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The use of chromatic information for motion segmentation: Differences between psychophysical and eye-movement measures

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Abstract. Previous psychophysical studies have shown that chromatic (red/green) information can be used as a segmentation cue for motion integration. We investigated the mechanisms mediating this phenomenon by comparing chromatic effects (and, for comparison, luminance effects) on motion integration between two measures: (i) directional eye movements with the notion that these responses are mediated mainly by low-level motion mechanisms, and (ii) psychophysical reports, with the notion that subjects' reports should employ higher-level (attention-based) mechanisms if available. To quantify chromatic (and luminance) effects on motion integration, coherent motion thresholds were obtained for two conditions, one in which the signal and noise dots were the same 'red' or 'green' chromaticity (or the same 'bright' or 'dark' luminance), referred to as homogeneous, and the other in which the signal and noise dots were of different chromaticities (or luminances), referred to as heterogeneous. 'Benefit ratios' ($\theta_{HOM}/\theta_{HET}$) were then computed, with values significantly greater than 1.0 indicating that chromatic (or luminance) information serves as a segmentation cue for motion integration. The results revealed a high and significant chromatic benefit ratio when the measure was based on psychophysical report, but not when it was based on an eye-movement measure. By contrast, luminance benefit ratios were roughly the same (and significant) for both measures. For comparison to adults, eye-movement data were also obtained from 3-month-old infants. Infants showed marginally significant benefit ratios in the luminance, but not in the chromatic, condition. In total, these results suggest that the use of chromatic information as a segmentation cue for motion integration relies on higher-level mechanisms, whereas luminance information works mainly through low-level motion mechanisms.

1 Introduction

Numerous psychophysical studies have demonstrated that the human visual system can use chromatic (red/green) information for motion processing. In different studies, chromatic information has been shown to be effective as (i) a motion-correspondence cue, and (ii) a segmentation cue for integration of local motion signals. As a motion-correspondence cue, the use of chromatic information has been demonstrated by employing red/green stimuli whose direction of motion can be discerned only by making correspondences between like chromaticities over space and time. The results from these studies (which have employed sinusoidal gratings, random-dot kinematograms, and periodic dot displays) have consistently shown that chromatic information can be used to establish motion correspondence, although the perceived motion is often weaker as compared to stimuli that contain luminance information (see Cropper and Wuerger 2005; Dobkins and Albright 2003; Gegenfurtner and Hawken 1996 for reviews).

As a segmentation cue for motion integration, the use of chromatic information has been demonstrated in two paradigms. The first involves the use of moving plaid patterns, in which two gratings are superimposed and moved in different directions (typically 90° apart). When the gratings are integrated perceptually, referred to as 'cohering', a single moving plaid pattern is perceived. When the gratings are segmented, they 'non-coherently' move across one another (see Stoner and Albright 1994 for review). Several psychophysical studies have compared the degree of integration (ie coherence) versus segmentation (ie non-coherence) between two conditions: one in which the component

gratings that make up the plaid pattern are chromatically the same (ie both red-bright/green-dark or both green-bright/red-dark—which we refer to as 'homogeneous'); the other in which the gratings differ chromatically (ie one grating is red-bright/green-dark and the other is green-bright/red-dark—which we refer to as 'heterogeneous'). The results of these studies show that, in the homogeneous condition, the component gratings are integrated into a single moving plaid pattern (they cohere), yet in the heterogeneous condition, the component gratings get segmented (they do not cohere) and appear to slide across one another (Dobkins et al 1998; Farell 1995; Kooi and De Valois 1992; Kooi et al 1992; Krauskopf and Farell 1990; Krauskopf et al 1996; but see Cropper et al 1996 for evidence that non-coherence in the heterogeneous condition depends on the angular difference between the two grating components). In sum, these psychophysical studies demonstrate that chromatic information can influence the integration versus segmentation of local motion signals.

The second way in which the influence of chromatic information on motion integration versus segmentation has been studied involves the use of stochastic motion displays (after Newsome and Paré 1988; Williams and Sekuler 1984). This display consists of a random array of dots, wherein a proportion of dots ('signal' dots) move in a coherent direction ('rightward' or 'leftward') while the others ('noise' dots) move in a random fashion. The signal proportion is varied across trials in order to obtain a coherent motion threshold (ie the percentage of signal dots required to yield 75%-correct directional discrimination). In several previous psychophysical studies coherent thresholds have been compared between two conditions: one in which the signal and noise dots are the same chromaticity (both red or both green—the homogeneous condition); the other in which the signal and noise dots are of different chromaticities (one red, the other green—the heterogeneous condition). The results of these studies demonstrate lower coherent motion thresholds (ie better performance) in the heterogeneous condition, presumably because the chromatic cue acts to segment the signal dots from the noise dots, allowing integration of only the former (Croner and Albright 1997, 1999; Festa-Martino et al 2005; Snowden and Edmunds 1999; and see Edwards and Badcock 1996 for similar benefits of chromatic cues in conditions where green dots are presented on a red background). Thus, like the results from moving plaid studies, these psychophysical results indicate that chromatic information can serve as a segmentation cue for motion integration.

Although the influence of chromatic information on both motion correspondence and motion integration/segmentation has been well established, the extent to which these effects are mediated by low-level versus high-level motion mechanisms is still a matter of some debate (eg Dobkins et al 2007; and see Cropper and Wuerger 2005 for review). Low-level motion mechanisms are typically considered those that are pre-attentive: the processing is passive/automatic and does not require attention. This processing is thought to be mediated by neural areas early on in the motion pathway hierarchy, such as primary visual cortex (V1) and the middle temporal (MT) visual area. As proof that motion mechanisms in V1 and MT can be considered 'low level', directionally selective responses in V1 (eg Churchland et al 2005; Mikami et al 1986) and MT (eg Albright and Desimone 1987; Maunsell and Van Essen 1983b) of monkeys are seen even under anaesthetized conditions [and see Rees et al (1997) for similar evidence of 'pre-attentive' MT responses obtained from human fMRI studies in which subjects are instructed to completely ignore motion stimuli]. This is not to say that directionally selective responses in V1 and MT cannot be modulated by attention [because they are, see Rezec and Dobkins (2004) for review], only that attention is not necessary. By contrast, high-level motion mechanisms are defined as those that require some sort of attentional process [see Claeys et al (2003) for a more comprehensive discussion of low-level versus high-level motion mechanisms].

In the current study, we investigated whether chromatic information as a segmentation cue for motion integration is mediated more by low-level than by high-level motion mechanisms by employing the homogeneous versus heterogeneous stochastic motion display paradigm and comparing chromatic (red/green) effects, as well as luminance (bright/dark) effects, between two measures: (i) directional eye movements (DEMs) and (ii) psychophysical reports. In the first measure, an experimenter judged the subject's eye-movement direction while the subject passively viewed a stochastic motion display. As we discuss in section 4, the passive eye movements elicited with this technique are likely to be mediated mainly by low-level motion mechanisms. In the second measure, subjects reported the perceived direction of motion in a stochastic motion display. Because subjects could use any strategy they wanted in order to perform the task, we assumed that if higher-level mechanisms were available for this task, subjects would use them. To quantify the effectiveness of chromatic (and luminance) information as a segmentation cue for motion integration, we computed a 'benefit ratio' ($\theta_{\mathrm{HOM}}/\theta_{\mathrm{HET}}$) separately for both the psychophysical and DEM measures. We hypothesized that if the use of chromatic information as a motion-segmentation cue relies on higher-level, attention-based mechanisms, chromatic benefit ratios should be higher in condition 2 (psychophysics) than in condition 1 (DEM). In addition to testing adults subjects, infants (3-month-olds) were tested with the DEM technique. We tested infants because previous infant studies, which used DEMs, showed that they an use chromatic information as a cue for motion correspondence (Dobkins and Anderson 2002; Dobkins and Teller 1996; Teller and Palmer 1996). Here, we asked whether infants can use chromatic information as a segmentation cue for motion integration.

2 Methods

2.1 *Subjects*

2.1.1 *Adults.* Seven adult subjects (aged 19 to 33 years) participated in this study. In addition, fourteen adult subjects (aged 20 to 32 years) provided psychophysical red/green isoluminant points to be used for setting an estimate of red/green equiluminance in the main experiment. Adult subjects had normal red/green color vision (as assessed by the Ishihara color plates) and no family history of color abnormalities. Each adult subject participated in all testing conditions.

2.1.2 *Infants.* Infant subjects were recruited from the San Diego area. Male infants with a 25% or greater chance of dichromacy (based on family reports of color blindness on the mother's side) were excluded from the study. In addition, female infants with a 25% or greater chance of being a carrier for dichromacy were also excluded since their red/green color vision is unpredictable [see Crone (1959) and Swanson (1991) for relevant studies in adult female carriers]. All infants were born within 14 days of their due date and were reported to have uncomplicated births. Testing for each infant was completed within a week. A total of sixty-five 3-month-old infants participated in this study. Forty-two infants failed to meet a minimum performance criterion (a score of greater than 85% correct on our eye-movement measure when presented with the strongest motion signal). Thus, data from a total of twenty-three infants (35%) were retained.

At first glance, one might suspect that the reason why the majority of infants did not reach a performance criterion is because they had trouble seeing the moving dots. This could happen if the dots were too small, since infants have poor spatial acuity. However, we do not believe this to be a likely explanation since previous studies on 3-month-olds from our and other laboratories have observed relatively low motion thresholds with moving dots that were even smaller than those used in the

current study (Banton et al 2001: 0.08 deg; Mason et al 2003: 0.26 deg; current study: 0.42 deg). Instead, we believe that other aspects of our stimuli may not have been optimal for motion processing by infants; for example, our stimuli may have been too fast for 3-month-olds. This seems a reasonable possibility since the speed of our dots was twice that employed in previous motion studies (Banton et al 2001: 11.0 deg s^{-1}; Mason et al 2003: 9.3 deg s^{-1}; current study: 25 deg s^{-1}). For the twenty-three infants whose data were retained, the mean age (and standard deviation) in days old on the first day of testing was 92.78 ± 4.45. Thirteen of these infants participated in the chromatic condition, eight participated in the luminance condition, and two participated in both.

2.2 *Apparatus*

Stimuli were generated on a Dell PC laptop with an ATI Radeon graphics card and were displayed on a 17 inch Eizo monitor. The stimulus monitor had a refresh rate of 60 Hz. Stimuli were created with Matlab (7.0). The CIE coordinates for the monitor phosphors were: red (0.616, 0.340), green (0.288, 0.599), and blue (0.162, 0.069). The voltage/luminance relationship was linearized independently for each of the three guns in the display (Cowan 1983) with a PR-650 SpectraColorimeter (Photoresearch). The PR-650 was also used for photometric measurements to standardize to V_λ equiluminance, as well to compute long-wavelength-selective (L) and medium-wavelength-selective (M) cone excitations produced by our visual stimuli.

2.3 *Stimuli*

2.3.1 *Stochastic motion stimulus.* The stimulus conditions used in these studies are shown in figure 1. Stimuli consisted of a stochastic motion display (after Newsome and Paré 1988; Williams and Sekuler 1984), which subtended 43 deg $\times$ 34 deg from a viewing distance of 38 cm. In total, 603 dots (0.42 deg in diameter) were presented (dot density = 0.41 dots deg^{-2}). A portion of these dots ('signal dots') were displaced 0.42 deg every vertical refresh (every 16.67 ms), which created coherent leftward or rightward motion at 25 deg s^{-1}. Signal dots had limited lifetimes; each dot lasted 333 ms (20 vertical refreshes) before disappearing and reappearing in a new location.[(1)] The rest of the dots ('noise' dots) were randomly relocated every 16.67 ms. The combination of low dot density and small spatial displacement of the signal dots resulted in a low probability of spurious motion signals occurring (Williams and Sekuler 1984). In order to obtain coherent motion thresholds, a range of signal coherence levels was presented. This range was tailored separately for the DEM and the psychophysical measures, and separately for adults and infants, such that thresholds could be obtained (see sections 2.5 and 2.6, respectively, for further details on the ranges employed). In separate blocks of trials, data were obtained for two different color conditions: chromatic (red/green) and luminance (bright/dark). Within each condition, the signal and noise dots were either the same (homogeneous) or different (heterogeneous).

2.3.2 *Chromatic condition.* In this condition red (CIE coordinates, $x = 0.616$, $y = 0.340$) and green ($x = 0.288$, $y = 0.599$) dots that were equiluminant with each other were used (both $\sim$16.4 cd m^{-2}), presented against a black background (0.3 cd m^{-2}). To give a sense of the chromatic difference between the red and green, going from red to green would modulate the activity of M-cones and L-cones by 36.4% and 14.6%, respectively [rms contrast = 27.7%, see Gunther and Dobkins (2002) for methodological details].

[(1)] We acknowledge that this dot lifetime is longer than is typically used in studies employing stochastic motion displays. However, in pilot studies with infants, we found we needed this longer dot lifetime to obtain thresholds, and therefore we used the longer dot lifetime in adults as well. We do not think that this longer dot lifetime affected our results, since the thresholds we observed in adult subjects tested psychophysically were on the order of those reported in other studies.

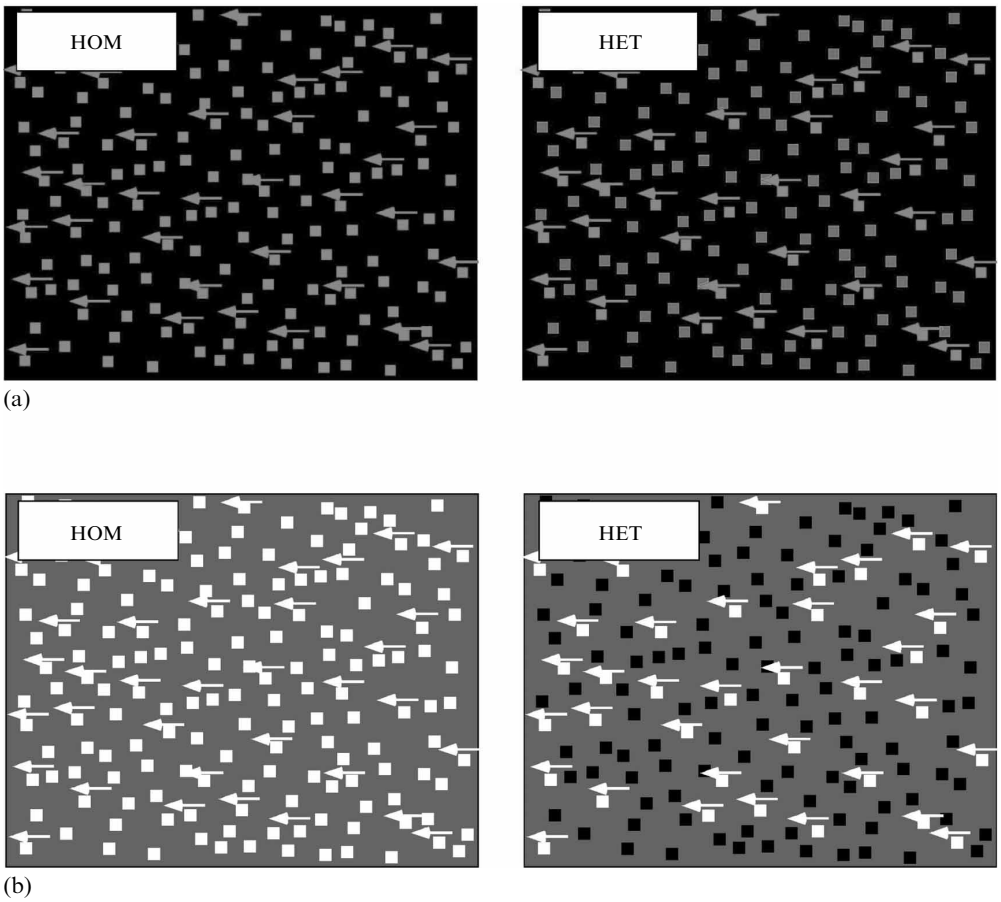

Figure 1. [In colour online, see http://dx.doi.org/10.1068/p59571] Stimuli consisted of a stochastic motion display (after Newsome and Paré 1988; Williams and Sekuler 1984), containing 603 dots presented on a 43 deg × 34 deg display (not all dots are shown in the figure). (a) Chromatic condition: in the homogeneous (HOM) condition, signal dots (moving coherently leftward or rightward at 25 deg s^{-1}, depicted by arrows) and noise dots were either all red or all green. In the heterogeneous (HET) condition, signal dots were red and noise dots were green, or vice versa. (b) Luminance condition: in the HOM condition, signal and noise dots were all bright or all dark. In the HET condition, signal dots were bright and noise dots were dark, or vice versa.

In the homogeneous condition, both the signal and noise dots were the same chromaticity, ie either both red or both green. In the heterogeneous condition, the chromaticity of the signal and noise dots differed, ie red signal and green noise dots, or vice versa. Note that, in addition to setting the red and green to be equiluminant on the basis of settings made by adult subjects, the high luminance contrast between the dots and the background ($\sim$100%) made it such that any small luminance mismatch between the red and green dots would be extremely difficult to notice. This is because luminance discrimination is poor at high contrasts, both in adults and in infants (Brown 1994).

2.3.3 *Luminance condition.* In this condition bright (66 cd m^{-2}) and dark (7.3 cd m^{-2}) dots were used. Against a background of 22 cd m^{-2}, these bright and dark dots produced 50% Michelson contrast [100(dot luminance − background luminance)/(dot luminance + background luminance)]. In addition, the luminance difference between the bright and dark dots would modulate the M-cones and L-cones by 80%, which is the same as the Michelson

contrast between the two [100(bright luminance − dark luminance)/(bright luminance + dark luminance)]. The CIE coordinates for the dots and background were $x = 0.333$, $y = 0.333$. In the homogeneous condition, both the signal and noise dots were the same luminance—either both bright or both dark. In the heterogeneous condition, the luminance of the signal and noise dots differed—bright signal dots and dark noise dots, or vice versa.

2.4 *Setting red/green equiluminance*

Fourteen adult subjects provided red/green equiluminance points obtained by heterochromatic flicker photometry (eg Gunther and Dobkins 2005; Kremers et al 2000; Smith and Pokorny 1975), to be used in setting the red/green in the main experiment. Subjects were presented with the same display of 603 dots as in the main experiment, except that, rather than moving, the dots alternated between red and green at a rate of 30 Hz. The red luminance was kept constant, and subjects adjusted the luminance of the green dots (with keypresses) until the percept of flicker was minimal. 20 trials were obtained for each subject. This mean equiluminant point was used in all adult and infant experiments. Our justification for using the red/green equiluminance settings from adults in our infant experiments is based on reports that equiluminance settings are the same between infants and adults (Bieber et al 1995; Brown et al 1995; Chien et al 2000; Dobkins et al 2001; Maurer et al 1989; Morrone et al 1993; Teller and Lindsey 1989; Teller et al 2000).

2.5 *Directional eye movement (DEM) paradigm: adults and infants*

In order to measure eye-movement-based direction discrimination, we used a DEM technique, which relies on the fact that both adults and infants make directionally appropriate eye movements in response to moving stimuli (eg Dobkins and Teller 1996; Hainline et al 1984; Kremenitzer et al 1979). These eye movements can include optokinetic nystagmus (OKN), smooth pursuit, and/or saccades when a medium-sized moving display is employed as in the current study (43 deg × 34 deg). Both chromatic (red/green) and luminance stimuli elicit DEM, although they are weaker for the former (Crognale and Schor 1996; Dobkins and Anderson 2002; Dobkins and Teller 1996; Hawken et al 1991). As discussed in section 4, we believe this DEM measure is mediated by low-level motion mechanisms. In adults, eye-movement responses typically correlate with psychophysical reports (Beutter and Stone 2000; Stone and Krauzlis 2003), although the point of the current study is to investigate whether this is true for the use of chromatic information as a segmentation cue for motion integration.

Both infants and adults viewed the monitor binocularly from a distance of 38 cm. On each trial, the direction of the signal dots was leftward or rightward. Different signal coherence levels were presented randomly intermixed across trials (infants: five coherence levels, ranging in equal log steps, base 0.08, from 33% to 85%; adults: nine coherence levels, ranging in equal log steps, base 0.12, from 9.0% to 79%). Also intermixed across trials were homogeneous and heterogeneous stimuli. Computer beeps provided feedback as to whether the decision was correct. For infants, an experimenter who was blind to the stimulus (because of a piece of cardboard blocking the view), used the subject's right-eye movements (viewed through the zoom lens of a camera) to judge the stimulus direction. Stimuli remained present until a decision was made. Adults were instructed to simply 'watch' the motion, and to do nothing special other than that, and eye-movement data were obtained in an identical fashion as for infants. Because in adult pilot studies we found that using the DEM technique with an unlimited duration (as employed for infants) yielded near-ceiling performance, which would not allow determination of a threshold, we used a limited duration stimulus for adults, specifically 800 ms. Note that, although it was our intention to use the same duration in the adult DEM measure as in the psychophysical measure, we were unable to do so as pilot DEM studies in adults showed that the duration used in the psychophysical measure (400 ms) was not long enough to produce reliable responses from the eye-movement measure.

Eye-movement data were obtained from each adult subject before the psychophysical data were obtained. Had we reversed the order, such that psychophysical reports were obtained first, we worried that this would increase the likelihood that during the subsequent eye-movement trials, subjects would inadvertently try to discern motion direction, and might, in turn, volitionally move their eyes in the perceived direction.

2.6 *Psychophysical paradigm: adults*

After adults finished the DEM measure, in separate blocks of trials, they provided self-reports ('leftward' versus 'rightward' via keypresses) about stimuli, which were identical to those presented in the DEM measure. Six different signal coherence levels were presented (ranging in equal log steps, base 0.3, from 0.14% to 4.75%), intermixed randomly across trials. Also intermixed across trials were homogeneous and heterogeneous stimuli. Computer beeps provided feedback after each trial. Stimulus duration was set at 400 ms. As stated above, it was our intention to use the same duration in the psychophysical measure as in the DEM measure, the latter employing an 800 ms stimulus. However, we were unable to do so, as pilot psychophysical studies in adults showed that 800 ms yielded ceiling performance, which would not allow determination of a threshold.

In sum, there were two stimulus parameters that differed between the psychophysical and DEM measures in adults: (i) a shorter duration for psychophysics (400 ms) than for DEM (800 ms) (also, infants were tested with an unlimited stimulus duration); and (ii) a lower range of coherence values for psychophysics (0.14% to 4.75%) than for DEM (9.0% to 79%), an issue we address further in section 4. Despite these differences, we nonetheless believe the comparison between the psychophysical and DEM data is meaningful because, if they were to account for results, we would expect similar results in the chromatic and luminance conditions. Since this was clearly not the case (see section 3), we feel strongly that these stimulus differences between the two measures cannot account for our findings.

2.7 *Data analysis*

For each subject, data for the two types of homogeneous trials (chromatic: signal and noise dots both red or both green; luminance: signal and noise dots both bright or both dark) were combined. Likewise, data for the two types of heterogeneous trials (chromatic: red signal dots, green noise dots, and vice versa; luminance: bright signal dots, dark noise dots, and vice versa) were combined. For each subject and condition, a motion coherence threshold was obtained by fitting percentage of correct performance versus percentage of coherence (ie percentage of signal dots) data with Weibull functions and maximum-likelihood analysis (Watson 1979; Weibull 1951). Coherence threshold was defined as the coherence yielding 75%-correct performance. For infants, at least 100 trials were obtained per psychometric function. For adults, 300 trials were obtained per psychometric function. For each subject, a 'benefit ratio' was then computed as follows: $\theta_{\mathrm{HOM}}/\theta_{\mathrm{HET}}$, with ratios greater than 1.0 indicating that chromatic (or luminance) information acts as a segmentation cue for motion integration. All analyses employed logged ratios, since subject data conform to normal distributions when log-transformed. However, in all figures, we plot the linear equivalent of the log mean—the geometric mean—because linear values are easier to understand.

3 Results

3.1 *Example data*

The psychometric functions from one adult subject are plotted in figure 2. Percentage of correct performance is plotted as a function of percentage of coherence (ie percentage of signal dots) for the heterogeneous and homogeneous conditions. Data are presented separately for the chromatic condition (a) and the luminance condition (b), and separately

for data obtained psychophysically versus with the DEM technique. For the chromatic condition, this subject's benefit ratio ($\theta_{HOM}/\theta_{HET}$) obtained psychophysically (2.33) was greater than 1.0, indicating the use of chromatic information as a segmentation cue for motion integration. In contrast, the chromatic benefit ratio obtained with DEM (1.08) was near 1.0, including a negligible influence of chromatic information. In the luminance condition, the benefit ratio obtained psychophysically (1.56) was only slightly higher than that obtained with DEM (1.24), and both were above 1.0.

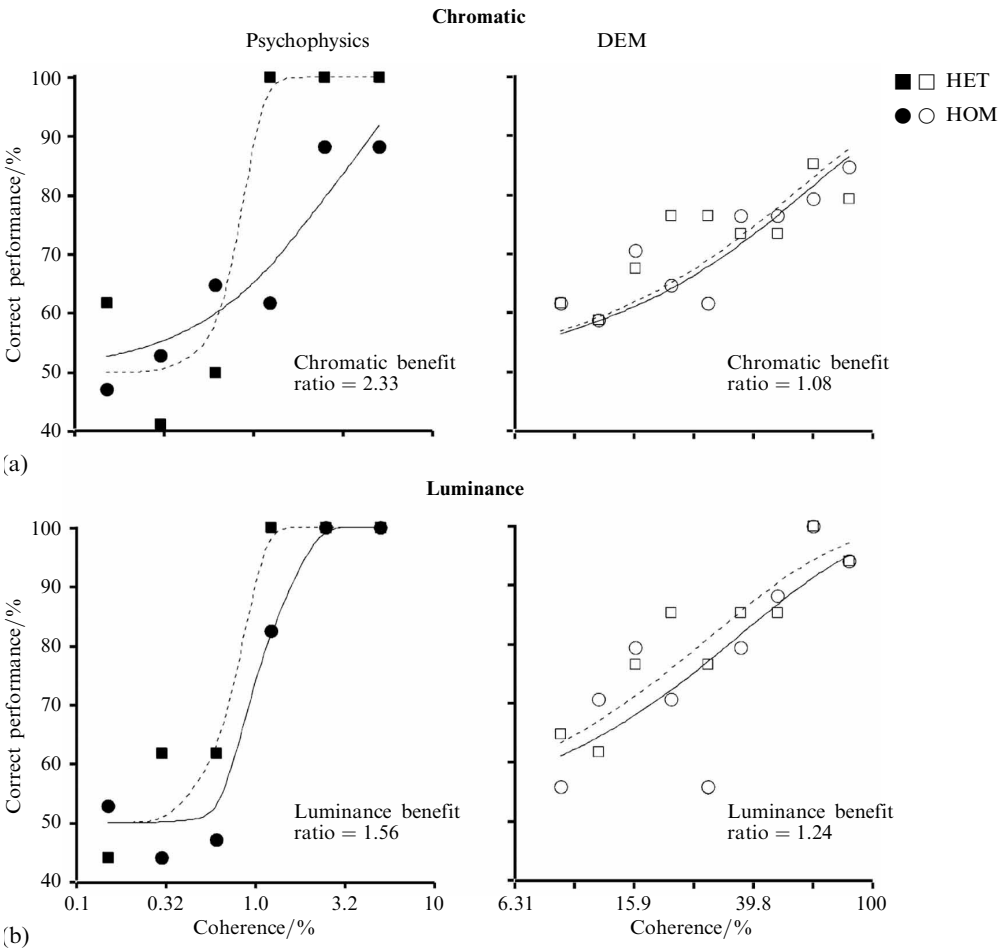

Figure 2. Psychometric functions from a representative adult subject. Percentage of correct performance plotted as a function of percentage of coherence (ie percentage of signal dots), for the heterogeneous (HET, squares) and homogeneous (HOM, circles) conditions. (a) Chromatic condition: for psychophysics (left, black symbols), the chromatic benefit ratio ($\theta_{HOM}/\theta_{HET}$) was greater than that obtained with directional eye movements (DEMs) (right, white symbols), and only for the former was the ratio substantially greater than 1.0. (b) Luminance condition: the luminance benefit ratio for psychophysics (left) was only slightly higher than that obtained with DEMs (right), and the ratio was substantially greater than 1.0 for both.

3.2 *Group mean benefit ratios*

Group mean benefit ratios from adults and infants are plotted in figure 3a for the chromatic condition and in figure 3b for the luminance condition. Benefit ratios obtained psychophysically are plotted next to data obtained with DEM. In the chromatic condition, the mean benefit ratio for adults tested psychophysically was 1.93, which was significantly greater than 1.0 ($p = 0.003$, one-tailed t-test), and in line with

previous reports (Croner and Albright 1997, 1999; Festa-Martino et al 2005; Snowden and Edmunds 1999). For adults tested with DEMs, the mean chromatic benefit ratio was 1.14, which was only marginally significant ($p = 0.07$, one-tailed t-test), and was significantly lower than the benefit ratio obtained psychophysically ($p = 0.009$, one-tailed t-test). For infants tested with DEMs, the chromatic benefit ratio was not significant ($p = 0.41$). These results suggest that the psychophysical use of chromatic information as a cue for motion segmentation relies, to a substantial extent, on higher-level, attention-based mechanisms. We elaborate on the nature of these mechanisms in section 4.

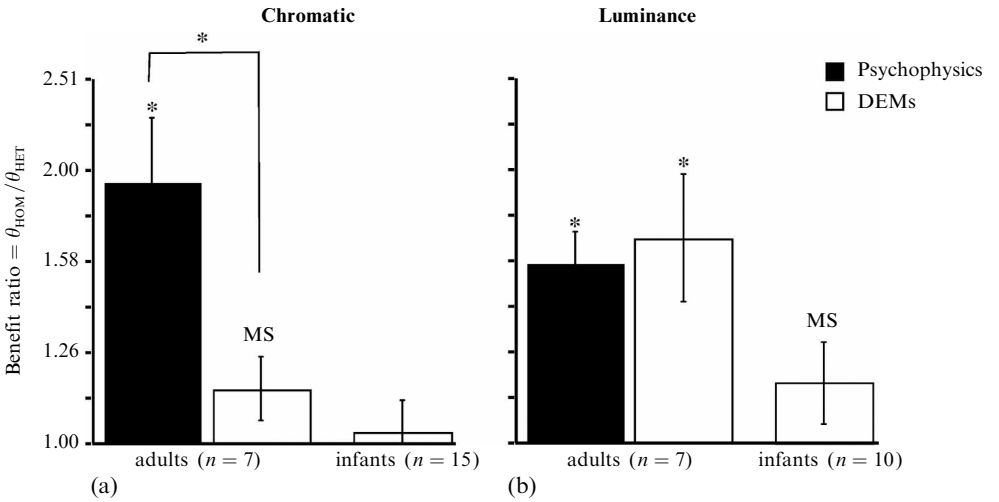

Figure 3. Group mean benefit ratios shown for the (a) chromatic and (b) luminance conditions, for psychophysical data and directional eye movement (DEM) data. Error bars denote SEM. Asterisks denote benefit ratios significantly greater than 1.0 and significant differences in benefit ratios between the psychophysical and the DEM measures ($p < 0.05$); MS denotes marginal significance ($p < 0.10$). (See text for actual benefit-ratio values.)

In the luminance condition, the mean benefit ratio for adults tested psychophysically was 1.58, which was significantly greater than 1.0 ($p = 0.001$, one-tailed t-test), and in line with previous reports [Croner and Albright (1999); Festa-Martino et al (2005); Snowden and Edmunds (1999); and see Anstis and Mather (1985); Edwards and Badcock (1994) for similar effects of luminance on motion processing]. For adults tested with DEMs, the luminance benefit ratio was 1.68, which was significant ($p = 0.009$, one-tailed t-test) and statistically indistinguishable from that obtained psychophysically ($p = 0.36$, one-tailed t-test). For infants tested with DEMs, the luminance benefit ratio was marginally significant ($p = 0.09$, one-tailed t-test). These patterns of results differ substantially from those observed in the chromatic condition. The fact that adult luminance benefit ratios were roughly the same for psychophysics and DEMs suggests that the psychophysical use of luminance as a segmentation cue for motion integration involves relatively low-level motion mechanisms.

It is perhaps important to point out that comparison of benefit ratios between the chromatic and luminance conditions is not meaningful. This is because we cannot know whether, on a perceptual level, the chromatic difference between the 'red' and 'green' dots in the chromatic condition is equivalent to the luminance difference between the 'bright' and 'dark' dots in the luminance condition. This would be true even if the contrast differences between the 'red versus green' and 'bright versus dark' dots were equated in some standardized metric [for example, in terms of the difference in excitation produced by the 'red versus green' or 'bright versus dark' in L-cones and M-cones—see Chaparro et al (1993), Dobkins et al (2000), Lennie and D'Zmura (1988), Mullen (1985)].

Table 1. Group mean geometric coherence thresholds for all conditions: infants (chromatic condition, $n = 15$; luminance condition, $n = 10$) and adults ($n = 7$). DEM = directional eye movement; HOM = homogeneous conditions; HET = heterogeneous conditions.

Subjects	DEM/%		Psychophysics/%	
	chromatic	luminance	chromatic	luminance
Adults				
HOM	26.39	21.82	1.57	1.19
HET	23.05	12.98	0.81	0.75
Infants	($n = 15$)	($n = 10$)		
HOM	49.36	61.84		
HET	48.37	53.25		

Because absolute thresholds are embedded in the benefit ratios, threshold values are presented separately in table 1. Note that we provide the mean geometric thresholds, which are the linear equivalents of the log means.

3.3 *Comparison of chromatic benefit ratios for human psychophysics, monkey psychophysics, and neural responses in MT*

In figure 4, we have re-plotted our chromatic benefit ratios from adults alongside chromatic benefit ratios from a set of studies conducted in adult humans and adult macaque monkeys (Croner and Albright 1997, 1999. The chromatic benefit ratios from the current study are plotted for data obtained psychophysically and with DEMs. As in the current study, Croner and Albright employed psychophysics to obtain benefit ratios in human subjects. In addition, they obtained chromatic benefit ratios in monkey subjects psychophysically, and, simultaneously, recorded from neurons in motion area MT so that they could derive a neural benefit ratio. To allow easier comparison between our results and those of Croner and Albright, benefit ratios are normalised relative to the human psychophysical data, which are set to 1.0 (linear equivalent of log 0), with values for the other measures (human DEMs, monkey psychophysics, monkey MT responses) reflecting a proportion. We did this because several stimulus parameters differed between the two studies, which might affect the absolute value of the chromatic benefit ratio (Croner and Albright: dot size = 0.1 – 0.2 deg, speed = 4 deg s^{-1}, stimulus duration = 2000 ms; current study: dot size = 0.42 deg, speed = 25 deg s^{-1}, stimulus duration = 400 and 800 ms for psychophysics and DEMs, respectively).

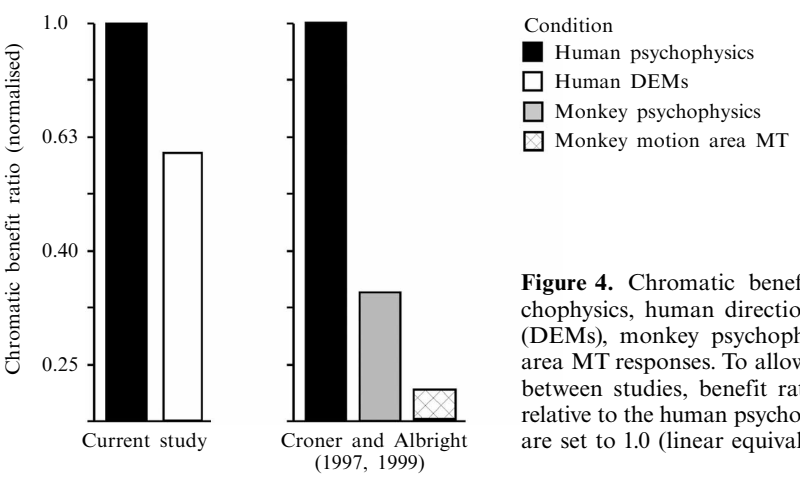

Figure 4. Chromatic benefit for human psychophysics, human directional eye movements (DEMs), monkey psychophysics, and monkey area MT responses. To allow easier comparison between studies, benefit ratios are normalised relative to the human psychophysical data, which are set to 1.0 (linear equivalent of log 0).

As can be seen in the data from Croner and Albright, monkeys tested psychophysically showed lower chromatic benefit ratios than humans tested psychophysically. We believe this difference reflects greater use of higher-level, attention-based mechanisms in humans, as compared to monkeys. We elaborate on the nature of this mechanism in section 4. In addition, chromatic benefit ratios in monkey motion area MT neurons were substantially lower than those obtained psychophysically from the same monkeys. Given that activity in area MT reflects low-level motion processes, the higher benefit ratios observed for psychophysical data (both in monkeys and in humans) suggest that the psychophysical use of chromatic information as a segmentation cue for motion integration relies on higher-level mechanisms, at least past the level of MT.

4 Discussion

The results from adults of the current study reveal significantly higher chromatic benefit ratios, reflecting stronger influence of chromatic information as a segmentation cue for motion integration, for psychophysical reports than for DEM. By contrast, luminance benefit ratios were roughly the same (and significant) for both measures. 3-month-old infants tested with the eye-movement measure (DEM) showed marginally significant benefit ratios in the luminance condition, but not in the chromatic condition. These results suggest that chromatic information as a segmentation cue for motion integration engages higher-level, attention-based mechanisms, whereas luminance information works mainly through low-level (pre-attentive and automatic) motion mechanisms.

These findings and their interpretations are discussed in several contexts. First, we discuss evidence for the notion that DEMs are mediated mainly by low-level motion mechanisms. Second, we discuss previous studies that have investigated the use of chromatic information as a segmentation cue for motion integration, with a particular focus on studies that have compared psychophysical responses with area MT and/or eye-movement responses. Third, we discuss the potential nature of higher-level, attention-based and low-level, pre-attentive motion mechanisms that use chromatic (and luminance) information as a segmentation cue for motion integration. On a final note, we discuss infants' use of chromatic information as a cue for motion correspondence and motion integration.

4.1 *Are directional eye movements mediated by low-level motion mechanisms?*

In the current study, we employed DEMs with the notion that they are mediated, to a substantial degree, by low-level motion mechanisms. As stated in section 1, we define low-level motion mechanisms as pre-attentive, ie the processing is passive/automatic and does not require attention (although, note that this does not mean that attention cannot modulate activity of low-level motion mechanisms). By this definition, directionally selective neurons in areas V1 and MT can be considered part of the low-level motion system. In turn, because the neurons in these areas feed directly into eye-movement systems, we consider DEMs to be an extension of the low-level motion system. More specifically, in our study, approximately half of the eye movements (in adults and infants) were of the OKN type, which is considered an automatic eye-movement response. OKN is mediated, in part, by directionally selective neurons in a subcortical structure of the midbrain called the nucleus of the optic tract (NOT). The NOT gets direct input from the retina and projects directly to motor regions that move the eyes (Hoffmann 1986; Hoffmann and Distler 1989; Hoffmann et al 1988; Simpson et al 1988; Telkes et al 2000). This subcortical 'loop' can be considered low-level, as attention is certainly not required. In adults, the NOT also receives descending input from area MT (Distler and Hoffmann 2001), which is thought to exert control over the subcortical eye-movement loop (see Hoffmann 1981). In very young infants (< 3 months old), the cortical descending projections have not developed fully and thus, in young infants, OKN is thought to be mediated almost exclusively by the

subcortical loop (Atkinson and Braddick 1981; Braddick 1996; Distler and Hoffmann 2003; Morrone et al 1999; and see Mason et al 2003 for further discussion). The other half of eye movements in our study were smooth-pursuit eye movements, which, in adults and infants, are thought to be mediated by areas MT and MST; lesions of these areas disrupt smooth pursuit as well as OKN (Dursteler and Wurtz 1988; Krauzlis 2004; Newsome and Paré 1988; Newsome et al 1985). On the basis of these data, we believe that the DEMs we observed in our study were mediated, to a large extent, by low-level motion mechanisms.

4.2 *Previous related studies*

In several previous psychophysical studies stochastic motion displays have been used to investigate chromatic information being employed as a segmentation cue for motion integration. Like the psychophysical data from adults of the current study, the results from these previous studies reveal chromatic benefit ratios greater than 1.0 [Croner and Albright (1997, 1999); Festa-Martino et al (2005); Snowden and Edmunds (1999); and see Edwards and Badcock (1996) for similar benefits of chromatic cues in conditions where green dots are presented on a red background]. Chromatic benefit ratios are found to vary somewhat across studies (ranging from 2 – 10), which is likely due to somewhat different stimulus parameters (eg dot speed, dot size, stimulus duration being used). Also, as in the current study, in some of these previous studies luminance (bright/dark) has been used as a segmentation cue and luminance benefit ratios have been found to be greater than 1.0 (Croner and Albright 1997; Festa-Martino et al 2005; Snowden and Edmunds 1999).

As mentioned in section 1, of particular relevance are the results from Croner and Albright (1997, 1999), who obtained chromatic benefit ratios psychophysically in humans and in macaque monkeys, as well as neurally in monkey area MT. The results of their study, presented in figure 4, show that chromatic benefit ratios obtained psychophysically are higher in human than in monkey subjects. This could be explained by supposing that humans, more so than monkeys, engage in higher-level strategies in the heterogeneous condition. The results of their study also show that psychophysical benefit ratios in monkeys are higher than those observed neurally in area MT. This result suggests that the psychophysical use of chromatic information as a segmentation cue for motion integration is mediated, at least in part, at a level past area MT. In further support of this suggestion, the results from this study show that the difference between the psychophysical and neural data is based mainly on differences in absolute thresholds in the heterogeneous condition; ie heterogeneous thresholds derived from MT neurons are much higher than those obtained psychophysically from the same monkey. This is in contrast to the homogeneous condition, where psychophysical and MT thresholds are much more similar—a finding that is corroborated in previous reports (eg Newsome et al 1989). Because area MT can be considered a low-level motion area, these results suggest that the psychophysical use of chromatic information as a segmentation cue for motion integration cannot be accounted for entirely by low-level motion mechanisms.

Also relevant are results from studies employing moving plaid patterns. As described in section 1, psychophysical studies have shown that chromatic information can influence the integration versus segmentation of two moving component gratings that make up a plaid pattern. In one study (Dobkins et al 1998), it was shown that these chromatic effects are significantly stronger when the measure is based on psychophysical reports than when it is based on eye movements or area-MT responses. Thus, like the results of the current study and those of Croner and Albright, these plaid findings suggest that the psychophysical use of chromatic information as a segmentation cue for motion integration relies on higher-level mechanisms.

4.3 *The nature of higher-level, attention-based mechanisms that use chromatic information as a segmentation cue for motion integration*

Given that the psychophysical use of chromatic information as a segmentation cue for motion integration relies on higher-level, attention-based mechanisms, here we speculate on the nature of these mechanisms. In our experiments, the two types of heterogeneous trials, red signal dots/green noise dots, and vice versa (as well as heterogeneous and homogeneous trials), were intermixed across trials, so that subjects could not predict which chromaticity would correspond to the signal and which to the noise dots. However, on heterochromatic trials, the signal dots were always the minority chromaticity because the range of signal-dot percentages stayed well below 50% (ranging from 0.14% to 4.75%; see section 2). We believe that, even with very-short-duration trials, subjects can figure this out, and, in turn, can attentively track the direction of the signal dots on each trial [and see Cavanagh (1992) and Cropper and Wuerger (2005) for further discussion of attentional tracking of chromatic motion]. In this scenario, even in the extreme case where there exists only one signal dot (eg red) amongst many noise dots (eg green), the task is very easy.

In addition to attentional tracking, attention could serve to group dots of similar chromaticity and/or decrease the gain of the chromaticity corresponding to the noise, lessening the weight of the noise in the motion integration process [see Croner and Albright (1997) and Snowden and Edmunds (1999) for further discussion; and Blaser et al (1999) for related effects of attention on the use of chromatic information as a motion correspondence cue]. In addition, the minority signal dots may automatically 'pop out', leading to selective attention to these dots (see Li and Kingdom 2001). In contrast to the psychophysical condition, pop-out of signal dots would not occur consistently in the eye-movement condition, where signal dots were the minority only half of the time (percentage of signal dots ranging from 9.0% to 79%). Although it is tempting to speculate that it is this difference in the degree of pop-out that accounts for the difference in chromatic benefit ratios between the psychophysical and eye movement measures, we feel strongly that this is not that case, since benefit ratios for the luminance condition (where these differences in the range of percentage of dot signals also existed) were found to be very similar between the two measures. In sum, any of the scenarios described above could explain why chromatic benefit ratios are greater than 1.0, without requiring direct chromatic input to low-level motion mechanisms.

4.4 *The nature of low-level mechanisms that use chromatic (and luminance) information as a segmentation cue for motion integration*

Despite the fact that the use of chromatic information as a motion segmentation cue appears to engage higher-level, attention-based mechanisms, the results from the current eye-movement measure and previous neurophysiological studies in area MT nonetheless support the existence of at least minimal low-level mediation. One way in which this could occur is if directionally selective neurons in the visual system were also chromatically selective. This, however, does not appear to be the case (Albright 1984; Baker et al 1981; Maunsell and Van Essen 1983b; Van Essen et al 1981; Zeki 1974). Instead, chromatic influence on motion integration versus segmentation could come from chromatically selective neurons that provide input to low-level motion areas like MT. Although such input to area MT is thought to be relatively minimal, it is not entirely absent; there is known feedforward input, via area V1, from chromatically selective neurons of the parvocellular pathway (Maunsell et al 1990; Nassi et al 2006), as well as lateral connections from chromatically selective neurons in area V4 (Desimone and Ungerleider 1986; Maunsell and Van Essen 1983a; Ungerleider and Desimone 1986). This chromatically selective input holds the potential to exert a modulatory, and low-level, influence on the integration of motion signals.

With respect to luminance information, our results showing equal effects of luminance contrast polarity between the psychophysical and DEM measures suggest that the psychophysical results are mediated by low-level motion mechanisms. This can potentially be accounted for by the known existence of directionally selective neurons in V1 that are selective for 'bright' and 'dark' (ie simple cells, see Hawken et al 1988). This could also explain the results from infants tested in the luminance condition, where luminance benefit ratios were marginally greater than 1.0, since directionally selective neurons in V1 are present very early in development (monkey neurophysiology: Hatta et al 1998; human VEP data: Braddick et al 2005; Hamer and Norcia 1994; Wattam-Bell 1991) and, as in adults, a subset of these neurons is likely to consist of simple cells.

4.5 *Infants*

In the current study, we were interested in obtaining chromatic benefit ratios in infants because in previous studies, which used DEMs, it has been demonstrated that infants can use chromatic information as a cue for motion correspondence (eg Dobkins and Anderson 2002; Dobkins and Teller 1996; Teller and Palmer 1996). Here, we asked whether infants can use chromatic information as a segmentation cue for motion integration. The results obtained with our eye-movement measure suggest they cannot. This, of course, is likely owing to the fact that the use of chromatic information as a cue for motion segmentation relies substantially on higher-level, attention-based mechanisms, which are not engaged in the eye-movement measure. The null result is unlikely to be due to a general lack of segmentation abilities in infants, since benefit ratios in the luminance condition were marginally greater than 1.0. Still, chromatic benefit ratios in infants are smaller than those in adults, suggesting that even the minimal use of chromatic information as a motion-segmentation cue (revealed with eye movements) may take time to develop. Future experiments on older infants will address this possibility.

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