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Contrast normalization in colour vision: the effect of luminance contrast on colour contrast detection

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While contrast normalization is well known to occur in luminance vision between overlaid achromatic contrasts, and in colour vision between overlaid colour contrasts, it is unknown whether it transfers between colour and luminance contrast. Here we investigate whether contrast detection in colour vision can be normalized by achromatic contrast, or whether this is a selective process driven only by colour contrast. We use a method of cross-orientation masking, in which colour detection is masked by cross-oriented achromatic contrast, over a range of spatio-temporal frequencies (0.375–1.5 cpd, 2–8 Hz). We find that there is virtually no cross-masking of colour by achromatic contrast under monocular or binocular conditions for any of the spatio-temporal frequencies tested, although we find significant facilitation at low spatio-temporal conditions (0.375 cpd, 2 Hz). These results indicate that the process of contrast nornalization is colour selective and independent of achromatic contrast, and imply segregated chromatic signals in early visual processing. Under dichoptic conditions, however, we find a strikingly different result with significant masking of colour by achromatic contrast. This indicates that the dichoptic site of suppression is unselective, responding similarly to colour and luminance contrast, and suggests that dichoptic suppression has a different origin from monocular or binocular suppression.

The visual response to contrast is continuously regulated by a process of contrast normalization, in which its contrast sensitivity is set by a combination of local contrasts. Such a process has been described in a number of contrast normalization models as divisive inhibition arising from a broad pool of oriented detectors operating on the response to a test stimulus[1–4]. The natural world, however, contains both colour as well as luminance contrast, each processed by the human visual system. The extent to which these are processed independently within the visual system or whether they combine and interact, is a controversial and complex question that has been unresolved for some time. While contrast normalization is well known to occur in luminance vision between overlaid achromatic contrasts[1,3,5–11], and also in colour vision between overlaid colour contrasts[12,13], it is unknown whether it transfers between colour and luminance contrast. In this paper, we investigate whether chromatic gain control is modulated by achromatic contrast, or whether it is an independent process driven only by colour contrast. It is important to understand this issue both from the point of view of making realistic models of the responses of the human visual system and for understanding how the gain control pools are established at the physiological level.

Psychophysically, the process of contrast normalization is revealed by cross-orientation masking, which occurs when the detection of an oriented test stimulus, such as a grating, is elevated by a superimposed stimulus at an orthogonal orientation[1,5,9,14–18]. This effect is thought to involve inhibitory interactions between separate neural detectors for the test and the orthogonal mask, tuned to different orientations, a so-called "cross-channel" effect.

Medina & Mullen[12] were the first to show not only that cross-orientation masking occurs in colour vision, but also that it is significantly greater for chromatic (red-green) stimuli compared to achromatic at equivalent spatial and temporal frequencies. Subsequently, Kim et al.[13] compared the relative strengths of suppression in colour and luminance vision for two different sites of cross-orientation masking: within-eye suppression that occurs for monocular stimuli, and an inter-ocular suppression that is isolated when dichoptic stimuli are used. They found that, the magnitude of masking was stronger for colour than luminance contrast for monocular and binocular viewing, whereas for the dichoptic presentations colour and luminance masking were similar. They concluded that the greater strength of chromatic cross-orientation masking has a monocular origin. This result also adds weight to the idea that monocular and dichoptic presentations tap into different sources of suppression. In

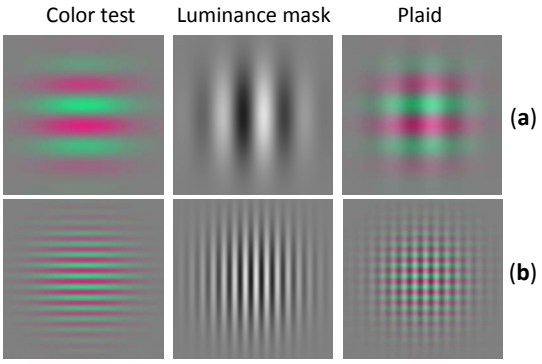

Figure 1 | Illustrations of the test and masking stimuli. All stimuli were Gabors with a fixed space constant of $\sigma = 2^{\circ}$. Test stimuli are horizontal red-green isoluminant Gabors superimposed on vertical achromatic Gabors (the mask stimuli), with their superimposition illustrated as a plaid. Examples show (a) the low spatial frequency (0.375 cpd) and (b) the mid spatial frequency (1.5 cpd) used.

addition, differences in the spatio-temporal tuning and the effect of stimulus duration for these two types of suppression lend weight to the idea that they originate from different sites[9].

Here, we explore the interactions between colour and luminance contrast using a method of cross-orientation masking. The presence of cross masking, in which colour grating detection is masked by cross-oriented achromatic contrast, would demonstrate a lack of colour selectivity in contrast normalization and imply a broadly tuned suppressive pool that includes both luminance and colour responses. On the other hand, a selective effect, in which a colour stimulus is only masked by cross-oriented colour contrast, would indicate that the suppressive mechanism is independent of achromatic contrast and pools only colour signals. (See Figure 1 for an illustration of the stimulus arrangement).

We measure the selectivity of cross-orientation masking for both monocular and dichoptic suppression with surprising results. We find that there is virtually no cross-orientation masking of colour by achromatic contrast under monocular or binocular conditions at any of the spatial and temporal frequencies tested (0.375–1.5 cpd, 2 & 8 Hz), although we do find a significant amount of facilitation at low spatio-temporal conditions (0.375 cpd at 2 Hz). These results indicate that the gain control pool is colour selective and independent of achromatic contrast, and supports the independence of chromatic signals in early visual processing. In contrast, under dichoptic conditions, there is significant masking of colour by achromatic contrast, indicating that the dichoptic site of suppression is unselective, pooling both colour and luminance contrast. These results suggest that the suppression arising under dichoptic viewing has a different origin from monocular or binocular suppression.

Results

Figure 2a shows masking functions for the red-green test stimulus, with colour detection thresholds plotted as a function of the increasing contrast of an orthogonal achromatic mask. Data are for monocular, dichoptic, and binocular stimulus presentations, for three spatio-temporal conditions (0.375, 0.75, and 1.5 cpd, at 2 Hz), and are averaged across four subjects. Results from each individual subject can be seen in the supplemental data (Figure S1). Functions for the dichoptic condition (red symbols) show the presence of masking, with thresholds rising as a function of mask contrast in all three spatio-temporal conditions. In comparison, for the monocular (blue symbols) and binocular conditions (open green symbols) there is no masking, but instead facilitation is observed at the two lowest spatio-temporal conditions (0.375 & 0.75 cpd, 2 Hz). At 1.5 cpd, the facilitation has disappeared and the colour test detection threshold is independent of the achromatic mask. These results show that the effect of an achromatic mask on a colour test stimulus is profoundly different depending on whether it is presented to different eyes (dichoptic), in which case masking occurs, or to the same eyes (monocular and binocular conditions), in which case there is no masking but may be some facilitation.

The fit of the modified two-stage model[13] of contrast gain control is shown by the solid lines. The model allows the dichoptic and monocular weights of suppression to be determined from the test threshold versus mask contrast data. Model fit parameters for w_d (dichoptic suppression), w_m (monocular suppression) and a (facilitation) for individual subjects and the fit of the averaged data are given in Table 1. The weight of binocular suppression (w_b) was always close to zero and is not included in the table. The goodness of fit of our model was assed by the adjusted R^2 metric with values given in the table legend (further details are given in Appendix A in Kim et al.[13]). Model fit parameters are compared below, however, we note at this point that the fitted weight of suppression for monocular masking (w_m) is zero under all conditions but there is significant suppression under dichoptic viewing (w_d). The monocular and binocular data are not significantly different (unpaired t-test, $p > 0.05$), showing that the dichoptic suppression is not revealed under the binocular viewing conditions.

In order to examine whether the colour-luminance interactions in cross-orientation masking depend on temporal frequency, we measured a complete set of data for 8 Hz stimuli. Figure 2b shows the masking functions across three spatio-temporal combinations (0.375, 0.75, and 1.5 cpd at 8 Hz) with data averaged across 4 subjects. Results for each individual subject (can be seen in the supplemental data (Figure S2). For the monocular and binocular conditions there is no masking or facilitation, whereas for the dichoptic conditions masking occurs. Model fit parameters are listed in Table 2 and the goodness of the model fits is given in the legend. As at 2 Hz, weight of suppression for monocular masking is close to zero under all conditions, while there is significant dichoptic suppression. As for the 2 Hz condition, the monocular and binocular data are not significantly different.

In Figure 3a, the fitted weights of monocular (w_m, blue symbols) and dichoptic suppression (w_d, red symbols) are plotted as a function of spatial frequency for the stimuli at 2 Hz and 8 Hz, with the fitted values averaged across four subjects. (Plotted values are in Table 1 & 2). The data set was analyzed using a three-factor repeated-measures ANOVA, with factors of viewing condition, spatial, and temporal frequency. When the main and/or interaction effects were significant, viewing condition differences were pursued further with t-tests comparing suppression at different viewing conditions, spatial frequencies or temporal frequencies. There was no significant main effect of spatial frequency ($F(2,6) = 0.939$, $p = 0.442$) or viewing condition ($F(1,3) = 7.888$, $p = 0.067$), however a significant effect of temporal frequency was found ($F(2,6) = 10.630$, $p = 0.047$). There was a significant two-way interaction between viewing condition and temporal frequency ($F(1,3) = 33.716$, $p = 0.010$), with all other interactions not significant.

Since our results show no effect of spatial frequency, consistent with previous results[12,13], we collapsed the data (suppression weights) across spatial frequency with results plotted in Figure 3b. The data were re-analysed using a 2-factor repeated-measures ANOVA (temporal frequency × viewing condition). The main effect of temporal frequency was significant ($F(1,11) = 9.115$, $p = 0.012$), indicating greater suppression at 2 Hz than 8 Hz. The main effect of viewing condition was also significant ($F(1,11) = 23.476$, $p = 0.001$), indicating greater dichoptic suppression than monocular. There was a significant interaction between temporal frequency and viewing condition ($F(1,11) = 9.115$, $p = 0.012$), which we followed up with t-tests as shown in Figure 3b. These show that the significantly lower

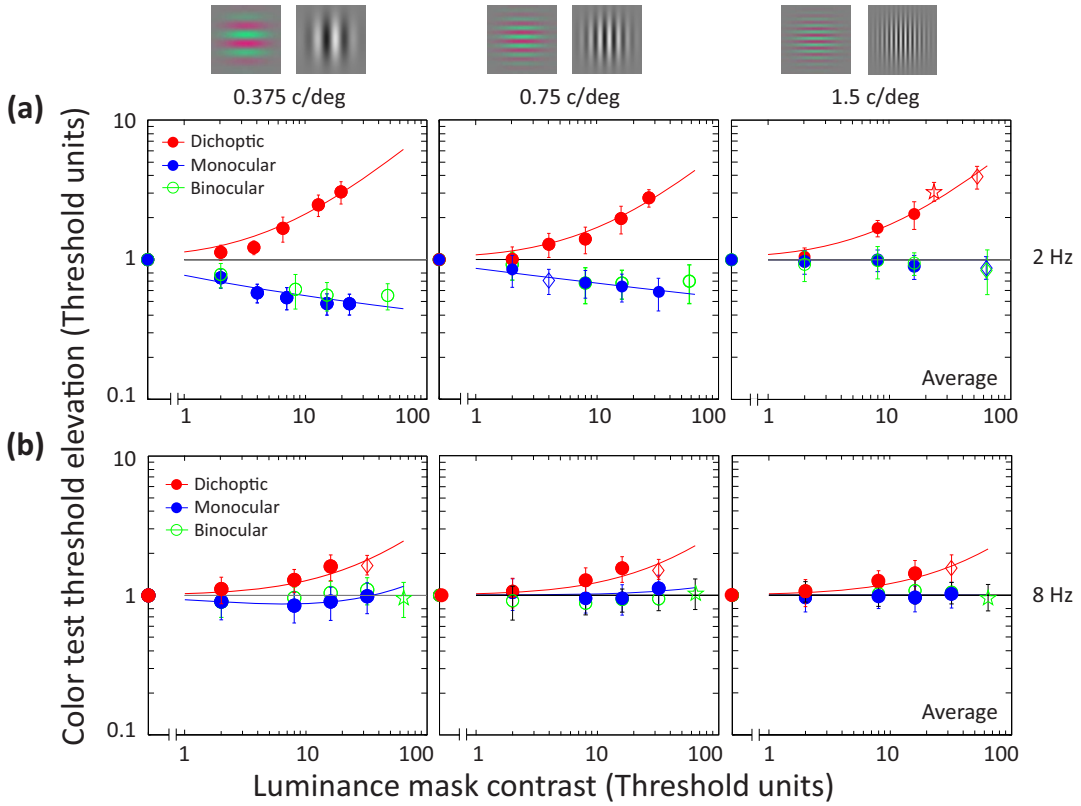

Figure 2 | Threshold elevations of the chromatic test stimuli plotted as a function of the achromatic orthogonal mask contrast (TvC functions). Results are for three viewing conditions: monocular (blue symbols), dichoptic (red symbols) and binocular (open green symbols), averaged across four subjects. Columns show results for the three spatial frequencies (0.375, 0.75 and 1.5 cpd) with the two temporal frequencies show in rows (a) 2 Hz and (b) 8 Hz. Axes show contrast normalized by the stimulus detection threshold in the absence of a mask (masked/unmasked thresholds). The data are fitted with the generalized two-stage model (solid lines) after Kim et al.[13] and described in the text. Weights of within-eye (w_m) and between-eye (w_d) suppression are estimated from the monocular and dichoptic viewing conditions, respectively. The model parameters and goodness of fit are reported in Table 1 & 2 for 2 Hz data and Table 3 for 8 Hz data. Error bars are ±1 SE. Note: Not all subjects used identical mask contrasts: open diamond symbols show the average of 3 subjects and open star symbols the average of 2 subjects for a particular mask contrast. Subjects used in (a) are YJK, JWZ, MG and KTM and in (b) are YJK, RW, MG and KTM.

suppression found at 8 Hz occurs in the dichoptic condition ($t(11) = 3.019$, $p = 0.012$).

So far we have shown that achromatic contrast only causes a significant cross-orientation suppression of colour under dichoptic viewing and this has a temporal frequency dependence. In order to confirm this effect, we collected additional data for a fixed supra-threshold mask contrast set to the highest value we could use (21 × threshold) at two spatial and temporal frequencies (0.375, 1.5 cpd, 2, 8 Hz). Data were collected for 6 subjects with new data collected on all subjects, even those that had participated in previous experiments. Results are shown in Figure 4. A 2-factor repeated-measured ANOVA confirmed that the main effect of temporal frequency is

Table 1 | Model parameters obtained from the fits of the data in Figure 2a (data averaged across subjects) and Figure S1 (individual data fits). w_m is the monocular weight of suppression, w_d is the dichoptic weight of suppression and a is a parameter reflecting the magnitude of any facilitation. Note that the fitted values of binocular suppression (w_b) under the monocular (Mon) and dichoptic (Dic) condition are close to zero for all masking conditions and so are not included in the table (w_b is zero to five decimal places). The last two rows show the average of the parameter fits across the four subjects and ±1 SE of the mean, respectively, which are also plotted in Figures 3 and 5. The model provides a good fit: the adjusted R^2 values for the average subjects are *0.97* for monocular and *0.88* for dichoptic viewing conditions (averaged across spatial frequency)

	0.375 cpd, 2 Hz				0.75 cpd, 2 Hz				1.5 cpd, 2 Hz			
	Mon		Dic		Mon		Dic		Mon		Dic	
Subjects	W_m	a	W_d	a	W_m	a	W_d	a	W_m	a	W_d	a
Average subject	0.00	1.05	0.22	0.00	0.00	0.52	0.13	0.00	0.00	0.00	0.14	0.00
JWZ	0.00	1.03	0.10	0.00	0.00	0.54	0.05	0.00	0.00	0.38	0.06	0.00
MG	0.00	0.75	0.07	0.32	0.00	0.19	0.05	0.01	0.00	0.00	0.10	0.00
YJK	0.00	1.04	0.07	0.00	0.00	0.27	0.19	0.00	0.00	0.08	0.05	0.00
KTM	0.00	1.24	0.35	0.00	0.00	1.99	0.14	0.00	0.00	0.00	0.17	0.00
Average of four subjects	0.00	1.01	0.15	0.08	0.00	0.75	0.11	0.00	0.00	0.11	0.09	0.00
SE	0.00	0.10	0.07	0.08	0.00	0.42	0.03	0.00	0.00	0.09	0.03	0.00

Table 2 | Model parameters obtained from the fits of the data in Figure 2b (data averaged across subjects) and Figure S2 (individual data fits) obtained for stimuli presented at 8 Hz. The model provides a good fit: the adjusted R^2 values for the average subject are *0.89* for monocular and *0.94* for dichoptic viewing conditions (averaged across spatial frequency). All parameter values are shown to two decimal places. (Full details of the model are in Kim et al.[13])

	0.375 cpd, 8 Hz				0.75 cpd, 8 Hz				1.5 cpd, 8 Hz			
	Mon		Dic		Mon		Dic		Mon		Dic	
Subjects	W_m	a	W_d	a	W_m	a	W_d	a	W_m	a	W_d	a
Average subject	0.00	0.00	0.05	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.04	0.00
RW	0.02	0.00	0.07	0.00	0.02	0.00	0.03	0.00	0.01	0.00	0.02	0.00
MG	0.00	0.23	0.03	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.05	0.00
YJK	0.00	0.30	0.05	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.01	0.00
KTM	0.00	0.00	0.14	0.00	0.00	0.00	0.15	0.00	0.00	0.06	0.13	0.00
Average of four subjects	0.01	0.13	0.07	0.00	0.01	0.00	0.06	0.00	0.00	0.02	0.05	0.00
SE	0.01	0.08	0.02	0.00	0.01	0.00	0.03	0.00	0.00	0.02	0.03	0.00

significant ($F(1, 5) = 8.492, p = 0.033$) and a follow-up t-test showed that dichoptic masking at 2 Hz is significantly greater than at 8 Hz ($t(11) = 3.086, p = 0.010$). The main effect of spatial frequency and the interaction are not significant.

A very noticeable effect of the monocular and binocular masking functions at 2 Hz is the presence of facilitation (Figure 2a). The facilitation of colour detection by luminance contrast has been reported previously under a variety of different stimulus conditions including spots and co-aligned gratings[19–22]. The chromatic test stimulus becomes more visible with increasing mask contrast and this effect is most pronounced for the lower spatial frequencies (0.375 and 0.75 cpd) at the low temporal frequency (2 Hz), disappearing at 8 Hz and at the higher spatial frequency (1.5 cpd). The effect was found in all subjects (Figure S1). A similar type of facilitatory interaction by luminance contrast on colour detection has been reported under other conditions[19,22–25]. A parameter (a) reflecting the facilitation can be obtained from the model fit and is plotted in Figure 5, showing that facilitation is only present for 2 Hz stimuli at 0.375 and 0.75 cpd.

The cause of the facilitation is unknown. We hypothesized that the effect might be due to the low spatial frequency achromatic mask increasing local luminance levels in the chromatic stimuli and enhancing threshold detection. In the next experiment, we test this by removing the grating from the mask but leaving its Gaussian envelope, creating a bright spot in the centre of the chromatic stimulus. We picked a Gabor mask of 4 × threshold, for which facilitation is known to occur, and set the value of the Gaussian mask to have the same peak luminance as the Gabor mask (L_{max} is match in the two stimuli). In all other respects the experiment was the same as in Figure 2a. As a control, we repeated the experiment when both Gabor and Gaussian masks equated in multiple of their own detection threshold (x4). Results are shown in Figure 6 as the average of the five subjects tested. A planned contrast comparison test with a Bonferroni corrected p-value (0.017) revealed significant facilitation of colour contrast detection by the luminance Gaussian mask ($t(133) = -4.330, p = 0.000$), as well as confirming the facilitation found previously by the luminance Gabor mask ($t(133) = -7.289, p = 0.000$). Both mask types significantly lowered threshold compared to the no mask condition, and no significant difference was observed for the two mask types ($t(133) = 3.959, p = 0.000$). Results suggest that removing the spatial structure from the mask does not significantly reduce facilitation and suggest that colour detection may be enhanced by the increased brightness provided by the low spatial frequency achromatic mask.

Discussion

We have investigated whether contrast gain control in colour vision is driven by achromatic contrast, or whether it is driven only by

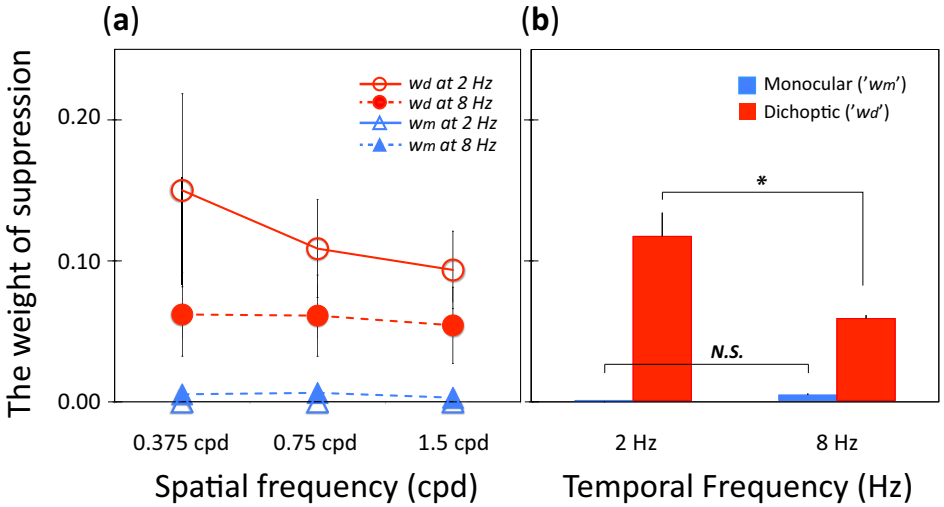

Figure 3 | Fitted weights of suppression. (a) Monocular (w_m, blue symbols) and dichoptic conditions (w_d, red symbols) for a chromatic test stimulus and achromatic mask modulated at 2 or 8 Hz as marked. The weights are the average of 4 subjects and error bars are ±1 standard error of the mean. (b) Monocular (w_m, blue bars) and dichoptic conditions (w_d, red bars) for a chromatic test stimulus and achromatic mask modulated at 2 or 8 Hz as marked. The weights are the average of 4 subjects collapsed across spatial frequency and error bars are ±1 standard error of the mean. * Indicates significant for $p < 0.05$. (Values are in Table 1 & 2).

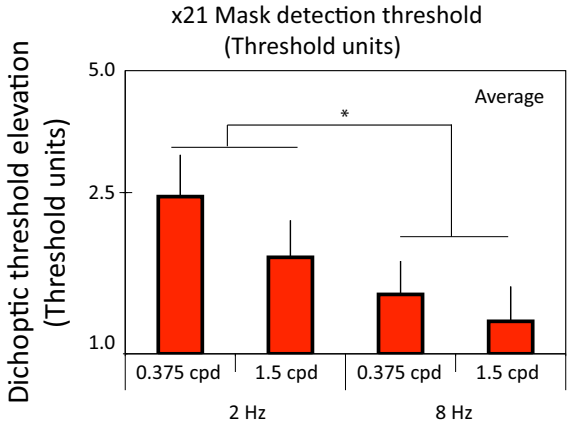

Figure 4 | Dichoptic threshold elevation. Threshold elevation, expressed as multiples of detection threshold, for the chromatic test stimulus in the presence of the achromatic mask at a fixed contrast (21 × detection threshold) for dichoptic viewing conditions. Results are for 6 subjects at two spatial and two temporal frequencies as marked.

colour contrast. We have tested this using the psychophysical method of cross-orientation masking. We have found that under binocular and monocular conditions, those closest to natural viewing, there is no evidence for the suppression of colour contrast detection by achromatic contrast. Even achromatic mask contrasts of high values (up to 30 times detection threshold) failed to raise colour detection thresholds. This lack of suppression was consistent over the range of spatial and temporal frequencies tested (0.375–1.5 cpd, 2–8 Hz). We conclude that for chromatic stimuli, cross-orientation suppression is a colour-selective process operating independently of achromatic contrast. Under dichoptic viewing conditions, however, which do not typically occur naturally, we found a strikingly different result: the achromatic mask produced a significant level of chromatic suppression, demonstrating a lack of colour selectivity. This suggests that dichoptic suppression is a fundamentally different process from the contrast normalization found under monocular and binocular conditions.

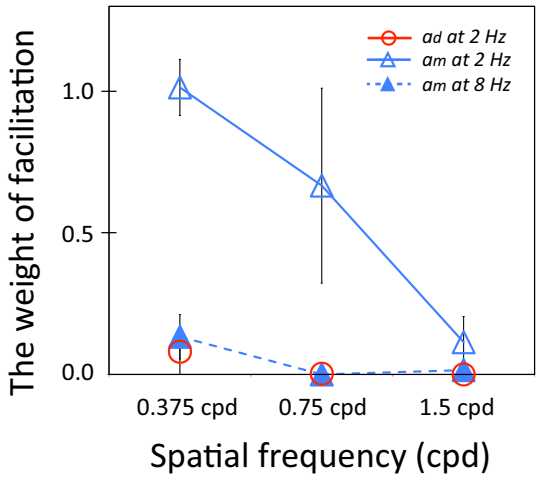

Figure 5 | Fitted weights of facilitation. Monocular (a_m, blue symbols) and dichoptic (a_d, red symbols) viewing conditions for chromatic test stimulus and achromatic mask stimuli modulated at 2 or 8 Hz as marked. The weights are the average of 4 subjects and error bars are ±1 standard error of the mean. (Values are in Table 1 & 2). Note that facilitation occurs at 0.375 and 0.75 cpd at 2 Hz under the monocular condition. No facilitation occurs under dichoptic conditions at 8 Hz and so this condition is omitted from the figure.

Colour selective contrast normalization implies that the activity-dependent signal driving the gain control is pooling colour-only neurons or at least neurons with high colour sensitivity. These results seem to be at odds with what is known about the responses of individual neurons in the visual cortex (V1) of primates. Most colour sensitive neurons in V1 respond to both colour and luminance contrast and are classed as colour-luminance cells[26–28]. Solomon and Lennie[29] have shown that these have a normalization pool driven primarily by achromatic contrast, at odds with the absence of achromatic masking we find psychophysically. A minority of neurons in V1, however, have a high sensitivity to colour and may be classified as colour-only; these have a normalization signal that includes a strong colour input but also some influence of achromatic contrast[28,29]. Neither of these categories accounts directly for our psychophysical results since both predict some modulatory influence of achromatic contrast on the chromatic response. The lack of a clear correspondence between single cell responses in V1 and the overall behavioral response suggests that the independence of the chromatic response from cross oriented luminance contrast is established elsewhere. Previous results have shown that cross-orientation suppression within colour vision (chromatic test and mask) is significantly stronger than in luminance vision for both binocular and monocular stimuli[12,13]. It is unclear where this effect originates. Parvocellular cells in the lateral geniculate nucleus (LGN), the pathway carrying red-green colour information, have been reported to show no contrast normalization[29], implying it originates at a higher level, although this effect may be an artifact of the anesthetic used, which reduces descending cortical modulation.

Achromatic contrast exerts a suppressive effect on colour contrast detection when presented dichoptically. This effect is greatest at 2 Hz but weakens as temporal frequency is increased to 8 Hz. No dependence on temporal frequency has been found for purely achromatic stimuli[30], showing that the temporal dependency of the dichoptic weights of suppression is different for achromatic-only and colour-plus-luminance conditions[13]. This dichoptic effect contrasts to the absence of masking for binocular or monocular viewing.

It is curious that the masking found for dichoptic presentations is not evident when the same stimuli are presented binocularly and suggests that this dichoptic suppression is driven by the fact that the two eyes are seeing different stimuli, whether different in orientation or contrast type (colour vs. achromatic). In other words, inter-ocular suppression occurs for stimuli that cannot binocularly summate. Our results suggest that this type of suppression is a broad, unselective effect that occurs with a similar magnitude regardless of whether the mask is of chromatic or achromatic contrast. It is not

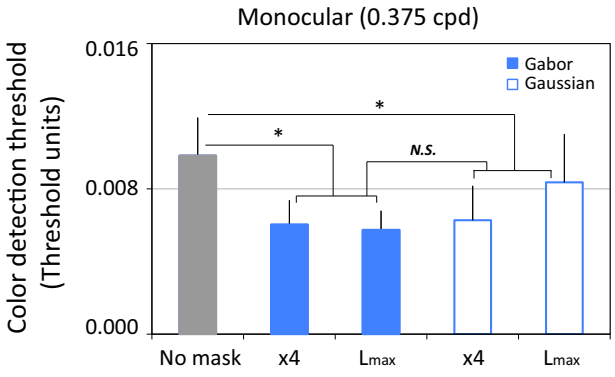

Figure 6 | Effect of Gaussian vs. Gabor masks on facilitation. Averaged colour detection thresholds plotted for Gabor or Gaussian masks, and with no mask, as marked. The masks are matched in their peak luminances (Lmax) or in their contrasts expressed as 4 × their detection threshold. Results are the average of five subjects (KTM, YJK, RW, NT and AR) and error bars are ±1 standard error of the mean.

Table 3 | Cross-orientation suppression in colour vision for monocular/binocular versus dichoptic conditions

	Monocular/binocular viewing	Dichoptic viewing
Selectivity	Colour selective (driven by colour but not luminance contrast)	Unselective (driven by both colour and luminance contrast
Magnitude	Stronger in colour vision than luminance vision, based on comparing colour test & mask with luminance test & mask[12,13].	Similar strength in colour and luminance vision
Facilitation	Present for colour test and luminance mask at low spatial frequencies	Absent
Orientation tuning	None	None
Spatio-temporal effects	Invariant across spatial and temporal frequency (TF)	Invariant, but luminance masking of colour decreases with TF

dependent on having orthogonal test and mask orientations for colour contrast[12], although dichoptic masking for achromatic stimuli is orientation tuned[31]. In colour vision, the key differences between dichoptic masking versus masking under monocular and binocular conditions are listed in Table 3. Such extensive differences suggest they have different physiological origins.

In luminance vision, previous studies have also demonstrated differences between dichoptic and monocular suppression including a differential dependence on time[9], spatial frequency (dichoptic suppression is spatio-temporally invariant, whereas monocular suppression is greatest at low spatial and high temporal frequencies[30]), and differences in adaptability (greater adaptation in the dichoptic condition)[9,18,32–34]. Dichoptic suppression is thought to involve a cortical site, either by feedback from V1 to the LGN or by intracortical modulation. Modulatory feedback from V1 to the LGN is well known and is the greatest source of input to the LGN[35–38]. If this forms the basis of dichoptic suppression, our results suggest that this descending suppression is broadly tuned across the achromatic and chromatic streams.

Our work demonstrates facilitation of colour detection by luminance contrast only for the low spatio-temporal stimuli, i.e., 0.375–0.75 cpd at 2 Hz. Some form of facilitation of colour detection by a luminance contrast pedestal has been reported before for spatially co-oriented and coextensive test and pedestal stimuli, including spot stimuli[20,21] and gratings[19,22,25]. These effects are robust across conditions including different phases and spatial frequencies of co-oriented test grating and mask[22], are monocular and may also be produced by a thin luminance ring surrounding the spot stimulus[20]. It is absent in the presence of noise pedestals[24,39], suggesting a role of luminance contrast in providing demarking spatial structure for the chromatic stimulus. It is interesting, however that this facilitation does not occur for luminance-luminance or colour-colour cross masking, but only for the cross-combination of colour and luminance contrast[13]. This facilitation remains largely unexplained, however, and may well have several different origins.

Arguments have been presented both for[19,25] and against[20,22] a direct input of attenuated luminance contrast into the chromatic system via a common detection channel, for example involving the colour-luminance neurons of V1. A common channel for colour and luminance contrast cannot readily explain our results for a number of reasons: 1. Facilitation occurs for orthogonal colour tests and luminance masks, whereas psychophysical detection channels are typically orientation tuned and do not respond to orthogonal stimuli. 2. The facilitation is largely contrast-independent, remaining relatively flat as mask contrast increases, whereas a common channel would be expected to follow the form of a standard dipper function switching from facilitation to masking as contrast increases. 3. The shape and location of the colour-colour dipper function does not change in the presence of luminance masking contrast, which is incompatible with a common colour-luminance transduction[22]. The role of the mask in reducing stimulus uncertainty (in space or time) is unlikely to account for our results, as this effect should apply to all spatial frequency stimuli, not just the low ones as we find.

We tested the hypothesis that facilitation in our data could be due to a local increase in mean luminance improving colour detection. This effect is compatible with the monocular origins of the facilitation and its presence for low spatial and temporal frequencies. The results were compatible with this explanation since Gaussian masks providing only a bright spot in the centre of the test grating were effective at providing facilitation of the test stimulus and there was no significant difference between facilitation by Gabor or Gaussian masks with the same peak luminances. We suggest that the facilitation we find may simply be due to a local enhancement of colour discrimination based on the increased mean luminance of the chromatic bars.

Methods

Apparatus. Stimuli were generated using a ViSaGe video-graphics card (Cambridge Research Systems, Kent, UK) with 14-bit contrast resolution and displayed on a Sony Trinitron (GDM 500 DIS) monitor (Sony Corporation, Tokyo, Japan) (120 Hz frame rate, 1024 × 768 spatial resolution, 51 cd/m^2 mean luminance, viewing distance of 58 cm). The monitor was gamma corrected and color calibrated as described previously[13]. Stimuli were viewed using a mirror stereoscope.

Observers. Eight subjects participated in the study, the three authors (YJK, MG, and KTM) and five naïve subjects (JWZ, AR, SK, NT and RW). All had normal or corrected-to-normal visual acuity and normal colour vision. The experiments were performed in accordance with the Declaration of Helsinki with approval from the institutional ethics committee of McGill University Health Center. Each subject signed an informed consent form.

Colour space. Stimuli were represented in a 3-dimensional cone-contrast space[40,41] in which each axis is defined by the contrast of the stimulus to each cone type. The calculation of this space has been described previously[13]. Stimulus contrast is defined as the vector length in cone contrast units (C_C):

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

where *Lc*, *Mc*, and *Sc* represent the L, M, and S Weber cone-contrast fractions in relation to the L, M, and S cone values of the achromatic background. The isoluminant point for the red-green mechanism was measured individually for each observer at each spatial and temporal frequency using a minimum motion task[42].

Stimuli. Test stimuli were chromatic horizontally oriented Gabor patterns (Figure 1) and mask stimuli were overlaid vertical, achromatic, Gabors with the same spatio-temporal frequency as the test. Three spatial frequencies were used (phase = 0): 0.375, 0.75, and 1.5 cpd. The Gabor stimuli were scaled to a fixed space constant ($\sigma = 2^\circ$). Stimuli were sinusoidally phase reversed at 2 or 8 Hz and were presented in a temporal Gaussian contrast envelope ($\sigma = 125$ ms). Test and mask stimuli were interlaced with frame-by-frame cycling and independently controlled by lookup tables. Test and mask were presented under monocular, dichoptic, and binocular viewing conditions using a stereoscope. Test and mask gratings were both presented to the right eye in the monocular condition, to both eyes in the binocular condition, and the test was presented to the right eye and the mask to the left eye in the dichoptic condition.

Procedure. Thresholds were measured using a two-interval forced-choice (2IFC) staircase procedure as previously described[13]. We first measured contrast detection thresholds for the horizontal colour test and vertical luminance mask stimuli presented alone. We then measured contrast detection thresholds for the horizontal test stimuli in the presence of the overlaid vertical masks at 4–6 fixed contrasts. Data were obtained using a pseudorandomized block design for the monocular, dichoptic or binocular conditions. Each block was repeated at least four times over the course of the experiment and each plotted threshold is based on the arithmetic mean of a at least four staircase measurements. Data for different spatial and temporal frequencies were

collected in different experiments. Contrast on all axes is expressed as threshold units (multiples of the detection threshold measured in the absence of a mask).

Model. We fitted the monocular and dichoptic test threshold versus mask contrast functions with a modified two-stage masking model[13] to determine the dichoptic and monocular weights of suppression, respectively. This model is one of a family of similar models that has been previously applied to colour-only[13] and luminance-only cross-orientation masking[1,8,30]. It separately weights the effects of inter-ocular (w_d), monocular (w_m) and binocular (w_b) contrast gain controls, and also has a facilitation parameter ('a'). The fit of each data set has three free parameters: a, w_b and w_m for monocular viewing, and a, w_b and w_d for dichoptic viewing.

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Author contributions

K.M. conceived the experiments. Y.J.K., M.G. and K.M. ran the experiments and analyzed the data. Y.J.K. programmed the model. K.M. and Y.J.K. wrote the manuscript.

Additional information

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