Blobs versus bars: Psychophysical evidence supports two types of orientation response in human color vision

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The classic hypothesis of Livingstone and Hubel (1984, 1987) proposed two types of color pathways in primate visual cortex based on recordings from single cells: a segregated, modular pathway that signals color but provides little information about shape or form and a second pathway that signals color differences and so defines forms without the need to specify their colors. A major problem has been to reconcile this neurophysiological hypothesis with the behavioral data. A wealth of psychophysical studies has demonstrated that color vision has orientation-tuned responses and little impairment on form related tasks, but these have not revealed any direct evidence for nonoriented mechanisms. Here we use a psychophysical method of subthreshold summation across orthogonal orientations for isoluminant red-green gratings in monocular and dichoptic viewing conditions to differentiate between nonoriented and orientation-tuned responses to color contrast. We reveal nonoriented color responses at low spatial frequencies (0.25–0.375 c/deg) under monocular conditions changing to orientation-tuned responses at higher spatial frequencies (1.5 c/deg) and under binocular conditions. We suggest that two distinct pathways coexist in color vision at the behavioral level, revealed at different spatial scales: one is isotropic, monocular, and best equipped for the representation of surface color, and the other is orientation-tuned, binocular, and selective for shape and form. This advances our understanding of the organization of the neural pathways involved in human color vision and provides a strong link between neurophysiological and behavioral data.

Introduction

Here we address a longstanding controversy in our understanding of the physiological versus the behavioral basis of human color vision. Based on neurophysiological recordings from single cells, the classic hypothesis of Livingstone and Hubel (1984, 1987) proposed two types of color pathways in primate visual cortex: a segregated, modular pathway that signals color per se but provides little information about shape or form and a second pathway that signals color differences, so defining forms without the need to specify their colors. Almost three decades later, although much of the detail has changed, the basic outline of this neurophysiological hypothesis still stands. Recent single cell recordings suggest that approximately only 10% of chromatic neurons in the primate cortex (area V1) respond exclusively to color, but because these lack orientation tuning they are not likely to be involved in form perception (Conway, 2001; Friedman, Zhou, & von der Heydt, 2003; Johnson, Hawken, & Shapley, 2008; Livingstone & Hubel, 1984; Shapley & Hawken, 2011). On the other hand, a much larger population of color responsive neurons in V1 (about 40%) is selective for the orientation of chromatic stimuli and so is equipped for form perception. These neurons, however, also respond to achromatic contrast and so are not exclusively dedicated to color vision (Friedman et al., 2003; Johnson et al., 2008; Leventhal, Thompson, Liu, Zhou, & Ault, 1995; Thorell, De Valois, & Albrecht, 1984).

The behavioral relevance of these two neural populations is controversial, however, with an apparent conundrum between the psychophysical and neurophysiological evidence. Under Livingstone and Hubel's (1988) original scheme, color vision was considered very poor at form perception and was even called "form blind" (Livingstone & Hubel, 1987), a view that

found support from the lowpass, low acuity color contrast sensitivity function (Kelly, 1983; Mullen, 1985). This view held that the boundaries and contours within the visual scene are primarily extracted from luminance contrast, with color vision filling in the surface color between contours and linking areas of common color to define objects, a role which is compatible with a population of nonoriented, color-selective neurons. Psychophysical research over ensuing decades, however, demonstrated that this could not be the only way the brain uses color. Instead, we now know that color vision can extract the key characteristics of edges with very little deficiency. Psychophysical experiments have shown that bandpass spatial frequency tuning, critical for edge detection, underlies the lowpass color contrast sensitivity function (Losada & Mullen, 1994, 1995; Vimal, 1998), orientation discrimination in color vision is only mildly deficient (Beaudot & Mullen, 2005; Reisbeck & Gegenfurtner, 1998; Webster, De Valois, & Switkes, 1990; Wuerger & Morgan, 1999), and chromatic oriented elements can readily be linked into contours and shapes (Mandelli & Kiper, 2005; Mullen, Beaudot, & Ivanov, 2011; Mullen, Beaudot, & McIlhagga, 2000). Hence, there is now little doubt that human color vision is well equipped to extract shape and form, and the large population of spatially selective, orientation-tuned neurons found in primate V1, referred to above, is thought to support this function. This raises the question of the psychophysical role of the small population of nonoriented neurons in V1. The role of these neurons as surface color detectors has largely been surmised, and psychophysical experiments have not yet revealed any direct evidence for nonoriented mechanisms in color vision. Yet, the fact that these neurons are the only population in V1 that exclusively responds to color suggests they have an important role.

Here we use a classic, psychophysical method of subthreshold spatial summation (Kulikowski & King-Smith, 1973; Sachs, Nachmias, & Robson, 1971; Wilson & Bergen, 1979) to investigate orientation tuning in human color vision. We aim to differentiate between nonoriented responses and orientation-tuned responses to color contrast with two crucial conditions. First, the method uses very low contrast stimuli, ensuring the color pathway is well isolated from the modulatory effects of cross-orientation masking that contaminate orientation tuning measurements at higher contrasts (Cass, Stuit, Bex, & Alais, 2009; Meese & Holmes, 2010). Second, we use a range of spatial frequencies since it is likely that nonoriented neurons (color blob detectors) are most sensitive to large, low spatial frequency stimuli (Schluppeck & Engel, 2002). We find behavioral evidence for two distinct pathways in color vision revealed at different spatial scales. At low spatial frequencies, our results reveal the presence of nonoriented (isotropic) color responses which appear to be predominantly monocular, switching to orientation-tuned responses at higher spatial frequencies and under binocular conditions. These results help to advance our understanding of the organization of the neural pathways involved in human color vision and provide a strong link between the behavioral and neurophysiological data.

Methods

Apparatus

Stimuli were displayed on a CRT color monitor (Iiyama Vision Master Pro 513, resolution of 1024 × 768, and a frame rate of 120 Hz) connected to a graphics card (Cambridge Research Systems, VSG Visage) in a generic PC. This graphics card has 14 bits of contrast resolution and is specialized for the measurement of visual thresholds. The gamma nonlinearity of the luminance output of the monitor guns was measured using a Cambridge Research Systems Opti-Cal photometer and corrected in vsgDesktop software. The spectral outputs of the red, green, and blue phosphors of the monitor were calibrated using a PhotoResearch PR-645 SpectraScan spectroradiometer. The CIE-1931 chromaticity coordinates of the red, green, and blue phosphors were ($x = 0.624$, $y = 0.335$), ($x = 0.293$, $y = 0.608$), and ($x = 0.147$, $y = 0.073$), respectively. The background was achromatic with a mean luminance of 43.2 cd/m^2 at the screen center.

Observers

Six observers were used, the three authors (MG, KTM, and TSM) and three observers naive to the purpose of the experiment (LGS, NN, and YJK). YJK only performed the monocular color condition. All had normal vision and normal color vision according to the Farnsworth-Munsell 100 Hue test and wore corrective lenses if required. The experiments were performed in accordance with the Declaration of Helsinki.

Stimuli

All stimuli were oriented sine-wave gratings (phase = 0) and were presented alone or as pairs of orthogonal gratings overlaid to form a plaid, as illustrated in Figure 1. The two component stimuli were generated independently and were combined using frame interleaving, with the two grating components presented in alternative monitor frames at 120 Hz using a frame-cycling option
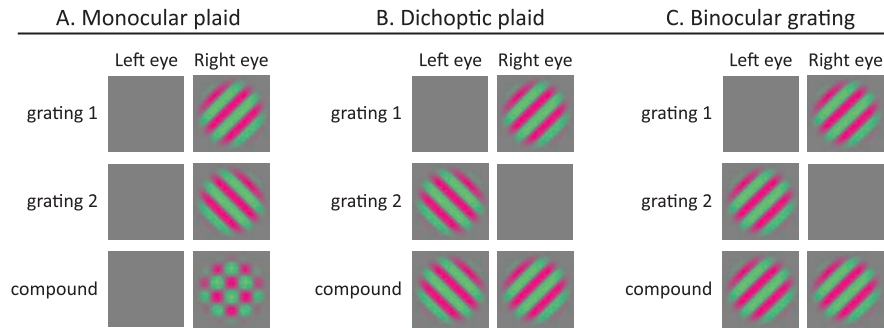
Figure 1. Diagram of the stimulus conditions. (A) Monocular plaid: Psychometric functions are obtained for detection of a right oblique grating, a left oblique grating, and their combination (plaid) all viewed by the right eye and with the other eye seeing the mean luminance. (B) Dichoptic plaid: Psychometric functions are obtained for a right oblique grating presented to the right eye, a left oblique grating presented to the left eye, and their simultaneous dichoptic presentation, which appears as a plaid. (C) Binocular grating: Psychometric functions are obtained for a right oblique grating presented to the right eye, an identical grating presented to the left eye, and their simultaneous dichoptic presentation, which is a binocular grating. For illustrative purposes, stimuli are shown at high contrasts.

in software. All stimuli were presented in a circular patch (10°, total diameter) with edges contrast enveloped with a spatial raised cosine (2.5°). Three different spatial frequencies were tested: 0.25, 0.375, and 1.5 c/deg. Stimulus size was fixed and was independent of the spatial frequency. Stimuli were static and were presented in a contrast modulated temporal Gaussian envelope ($\sigma = 0.125$ s; interval duration $= 0.5$ s, interstimulus interval $= 0.4$ s). All stimuli were presented using a stereoscope with stimuli at 58 cm from the eye. Viewing conditions were monocular, dichoptic, or binocular as illustrated in Figure 1.

Stimuli were achromatic (black/white) or chromatic (red/green). Chromatic stimuli were isoluminant and calibrated to activate the L/M cone opponent pathway. Isoluminance was determined for each subject and condition using a minimum motion method as described previously (Medina & Mullen, 2009). Stimuli were represented in a three-dimensional cone-contrast space (Cole, Hine, & McIlhagga, 1993; Sankeralli & Mullen, 1996). Each axis is defined by the Weber contrast of the stimulus to each of the three cone types, respectively, (i.e., incremental stimulus intensity for the cone type normalized by the respective intensity of the fixed adapting white background to that cone type). Stimulus contrast is defined as the vector length in cone contrast units (C_C):

$$C_C = \sqrt{(L_C)^2 + (M_C)^2 + (S_C)^2} \qquad (1)$$

where L_C, M_C, and S_C, represent the L, M, and S cone Weber contrasts as described above.

Protocols

For each summation experiment, the detection threshold was obtained for a left oblique grating, a right oblique grating orthogonal to the first grating, and a plaid composed of the superimposition of the two gratings. Detection thresholds were derived from fits of the psychometric functions, which plot percent correct for stimulus detection as a function of cone contrast (achromatic or chromatic). Stimulus detection was measured using a two-alternative-forced choice (2AFC) method of constant stimuli, in which a stimulus was presented in one interval and the other was a blank. Each psychometric function was measured with at least six contrast levels and at least 100 trials per contrast level and was obtained over several sittings with presentations of the two orthogonal gratings and their combination ordered in a balanced block design. Psychometric functions were fitted with a standard Weibull function (Nachmias, 1981; Weibull, 1951) with the chance level set to 0.5 for the 2AFC paradigm to extract the parameters for contrast detection threshold corresponding to 81.6% correct detection and the slope of the function:

$$\psi(C) = 0.5 + (0.5 - \lambda)\left(1 - e^{-\left(\frac{C}{\alpha}\right)^\beta}\right) \qquad (2)$$

where C is the contrast of the grating, α is threshold (contrast at 81.6% when $\lambda = 0$), β is the slope of the psychometric function, and λ is the lapse rate (constrained to ≤ 0.02 in all fittings). Fitting was done using the psignifit toolbox of Matlab (Wichmann & Hill, 2001a), and estimates of variability for each parameter were found using the bootstrap method based on 4,999 simulations (Wichmann & Hill, 2001b).

To quantify the amount of visual summation between the two added component gratings we use a summation ratio (SR), expressed in dB, which is defined as the ratio of the contrast detection threshold for a component grating presented alone to the contrast of the component grating at detection threshold of the compound stimulus:

$$SR(dB) = 20\log_{10}\left(\frac{Thresh_{compt}}{Thresh_{compt\ in\ plaid}}\right) \qquad (3)$$

For every condition in every subject, we used a *t* test to determine whether the detection thresholds for the two orthogonal component gratings presented alone were significantly different from each other. We found no significant difference in any condition except for one (NS, chromatic grating detection by the left and right eyes). Hence we used the average of the two orthogonal component gratings to represent threshold detection of the components presented alone. The summation ratio is measured for the achromatic and chromatic stimuli under three different viewing conditions as illustrated in Figure 1. In monocular viewing (Figure 1A), the two orthogonal component gratings and their combination (plaid) are presented to one eye while the other eye views a blank field of the same mean luminance and chromaticity as the stimulus. In dichoptic viewing (Figure 1B), the two orthogonal component gratings are presented to different eyes and a plaid is seen dichoptically. In a control condition, we measure binocular summation (Figure 1C), in which detection thresholds are measured for the co-oriented gratings viewed by the left and right eyes separately (monocular) and by the two eyes together (binocular).

Model

Subthreshold summation experiments measure the extent to which responses to two stimuli summate to improve detection threshold when the two stimuli are physically combined (added) compared to when they are presented alone (Bergen, Wilson, & Cowan, 1979; Georgeson & Shackleton, 1994; Graham, 1989; Meese & Baker, 2011; Watson, 1982; Wilson & Bergen, 1979). In our experiments, we measure summation between two gratings of orthogonal orientations. The level of response summation across orthogonal orientations can be used to infer whether response mechanisms are orientation tuned or isotropic. Below we derive predictions at threshold for response summation by orientation-tuned and isotropic detectors.

The predicted response summation by orientation-tuned mechanisms

If the neural detectors are orientation tuned, response summation will be very low and similar to the levels previously found for achromatic stimuli. Low summation suggests that the two components of the plaid are filtered by different, independent orientation-tuned linear mechanisms with each orientation filter having no response to the orthogonal component. The response to the combined stimulus still shows some summation effect, however, depending on how the responses to the two independent oriented components of the plaid are combined prior to the detection decision. Exactly how this occurs is not fully understood, but several different arrangements all lead to similar predictions. For example, linear summation across each orientation following square-law transduction and the addition of independent noise in each oriented channel predicts a summation ratio of 1.5 dB (Meese, 2010). Probability summation across linear filter outputs with intrinsic uncertainty or following square-law transduction with no uncertainty also predicts summation ratios around 1.5 dB. The predicted level of summation diminishes if intrinsic uncertainty is combined with nonlinear transduction or if the observer's ability to monitor the relevant channels is suboptimal (Tyler & Chen, 2000). Thus in general, a summation ratio of around 1.5 dB or less is consistent with the assumption that the orthogonal component stimuli are filtered by orientation-tuned mechanisms prior to some form of signal combination.

The predicted response summation by isotropic mechanisms

If the neural detectors are not orientation tuned, a single mechanism will respond to the orthogonally presented gratings and summation will occur between the responses to each. To quantify this, we must first consider the effects of spatial summation across the stimulus (Bergen et al., 1979; Georgeson & Shackleton, 1994; Meese & Holmes, 2010). This is important because the beating effects of the plaid components mean that the full benefit of cross-orientation summation is not available across the entire stimulus (Bergen et al., 1979). We assume there is linear summation across space following square-law nonlinear contrast transduction. A square-law exponent of contrast transduction (c^b), with $b = 2$, is used for two reasons. First, it is consistent with previous psychophysical results and models (Meese, 2010; Meese & Summers, 2009; Petrov, Dosher, & Lu, 2005, see also Watson & Ahumada, 2005). Second, it is consistent with the average slope of the psychometric functions (β) measured from our data since, from Pelli (1987), $\beta \sim 1.247b$, (see also Meese & Summers, 2009). This implies $\beta \sim 2.49$, which is very close to the (geometric) average $\beta = 2.40$ estimated from the average Weibull fits we obtain here.

With the assumption above, we can say that the contrast response over a set of linear isotropic mechanisms for our stimuli here is given by:
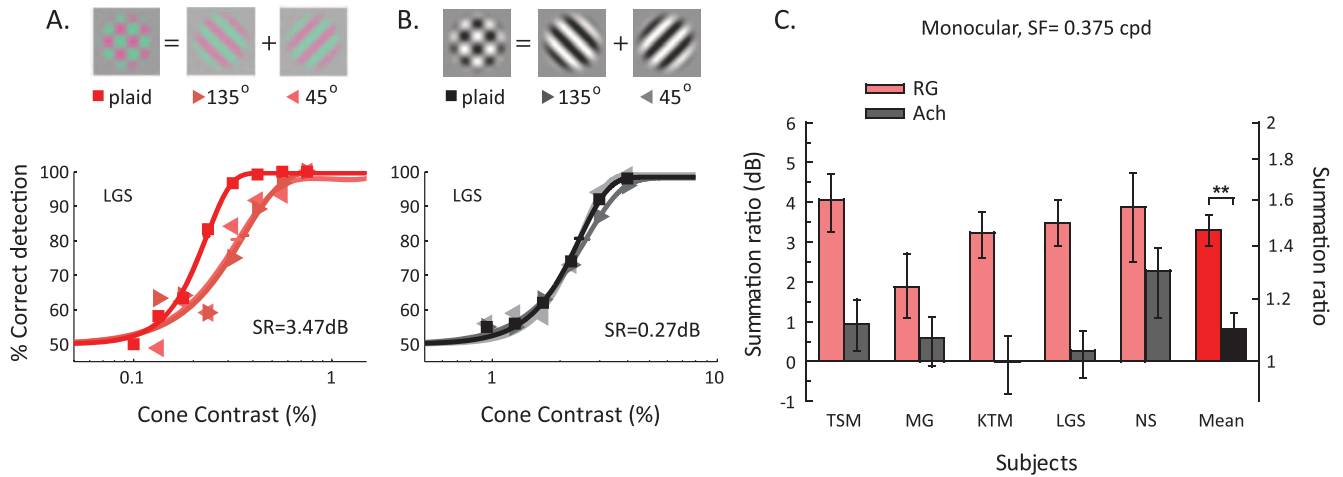
Figure 2. Monocular cross-orientation summation for chromatic and achromatic stimuli at a low spatial frequency (0.375 c/deg). Panels A and B show graphs of performance level (% correct detection) plotted as a function of stimulus cone contrast (%) for two orthogonal component gratings (45° and 135° of orientation) and their combination (plaid) for chromatic (A) and achromatic (B) stimuli, presented monocularly. The icons above each graph are schematics of the stimuli used in the summation experiments in either isoluminant red-green color contrast (A) or achromatic contrast (B). The symbols below each icon refer to the data points shown in the graph below and the solid lines show the fits of the psychometric function. Data are shown for an example subject (LGS). The horizontal error bar on each fit shows the standard deviation of the threshold estimate found from bootstrap method based on 4,999 simulations but in some cases is too small to be clearly visible. The summation ratio (SR) in dB (Equation 3) is given on the graph. Note the summation ratio is higher for the chromatic than the achromatic stimuli. (C) Summation ratios expressed in dB (left axis) and directly as a ratio (right axis) are plotted for five subjects for chromatic stimuli (pink bars) and achromatic stimuli (grey bars), with the group average given in the last pair of bars (red/black). ** Indicates significantly higher summation is obtained for the chromatic than the achromatic condition, (t test, p < 0.01). The error bars on the means are the standard error (SE) across five subjects, and the error bars for each subject indicate the standard deviation of the SR based on the sum of the variances for the grating and plaid thresholds.

$$Resp_{Iso} = \sum_{i=1}^{n} (|m_i|c)^b \qquad (4)$$

where n is the number of mechanisms tiling the image space (e.g., the number of image pixels), m_i is the spatial modulation of the stimulus (this has unit amplitude for the grating and twice that for the plaid), and c is the component contrast. Assuming an internal response of one arbitrary unit at detection threshold ($Resp_{Iso} = 1$), we can rearrange Equation 4 to solve for contrast at detection threshold ($c = Thresh_{stim}$):

$$Thresh_{stim} = \left(\sum_{i=1}^{n} |m_i|^b \right)^{\frac{-1}{b}} \qquad (5)$$

We used Equation 5 for grating and plaid stimuli to calculate the detection threshold ratio to predict the empirical summation ratios. For $b = 2$, this gave SR = 3.01 dB for integer periods of the plaid and grating with matched areas. This analysis suggests that for a summation ratio of around 3 dB or higher chromatic responses are unselective for orientation, consistent with the presence of isotropic or very broadly tuned detectors responding to orthogonal orientations. For summation ratios in between 1.5 and 3 dB, it remains

unclear whether responses are untuned or tuned for orientation.

Results

As explained in the Model section above, low summation of around 1.5 dB or less is consistent with the detection of the orthogonal grating stimuli on the basis of separate, independent neural responses and implies the selective orientation tuning of these responses. Summation of around 3 dB or higher is compatible with the detection of the two orthogonal stimuli on the basis of a summed neural response, consistent with detection by an isotropic or very broadly tuned neural mechanism that responds to both stimuli.

Chromatic versus achromatic subthreshold summation

In Figure 2, panels A and B each show example psychometric functions for the detection of two orthogonal component gratings of a low spatial

	Summation ratio (dB)					
	Monocular plaid			Dichoptic plaid	Binocular grating	Binocular plaid
Condition	0.375 c/deg	0.25 c/deg	1.5 c/deg	0.375 c/deg	0.375 c/deg	0.375 c/deg
Chromatic	3.31 ± 0.27	2.88 ± 0.12	1.26 ± 0.27	1.2 ± 0.43	4.48 ± 0.52	3.94 ± 0.3
Achromatic	0.81 ± 0.4	-	-	−0.27 ± 0.37	-	-

Table 1. Group average summation ratios (in dB) ± standard errors for all conditions. Note: 20 dB = 1 log unit, n = 6 for the monocular chromatic condition, and n = 5 for all other conditions.

frequency (0.375 c/deg) and their combination (plaid), presented monocularly. Figure 2A shows results for isoluminant chromatic stimuli and Figure 2B shows results for achromatic gratings. The calculated summation ratio (SR) in dB is indicated on each graph. In the chromatic condition, the data show a clear threshold improvement for detection of the plaid compared to the component stimuli, indicating a summation of the responses to the two orthogonal component gratings. By contrast, in the achromatic condition, thresholds for the two component stimuli and the plaid are very similar, indicating very low or absent response summation. The bar chart in Figure 2C shows the summation ratios for chromatic and achromatic conditions for each of five subjects and the average across subjects. Average values (in dB) are given in Table 1. Average summation is significantly higher for the chromatic condition compared to the achromatic condition with an average summation ratio of 3.3 dB ± 0.39 SE for chromatic stimuli and 0.81 dB ± 0.4 SE for achromatic stimuli, paired t test: $t(4) =$ 5.729, $p = 0.0046$. This is consistent with a lack of orientation tuning for the responses to the chromatic gratings but orientation-tuned responses to the achromatic gratings.

The summation experiments for chromatic stimuli were repeated at a higher (1.5 c/deg) and a lower (0.25 c/deg) spatial frequencies under monocular conditions for six subjects, and results are shown in Figure 3 with group averages given in Table 1. Summation shows an inverse relationship with spatial frequency with greater summation at the two lower spatial frequencies (0.25 and 0.375 c/deg) compared to the higher (1.5 c/deg). A one-way ANOVA demonstrates a significant effect of spatial frequency on the summation ratio, $F(2, 5) =$ 16.83, $p = 0.0006$, with Bonferroni's post-hoc test showing a significant effect for 0.375 c/deg versus 1.5 c/deg and for 0.25 c/deg versus 1.5 c/deg. At a spatial frequency of 1.5 c/deg, the average chromatic summation (SR = 1.26 dB) falls within the range compatible with orientation-tuned responses.

In a control experiment, we tested whether the number of cycles (bars) displayed in the grating stimuli influenced the summation ratio. For the main experiments, the stimulus diameter was fixed (10°), which means that the number of cycles displayed in the

stimulus increased with spatial frequency. To test whether this was a factor influencing the loss of summation, two subjects (MG and YJK) repeated the 1.5 c/deg monocular chromatic condition using a smaller diameter (2.5°) and the same number of cycles (3.75) as in the low frequency condition (0.375 c/deg). This produced a similar level of cross-orientation summation in both subjects (SR = 0.14 dB for MG; 0.96 dB for YJK) as was found for the higher cycle number (SR = 0.69 dB for MG; 0.6 dB for YJK), indicating that spatial frequency, not stimulus cycle number, is the critical factor.

Subthreshold summation in dichoptic presentations

In this section, we explore the binocularity of the chromatic responses and their orientation selectivity. As a control experiment, we first measured binocular
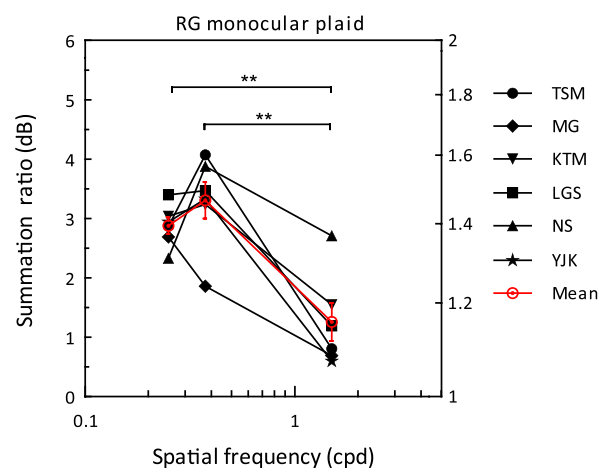

Figure 3. Summation ratios expressed in dB (left axis) and directly as a ratio (right axis) are plotted as a function of stimulus spatial frequency (0.25, 0.375, and 1.5 c/deg) for the chromatic monocular condition for six subjects as marked with the mean plotted in red and error bars showing the standard error (SE). The average summation ratio at 1.5 c/deg is significantly lower compared to 0.375 c/deg and 0.25 c/deg, one-way ANOVA F(2, 5) = 16.83, p = 0.0006, Bonferroni post-hoc test: p < 0.01 for the two conditions.
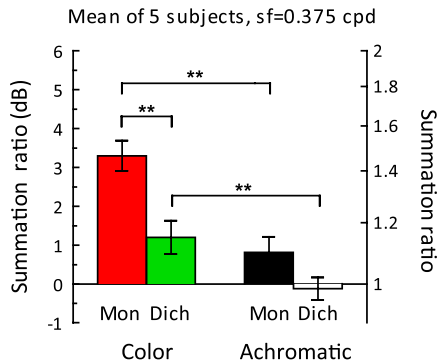
Figure 4. Average summation ratios over five subjects are plotted for the following conditions: chromatic monocular (red bar), chromatic dichoptic (green bar), achromatic monocular (black bar), and achromatic dichoptic (white bar) all expressed in dB (left axis) and directly as a ratio (right axis). The error bars show the standard error (*SE*) across five subjects and ** indicates a significant difference (paired *t* test, *p* < 0.01). Across subjects the summation ratio is significantly higher for the monocular chromatic compared to the dichoptic chromatic condition whereas there is no significant difference between monocular and dichoptic achromatic conditions. The summation ratio is also significantly higher for the dichoptic chromatic compared to the dichoptic achromatic condition.

summation ratios for identical, co-oriented chromatic grating stimuli (0.375 c/deg) presented monocularly to each eye and binocularly to both eyes. The summation ratio is defined by Equation 3, as before. The averaged binocular summation ratio between our subjects is 4.48 dB ± 0.52 *SE* (see Table 1) and establishes that there is binocular summation for identical stimuli in color vision (Medina & Mullen, 2007; Simmons, 2005), presumably mediated at the cortical level by color sensitive, binocular neurons (Peirce, Solomon, Forte, & Lennie, 2008).

We measured summation for dichoptic presentations of orthogonal component gratings. The dichoptic experiment measures the cross-orientation summation that occurs when two orthogonal component gratings are presented to different eyes rather than to the same eyes as in the monocular condition. Figure 4 shows the results averaged across five subjects for low spatial frequency stimuli (0.375 c/deg), with group average values given in Table 1. Summation ratios are shown for monocular and dichoptic presentations of chromatic component gratings (red and green bars, respectively) and for achromatic component gratings (black and white bars, respectively). If the chromatic mechanisms at threshold were isotropic and binocular, we would expect to find summation of 3 dB or above and of similar strength as in the monocular presentation, whereas low dichoptic cross-orientation summation (<1.5 dB) indicates orientation tuning. For the chromatic stimuli in dichoptic presentation, the average

summation ratio is 1.2 dB ± 0.43 *SE* and is significantly lower than the monocular condition, paired *t* test: $t(4) = 5.133$, $p = 0.0068$. This suggests that the neural responses under dichoptic conditions are orientation-tuned. Cross-orientation summation in the dichoptic condition is also significantly reduced compared to the binocular condition in which the component gratings presented to the two eyes are co-oriented (see Table 1), also suggesting that the chromatic pathway is orientation-tuned under binocular/dichoptic conditions when both eyes are active.

For achromatic stimuli presented dichoptically, we find almost no cross orientation summation between eyes and there is no significant difference between the monocular and dichoptic summation ratios, indicating that there is orientation tuning of the achromatic responses under both conditions. There is significantly more summation for the chromatic dichoptic than the achromatic dichoptic condition, paired *t* test: $t(4) = 5.729$, $p = 0.0046$, although both fall within the range compatible with the presence of orientation tuning. Possible reasons for this difference are raised in the Discussion.

Figure 5 illustrates a scheme with two types of chromatic pathways that is consistent with our results: an orientation-tuned, binocular pathway and a monocular, isotropic pathway. We assume that the binocular orientation-tuned pathway responds to a broad range of spatial frequencies, including the low spatial frequencies used in our experiments (0.25–0.375 c/deg). For low spatial frequency color stimuli, an additional monocular pathway is available that has isotropic responses. Under dichoptic presentations at detection threshold, both monocular and binocular pathways are likely to be active. Under monocular conditions, the isotropic pathway is the most sensitive, and under binocular conditions, the binocular pathway is the most active and so determines threshold.

In addition, based on our results we can estimate the exponents for the binocular and monocular stages illustrated in Figure 5. We measured binocular summation ratios for grating stimuli (Table 1) which produced binocular summation ratios of 4.48 dB (factor of 1.68), consistent with previous estimates for achromatic (Meese, Georgeson, & Baker, 2006) and chromatic stimuli (Simmons, 2005; Simmons & Kingdom, 1998). From this we can deduce the exponent of the nonlinear contrast transducer (μ in Figure 5) prior to binocular summation. Since the binocular response is the linear sum of the identical components in the two eyes, $Resp_{Bin} = c^{\mu} + c^{\mu}$ and $Resp_{Mon} = c^{\mu}$, we can solve each for c at detection threshold leading to the following expression for the binocular summation ratio (in dB): $BinSR = 20\log_{10}(2^{1/\mu})$ (see Baker, Meese, & Summers, 2007, appendix 1 for further details). From this it follows that $\mu = 1.34$. By allowing the overall
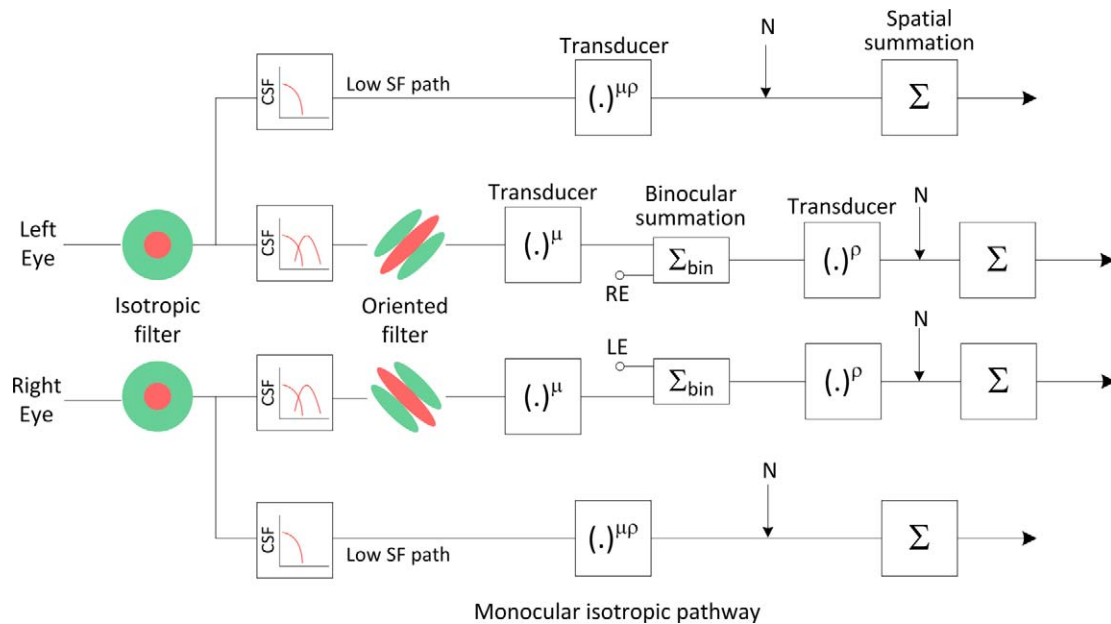
Figure 5. A schematic model of contrast detection for chromatic stimuli. The monocular outputs of the isotropic chromatic mechanisms are available only for stimuli at low spatial frequencies. There is a binocular pathway for each filter orientation. The outputs across oriented filters are combined according to probability summation. The location of the performance-limiting noise (N) is consistent with other work (Meese, 2010).

exponent to derive from a cascade of transducers, one pre- and one post-binocular summation (Meese & Summers, 2009) with post-binocular transduction $\rho = 1.49$, we obtain the same overall nonlinear contrast transduction for binocular and monocular conditions, with $b = \mu\rho = 2$.

Discussion

The psychophysical approach of measuring subthreshold summation of grating stimuli at different orientations has been used to demonstrate orientation tuning for achromatic vision under a wide range of conditions (Kulikowski & King-Smith, 1973; Meese & Baker, 2011; Phillips & Wilson, 1984; Sachs et al., 1971). For achromatic stimuli, the lack of contrast summation within the visual system for orthogonal grating stimuli that are physically combined on the screen has been considered key psychophysical evidence for the presence of orientation tuning in the human visual system. Here we have applied this classic method to the study of orientation tuning in color vision. Under monocular conditions, we have found evidence for nonoriented responses at low spatial frequencies (0.375 c/deg and below), with clear evidence for contrast summation between orthogonal orientations. This switches to orientation-tuned responses as spatial frequency increases (to 1.5 c/deg). Under dichoptic conditions, we found orientation-tuned re-

sponses at all spatial frequencies. Our results thus provide direct evidence for an isotropic mechanism in color vision that is biased towards low spatial frequencies and is monocular. A binocular, orientation-tuned pathway is also available at low spatial frequencies whereas at higher spatial frequencies there is only an orientation-tuned response.

This is the first psychophysical study to find direct evidence for isotropic responses at the behavioral level. In contrast, there is already a large body of psychophysical data providing evidence for the presence of orientation tuning in color vision, consistent across a range of different methods including adaptation (Bradley, Switkes, & De Valois, 1988), orientation discrimination (Beaudot & Mullen, 2005; Webster et al., 1990), masking (Pandey Vimal, 1997), contour linking (Mullen et al., 2000), and the tilt aftereffect (Clifford, Spehar, Solomon, Martin, & Zaidi, 2003). There are several likely reasons why nonoriented responses have not been revealed in these previous studies of color vision. First, psychophysical studies of orientation tuning in color vision have typically, although not always (Pandey Vimal, 1997), used spatial frequencies of 1 c/deg or higher and report orientation tuning bandwidths only slightly broader for chromatic compared to achromatic contrast (Beaudot & Mullen, 2005; Reisbeck & Gegenfurtner, 1998; Webster et al., 1990; Wuerger & Morgan, 1999). Our results also reveal an orientation tuned chromatic response at mid-spatial frequencies (1.5 c/deg), supporting previous psychophysical work. Second, in this study we have

used a method that relies on the use of very low contrasts spanning detection threshold. The use of low contrast, sub-threshold stimuli has the advantage of revealing the most sensitive chromatic responses which may be obscured by methods that use higher contrasts and allow other less sensitive responses to be recruited. It also avoids the influence of contrast gain controls, which operate across the broad range of orientations and are likely to confound measurements of orientation tuning (Cass et al., 2009; Meese & Holmes, 2010).

Our finding of nonoriented blob detectors sensitive to low spatial frequencies may reflect the activity of the nonoriented chromatic neurons in primate V1 and V2. Since the earliest neurophysiological studies, isotropic chromatic receptive fields have been found in primate V1 (Conway, 2001; Conway, Hubel, & Livingstone, 2002; Hubel & Wiesel, 1968; Johnson et al., 2008; Livingstone & Hubel, 1984; Peirce et al., 2008), and these are now thought to form around 10% of the total V1 population (Shapley & Hawken, 2011). The isotropic color cells were thought to be selectively located in the cytochrome oxidase blobs of V1, forming a modular pathway dedicated to color vision that continues to V2 via the thin stripes of V2 (Livingstone & Hubel, 1984, 1987), a claim which has been questioned and remains controversial and unresolved to this day (Economides, Sincich, Adams, & Horton, 2011; Gegenfurtner, Kiper, & Fenstemaker, 1996; Lennie, Krauskopf, & Sclar, 1990). There is also good evidence that the responses of color-preferring isotropic neurons in V1 are lowpass with greatest sensitivity at low spatial frequencies (Schluppeck & Engel, 2002; Shapley & Hawken, 2011), which is compatible with the low spatial frequency bias we find behaviorally. Nonoriented and spatially lowpass chromatic neurons are likely to play a role in determining surface color and in color identification without providing specific information about shape or form. It is likely that this type of isotropic response is involved in the representation of surface color at a cortical stage (Goddard, Solomon, & Clifford, 2010).

Our results also provide strong psychophysical evidence for orientation selective responses at higher spatial frequencies (1.5 c/deg) and for binocular pathways. These results lend quantitative psychophysical support to the idea that color vision has a dual role, providing form information via a pathway with spatial and orientation tuning as well as surface information through an isotropic, spatially lowpass pathway. Neurophysiological data from V1 demonstrate a substantial population of chromatic neurons in V1 that are selective for orientation and are bandpass for spatial frequency, typically peaking around 1–3 c/deg, responding to contours and edges (Friedman et al., 2003; Johnson, Hawken, & Shapley, 2001; Johnson et al., 2008; Lennie et al., 1990; Leventhal et al., 1995;

Thorell et al., 1984), with a similar organization likely in V2 (Gegenfurtner et al., 1996). A key characteristic of these neurons, however, is that their response to color is not unique but is typically confounded with their response to luminance contrast. This has led some to question whether these neurons could have a significant role in color vision (Conway et al., 2002). Others, on the other hand, argue that neurons with a combined response to color and luminance contrast can have an important role in color and form processing, proposing that in early cortical vision color contrast, luminance contrast, and orientation tuning are combined ("multiplexed") in common cortical signals (Friedman et al., 2003; Lennie, 1998; Shapley & Hawken, 2011). The multiplexing model, however, remains to be reconciled with the psychophysical evidence demonstrating that responses to color and luminance contrast are more or less independent at detection threshold supporting the presence of separate pathways; for example, at detection threshold color and luminance responses do not summate and do not show significant cross adaptation (Cole et al., 1993; Krauskopf & Gegenfurtner, 1992; Mullen, Cropper, & Losada, 1997; Mullen & Losada, 1994). In general, interactions between color and luminance contrast are found to occur at higher suprathreshold contrasts, but these are complex and are not accounted for by a simple scheme with a common pathway for color and luminance contrast.

Two possible solutions present themselves to the question of whether there is multiplexed versus modular processing of color and luminance contrast. First, single cell responses in V1 and V2 may not be directly relevant to behavioral thresholds. There is emerging evidence that form processing in color vision may occur in extrastriate areas such as V4, where populations of neurons selective for isoluminant color and form have been reported (Bushnell, Harding, Kosai, Bair, & Pasupathy, 2011). Hence, the separation of color and luminance contrast for form processing may occur at a higher, extrastriate stage. Alternatively, assessments of the independence of the responses to color and luminance contrast have typically involved measurements of detection thresholds. Detection thresholds, by definition, reveal the mechanisms most sensitive to color and are likely to be based on a relatively small population of cells. This population may have little or no response to luminance contrast at such low color contrasts, so appearing independent of luminance contrast at threshold. In support of this view, there is evidence that interactions occur between color and luminance contrast at higher contrasts (De Valois & Switkes, 1983; Forte & Clifford, 2005; Kingdom, Bell, Gheorghiu, & Malkoc, 2010) when larger neural populations may be recruited and mixed color and luminance responses revealed.

Monocular versus binocular summation

Our results have shown evidence for both monocular and binocular mechanisms in color vision. We found binocular summation for isoluminant, low spatial-frequency stimuli (0.375 c/deg), demonstrating the presence of binocular chromatic mechanisms under these conditions. The binocular summation disappeared under conditions of cross orientation (the dichoptic condition) indicating the presence of orientation tuning in binocular combination. Other factors, such as interocular suppression, may also contribute. In contrast, under monocular viewing conditions we found isotropic chromatic mechanisms. The most parsimonious interpretation of these results is that at low spatial frequencies there are two pathways available, a monocular, isotropic pathway and a binocular orientation-tuned pathway, whereas at high spatial frequencies there is only an orientation-tuned pathway. Under conditions of higher spatial frequencies, we presume the monocular isotropic response is obscured because it is less sensitive to these spatial frequencies. For binocular presentations at low spatial frequencies, the binocular pathways have a summation advantage over the monocular pathway and their response may determine threshold. Similar methods have revealed isotropic responses in achromatic vision under conditions of low spatial and high temporal frequency, which also appear to be monocular (Meese & Baker, 2011).

Although dichoptic summation is low for both chromatic and achromatic stimuli, we find significantly more summation for the chromatic than the achromatic stimuli (Figure 4b). Based on the proposed model scheme, one simple explanation for this is that for chromatic low spatial frequencies four pathways are available under dichoptic viewing: the monocular isotropic pathway in the left and right eye and the orientation-tuned binocular pathway in the left and right eye (see Figure 5). Probability summation over four pathways will be higher than over the two available for achromatic stimuli (orientation-tuned binocular in left and right eye). An alternative explanation is that there is a mixture of orientation tuned binocular and monocular responses in color vision. Neurophysiological results have shown the presence of binocular neurons in primate V1 and V2 that are color sensitive, spatially lowpass, and isotropic, as well as binocular neurons that show more defined spatial tuning (Peirce et al., 2008). There may be a wider range of binocular and monocular responses among chromatically-tuned neurons contributing to the higher dichoptic summation that we find for color vision, at least at low spatial frequencies.

These results suggest that the brain has access to the monocular response at the behavioral level. Although a monocular psychophysical response need not be associated with conscious awareness of the eye of origin of the stimulus, there is some evidence that utrocular discrimination is possible in human vision (Blake & Cormack, 1979), supporting the idea that monocular responses can be accessible at a behavioral level. In addition, eye specific signals can be identified in V1 using fMRI at low spatial frequencies (0.5 c/deg) (Schwarzkopf, Schindler, & Rees, 2010), indicating the presence of monocular responses, although it is not known whether these overall levels of neural activity relate to behavior.

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