Vision Research 116 (2015) 80–91

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

The dynamics of cross-orientation masking at monocular and interocular sites

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ARTICLE INFO

Article history:
Received 26 May 2015
Received in revised form 9 September 2015
Accepted 21 September 2015

Keywords:
Color vision
Temporal properties
Psychophysics
Dichoptic
Isoluminance

ABSTRACT

We investigated the temporal properties of monocular and dichoptic cross-orientation masking (XOM) mediating suppressive or facilitatory cross-channel interactions between the neural detectors for the test and orthogonal mask stimuli. We measured the evolution of masking as a function of the duration of the test and mask stimuli to determine its time constant, and determined its dependence on stimulus onset asynchrony (SOA), for three contrast combinations: color-only (red–green color test and mask), luminance-only (luminance test and mask) and color-luminance (color test and luminance mask). Results show that the temporal properties of monocular and dichoptic masking differ markedly from each other and across contrast type. For the color-only condition, the dichoptic suppressive interaction is significantly longer than for the monocular one and both are largely independent of SOA. For the luminance-only condition, the suppressive interactions in both presentations are faster than for color, have similar time constants, but have different dependencies on SOA. For the color-luminance condition under the monocular conditions, cross-orientation facilitation (XOF) occurs with the luminance mask speeding up the processing of the color test with greatest XOF when the luminance mask precedes the color test by around 22 ms. No significant effects are observed for the dichoptic condition. Effects are invariant across spatial frequency. These strongly differential dynamic effects suggest that there is separate encoding of color contrast, luminance contrast, and their combination at the relatively early within-eye stage of processing, which is distinct from the dichoptic site.

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1. Introduction

Cross-orientation masking (XOM) is a widely-known psychophysical phenomenon, in which the detection of a test stimulus, such as a grating, is masked by a superimposed stimulus with an orthogonal orientation. This phenomenon, also called overlay masking, is one of the most prevalent forms of suppression in the visual system, and has been extensively investigated in luminance vision (Cass, Stuit, Bex, & Alais, 2009; Foley, 1994; Holmes & Meese, 2004; Meese & Hess, 2004; Meese & Holmes, 2007; Meier & Carandini, 2002; Petrov, Carandini, & McKee, 2005), but less so in color vision (Kim, Gheiratmand, & Mullen, 2013; Medina & Mullen, 2009; Mullen, Kim, & Gheiratmand, 2014). XOM is widely thought to be the result of cross-channel interactions, based on mutual suppression between the neural detectors for the test and for the orthogonal mask stimuli, tuned to different orientations. This mutual suppression in neural activity is referred to as contrast gain control, and has been well characterized by several models of contrast normalization, in which the activity of a neural detector at an early visual stage (V1) is divided by the pooled activities of a number of neural detectors forming a contrast gain control pool, in a so-called "divisive normalization" process (Bonds, 1989; Carandini & Heeger, 2012; Carandini, Heeger, & Movshon, 1997; Foley, 1994; Geisler & Albrecht, 1992; Heeger, 1992).

Suppression underlying psychophysical XOM is thought to occur in at least two different ocular sites. One is within-eye suppression that occurs within a monocular channel, and the other is interocular suppression that occurs between monocular channels. These two types of suppression have been well accounted for by contrast normalization models of cross-orientation masking in luminance contrast (Baker, Meese, & Summers, 2007; Kim et al., 2013; Meese & Baker, 2009), color contrast (Kim et al., 2013), and color and luminance contrast in combination (Mullen et al., 2014). Evidence suggests that for luminance vision these two types of suppression engage mechanisms that are distinct in terms of their spatio-temporal properties (Meese & Baker, 2009), their response to stimulus duration and their response to adaptation

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http://dx.doi.org/10.1016/j.visres.2015.09.008
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(Baker et al., 2007), and in terms of orientation tuning (Baker & Meese, 2007). Likewise for color vision, within-eye and interocular suppression appear distinct in several ways. For within-eye conditions, chromatic cross-orientation suppression (XOS) is stronger than the equivalent achromatic effect and is selective for color contrast, whereas under dichoptic conditions the two effects have a similar magnitude and suppression is not chromatically selective, with both achromatic and chromatic contrast suppressing chromatic stimuli (Kim et al., 2013; Mullen et al., 2014).

Studying the dynamics of XOM will help our understanding of the underlying mechanisms involved in these two types of suppression. Smith, Bair, and Movshon (2006) have investigated the temporal dynamics of XOS in macaque V1 neurons (using achromatic contrast) searching for indications of the source of within-eye suppression. They found that the onset of XOS was fast and appeared to act on the neuron even before the response onset for the preferred grating (Smith et al., 2006). They suggested that the underlying mechanism must be a rapid direct feed-forward intracortical inhibition forming divisive normalization signals in V1 cortex.

Psychophysical studies have also investigated the temporal properties of monocular and dichoptic masking. Baker et al. (2007) compared the evolution of monocular and dichoptic XOM in luminance contrast as a function of the stimulus duration of the test and mask stimuli and found that monocular masking is markedly different from dichoptic masking, with monocular masking being more dependent on stimulus duration than dichoptic masking (Baker et al., 2007). Interestingly, a recent clinical approach by Zhou et al. (2014) examined the time course of dichoptic masking using broadband noise masks in normal vision and suppression in amblyopia to understand the relationship between them. They found that interocular suppression derived from dichoptic stimuli and suppression in amblyopia have similar temporal properties in that both are strongest at short durations and decreased to approach a plateau as stimulus duration increased. Other studies have investigated the temporal properties of masking by varying the temporal interval between test and mask stimuli under other conditions (Brietmeyer, 1984; Brietmeyer & Ogmen, 2000; Essock, Haun, & Kim, 2009; Georgeson & Georgeson, 1987; Macknik & Livingstone, 1998; Saarela & Herzog, 2008). The agreement across studies is that masking occurs when the transient responses to the target are inhibited by the transient onset or offset responses to the mask stimuli, indicating a critical role of the temporal interactions between specific parts of the responses elicited by each of the test and the mask stimulus (i.e., Macknik & Livingstone, 1998).

Here we use XOM to investigate the temporal properties of monocular and dichoptic contrast normalization, mediating either suppressive or facilitatory cross-channel interactions for color-only (color test and mask), luminance-only (luminance test and mask) and color-luminance (color test and luminance mask) conditions. We first investigate the integration time for the color and luminance test stimuli presented alone. We then explore the time course of XOM by measuring the masking effect as a function of the duration of the test and mask stimuli and determining its time constant (Experiment 1). This reveals how the mask influences the time course of the detection of the test stimulus in monocular as compared to dichoptic conditions under our three contrast types at two spatial frequencies (0.375 and 1 cpd). In a second experiment, we explore the temporal resolution of the XOM by measuring masking as a function of stimulus onset asynchrony (SOA) between the test and mask stimuli in two viewing conditions (at 0.375 cpd) across the three contrast types, and determining its temporal bandwidth (Experiment 2).

Results show that the temporal properties of monocular and dichoptic cross-channel interactions are markedly different from each other, and differ profoundly across the three contrast types. For color contrast (color-only condition), the suppressive interactions under dichoptic viewing are significantly more prolonged than those for monocular viewing, and both types of suppression are prolonged across a wide range of SOAs. For achromatic contrast (luminance-only condition), the suppressive interactions under both viewing conditions are faster than in color vision, and show differential tuning for SOA. Interestingly, for a color test in the presence of an achromatic mask (color-luminance condition), we observe a different set of interactions particularly for the monocular condition, with strong *facilitation*. The luminance mask speeds up processing of the color test, and the greatest facilitation occurs when the luminance mask precedes the color test by around 22 ms (forward facilitation). For dichoptic viewing, there is no significant temporal effect of the luminance mask on the color test. These results suggest that there is differential dynamic encoding of color contrast, luminance contrast and their combination at a relatively early monocular site, which is independent of the interocular site.

2. Methods

2.1. Apparatus

Stimuli were displayed on a Sony Trinitron (GDM 500DIS) monitor (Sony Corporation, Tokyo, Japan) at 120 Hz frame rate and 1024×768 spatial resolution. A ViSaGe video-graphics card (Cambridge Research Systems, Kent, UK) was used to provide 14-bit contrast resolution using CRS Toolbox for MATLAB (MathWorks version 2008b). The monitor was gamma corrected and color calibrated as described previously (Kim et al., 2013). The background was achromatic with a mean luminance of 51 cd/m^2 at the screen center. All stimuli were viewed through a mirror stereoscope in a dimly lit room with a viewing distance of 58 cm.

2.2. Observers

Three subjects participated in this study, the one author (YJK) and two naïve subjects (AR and IO). All had normal or corrected-to-normal visual acuity and normal color vision. The experiments were performed in accordance with the Declaration of Helsinki and approved by the institutional ethics committee of McGill University Health Center. Each subject signed an informed consent form.

2.3. Color space

Stimuli were represented in a 3-dimensional cone-contrast space (Cole, Hine, & McIlhagga, 1993; Sankeralli & Mullen, 1996) 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 (Kim et al., 2013). 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 L_c, M_c, and S_c 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 isoluminance point for the red–green mechanism was estimated by a minimum motion task (Cavanagh, Tyler, & Favreau, 1984) for each observer and for each spatial frequency.

2.4. Stimuli

Test stimuli were chromatic (red/green) or achromatic horizontal Gabor patterns. Chromatic stimuli were isoluminant and

calibrated to activate the L/M cone pathway. Both chromatic and achromatic mask stimuli were vertically oriented, with the same duration, spatial frequency, and phase as the test stimulus. Two different spatial frequencies were used (phase = 0): 0.375 and 1 cpd (Fig. 1a). The Gaussian envelopes of the Gabor stimuli had a fixed space constant ($\sigma = 2°$). All Gabors were presented in a contrast modulated temporal profile characterized as fixed ramped onset/offset (3 frames for each onset and offset and each dot indicates one frame which is 8.3 ms) and a plateau (Fig. 1b). Contrast is expressed as a multiple of detection threshold, with contrast at detection threshold measured for the relevant stimulus, test or mask, presented alone. Mask contrast for the chromatic and achromatic stimuli was fixed at 10× contrast detection threshold based on previous work (Kim et al., 2013; Mullen et al., 2014). The test and mask stimuli were controlled independently by lookup tables and were interlaced with frame-by-frame cycling. The test and mask were presented under monocular and dichoptic viewing conditions using a mirror stereoscope. In the monocular condition, the test and mask grating were both presented to the right eye. In the dichoptic condition, the test was presented to the right eye and the mask to the left eye.

2.5. Procedure

Thresholds were measured using a two-interval forced-choice (2IFC) staircase procedure as previously described (Kim et al., 2013). We first measured contrast detection thresholds for the horizontal test and vertical mask stimuli in the absence of a mask for both color and luminance contrast in Experiment 1 and 2. In Experiment 1, we measured contrast detection thresholds for the horizontal test stimuli in the presence of the overlaid vertical mask stimulus as a function of the duration of the test and mask stimuli simultaneously (Threshold vs. Duration, TvD) under both monocular and dichoptic viewing conditions at two spatial frequencies (0.375 and 1 cpd). Up to seven stimulus durations (58.1, 66.4, 83, 116.2, 182.6, 315.4 and 531.2 ms) were used. For the color-only condition, four durations of the stimulus (116.2, 182.6, 315.4 and 531.2 ms) were used in both viewings at two spatial frequencies, since color thresholds were out of the range of the color gamut at the shortest durations (58.1, 66.4, and 83 ms). In Experiment 2, we measured contrast detection thresholds for horizontal test stimuli in the presence of the overlaid vertical mask stimulus as a function of the SOAs in both viewings at the 0.375 cpd. For the 116 ms (14 video frames) duration of the test and mask stimuli, nine SOAs were used: −229, −174, −133, −17, 0, +17, +133, +174 and +229 ms. SOA was defined as mask onset minus test onset: negative SOA conditions indicate that the mask precedes the test stimulus (a top in Fig. 1c), and positive SOA indicates that the mask follows the test (a bottom in Fig. 1c). We used three contrast types in both experiments. In the color-only condition, the test and mask were isoluminant and red–green. In the luminance-only condition, the test and mask were achromatic. In the color-luminance condition, the test was chromatic and the mask was achromatic. Thresholds were measured in a block design. In one block, thresholds were measured at seven (or four for the color-only condition) different durations of the stimuli (short to long) for one viewing condition (monocular or dichoptic). The order of the blocks was chosen pseudorandomly. Each block was repeated at least four times over the course of the experiment. Each plotted threshold is based on the arithmetic mean of a minimum of four staircase measurements. Data for each spatial frequency and each contrast type were collected in different experimental sessions, each using the same block design.

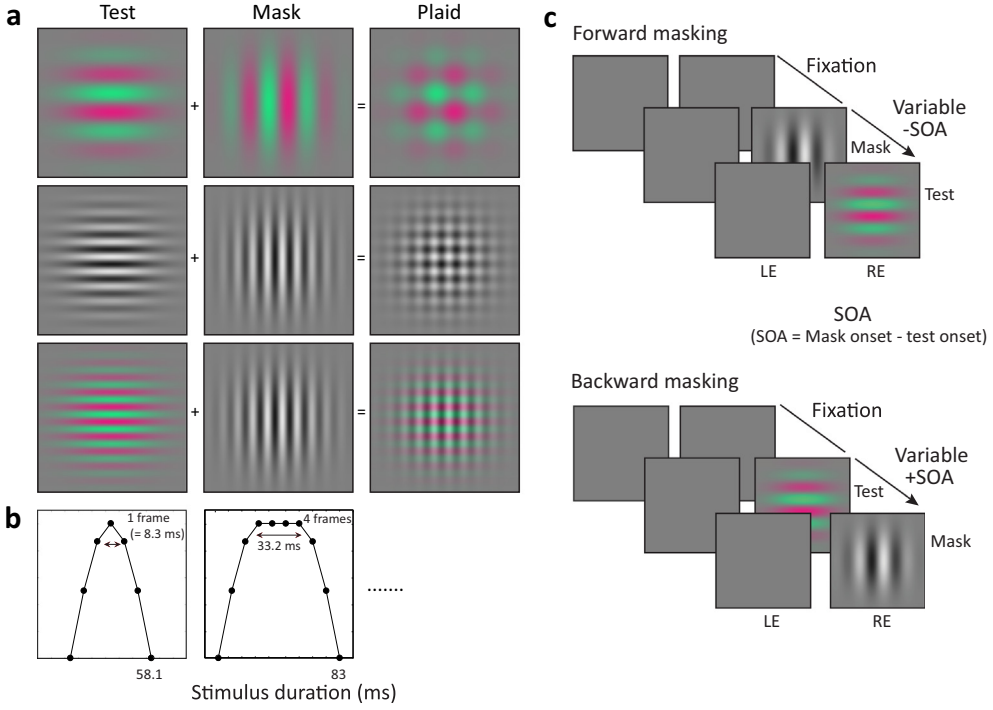

Fig. 1. Stimuli and experimental design. All stimuli are Gabors with a fixed a space constant of $\sigma = 2°$. (a) Three examples of test and mask combinations are shown. Top row, color-only condition: test and mask stimuli are both red–green isoluminant Gabors (0.375 cpd shown here). Middle row, luminance-only condition: test and mask stimuli are achromatic (1 cpd shown here). Bottom row, color-luminance condition: test is chromatic and mask is achromatic (1 cpd shown here). (b) Examples of stimuli durations, 8.3 ms (left) and 33.2 ms (right), presented using a fixed ramped onset/offset (each dot indicates one frame which is 8.3 ms). (c) Examples of the stimulus display sequences used in Experiment 2. Top shows forward masking condition in which the mask precedes the test (negative SOA). Bottom shows backward masking in which the mask follows the test (positive SOA). Monocular viewing under the color-luminance condition is illustrated. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3. Results

3.1. Experiment 1: The time course of XOM

3.1.1. Time course of detection threshold with no mask

Fig. 2 shows test detection thresholds in the absence of the mask as a function of the duration (TvD), for the color and luminance tests at two spatial frequencies (0.375 and 1 cpd). Individual data (YJK, AR and IO) are shown, with the average in the top row of the figure. The time courses of detection thresholds for the color and luminance stimuli are markedly different. To compare the temporal properties across conditions, the data were fitted with an exponential function with four parameters (solid lines):

$$X = A_1 \cdot \exp\left(-\left(\frac{t - t_0}{\tau}\right)\right) + C_1 \quad (2)$$

where τ is a time constant, revealing the ability of the visual system to integrate visual input over time (temporal integration). A_1 is a magnitude, measuring the maximum minus minimum responses. C_1 is a vertical shift. t_0 is a temporal offset fixed as 50 ms for all conditions. The values of the three free parameters (τ, A_1 and C_1) were determined from the data using a Matlab *fminsearch* function to optimize the fits. Exponential model fit parameters for individual subjects and the fit of the averaged data are given in Table S1. The goodness of fit was assessed by the adjusted R^2 metric (see further details in Kim et al., 2013) with values given in the legend of Table S1.

Fig. 3 shows the fitted values of time constant (τ) for the color and luminance test averaged across two spatial frequencies and three subjects. These were analyzed using a 2-factor repeated-measures ANOVA, with factors of contrast type and spatial frequency. The main effect of contrast type was significant ($F(1,2) = 65.68$, $p = 0.02$), showing that the fitted time constant values for the color test and luminance stimuli were significantly different ($t(5) = 3.09$, $p = 0.03$, $d = 1.42$): the color test ($\tau = 44.84$ ms) has longer processing time than the luminance stimulus ($\tau = 30.16$ ms). (No significant main effect of spatial frequency ($F(1,2) = 0.89$, $p = 0.44$) and no interaction between contrast type and spatial frequency ($F(1,2) = 4.20$, $p = 0.18$) were found.) This result is compatible with previous psychophysical results (i.e., Bowen, 1981; Burr & Morrone, 1993; Schwartz & Loops, 1983; Smith, Bowen, & Pokorny, 1984) as well as results from single cell recordings in primates (Nowak, Munk, Girard, & Bullier, 1995), indicating that neurons in the P-cell pathway are activated on average on 20 ms later than those in the M-cell pathway in V1.

With respect to the fitted values of vertical shift (C_1), significant effects were found for two contrast types ($F(1,2) = 684.89$, $p = 0.001$), reflecting higher luminance detection thresholds than color ones ($t(5) = 4.12$, $p = 0.01$, $d = 2.39$). However, no significant main effect of spatial frequency ($F(1,2) = 14.73$, $p = 0.06$) and no interaction ($F(1,2) = 19.19$, $p = 0.06$) were found.

Regarding the fitted values of magnitude (A_1), no significant effects of contrast type ($F(1,2) = 0.46$, $p = 0.57$), spatial frequency ($F(1,2) = 0.04$, $p = 0.86$) and interaction ($F(1,2) = 0.28$, $p = 0.65$) were observed for any of the conditions.

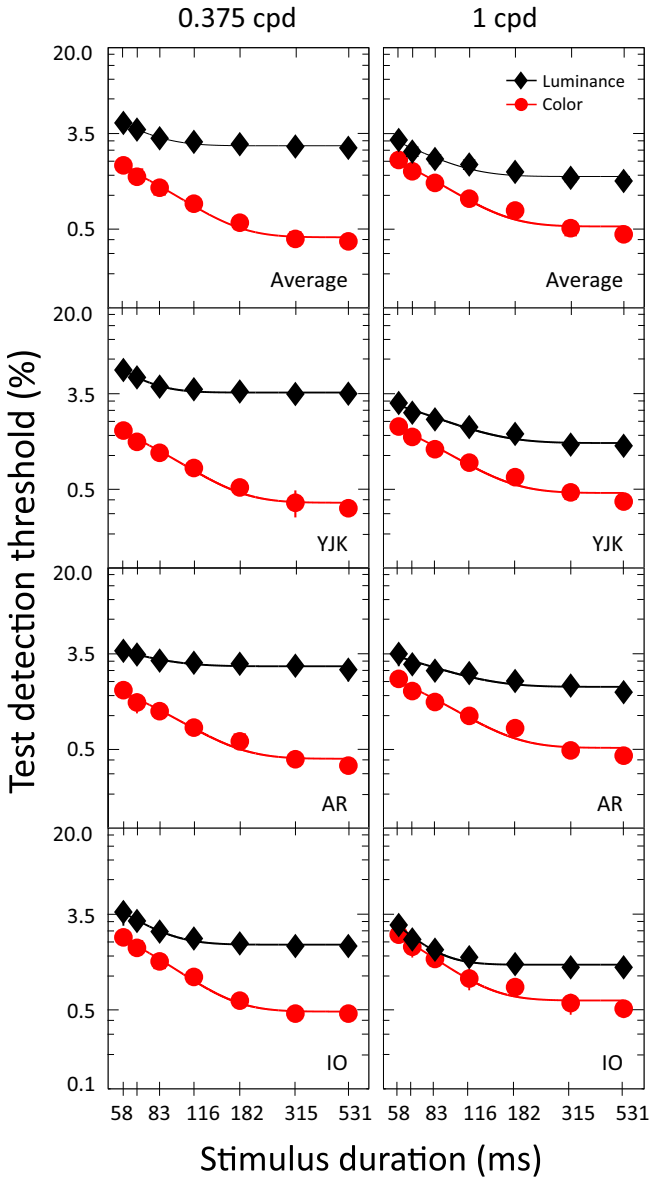

Fig. 2. Detection thresholds as a function of stimulus duration for color and luminance stimuli without mask. Detection thresholds for each color (circles) and luminance test (diamonds) as a function of the stimulus duration at two spatial frequencies (0.375 and 1 cpd) plotted on double-log axes. The average across two subjects is shown in the top panel. Error bars are ±1 SE of the mean. The individual subjects' data are shown under top panel (YJK, AR & IO) (±1 SD of the mean of the four replications is shown). The data are fitted with an exponential function (solid lines, Eq. (2)). All fitted values are provided in Table S1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

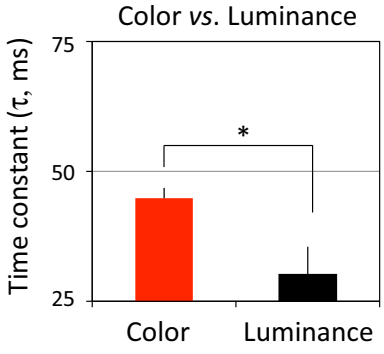

Fig. 3. Fitted values of time constant. Fitted values of the time constant (τ) are plotted for color and luminance test stimuli. Fitted values of the vertical shift (C_1) are 0.48 for color and 2.34 for luminance test. Fitted values of the magnitude (A_1) are 1.71 for color and 1.98 for luminance test. Note that the values are the average of 3 subjects (YJK, AR & IO) collapsed across two spatial frequencies (0.375 and 1 cpd) and error bars are ±1 SE of the mean. *Indicates significant for $p < 0.05$. Fitted values are in Table S1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

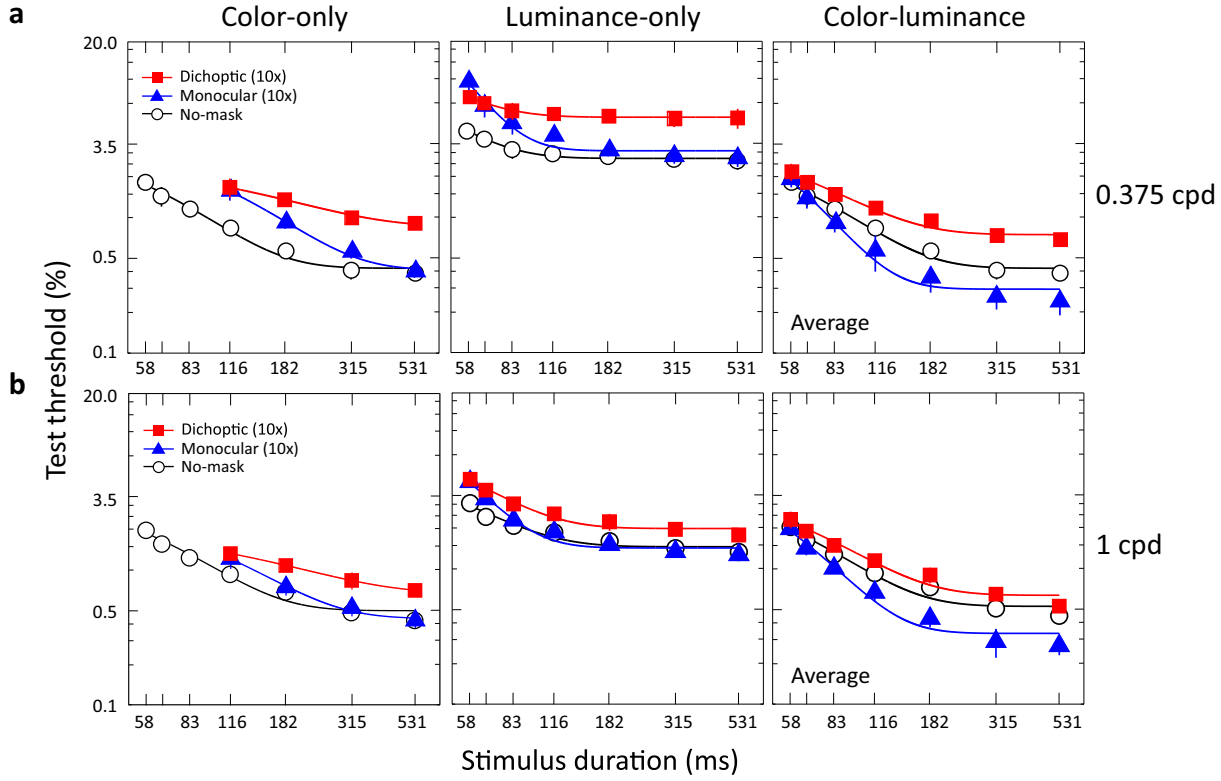

Fig. 4. Detection thresholds as a function of the duration of the test and mask stimuli with mask across three contrast types for two viewings: monocular (triangles) and dichoptic (squares). Mask contrast for the chromatic and achromatic stimuli is fixed at 10× contrast detection threshold. No-mask data (open circles) are re-plotted from Fig. 2. Results are the average across 3 subjects. Two spatial frequencies shown as marked (0.375 and 1 cpd). The data are fitted with the same function (solid lines) as used in Fig. 2. Error bars are the mean of ±1 SE. All fitted values are provided in Table S2.

3.1.2. Time course of XOM under monocular and dichoptic presentations

Fig. 4 shows thresholds in the presence of the mask as a function of the stimulus duration (TvD) under the monocular and dichoptic conditions for three contrast types at two spatial frequencies (0.375 and 1 cpd) averaged across three subjects. The thresholds in the absence of the mask (on the top panel from Fig. 2) (open circles) are re-plotted with the exponential model fit (solid lines). Individual data are plotted in Fig. S1a and b. Under most conditions masking occurs, but under the color-luminance condition for monocular viewing, there is facilitation of the color test. To determine the temporal parameters underlying XOM and XOF, the TvD masking data are fitted with the exponential function of equation 2 with four parameters (solid lines). Model fit parameters are listed in Table S2 and the goodness of the model fits is given in the legend of Table S2.

Since a 3-factor repeated-measures ANOVA on the data (time constant) (viewing condition × spatial frequency × contrast type) revealed no significant main effect of spatial frequency, consistent with the no-mask data, we collapsed the data across two spatial frequencies. The data were then re-analyzed using a 2-factor repeated-measures ANOVA (contrast type × viewing). The main effect of viewing condition was significant ($F(1, 5) = 13.05$, $p = 0.02$). There was a significant difference between the time constants for the dichoptic and monocular conditions ($t(17) = 3.83$, $p = 0.001$, $d = 0.66$), as shown in Fig. 5a. This finding confirms that the time course of dichoptic masking ($\tau = 73$ ms) is significantly longer than that for monocular masking ($\tau = 44$ ms).

As reflected in Fig. 5b, the main effect of contrast type was also significant ($F(2,10) = 70.70$, $p = 0.00$). A follow-up Bonferroni post hoc test showed that the fitted time constants for the color-only ($\tau = 114$ ms) condition were significantly longer than those for the luminance-only ($\tau = 24$ ms) ($p = 0.001$, $d = 2.91$) or color-luminance ($\tau = 39$ ms) ($p = 0.001$, $d = 2.41$) conditions. However, the fitted time constants for luminance-only condition were not significantly different from those for the color-luminance condition ($p = 0.54$, $d = 1.57$). These findings indicate that the timing of masking for the color-only conditions has the longest processing. Furthermore, there was significant two-way interaction between contrast type and viewing condition ($F(2,10) = 17.28$, $p = 0.001$). Particularly, for the color-only condition the fitted time constants under dichoptic viewing ($\tau = 145$ ms) were significantly longer than those for the monocular case ($\tau = 83$ ms) ($t(5) = 4.10$, $p = 0.01$, $d = 2.08$), as shown in Fig. 5c. This indicates that the processing time under the dichoptic presentation for the color-only condition is the longest.

Other significant effects were observed on the fitted values of magnitude (A_1) across the three contrast types ($F(2,33) = 7.95$, $p = 0.002$). A follow-up Bonferroni post hoc test revealed that the fitted magnitude values for the luminance-only condition were significantly greater than those for the color-luminance ($p = 0.005$, $d = 1.14$) and color-only ($p = 0.004$, $d = 1.17$) conditions. However, there was no significant difference between the magnitudes for the color-only and color-luminance conditions ($p = 1.0$, $d = 1.20$). These findings indicate that thresholds derived from the luminance test by the luminance mask (luminance-only) are more dependent on the stimulus duration than the color-only and color-luminance conditions. With respect to the fitted values of vertical shift (C_1), the significant effects were found for three contrast types ($F(2,33) = 29.06$, $p = 0.001$). As expected, masking thresholds for the luminance-only condition were significantly higher than those for the color-only ($p = 0.001$, $d = 2.17$) and color-luminance conditions ($p = 0.001$, $d = 2.26$).

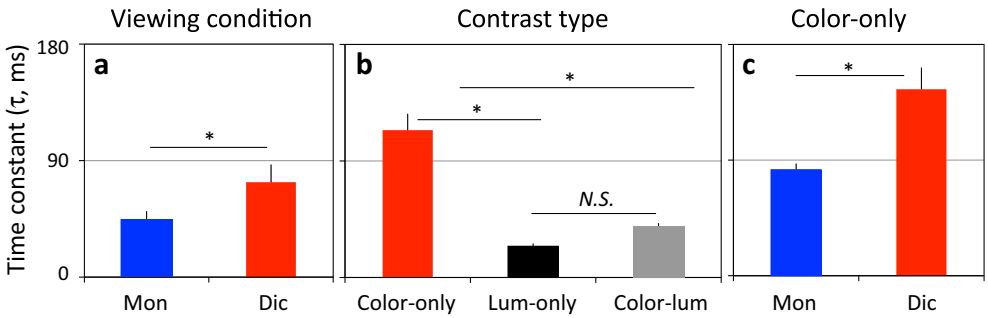

Fig. 5. Fitted values of the time constant. (a) Fitted values of the time constant (τ) for monocular and dichoptic viewings averaged across spatial frequency, contrast type, and subject. (b) Fitted values of the time constant for color-only, luminance-only and color-luminance contrast types averaged across spatial frequency, viewing condition, and subject. (c) For the monocular and dichoptic presentations in the color-only condition, the fitted time constants averaged across spatial frequency and subject. Note: the fitted values of vertical shift (C_1) for all conditions are 0.61 for the color-only, 3.24 for luminance-only, and 0.75 for color-luminance condition. The fitted values of magnitude (A_1) for all conditions are 1.81 for color-only, 5.41 for luminance-only and 1.92 for color-luminance conditions. Error bars are ±1 SE of the mean. *Indicates for $p < 0.05$. Fitted values are in Table S2. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.1.3. How does the orthogonal mask influence the processing time of the test?

In order to reveal how the mask stimulus affects the processing time (τ) of the test stimulus, in Fig. 6 we compare the fitted time constants for the no-mask (Fig. 3) and each of the masking conditions (Fig. 5). As the time constants for the chromatic and luminance test stimuli presented alone are different, it is useful to compare the with-mask and no-mask time constants to reveal the temporal effects of the mask. We use Welch's F test and Games-Howell post hoc test on the data set when the sample sizes are unequal.

The fitted time constants for the color test with no mask, with a color mask (color-only) and an achromatic mask (color-luminance) are shown in Fig. 6a. There was a significant effect of masking on the time constant for these conditions (Welch's $F(2, 17.47) = 16.13$, $p = 0.001$). A follow-up Games-Howell post hoc test revealed that the time constant for the color-only condition was significantly longer than that for the no-mask color-test ($p = 0.001$, Hedges' $g = 1.9$) and color-luminance ($p = 0.001$, $g = 2.23$) conditions. However, no significant difference between the no-mask color-test and color-luminance condition was observed ($p = 0.27$, $g = 0.63$). These findings show that the color mask significantly delays the processing time of the color test, but the luminance mask does not.

The fitted time constants for the color test with the same masks as above, but split into the monocular and dichoptic viewing conditions are shown in Fig. 6b. There was a significant effect on the time constants across the five conditions (Welch's $F(4, 12.10) = 32.97$, $p = 0.001$). With a Games-Howell test, the time constants for the monocular color-only ($p = 0.001$, $g = 4.18$) and dichoptic color-only ($p = 0.01$, $g = 3.41$) conditions were significantly longer than those for the no-mask, indicating that the color mask significantly delays the processing of the color test. In comparison, the time constants for the monocular, color-luminance condition were significantly shorter than those for the no-mask ($p = 0.002$, $g = 3.12$). No significant difference between the dichoptic

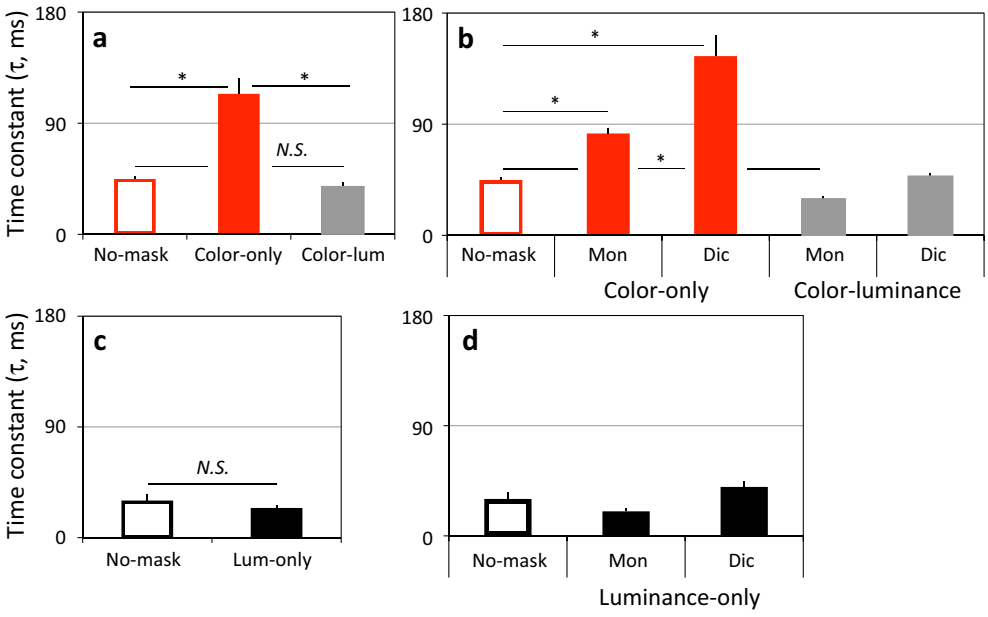

Fig. 6. The role of the mask in the processing time for the test. Time constant (τ) derived from no-mask and mask conditions. (a) Fitted values of time constant for the no-mask color-test, color-only, and color-luminance conditions averaged across subject and spatial frequency, (b) Fitted time constants for the no-mask color-test, the monocular and dichoptic conditions in the color-only and color-luminance contrast averaged across subject and spatial frequency. (c) Fitted time constants for the no-mask luminance-test, and luminance-only conditions averaged across subject and spatial frequency. (d) Fitted time constants for the no-mask luminance-test, monocular and dichoptic conditions in the luminance-only condition averaged across subject and spatial frequency. Error bars are ±1 SE of the mean. *Indicates for $p < 0.05$. Fitted values are in Tables S1 and S2. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

color-luminance and the no-mask conditions was observed ($p = 0.85$, $g = 0.58$). This finding indicates that the luminance mask speeds up the processing of the color test for the monocular site, while no significant effect is observed for the dichoptic site. These results demonstrate the role of the mask in altering the processing time for the test in the monocular and interocular sites.

Fig. 6c shows the fitted time constants for the luminance test with no mask and with a luminance mask (luminance-only condition). We found no significant main effect with the luminance data set (Welch's F (1, 6.617) = 1.11, $p = 0.33$), indicating no significant difference between the two conditions ($t(16) = 1.27$, $p = 0.22$, $g = 0.57$). Dichoptic and monocular viewing are shown separately in Fig. 6d and our data show an interesting trend in which the luminance mask speeds up the processing of the luminance test under monocular viewing. A consistent trend with the luminance mask speeding up the processing time of the luminance test has been reported previously under monocular viewing (see Figs. 2 and 4 from Smith et al., 2006).

3.2. Experiment 2: Temporal resolution of XOM

Fig. 7 shows masking thresholds as a function of the stimulus onset asynchrony (SOA) between the test and mask, under the monocular and dichoptic conditions for the three contrast types. Results are shown for three subjects and their average (top row). No-mask thresholds are plotted as open circles. The shapes of the monocular and dichoptic masking functions with respect to SOAs are markedly different from each other, and also differ according to the three contrast types. To compare their tuning properties, the data were fitted with a skewed Gaussian function (solid lines) with five parameters, given in the following equations:

$$\begin{aligned} G_1 &= m \cdot \exp\left(-0.5 \cdot \left(\frac{t-p}{\sigma_{\text{left}}}\right)^2\right) \\ G_2 &= m \cdot \exp\left(-0.5 \cdot \left(\frac{t-p}{\sigma_{\text{right}}}\right)^2\right) \\ G &= G_1 \cdot (t < p) + G_2 \cdot (t \geqslant p) + d \end{aligned} \tag{3}$$

where t is time corresponding to mask – test onset SOAs. m is amplitude indicating either facilitatory or suppressive effects, σ_{left} and σ_{right} are half standard deviations with at 1/e height of the forward (left) and backward (right) of the distribution respectively, p is the peak time, and d is the vertical offset. The values for the free parameters m, σ_{left}, σ_{right}, p and d were determined for each subject and condition using the same Matlab function as in Experiment 1. Fitted values are given in Table S3.

For the color-only condition, masking thresholds for monocular and dichoptic conditions are independent of SOA over the range measured (left column, Fig. 7). For the luminance-only condition, masking thresholds with respect to SOA show tuning but with differently shaped functions for the monocular and dichoptic conditions (middle column, Fig. 7); under monocular viewing, the masking is asymmetric showing backward masking (positive SOAs), whereas it is symmetric under dichoptic viewing. For the color-luminance condition, the shape of the masking functions differ between the monocular and dichoptic conditions (right column, Fig. 7), showing forward facilitation (negative SOAs) under monocular viewing but symmetric masking for dichoptic viewing.

The fitted values of forward and backward temporal bandwidths ($\sigma_{\text{left}} + \sigma_{\text{right}}$) are shown in Fig. 8. These are shown in Fig. 8a averaged across the monocular and dichoptic conditions for the three contrast types. A 2-factor repeated-measures ANOVA (contrast type × viewing condition) provided a significant main effect of contrast type ($F(2,4) = 257.05$, $p = 0.001$). A follow-up Bonferroni post hoc test showed that the temporal bandwidth for the color-only condition was significantly broader than that for the luminance-only ($p = 0.001$, $d = 9.91$) or color-luminance conditions ($p = 0.001$, $d = 17.04$). These results confirm that masking thresholds underlying the chromatic system have a poor temporal resolution resulting in extended constant masking across the SOAs. In comparison, masking thresholds underlying the luminance and color-luminance systems have a better temporal resolution. There was a significant main effect of viewing condition ($F(1,2) = 33.19$, $p = 0.03$), although the difference between the two conditions was not significant ($t(8) = 1.36$, $p = 0.21$, $d = 0.24$). That is, the temporal bandwidths for monocular and dichoptic conditions, if averaged across all other conditions, are not significantly different from each other. There was a significant two-way interaction between contrast type and viewing condition ($F(2,4) = 52.39$, $p = 0.001$), implying that masking thresholds obtained from the three contrast types and two viewing conditions are mediated by distinct mechanisms.

Fig. 8b compares the fitted values of forward (σ_{left}, filled rectangle) and backward distribution (σ_{right}, open rectangle) for the luminance-only and color-luminance conditions under monocular viewing. Since the masking thresholds do not show any tuning for the color-only condition, they are not included here. The shape of the monocular masking function with respect to SOAs is largely asymmetric. For the luminance-only condition, the σ_{right} values were significantly broader than the σ_{left} values ($t(4) = 5.32$, $p = 0.01$, $d = 4.35$), revealing significant backward masking (positive SOAs). A similar asymmetry with stronger backward masking has been reported under binocular viewing using a broadband mask pattern in luminance vision (Essock et al., 2009). For the color-luminance condition, the σ_{left} values were markedly broader than the σ_{right} values ($t(4) = 10.98$, $p = 0.001$, $d = 8.95$), indicating significant forward facilitation (negative SOAs). These results show the temporal order of the test and mask stimuli has an important differential effect between luminance-only and color-luminance selective detecting-mechanisms in the monocular site.

In Fig. 8c we show the fitted σ_{left} and σ_{right} values for both contrast types under dichoptic viewing. The σ_{left} and σ_{right} values were not significantly different for the luminance-only ($t(4) = 0.09$, $p = 0.93$, $d = 0.07$) and color-luminance ($t(4) = 1.26$, $p = 0.28$, $d = 0.34$) conditions, indicating a symmetric shape of the masking function for the dichoptic site. Together, our results provide evidence that temporal resolution evoked by varying SOA between the test and mask stimuli plays a critical role in determining the shape of the masking function for the luminance-only and color-luminance conditions and two viewing conditions, indicating that different mechanisms are involved.

The fitted values of amplitude (m) indicate the size of the facilitatory or suppressive effects. For the luminance-only condition, the fitted amplitude values for dichoptic viewing were greater than those for monocular viewing ($t(4) = -4.02$, $p = 0.02$, $d = 3.30$). For the color-luminance condition, the fitted amplitude values in both viewings are markedly different each other ($t(4) = -14.07$, $p = 0.001$, $d = 10.97$), and in particular for monocular viewing strong facilitation was observed.

The parameter p indicates the time of the maximal cross-channel interaction (either suppressive or facilitatory); values are listed in Table S3. For the color-luminance condition, the facilitation had a peak time averaged across subjects of −22-ms SOA. Apart from this condition, the peak time is around 0-ms SOA for all conditions. A similar result has been reported with maximal facilitation at around −20-ms SOA (Eskew, Stromeyer, & Kronauer, 1994). For the color-only condition, there is no peak time since the masking thresholds in both viewings are largely independent of SOA. Other significant effects on the fitted values of vertical shift (d) were observed for three contrast types, indicating that masking thresholds for the luminance-only condition are

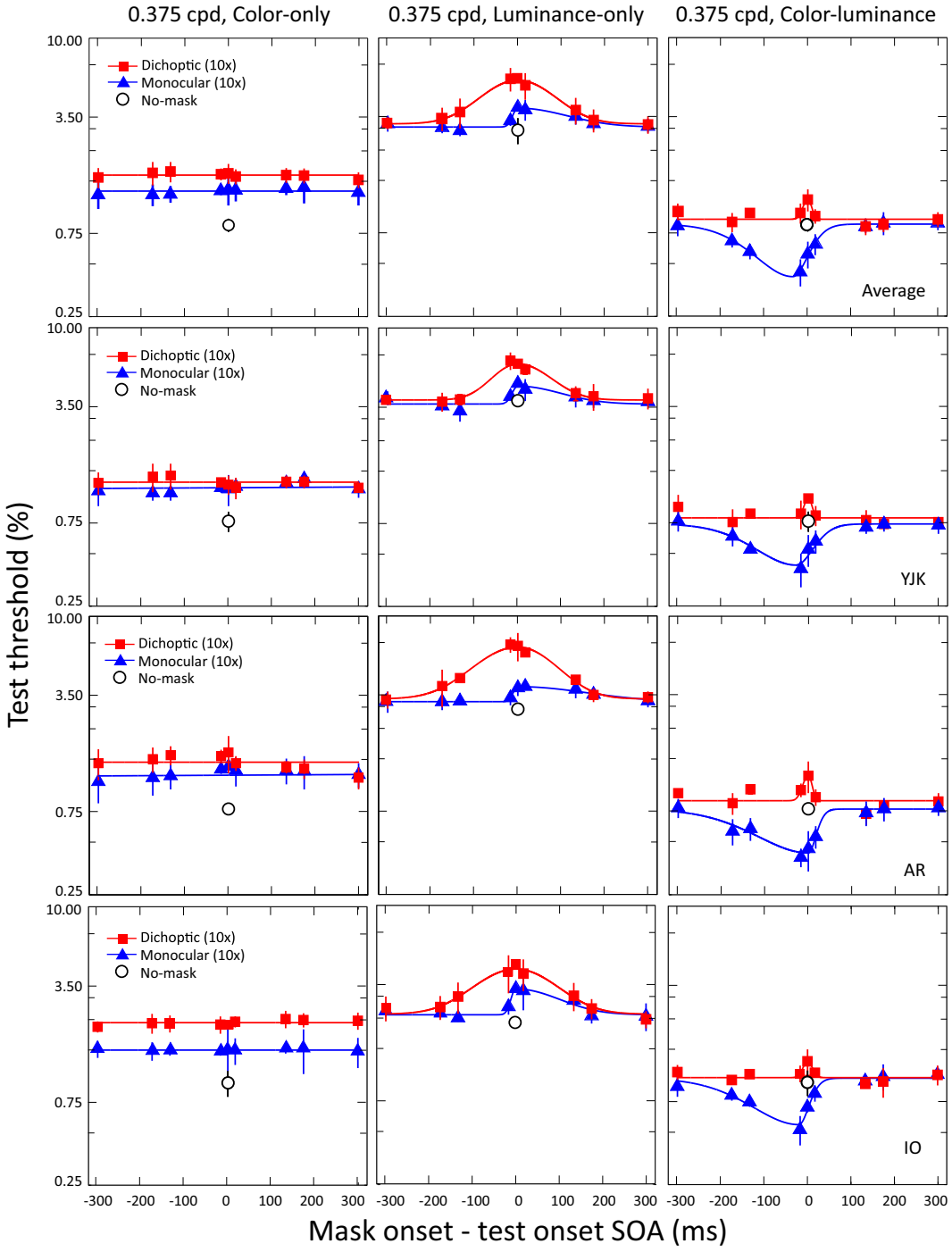

Fig. 7. Detection thresholds for 0.375 cpd as a function of the SOA for the 116 ms duration of the test and mask stimuli. Test detection thresholds for 0.375 cpd as a function of mask onset – test onset SOA under monocular (triangles) and dichoptic (squares) viewings in the presence of either color-only, luminance-only, color-luminance mask, or no-mask test conditions (open circles). The average of the 3 subjects (YJK, AR & IO) is shown in the top row. The data are fitted with the skewed Gaussian function (solid lines) of equation 3. Error bars are the mean of ±1 SE. Individual data are shown under the top rows (±1 SD of the mean of the four replications is shown). All fitted values are provided in Table S3. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

significantly higher than those for the color-only and color-luminance conditions.

3.3. Control conditions

In the main experiments, mask contrasts were limited to 10 times detection threshold so that chromatic and achromatic masks could be presented at equivalent suprathreshold contrasts, and this limited the amount of masking that could be obtained. Because of the color gamut of the display screen, higher color contrasts could not be obtained. As a control, however, we increased the luminance mask contrast from 10× threshold to the maximum available contrast (18–30× thresholds) in the two main experiments. Data for each control condition with the model fit are plotted in Fig. S2 (control 1) and S3 (control 2). Model fits are listed in Tables S4 and S5. The results for Control 1 show that the higher luminance mask contrast produced greater masking (higher vertical shift parameter). However, fitted values of the time constant and

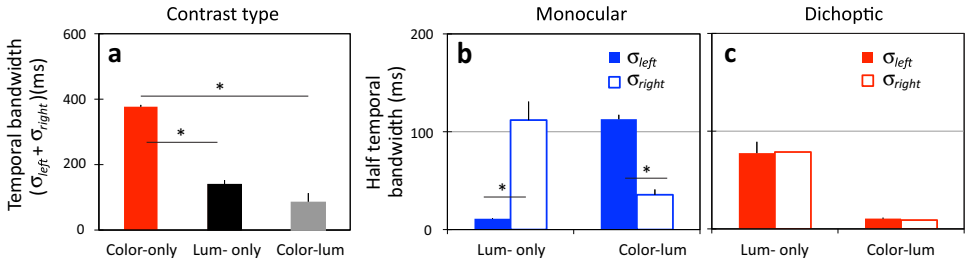

Fig. 8. Fitted values of temporal tuning bandwidth. (a) Fitted values of full bandwidth ($\sigma_{left} + \sigma_{right}$) for the color-only, luminance-only and color-luminance conditions averaged across viewing and subject. (b) For monocular viewing, fitted values of σ_{left} (forward distribution) and σ_{right} (backward distribution) for the luminance-only and color-luminance conditions averaged across subject. (c) For dichoptic viewing, fitted values of σ_{left} and σ_{right} for the luminance-only and color-luminance conditions averaged across subject. Error bars are ±1 SE of the mean. *indicates for $p < 0.05$. Fitted values are in Table S3. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

magnitude parameters showed no significant difference at the higher mask contrast. The results of Control 2 show a similar effect with increased masking but no effect on the fitted values of temporal bandwidth, magnitude and peak parameters.

4. Discussion

We have used cross-orientation masking (XOM) to investigate the temporal properties of monocular and dichoptic contrast normalization in both color and luminance vision, and their combination. We have found quite a complex set of temporal properties that clearly differ between dichoptic and monocular presentations, and also depend on whether test and mask stimuli are both chromatic, both achromatic, or with a chromatic test and luminance mask. Effects, however, were invariant across spatial frequency. The effect of the mask was predominantly suppressive, although in one specific condition (monocular color test with achromatic mask), facilitation occurred. Temporal properties were investigated in two ways, by measuring the dependence of the masking effect on the duration of the test/mask combination to extract a time constant, and by measuring the effect of SOA between the test and mask to obtain a measure of temporal tuning. Results are summarized in Table 1. After a brief description below they are discussed more fully under separate headings.

For color vision (color-only condition), the presence of the color mask significantly delayed the processing of the color test in both monocular and dichoptic cases but much more so under dichoptic viewing (Fig. 6b). Both suppressions were largely independent of SOA over the range tested (left column, Fig. 7) indicating very sluggish and prolonged responses to the test and mask. For luminance vision (luminance-only condition), the presence of the luminance mask has no significant effect on the processing time of the test (Fig. 6d), although there was an observable trend for the monocular mask to speed up the test response and for the dichoptic mask to slow it down. Both effects are selective for SOA but with different shapes, showing symmetric temporal tuning for the dichoptic condition and asymmetric backward masking for the monocular condition (middle column, Fig. 7), indicating distinct masking mechanisms for each condition. Interestingly, for the combination of a color test and luminance mask under monocular conditions, for which we observed strong XOF, the luminance mask significantly speeds up the processing time of the color test (Fig. 6b), with greatest facilitation when the luminance mask precedes the color test by 22 ms (forward facilitation) (right column, Fig. 7). In comparison, a color mask slows it down. Under the dichoptic conditions, no significant effects of the luminance mask on the color test were observed. Together, our results suggest that distinct dynamic and separate encoding of color contrast, luminance contrast, and their combination emerges at a relatively early within-eye stage of processing, which is independent of the dichoptic site.

In previous work using a similar approach, key differences have emerged between dichoptic and monocular/binocular masking effects under color-only, luminance-only and color-luminance conditions, supporting the idea of separate within-eye and between eye normalization mechanisms. Kim et al. (2013), using a modified two-stage masking model of contrast normalization (Meese & Baker, 2009), provided evidence for separate neural pathways for color and luminance contrast normalization at the monocular/binocular sites, which are independent of the dichoptic site. Mullen et al. (2014) demonstrated significant facilitation of the color test by the luminance mask under monocular/binocular conditions at low spatio-temporal conditions (0.375 cpd, 2 Hz), but suppression under dichoptic conditions at 2 Hz. Together, these previous findings suggested that monocular and dichoptic

Table 1
Temporal properties of cross-orientation masking for the monocular and dichoptic conditions for three different contrast combinations.

	Monocular	Dichoptic
Processing time	The processing time of the dichoptic XOM for all conditions is significantly longer than for the monocular one.	
Color-only	The color mask significantly delays the processing of the color test in both viewing conditions, with the greatest effect in the dichoptic condition.	
Luminance-only	No significant effect on the processing time of the luminance test by luminance mask is observed in any condition.	
Color-luminance	The luminance mask significantly speeds up the processing of the color test, revealing facilitation.	No significant effect is shown.
Temporal variation	The temporal resolutions of the dichoptic and monocular XOM for all conditions are not significantly different.	
Color-only	The shape of XOM function in both viewing conditions is largely constant regardless of the SOAs, revealing a poor temporal resolution of the underlying mechanism.	
Luminance-only	The shape of XOM is a skewed Gaussian with the masking effect larger for backward masking (positive SOAs) conditions.	The shape of XOM is a symmetric Gaussian, with the masking effect.
Color-luminance	The shape of tuning is asymmetric, with the facilitation effect larger for forward masking (negative SOAs) conditions.	The shape of tuning is a symmetric masking effect.

cross-orientation interactions, driven by the color-only, luminance-only, or the combination of the test and mask, arise from distinct neural mechanisms. The distinct temporal properties that we find here for each condition support this conclusion.

4.1. The origin of dynamic monocular XOS

The neurophysiological results of Smith et al. (2006) match well with the current psychophysical study for achromatic contrast, with both results indicating a relatively rapid effect of the mask on the processing time of the test. Their results show that the onset of XOS (42.5 ± 11.1 ms) appeared at or even before the response onset for the preferred grating stimulus (50 ± 15.8 ms). However, the onset of XOS occurs with some delay after the response offset for the preferred grating (30.1 ± 9.3 ms). These findings indicate that the luminance mask may speed up the processing time involved in temporal integration for the luminance test (see Fig. 4 from Smith et al., 2006). We found a similar trend in the present study under monocular viewing (see Fig. 6d). To account for their results, Smith et al. (2006) considered the offset response for the preferred grating as a measure of the earliest excitatory signal, and argued that the ~13.5 ms delay between the onset of XOS and the offset response for the preferred grating is sufficient time to build *local* inhibition forming contrast normalization signals within V1, which acts before the threshold for the preferred grating is reached. Therefore, they concluded that XOS results from delayed inhibition (~13.5 ms) evoked by the local inhibition within V1 that reduces feed-forward excitation from the LGN (termed the excitatory feed-forward model). This type of very fast intracortical inhibition (in the millisecond range) also accounts for why XOS actually precedes the onset response for the preferred grating. Their findings provide physiological evidence that XOS is mediated by a dynamic divisive normalization, which is also thought to underlie psychophysical XOM. This interpretation is consistent with the idea that the dynamic divisive normalization is a possible mechanism of suppression in V1 under other conditions (Albrecht, Geisler, Frazor, & Crane, 2002; Bonds, 1991; Heeger, 1992).

Other studies have explored the temporal properties of masking by varying SOA between the test and mask stimuli while searching for the source of suppression (Brietmeyer, 1984; Brietmeyer & Ogmen, 2000; Essock et al., 2009; Macknik & Livingstone, 1998; Saarela & Herzog, 2008). The common agreement across these studies is that the masking effect is mediated by temporal interactions between specific parts of the neural responses elicited by each of the test and mask stimulus: the transient onset-response and the transient offset-response. Specifically, forward masking occurs when the transient on-response of the target is inhibited by the transient off-response of the mask, while backward masking occurs when the transient off-response of the target is suppressed by the transient on-response of the mask (i.e., Macknik & Livingstone, 1998). So, it is logical to assume that the different shapes of masking functions shown in the current study (Fig. 7) might be mediated by different temporal interactions between the stimuli, depending on the viewing conditions and contrast types.

There is a very significant difference between the within-eye dynamics of the chromatic (color-color) and achromatic (luminance-luminance) masking effects. The luminance contrast displays backward masking; it is greatest when the test and mask are temporally co-extensive, declines as the mask is delayed relative to the test, and disappears once they no longer overlap. In comparison, the color contrast shows both forward and backward masking that is invariant over the SOA used (+/- 300 ms) and even when the test and mask are temporally well separated, suggesting a very sluggish effect of chromatic contrast normalization, also supported by the long time constant of monocular, chromatic masking.

4.2. The origin of dynamic interocular XOS

Several studies have investigated the temporal properties of dichoptic masking to understand the origin of interocular suppression under different conditions (Bair, Cavanaugh, & Movshon, 2003; Baker et al., 2007; Huang, Baker, & Hess, 2012; Macknik & Martinez-Conde, 2004; Petrov et al., 2005; Webb, Dhruv, Solomon, Tailby, & Lennie, 2005; Zhou et al., 2014). A common agreement in these studies is that the plausible source for dichoptic masking is intracortical inhibition. In the current study, we showed that the processing time of dichoptic masking is significantly longer (τ = 73 ms) than that for monocular viewing (τ = 44 ms) across all conditions (Experiment 1). This is compatible with a temporal frequency dependence of dichoptic suppression that is greater at 2 Hz than at 8 Hz (Kim, Gheiratmand, & Mullen, 2014; Mullen et al., 2014). Our findings also showed that the temporal interaction evoked by varying SOA between the test and mask stimuli forming the temporal tuning function plays a critical role in determining the different shapes of monocular and dichoptic masking across the three contrast types. It showed a symmetric shape of the temporal tuning function for the dichoptic site that is markedly different from the asymmetric shapes for the monocular site, with backward masking for the luminance-only and forward facilitation for color-luminance conditions (Experiment 2). These findings provide psychophysical evidence that the monocular and dichoptic XOMs are mediated by different dynamic mechanisms. In addition, the chromatic dichoptic masking is significantly more sluggish than the achromatic, in both its time constant and dependence on SOA.

Interestingly, there is psychophysical evidence that dichoptic suppression is a part of surround suppression mechanisms regarding their temporal properties. Physiological studies provide evidence that surround suppression has two components, one relating to spatio-temporal selectivity (Webb et al., 2005) and another relating to propagation time (Bair et al., 2003) in V1. Psychophysically, it has been first reported that suppression arising from dichoptically presented stimuli (Baker & Meese, 2007) and surround stimuli (Petrov et al., 2005) shows strong orientation selectivity. Second, the time course of threshold-elevation functions (masked threshold/unmasked thresholds) under dichoptic viewing (Fig. 2 from Petrov & McKee, 2009) are markedly similar to our data plotted in the same units as threshold-elevation (Kim, 2014). In particular, threshold elevations from both studies are largely independent of stimulus duration. Finally, the spatio-temporal properties of interocular suppression have been investigated using three types of broadband noises (full field, overlaying, or surrounding) (Huang et al., 2012). The results showed that the spatio-temporal properties of suppression were not markedly different across the three mask types, showing lowpass spatio-temporal properties with similar contributions from both surround and overlay suppression, which resemble the response properties shown in the early suppressive mechanism (see Fig. 11 from Webb et al., 2005).

4.3. The origin of dynamic monocular XOF

The existence of facilitatory interactions between color and luminance contrast are well established in the literature (Chen, Foley, & Brainard, 2000; Gegenfurtner & Kiper, 1992; Gowdy, Stromeyer, & Kronauer, 1999; Losada & Mullen, 1995; Mullen & Losada, 1994; Switkes, Bradley, & DeValois, 1988). Our results show that the temporal order of the test and mask stimuli has an important differential effect across the color-only and

color-luminance cross-orientation mechanisms in the monocular site (Fig. 7). A similar temporal order of color facilitation by luminance stimuli was reported (Eskew et al., 1994). One possible explanation for the strong facilitation of the color test by the luminance orthogonal mask found under monocular conditions is that color and luminance contrast are combined into a single color-luminance channel (right column, Fig. 7). However, to play a role in the facilitation, the channel would have to be isotropic, given the orthogonal presentation of test and mask. Such responses are known to occur early in the visual pathway in the P cells of the LGN, and are also found in the input layers of V1 (layers 4C) that show the strongest combined responses to color and luminance stimuli with less selectivity to stimulus orientation, direction and spatial frequency (Fig. 9 from Li et al., 2014). In the other cortical layers of V1, however, color-luminance responses are typically orientation tuned (Johnson, Hawken, & Shapley, 2001, 2008; Shapley & Hawken, 2002, 2011). It is plausible that the facilitation is mediated by the isotropic color-luminance neurons in the cortex, or by any neural pathway that is activated by both color and luminance contrast. A simple combination of color and luminance contrast into a common response mechanism, however, cannot explain the feed forward nature of the facilitation.

Chromatic facilitation is observed under monocular viewing in the forward masking condition (negative SOA) with greatest facilitation when the luminance mask precedes the color test by around 22 ms. However, given that, in the absence of a mask, the color response lags the luminance response by on average 15 ms (Fig. 3), we would expect that the maximal facilitation would occur at +15-ms SOA based on a simple temporal synchronization of the two stimuli. Instead the maximal facilitation occurs at around −22-ms SOA, in which case color test response lags the luminance mask response by around 37 ms (15 + 22 ms), demonstrating an even longer forward facilitation effect. We speculate that such a feed forward facilitatory effect might be accounted for if rapid local changes in light adaptation (Mullen et al., 2014) or an attentional effect mediated the facilitation.

Acknowledgments

We thank Daniel Baker and Andrew M. Haun for early discussion of this work. This research was supported by a Canadian Institutes of Health Research (CIHR) grant MOP-10819 and a Natural Science and Engineering Research Council grant (NSERC) RGPIN 183625-05 to KTM. We thank Dorita Chang for proofreading. We also thank two naive subjects for participating in the experiment.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.visres.2015.09.008.

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