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Colour–luminance interactions in binocular summation

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Abstract

Using a noise-masking paradigm we test the notion of binocular detection mechanisms that combine luminance and colour contrast. Binocular summation was measured for achromatic and red-green isoluminant Gabor stimuli over a range of temporal frequencies and was compared with and without the presence of a two-dimensional, dynamic, luminance noise mask (correlated). While we found that luminance noise reduced binocular luminance summation at all temporal frequencies, binocular red-green summation was reduced only at frequencies of 8 Hz and above. Our results suggest the existence of binocular colour–luminance interactions restricted to high temporal frequencies.

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1. Introduction

Based on physiological and psychophysical results, colour-vision models stipulate that L (long)-, M (middle)-, and S (short wavelength)-cone signals are combined to form three different detection mechanism from retina to cortex: two cone opponent mechanisms (red-green $(L-M)$ and blue-yellow $[S-(L+M)]$), and a luminance mechanism $(L+M)$. While different psychophysical methods have demonstrated separable responses of these three mechanisms at threshold (e.g., Cole, Hine, & McIlhagga, 1993; Gunther & Dobkins, 2003; Hughes & De Marco, 2003; Krauskopf, 1999; Krauskopf, Williams, & Heeley, 1982; Losada & Mullen, 1995; Mullen & Sankeralli, 1999; Sankeralli & Mullen, 1997), at suprathreshold contrast levels there is evidence for interactions between chromatic and luminance responses (e.g., Cole, Stromeyer, & Kronauer, 1990; Krauskopf, 1999; McGraw, McKeefry, Whitaker, & Vakrou, 2003; Sankeralli, Mullen, & Hine, 2002; Ueno & Swanson, 1989; Webster & Mollon, 1994). Physiological results also support the idea of a combination of the cone opponent and luminance signals at an early cortical stage (Gegenfurther & Kiper, 2003; Johnson, Hawken, & Shapley, 2001, 2004; Lennie & Movshon, 2005).

Relatively little attention has been focused on the study of the binocular system in colour vision. Binocular summation, defined as superior performance when using two eyes, is known to occur in luminance vision under different spatial and temporal conditions (e.g, Anderson & Movshon, 1989; Blake & Fox, 1973; Blake, Martens, & Di Gianfilippo, 1980; Blake, Sloane, & Fox, 1981; Campbell & Green, 1965; Howard, 2002; Reading, 1983). How achromatic contrast is combined between the two eyes is an issue addressed by current models of contrast gain control processing that include both within and between eyes interactions at several stages (e.g. Ding & Sperling, 2006; Foley, 1994; Howard, 2002; Meese, Georgeson, & Baker, 2006).

In red-green colour vision, binocular studies have supported the presence of interocular excitatory and inhibitory interactions (Forte, 2005; Howard, 2002; Jimenez, Medina, Jimenez del Barco, & Diaz, 2002; Jimenez, Valero, Anera, Martinez, & Salas, 2003; Shevell & Wei, 2000; Simmons, 2005; Simmons & Kingdom, 1998). Although comparisons have indicated similar binocular summation for achromatic

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and red-green isoluminant dichoptic gratings at low spatial frequencies (Forte, 2005; Simmons, 2005; Simmons & Kingdom, 1998), a wide range of experimental conditions are known to affect binocular summation (e.g., Blake & Fox, 1973; Blake et al., 1981; Howard, 2002; Reading, 1983). Thus the comparison of summation in the chromatic and luminance systems may depend on the spatial, temporal as well as interocular adapting conditions used (Anderson & Movshon, 1989; Jimenez et al., 2002, 2003; Simmons, 2005; Wildsoet, Wood, Maag, & Sabdia, 1988). Any differential effects in the magnitude of binocular summation between colour and luminance vision would support the presence of distinct mechanisms segregated along $L+M$ and $L-M$ cone axes. Nevertheless, a notion of segregation is at odds with the existence of colour–luminance interactions in others tasks involving dichoptic vision (Cole et al., 1990), or stereopsis (e.g. den Ouden, van Ee, & de Haan, 2005; Howard, 2002; Howard & Rogers, 2002; Simmons & Kingdom, 1997, 2002; Kingdom, 2003; Kingdom, Rangwalla, & Hammamji, 2005).

In this paper, we test for binocular interactions between luminance and red-green isoluminant mechanisms. Few studies have explored binocular summation in colour vision in the temporal domain. Differences between achromatic and isoluminant stimuli have revealed limited binocular excitatory interactions at isoluminant suprathreshold conditions in reaction time tasks (Hughes & Townsend, 1998; Jimenez et al., 2002; Medina, 2006). For the luminance system, previous studies have found that binocular contrast sensitivity depends on the temporal frequency, and binocular summation decreases above 10–15 Hz (Blake & Fox, 1973; Reading, 1983; Rose, 1980). In addition, Blake and Rush (1980) suggested that the temporal aspects of binocular summation vary with the spatial frequency, concluding the existence of at least two separate temporal mechanisms in the luminance system. No studies have investigated the effects of temporal frequency on chromatic binocular summation, its foundations and the summation values in relation to the luminance system.

For this purpose, we studied binocular summation across different temporal frequencies at isoluminance. Previous studies have reported that the binocular red-green contrast sensitivity may be confounded by luminance responses, especially at frequencies higher than 8 Hz (e.g., Dobkins, Gunther, & Peterzell, 2000). For luminance vision, the effect of external visual noise (static or dynamic) in binocular summation has been examined previously and it has been shown that binocular summation decreases as white noise strength increases (e.g. Anderson & Movshon, 1989; Blake, 1982; Blake et al., 1980; Blake et al., 1981; Braccini, Gambardella, & Suetta, 1980; Pardhan & Rose, 1999). Therefore, we measured binocular and monocular contrast detection thresholds for a variety of temporal frequencies for red-green isoluminant gratings, using achromatic stimuli as a control condition, with and without two-dimensional dynamic luminance correlated noise. If chromatic binocular contrast sensitivity mechanisms are responsive to luminance noise, a lowering of binocular summation should be expected for isoluminant stimuli, similar to that found in the luminance case. On the other hand, purely chromatic binocular contrast mechanisms will be robust to luminance noise across the temporal domain.

2. Methods

2.1. Observers

The subjects were the two authors (JM and KTM) and an additional volunteer (LA). All had experience in contrast threshold experiments. All had normal vision and colour vision according to the Farnswoth-Munsell 100-Hue test. Observers wore corrective lenses if required.

2.1.1. Apparatus and stimuli

The display system consisted of a CRT colour monitor (Mitsubishi Diamond Pro 2070SB) connected to a graphics card housed in a PC (VSG2/5, Cambridge Research Systems). This graphics card has over 14 bits of contrast resolution and is specialized for the measurement of visual thresholds. The monitor had a resolution of 1024 × 768 with a frame rate of 120Hz. The gamma nonlinearity of the luminance output of the CRT guns was corrected in look-up tables using the OptiCal, (Cambridge Research Systems). The spectral outputs of the red, green, and blue phosphors of the monitor were calibrated using a PhotoResearch PR-605-PC SpectralScan. The CIE-1931 chromaticities coordinates of the red, green and blue phosphors were ($x=0.628$, $y=0.339$), ($x=0.300$, $y=0.609$) and ($x=0.147$, $y=0.074$), respectively. The background was achromatic with a mean luminance of 18.8 $\mathrm{cd/m^2}$ at the screen centre. Observers were seated 60 cm from the monitor in a dimly lit room.

Stimuli were represented within a 3 dimensional cone-contrast space, with each axis defined by cone contrast (the incremental stimulus intensity for each cone type to a given stimulus normalized by the respective intensity of the fixed white background). Stimulus contrast is defined as the vector length in cone contrast units. The cone fundamentals of Smith and Pokorny (1975) were used for the spectral absorption of the L, M, and S-cones and a linear transform was calculated to specify the required phosphor contrasts of the monitor for given cone contrasts. Post receptoral luminance and red-green cone-opponent mechanisms were isolated in the achromatic ($L+M+S$) and red-green ($L-a\mathrm{M}$) cardinal directions respectively, where a is a numerical constant obtained at isoluminance (e.g., Cole & Hine, 1992; Cole et al., 1993; Mullen & Sankeralli, 1999; Sankeralli & Mullen, 1996). Stimuli were foveally presented, vertically oriented Gabor patterns (1.5 cycle/deg) in a spatial Gaussian contrast enveloped ($\sigma=2°$). Gratings were sinusoidally phase reversed at the 2, 8 and 16 Hz in the achromatic and 2, 8, and 12 Hz in the red-green isoluminant condition. All the gratings were presented in a contrast modulated temporal Gaussian envelope ($\sigma=0.125$ s; interval duration, 1 s). For each observer and for each temporal frequency, red-green isoluminance (value of a above) was estimated by the minimum perceived motion of a Gabor using a method of adjustment (Cavanagh, Tyler, & Favreau, 1986). A small black fixation point was displayed during the minimum motion task. No significant differences were found between binocular, left and right eye settings confirmed by the Kruskall–Wallis test (all cases, $p>0.05$). For each temporal frequency, isoluminance was calculated as the mean of at least 30 minimum motion settings.

Gabor stimuli were displayed alone or embedded in a 9° × 9° circular luminance noise patch with flat spatial and temporal Fourier spectrum (dynamic white noise). The grating stimulus and white noise were interlaced with frame by frame cycling. The noise contrast was defined in cone contrast units (Cc). RMS noise contrast differs by a factor of $\sqrt{3}$ from Michelson contrast ($C_{\mathrm{RMS}}=\mathrm{Cc}/\sqrt{3}$). Thus, the root mean squared (RMS) noise contrast value used was 28.9% ($50/\sqrt{3}$), while in the no noise condition, the level established was less than 0.3% ($0.5/\sqrt{3}$). In binocular vision, both eyes received the same external (correlated) noise level at the same time.

2.1.2. Procedure

We measured detection threshold contrasts for both binocular and monocular vision (left and right eye). A conventional semi-translucent white patch was used to cover the non-tested eye in all conditions. A two alternative forced choice staircase procedure (2AFC) was used with presentation intervals (1 s each), separated by 500 ms. The subject indicated in which interval the test stimulus appeared (the other was blank). A small black fixation point was displayed during stimulus presentation at the centre of the screen. Audio feedback was provided. In noise masking tasks, luminance noise was the same in the two intervals and was presented 250 ms before and centred in the time sequence in relation to stimulus presentation. A reversal was defined when the subject responded incorrectly after a minimum of two consecutive correct responses. Each staircase terminated after six reversals. The first reversal was used to establish the threshold level. After first reversal, stimulus contrast was raised by 25% following one incorrect response, and lowered by 12.5% following two consecutive correct responses. For a given 2AFC staircase session, the number of total trials fluctuated between 30 and 60 trials. This number guarantees a reliable threshold estimation according to the number of reversals used (Rammsayer, 1992). The threshold value was calculated as the arithmetic mean of the last five reversals of the staircase at the 81.6% correct detection level (Mullen & Sankeralli, 1999; Sankeralli & Mullen, 1996, 1997; Sankeralli et al., 2002). Each plotted threshold is based on the average of a minimum of four staircase measurements. Data were collected first for achromatic and then red-green isoluminant gratings using interleaved sessions balanced between observational conditions (i.e., binocular, right and left eye).

3. Results

3.1. The effect of dynamic luminance noise on the temporal contrast sensitivity function

Fig. 1 presents in a semilogarithmic plot the luminance and red-green isoluminant temporal contrast sensitivity functions for binocular and monocular vision (right and left eye separately). Thresholds for subject LA for red-green isoluminant stimuli at 12 Hz were too high to be measurable.

A two-way (viewing modality × temporal frequency) analysis of variance (ANOVA) (Montgomery, 1991), with $\alpha = .05$ was made on contrast thresholds for achromatic and red-green isoluminant stimuli separately. Our results support previous studies in terms of the effect of temporal frequency on contrast sensitivity (all cases, $p < 0.05$) with a band-pass achromatic temporal contrast sensitivity function with maximum sensitivity around 8 Hz, and a low-pass red-green function (e.g., Dobkins et al., 2000; Kelly, 1983; Kulikowski & Tolhurst, 1973; McKeefry, Murray, & Kulikowski, 2001; Reading, 1983; Robson, 1966; Swanson, 1994; Watson, 1986).

For luminance contrast thresholds without noise masking, a significant effect of the viewing modality was found [JM, $F(2,27) = 6.75$, $p = 0.004$; KTM, $F(2,36) = 16.45$, $p < 0.001$; LA, $F(2,27) = 8.58$, $p < 0.002$]. The interaction term (viewing × frequency) was significant for KTM [$F(4,36) = 3.26$, $p = 0.022$] but not for JM and LA [$F(4,27) = 0.38$, $p = 0.818$; $F(4,27) = 0.88$, $p = 0.491$, respectively]. A *post hoc* analysis (the Scheffé F test)[1] (Montgomery, 1991) revealed the existence of significant differences between binocular and right eye conditions (JM, $p = 0.036$; KTM, $p < 0.001$; LA, $p = 0.013$) and between binocular and left eye conditions (JM, $p = 0.005$; KTM, $p < 0.001$; LA, $p = 0.003$). There were no differences between the two eyes for monocular viewing (right eye vs. left eye, JM, $p = 0.544$; KTM, $p = 0.970$; LA, $p = 0.806$).

For red-green isoluminant thresholds without luminance masking noise, the ANOVA also revealed a significant effect of the viewing modality [JM, $F(2,27) = 40.55$, $p < 0.001$; KTM, $F(2,33) = 4.89$, $p = 0.014$; LA, $F(2,27) = 5.944$, $p = 0.010$]. The results for the interaction term were not uniform among subjects [only JM, $F(4,27) = 4.91$, $p = 0.004$]. The post hoc Scheffé test showed significant differences between binocular and right eye (JM, $p < 0.001$; KTM, $p = 0.015$; LA, $p = 0.045$, marginal value), between binocular and left eye (only, JM, $p < 0.001$ and LA, $p = 0.017$) and no significant differences between right and left eye (only KTM, $p = 0.174$ and LA, $p = 0.893$). Therefore, for each observer the patterns found without luminance masking noise verify previous results, that is, the presence of a binocular summation effect in both the luminance system (Blake & Fox, 1973; Blake & Rush, 1980; Blake et al., 1981; Reading, 1983; Rose, 1980), and in the red-green system at isoluminance.

For achromatic stimuli, both monocular and binocular thresholds were masked by dynamic luminance noise. A Mann–Whitey U-test between noise and no noise conditions combined across temporal frequency revealed significant overall differences ($p < 0.05$) in all cases except in observer JM, left eye ($p = 0.083$, marginal value). Sensitivity decreased at all temporal frequencies tested, but especially at 8 Hz and so the temporal contrast sensitivity functions become low-pass with poor achromatic sensitivity. Luminance noise had a greater effect on binocular than monocular vision (Anderson & Movshon, 1989; Blake, 1982; Braccini et al., 1980; Pardhan & Rose, 1999). Observer JM preserved lower binocular than monocular contrast threshold in the presence of dynamic luminance noise, an effect confirmed by a two-way ANOVA. The statistical analysis revealed the existence of significant differences in the viewing modality for JM [$F(2,27) = 12.95$, $p < 0.001$] but not for KTM and LA [$F(2,36) = 0.39$, $p = 0.679$; $F(2,27) = 0.76$, $p = 0.276$, respectively]. For observer JM, the Scheffé test indicated significant differences between binocular and right eye viewing ($p < 0.001$), and binocular and left eye ($p < 0.001$), with no significant differences between monocular conditions ($p = 0.869$). The interaction term was only significant for JM [$F(4,27) = 3.71$, $p = 0.016$].

For the isoluminant red-green stimuli, the presence of dynamic luminance noise preserves the low-pass contrast sensitivity function over the selected frequency range. For each observer and in each viewing condition, a Mann–Whitey U-test between noise and no noise conditions combined across temporal frequency revealed no overall differences (all cases, $p > 0.05$). This supports the

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[1] The same conclusions are obtained using the Bonferroni test.

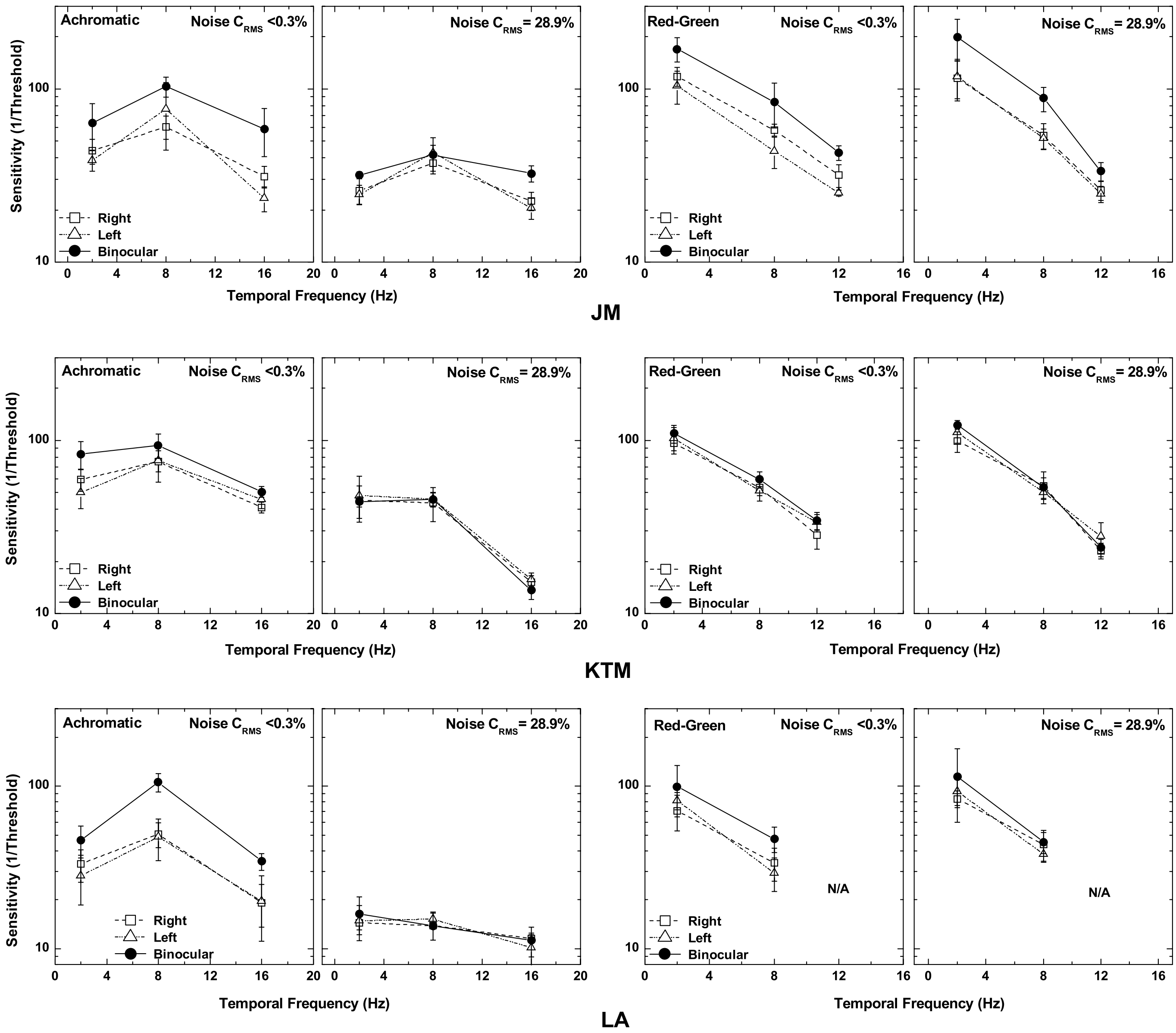

Fig. 1. Semilogarithmic plot of the temporal contrast sensitivity functions for achromatic and isoluminant red-green stimuli. Reciprocal of thresholds in cone contrast are represented in separate panels with or without dynamic luminance masking noise ($C_{RMS} = 28.9\%$ and $C_{RMS} < 0.3\%$, respectively). Solid circles, open squares and open triangles indicate binocular vision, right eye and left eye, respectively. Data are plotted separately for three observers (JM, KTM and LA). Error bars show ±1 standard deviation. N/A, not available.

notion that monocular thresholds are mediated by chromatic-based mechanisms and corroborates previous studies in monocular vision, where residual or no masking effects were found in chromatic contrast detection tasks with luminance noise including the temporal frequency range between 6 and 9 Hz (Losada & Mullen, 1995; Sankeralli & Mullen, 1997; Mullen, Yoshizawa, & Baker, 2003).

A two-way ANOVA between viewing modality and temporal frequency verified the presence of significant differences in the viewing modality for JM [$F(2,27) = 19.93$, $p < 0.001$] but not for KTM and LA [$F(2,36) = 1.25$, $p = 0.299$; $F(2,18) = 1.24$, $p = 0.313$, respectively]. For JM, the Scheffé test indicated significant differences between binocular and right eye viewing ($p < 0.001$), and binocular and left eye ($p < 0.001$), with no significant differences between the monocular conditions ($p = 0.849$). For all subjects, the interaction term was not significant [JM, $F(4,27) = 1.31$, $p = 0.291$; KTM, $F(4,33) = 1.57$, $p = 0.206$; LA, $F(2,18) = 0.69$, $p = 0.513$]. The absence of significant effects in the interaction term of the ANOVA confirmed no cross-effects between temporal frequency and observational conditions. However, binocular and monocular contrast sensitivity functions in luminance noise shows a trend in which their threshold differences are greater at low temporal frequencies and less at high temporal frequencies (KTM, 8 and 12 Hz, LA, 8 Hz, and JM, 12 Hz).

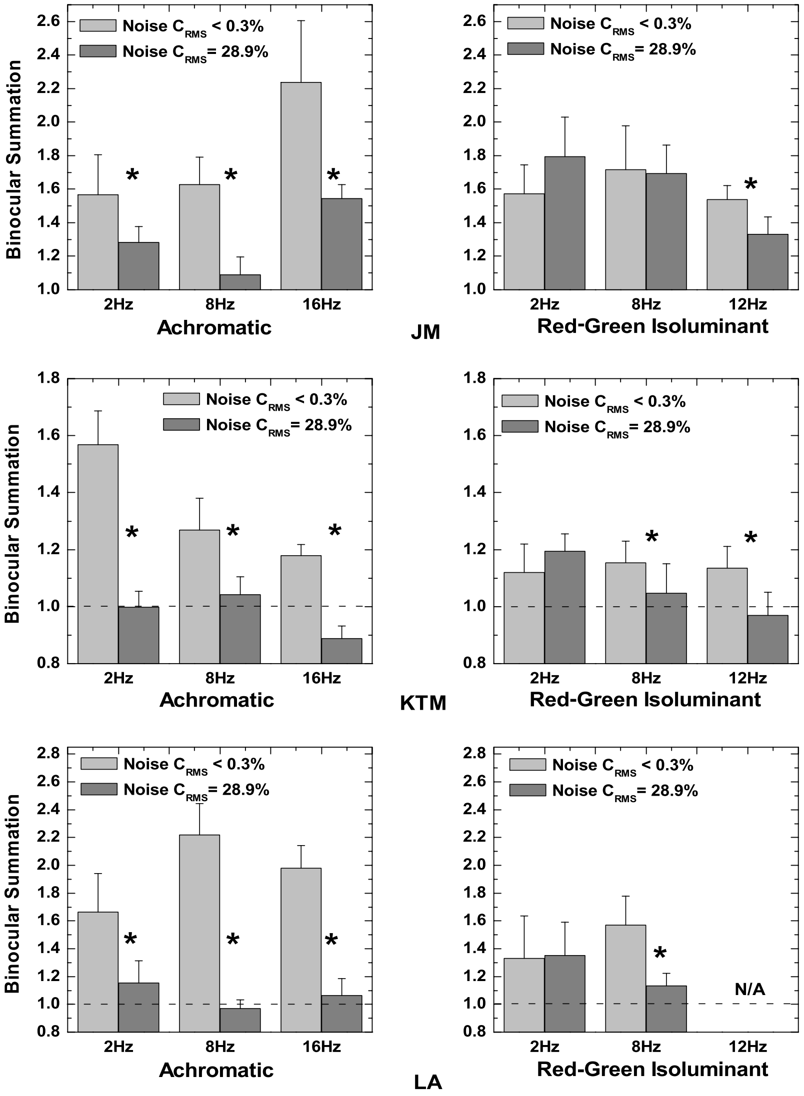

Fig. 2. Binocular summation for each temporal frequency (error bars indicate 95% confidence limits). Data are plotted separately for three observers (JM, KTM and LA). Light and dark grey bars represent mean summation in the absence of luminance masking noise ($C_{RMS} < 0.3\%$) or presence of noise ($C_{RMS} = 28.9\%$), respectively. For each temporal frequency, an asterisk shows the existence of significant differences between masked and unmasked noise conditions. Dashed lines indicate no summation. N/A, not available.

3.2. The effect of dynamic luminance noise on binocular summation

In Fig. 2 and Table 1 we show the influence of dynamic luminance noise on binocular summation for the chromatic and luminance stimuli. Binocular summation was defined as the ratio of the binocular to the monocular arithmetic average contrast sensitivity (e.g., Campbell & Green, 1965; Blake & Fox, 1973; Blake et al., 1981; Jimenez et al., 2003; Reading, 1983; Simmons, 2005; Simmons & Kingdom, 1998). For each temporal frequency, we made all possible binocular-monocular combinations for all the thresholds measured, and the mean binocular summation ratio in each temporal frequency was averaged as the arithmetic mean of the ratios generated[2]. Similar procedures have been used previously (e.g., Blake et al., 1980; Jimenez et al., 2002; Simmons, 2005; Simmons & Kingdom, 1998). For each observer and each condition, Table 1 summarizes the mean binocular summation obtained.

Fig. 2 shows, for each temporal frequency, the mean binocular summation obtained for the luminance and the red-green system stimuli in both the absence (light grey) and presence (dark grey bars) of dynamic luminance noise. Plotted data are presented for each observer separately and error bars represent 95% confidence limits. For luminance stimuli, the magnitude of binocular summation with unmasked gratings varied across observers within the range 1.18–2.24. These values are, on average, compatible with those found previously at low spatial frequencies (Reading, 1983; Rose, 1980). There were significant differences for temporal frequency [one-way ANOVA, JM, $F(2,45) = 8.60$, $p < 0.001$; KTM, $F(2,72) = 18.75$, $p < 0.001$; LA, $F(2,45) = 6.83$, $p = 0.010$], but no dependency of bin-

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[2] No significant differences were obtained using geometric means.

Table 1
Mean binocular summation obtained for the detection of achromatic and red-green isoluminant gratings for each temporal frequency selected

Subject	Noise (%)	Achromatic			Red-green isoluminant		
		2 Hz	8 Hz	16 Hz	2 Hz	8 Hz	12 Hz
JM	<0.3	1.57	1.63	2.24	1.57	1.71	1.53
	28.9	1.18	1.08	1.54	1.79	1.69	1.33
KTM	<0.3	1.57	1.27	1.18	1.12	1.15	1.13
	28.9	0.99	1.01	0.89	1.19	1.04	0.97
LA	<0.3	1.66	2.22	1.98	1.33	1.57	N/A
	28.9	1.15	0.97	1.06	1.33	1.13	N/A

Luminance noise contrast values are in RMS cone contrast units. Note—N/A, not available.

ocular summation and temporal frequency was found among subjects in the frequency range tested. The noise contrast level was sufficient to lower binocular summation. The ratio fell below unity in KTM and LA at frequencies above 2 Hz. If probability summation is taken into account as a test benchmark (a ratio of 1.2), this will reflect the existence of interocular inhibitory effects (e.g. Blake & Fox, 1973; Howard, 2002; Medina, 2006; Meese et al., 2006; Simmons, 2005; Simmons & Kingdom, 1998). For each observer and at each temporal frequency, comparisons between masked and unmasked conditions were statistically significant (Mann–Whitney *U*-test, all cases, $p < 0.05$). These results show, that for luminance vision, binocular summation decreases using two-dimensional dynamic luminance correlated noise, as suggested in previous studies (Anderson & Movshon, 1989; Blake, 1982; Blake et al., 1980; Pardhan & Rose, 1999).

For red-green isoluminant gratings without dynamic luminance noise, results demonstrate the existence of binocular summation at isoluminance (Howard, 2002; Jimenez et al., 2002, 2003; Simmons, 2005; Simmons & Kingdom, 1998). The summation range varied across observers between 1.12 and 1.71. No significant differences were found between the temporal frequencies (for each subject, one-way ANOVA, $p > 0.05$). Comparisons between red-green and luminance conditions were possible at low temporal frequencies (2 and 8 Hz separately), revealing that binocular summation at isoluminance was significantly lower only in KTM at 2 Hz (Mann–Whitney *U*-test, $p < 0.001$) and LA at 8 Hz ($p < 0.001$).

For red-green isoluminant gratings in dynamic luminance noise at 2 Hz results revealed binocular summation in all three subjects (JM, a ratio of 1.79; KTM, a ratio of 1.19; LA, a ratio of 1.33). For all subjects, at 2 Hz there were no significant differences between the masked and unmasked red-green condition (Mann–Whitney *U*-test, JM, $p = 0.187$; KTM, $p = 0.101$ and LA, $p = 0.291$). At higher temporal frequencies, however, differences were obtained, in which noise masking mimicked the effect found in the luminance system. At 8 Hz for JM, the noise had no influence on the binocular summation value (a ratio of 1.69), which was similar to the no-noise condition (a ratio of 1.71, Mann–Whitney *U*-test, $p = 0.706$). For KTM and LA, however, lower summation values were obtained in the presence of noise [ratios, 1.04 (no summation) and 1.13, respectively]. Comparisons between noise masked and unmasked gratings revealed that differences were statistically significant (Mann–Whitney *U*-test, KTM, $p = 0.016$; LA, $p = 0.006$). At 12 Hz, binocular summation decreased for JM to a level different from the unity (a ratio of 1.33), a significant decrease in relation to the unmasked red-green grating (a ratio of 1.53, Mann–Whitney *U*-test, $p = 0.005$). The same effect was obtained for KTM at 12 Hz with no summation found in the presence of the noise mask (a ratio of 0.97), with differences that were statistically significant in relation to the no noise condition (a ratio of 1.13, Mann–Whitney *U*-test, $p = 0.006$). We thus conclude that luminance noise significantly reduced chromatic binocular summation at temporal frequencies of 8–12 Hz, but not at lower frequencies (2 Hz).

4. Discussion

In the absence of noise masking, we find binocular summation for red-green isoluminant stimuli that has no dependency on temporal frequency, with binocular summation values from 1.12 to 1.71, broadly similar to those found in the luminance case (from 1.18 to 2.24). These values are compatible with the range obtained in previous work and suggest neural summation of contrast sensitivity or a ratio higher than 1.2 (Blake & Fox, 1973; Blake et al., 1981; Campbell & Green, 1965; Howard, 2002; Jimenez et al., 2003; Meese et al., 2006; Pardhan & Rose, 1999; Rose, 1980; Simmons, 2005; Simmons & Kingdom, 1998), although in two out of six conditions (KTM 2 Hz & LA, 8 Hz), summation for red-green was significant below that for luminance. Our results demonstrate robust interocular excitatory interactions at red-green isoluminance at threshold across the temporal domain, whereas previous work has only investigated chromatic binocular summation for stationary gratings (Jimenez et al., 2003; Simmons, 2005; Simmons & Kingdom, 1998). While ratios above probability summation levels do not exclude interocular inhibitory interactions, they reflect that net excitatory summation prevails. On the other hand, summation values below probability summation (KTM, 2 Hz, 1.12, 8 Hz, 1.15 and 12 Hz, 1.13) suggest that interocular suppression can be greater at isoluminance (e.g. Medina, 2006; Simmons, 2005).

The effects of dynamic luminance noise reveal different and interesting properties of the red-green chromatic system. First, we note that luminance noise did not affect monocular red-green thresholds for isoluminant stimuli, supporting the idea that detection thresholds are mediated by purely chromatic mechanisms that have no response to luminance contrast (Losada & Mullen, 1995; Mullen et al., 2003; Sankeralli & Mullen, 1997). Binocular summation, on the other hand, demonstrates an effect of luminance noise that is confined to the mid-high temporal frequencies (8–12 Hz), with luminance noise inducing a lower summation value only at high temporal frequencies. For luminance stimuli, we find that luminance noise suppresses binocular summation across all temporal frequencies. An effect reported previously only at 4Hz (Anderson & Movshon, 1989). Our results thus indicate that there is a mechanism of interocular inhibition arising from a cross-interaction between luminance and chromatic contrast-sensitive mechanisms that serve to modify red-green binocular summation. Stimulus-based luminance artifacts are improbable because the spatial frequency chosen (1.5 cpd, $\sigma = 2°$) minimizes chromatic aberration (Bradley, Zhang, & Thibos, 1992), and departures from the isoluminant point were minimized by establishing isoluminance for each observer and for each temporal frequency separately. Such luminance artifacts would also be revealed by luminance noise masking of the monocular chromatic thresholds. Previous work has examined the different constraints imposed by the relative number of L- and M-cones to the luminance and chromatic contrast sensitivity functions. In binocular vision, it was found that subjects with L:M ratios far from cone homogeneity (1:1) are correlated with a lower chromatic contrast sensitivity (Dobkins et al., 2000; Gunther & Dobkins, 2002). At isoluminance and at higher temporal frequencies (8–16 Hz), a higher L:M ratio was correlated with a higher luminance contrast sensitivity (Dobkins et al., 2000). Of the three subjects tested, JM had the lowest L:M ratio (1:3.5) at isoluminance at 8 Hz, a favourable condition for reducing the masking effects of luminance noise in the red-green system (see Fig. 2).

Current models of binocular contrast vision at and above threshold seek to provide a unified model for how contrast is combined between the two eyes and include divisive interactions within and between eyes that contribute to achromatic contrast gain control (Blake & Fox, 1973; Blake et al., 1981; Campbell & Green, 1965; Ding & Sperling, 2006; Howard, 2002; Meese et al., 2006; Meese & Hess, 2004; Pardhan & Rose, 1999; Reading, 1983). Although our mask is dynamic (correlated) white noise in both eyes and previous studies have typically used spatially narrowband masks (Foley, 1994; Li, Peterson, Thompson, Duong, & Freeman, 2005; Morrone, Burr, & Maffei, 1982; Sengpiel & Vorobyov, 2005), the mechanisms of contrast gain control are likely to act similarly. Several different models of binocular interactions that include contrast gain control predict a reduction in binocular summation at high mask contrasts and might account for the loss of binocular summation that we find for luminance stimuli in high contrast luminance noise in the temporal contrast sensitivity function (Meese et al., 2006; Meese & Hess, 2004). Our results for the red-green chromatic stimuli in luminance noise, however, indicate the presence of cross channel suppression that combines luminance and colour contrast but is confined only to mid and high temporal frequencies. We are presently unable to conclude whether this colour–luminance contrast interaction operates prior to binocular summation, and therefore involves dichoptic pathways, or occurs later, at a purely binocular site. The temporal frequency characteristics of the colour–luminance interaction that we find suggest that it might be mediated via M cell based responses.

Possible interactions between colour and luminance contrast that are specific to mid temporal frequencies have been reported in the literature in other contexts. Motion onset VEPs to chromatic stimuli resemble the responses to luminance stimuli at higher velocities suggesting a change in chromatic processing that is temporally dependent (McKeefry, 2002). Furthermore, differences in the contrast dependency of the perceived speed of chromatic motion have been reported to change and to resemble the responses to luminance stimuli above 4 Hz (Gegenfurther & Hawken, 1995). A covariance analysis of detection thresholds by Dobkins et al. (2000) suggests that the high (8–16 Hz) temporal frequency factor underlying red-green isoluminance is governed predominantly by luminance mechanisms, while the low temporal frequency factor receives contribution from chromatic mechanisms. Such temporally specific effects are reminiscent of the distinction made between flicker detection versus pattern detection mechanisms reported previously in the literature (e.g., Blake & Rush, 1980; Kulikowski & Tolhurst, 1973; Howard, 2002; McKeefry et al., 2001; Watson, 1986), and suggest that interactions between responses red-green and luminance contrast may be associated within the flicker and pattern mechanisms. On the other hand, in a more direct example of colour and luminance interactions, Mullen et al. (2003) reported a selective luminance contribution to red-green motion thresholds but not detection thresholds (luminance noise masked red-green direction discrimination thresholds but not detection), which occurred over a wide range of temporal frequencies (0.75–9 Hz).

In summary, our findings reveal an interaction between colour and luminance contrast such that binocular red-green summation decreases in the presence of luminance noise masking. This masking effect is manifest specifically under conditions of mid and high temporal frequencies. Finally, our results show that binocular summation is a useful psychophysical paradigm to examine interactions between binocular colour and luminance contrast processing.

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