitivity and markedly lower resolution than the achromatic functions.

The detection resolution limits for achromatic gratings were approximately 30 Hz and for the

conventional 18° chromatic grating were about 18Hz. Use of the PIG resulted in a 60% to 75% reduction in sensitivity (by 8–12dB at 2 Hz) and a marked reduction in resolution limit (to between 7 Hz and 12 Hz).

Movement sensitivity to the PIG was generally lower than for pattern detection; one subject (AGR) was barely able to detect temporal modulation at any temporal frequency. The shape of the tuning functions was dependent on the stimulus configuration. Tuning characteristics for the achromatic and conventional tritan grating showed a flattening below about 10 Hz (Figure 4A-D) or a low-frequency cut (Figure 4E-F) that was not seen in the low-pass tuning function generated by the PIG or the small conventional tritan grating.

Visual evoked potentials

Figure 6 shows examples of onset-offset VEPs to achromatic and chromatic (vector 1) stimulation. The achromatic response is characterized by a prominent positive component with a peak-time of 133 ms to 144 ms. The achromatic offset component is a broader positive-going wave. The response to the 18° conventional chromatic grating has a major negative component to stimulus onset but additionally there is an earlier positive component in VEPs from both subjects. This is of similar amplitude to the onset negative wave

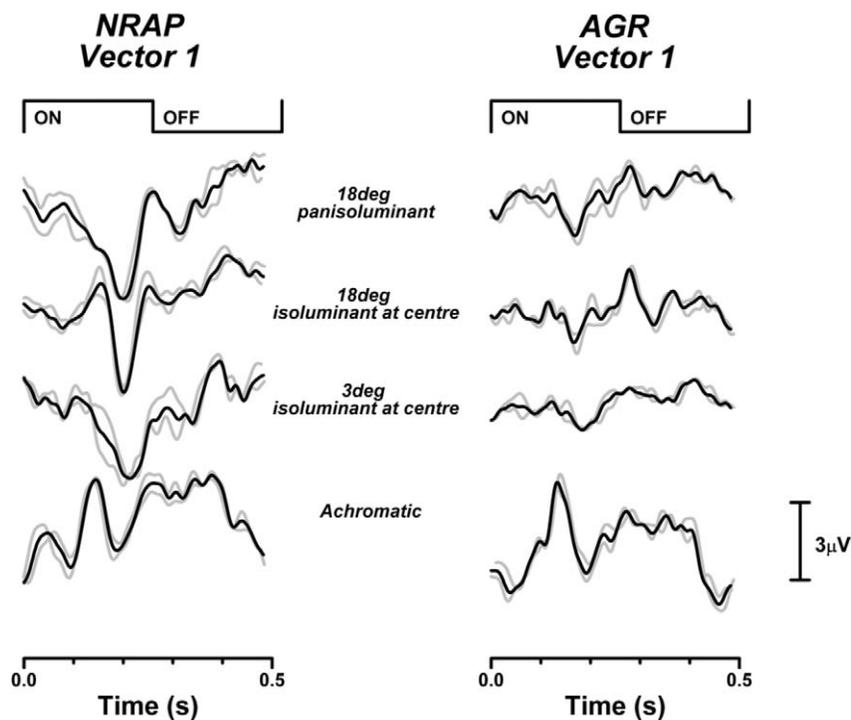


Figure 6. Vector 1 VEPs for both subjects. For the central isoluminance conditions (rows 2 and 3), isoluminance was determined for the central 1.2° and then applied across the whole stimulus. All responses were repeated and waveforms are superimposed to demonstrate consistency (gray traces). The grand average is shown in black.

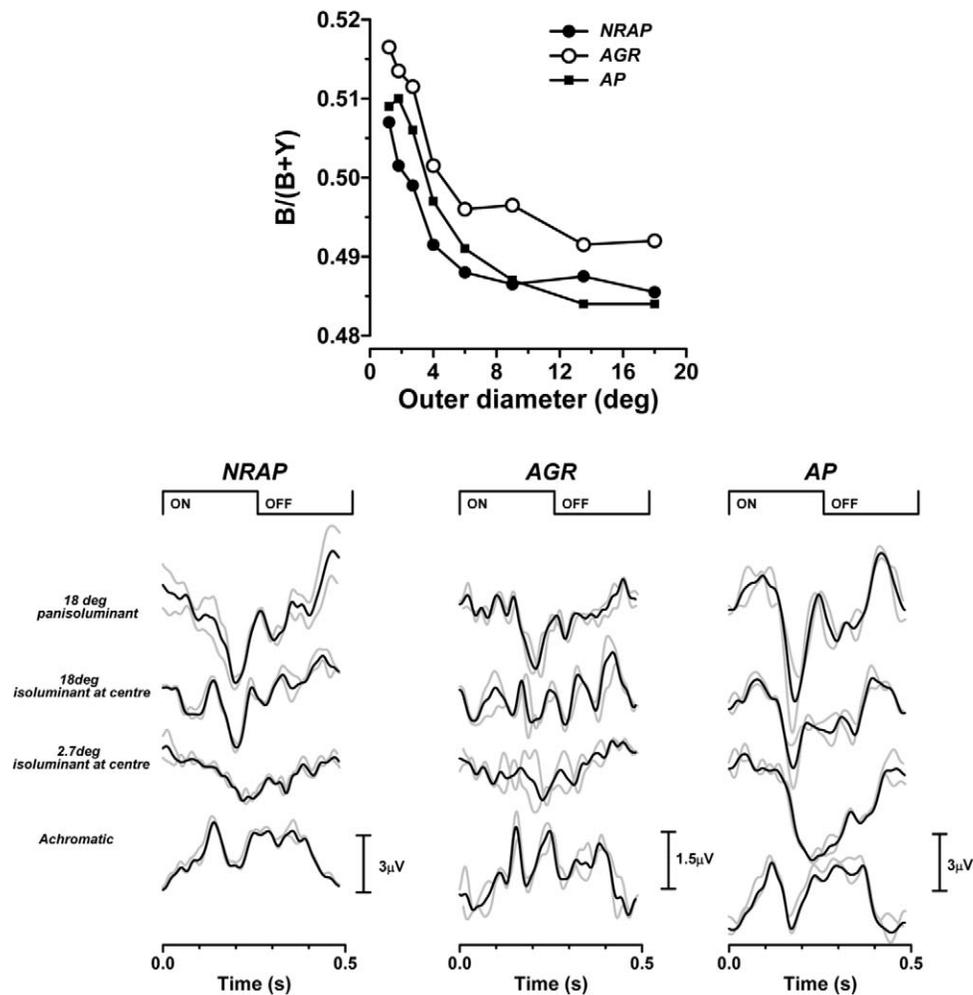


Figure 7. Blue-yellow ratios at isoluminance for vector 2 measured using the individual annular components of the PIG (top) and VEPs recorded from the same three subjects (bottom).

and of the same positive polarity as the achromatic VEP. The presence of an early positivity has been attributed to significant luminance-contrast response intrusion (Robson & Kulikowski, 1998). The onset response to the 3° centrally isoluminant stimulus is characterized by a largely negative chromatic-specific component at approximately 200 ms that is similar to that evoked by the much larger PIG; neither of these configurations elicited significant early positive components.

Figure 7 shows examples of onset-offset chromatic VEPs using vector 2. To achieve minimally distinct borders, the vectors were rotated by 5° for subjects NRAP and AP and 6° for AGR. Despite the fact that, for this vector, there was a relatively small change in the isoluminant blue-yellow ratio from the center to the periphery (of the order of 0.025, compared with about 0.04 for vector 1), there is still a marked difference between the VEPs recorded to the PIG stimulus compared with those recorded to the conventional 18° chromatic grating. The difference varies between the

three subjects but is greatest for subject AGR; the 18° grating elicits a complex VEP dominated by positive peaks that resemble the shape of the achromatic VEP. VEPs to the conventional 2.7° chromatic field are close to noise levels in two of the subjects (NRAP and AGR); with the PIG there is a larger chromatic-specific negative VEP without the achromatic VEP intrusions associated with the conventional large chromatic stimulus.

Further evidence of the likely achromatic intrusion from paracentral areas of the nonoptimized stimulus is presented in Figure 8. VEPs were recorded to a small (2.7°) blue-yellow (vector 2) stimulus which was either panisoluminant or only centrally isoluminant. The same settings were used to record VEPs to a large stimulus comprising all the annuli except the central 2.7°. When the chromatic results are compared with a standard achromatic response, it can be seen that the basic chromatic-achromatic difference (negative vs. positive waves) is seen for all but the peripheral nonoptimized stimulus. Here, there is very little

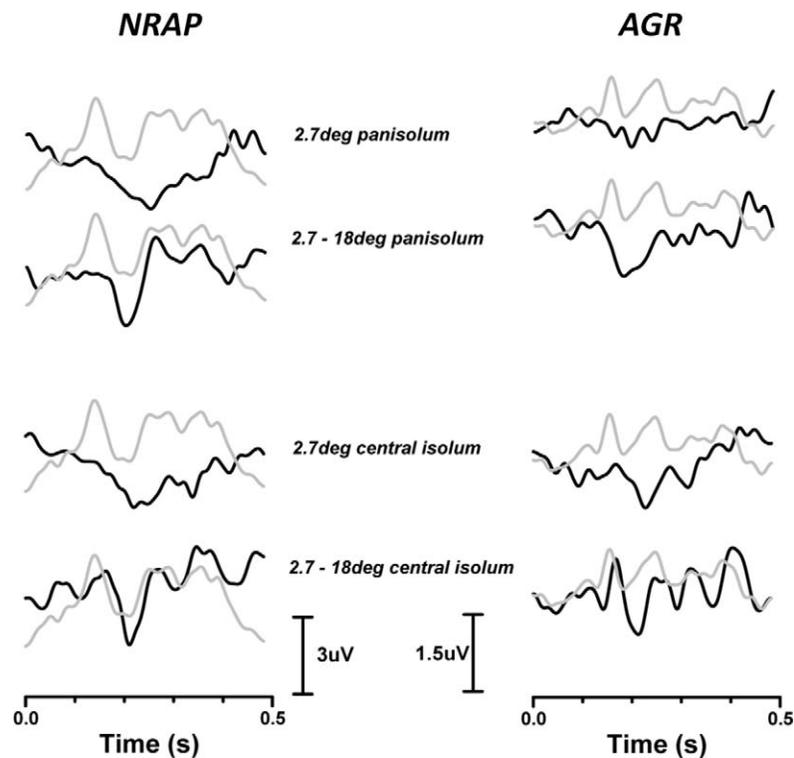


Figure 8. Blue-yellow VEPs recorded to a 2.7° disk and a 2.7°–18° annulus using either the PIG stimulus (top two rows) or a stimulus in which isoluminance was set for the central 1.2° (bottom two rows). For each subject, the same achromatic VEP is superimposed on all four responses (gray lines).

difference between the achromatic and chromatic VEPs.

Discussion

This study addresses the problem of testing the S-cone-driven (koniocellular) pathway using large, nominally tritan stimuli. A novel composite panisoluminant grating (PIG) was generated from multiple concentric annuli, each made to be isoluminant according to HFP. Chromatic selectivity was tested by measuring psychophysically-determined temporal tuning functions. The changing shape of cortical visual evoked potentials with and without optimization was also examined for evidence of achromatic intrusion. The study demonstrates the limitations of using large chromatic stimuli and the greater chromatic selectivity achieved by using the PIG.

It is well established that isoluminance varies between individuals due to retinal inhomogeneity (Livingstone & Hubel, 1987; Zrenner, 1983), lens yellowing (Said & Weale, 1959), and MP (Ruddock, 1963; Stabell & Stabell, 1980). Isoluminance may also be disrupted due to transverse and longitudinal chromatic aberration (Bedford & Wyszecki, 1957;

Cavanagh & Anstis, 1991; Charman & Kulikowski, 1991; Livingstone & Hubel, 1987; Mullen, 1985) and changes in MP with eccentricity (Chen, Chang, & Wu, 2001; Degli Esposti et al., 2012; Hammond, Wooten, & Snodderly, 1997; Moreland & Bhatt, 1984; Moreland, Robson, Soto-Leon, & Kulikowski, 1998; Robson, Moreland et al., 2003). It is implicit in routinely-used psychophysical assessments of MP (Bernstein, Delori, Richer, van Kuijk, & Wenzel, 2010; Howells, Eperjesi, & Bartlett, 2011) that isoluminance varies with eccentricity and it is clear that large stimuli with short-wavelength components cannot be wholly isoluminant (Robson et al., 2006; Robson & Parry, 2008). However, psychophysical investigations of color vision are not confined to the macula and an adequately large stimulus is needed to elicit recordable suprathreshold responses in electrophysiological and functional brain imaging tests.

This study proposes the use of a large panisoluminant grating (PIG) capable of eliciting robust suprathreshold responses that are specific to the koniocellular system. It is demonstrated that such responses are of similar or better selectivity than those evoked by conventional but much smaller tritan gratings, even when the central area of the smaller stimuli is optimized for the observer using HFP. The higher chromatic specificity associated with the (large)

PIG additionally implies that the effects of chromatic aberration are likely to be small compared with those of MP, superseding the conclusions of earlier studies that emphasized the effects of chromatic aberration on chromatic stimuli involving B/Y and tritan gratings (Kulikowski et al., 1997; McKeefry et al., 2001; Robson, McKeefry, & Kulikowski, 1997) and corroborating those that have quantified this effect (Robson et al., 2006; Robson & Parry, 2008).

The paradigms used in the current study are based on the respective temporal response properties of sustained color-opponent neurons and a highly transient subset of magnocellular neurons sensitive to movement. Chromatic opponent responses exhibit low-pass temporal tuning and low temporal resolution (Burr & Morrone, 1993; Green, 1969; Kelly, 1974, 1983; McKeefry et al., 2001). Lower temporal resolution is consistent with greater S-cone pathway selectivity (Figure 5); high temporal resolution or band-pass temporal tuning with intrusion from the achromatic system. The chromatic mechanisms respond poorly to high temporal frequencies and to temporal transients (McKeefry et al., 2001), and temporal resolution is low. For the conventional large centrally isoluminant chromatic grating, the shape of the tuning functions are closer to those for the achromatic than for the PIG stimulus.

Large conventional tritan gratings elicit VEPs with both negative chromatic components and earlier positive achromatic components (Figures 6 and 7). The early positive components have been used to quantify achromatic intrusions in chromatic VEPs (Robson et al., 2006; Robson, Kulikowski et al., 2003). For a large chromatic field, the relative contribution of chromatic and achromatic activity varies between subjects and arises in relation to differences in spectral sensitivity over the large areas that are stimulated and which include the MP (Moreland et al., 1998; Robson et al., 2006). The magnitude of achromatic VEP intrusion may be related to subject-specific MP optical density (or lack of pigment over paracentral areas) and can be used to estimate peak levels and the spatial profiles of MP (Robson & Parry, 2008).

Figure 8 shows that, when the central field is masked, the nonoptimized chromatic VEP is almost indistinguishable from the achromatic response. Thus, even though the VEP is generally considered to be weighted towards the central field (e.g., Meredith & Celesia, 1982; Potts & Nagaya, 1965), paracentral areas also exert a strong effect. This may help explain why VEPs exhibit band-pass temporal tuning to large tritan gratings (Kulikowski et al., 1997; Kulikowski et al., 1996; Rabin et al., 1994; Robson & Kulikowski, 1998; Switkes, Crognale, Rabin, Schneck, & Adams, 1996) but show low-pass tuning to small isoluminant stimuli

(Kulikowski et al., 1997; Kulikowski et al., 1996; Robson & Kulikowski, 1998). The latter studies are consistent with the color psychophysics (Figure 4) but a problem with VEPs is that small gratings may not be large enough to generate a robust chromatic onset VEP in all subjects (e.g., Figure 7; subject AGR) and thus have limited clinical application. It has also been argued that the achromatic intrusions associated with large stimuli are of limited significance in VEP studies as the timing of the chromatic negativity may be unaffected (see Rabin et al., 1994, Kulikowski et al., 1996, and Switkes et al., 1996 for a debate). The data presented above show that the chromatic onset negativity may be abolished if high selectivity is not maintained (Figure 7, subject AGR) and reliable identification of residual chromatic components may be difficult unless a more selective waveform is available for comparison (e.g., Figure 6, subject AGR). The shape of the VEP waveform offers an objective method of exposing luminance contrast intrusions that may not otherwise be perceived and which may be difficult to expose. Generating a subject-specific PIG is currently relatively time-consuming and requires central fixation, but offers the possibility of generating large suprathreshold responses without compromising chromatic selectivity. A more generic version of this stimulus may still offer advantages (see below).

Large red-green stimulus fields are less prone to achromatic intrusions (Kulikowski et al., 1997; Robson et al., 2006) as red-green isoluminance changes less with eccentricity (Robson & Parry, 2008). However, the effect may be significant because small departures from isoluminance can generate additional achromatic VEP components (Berninger, Arden, Hogg, & Frumkes, 1989a; Murray et al., 1987) and may combine with the effects of residual nonlinear magnocellular responses to red/green borders (Lee, Martin, & Valberg, 1988; Schiller & Colby, 1983; White, Wilder, Goodchild, Sefton, & Martin, 1998).

Specification of vector 1 involved rotating the chromatic axis around the yellow point specified by Porciatti and Sartucci (1999), through the copunctal point for blue, for each subject. We chose copunctal blue because, in the Porciatti and Sartucci study, the blue component of the stimulus (Figure 1) was of a relatively long wavelength, and indeed lay outside the gamut of the monitor. This is possibly the result of a misprint, but this nonoptimal axis has subsequently been described in several other studies from the same group; it is obvious from Figure 1 that such a stimulus would not isolate the blue-yellow or S-cone pathway. In keeping with this, the blue-yellow VEPs in Porciatti and Sartucci's (1999) study have strikingly short latencies—similar to their red-green data. The timing of the response is evidently a useful marker of

selectivity. Rabin et al. (1994) showed how small departures from the blue-yellow chromatic axis can dramatically shorten latency. It is evident from Figures 6 and 7 that onset VEPs to the PIG had a largely monophasic shape with a peak time of approximately 200 ms; this is of significantly longer peak time than the negative onset VEPs associated with R/G (parvocellular) and nontritan B/Y stimulation (Robson & Kulikowski, 1998). Integration times for R/G VEPs are additionally shorter than for tritan VEPs (Robson, Kulikowski et al., 2003). Reaction time (RT) studies suggest that there is perhaps a 30 ms to 40 ms lag with blue-yellow stimuli, in comparison with those along the red-green axis (McKeefry, Parry, & Murray, 2003; Smithson & Mollon, 2004). Thus VEP and RT data are consistent with slower koniocellular processing, although there is some controversy about how sluggish the konio pathway actually is (Chichilnisky & Baylor, 1999; Cottaris & De Valois, 1996; Xu et al., 2001; Yeh, Lee, & Kremers, 1995).

The spatial configuration of the PIG was designed to compensate for the effects of MP; smaller annuli were used over parafoveal areas where MP optical density was likely to show the greatest change (Robson, Moreland et al., 2003). The technique can be adapted to quantify MP (Robson & Parry, 2008) and, although red-green isoluminance varies less with eccentricity (Murray et al., 1987; Robson & Parry, 2008), the stimulus can easily be configured to stimulate the parvocellular (R/G) color-opponent pathways. Preliminary studies suggest a coarser arrangement of annuli is capable of achieving higher chromatic selectivity than a conventional grating of similar diameter. Further compromise may still offer advantages over more conventional methods. For example, predetermined eccentricity-dependent isoluminant ratios could be averaged across individuals and used to test naïve subjects or patients with limited ability to comply with testing. A better option might be to use fast flicker VEPs to objectively specify eccentricity-dependent changes in isoluminance (Robson & Parry, 2008)

Numerous investigations have attempted to characterize normal chromatic processing or congenital and acquired disorders of the color systems using large chromatic gratings (Crognale et al., 2001; Davis et al., 2003, 2006; Elia et al., 2005; Mullen, Sankeralli, & Hess, 1996; Parry & Murray, 1997; Porciatti & Sartucci, 1996, 1999; Rabin et al., 1994; Suttle & Harding, 1999). It is well-established that isoluminance varies between individuals and varies with eccentricity. This study highlights the limitations of using large conventional tritan gratings and describes a novel stimulus that may greatly improve the selectivity of suprathreshold responses. To the best of our knowledge this is the first study to use a large panisoluminant tritan stimulus capable of eliciting robust responses of

the S-cone-driven pathway at threshold and at supra-threshold levels, without compromising chromatic specificity.

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Corresponding author: Neil R.A. Parry.

Email: Neil.Parry@manchester.ac.uk.

Address: Vision Science Centre, Manchester Royal Eye Hospital, Manchester, UK.

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