Effects of spatial attention and salience cues on chromatic and achromatic motion processing

Karen R. Dobkins [a,*], Amy A. Rezec [a], Bart Krekelberg [b]

[a] *Department of Psychology, University of California, San Diego, La Jolla, CA 92093, USA*
[b] *Center for Molecular and Behavioral Neuroscience, Rutgers University, USA*

Abstract

While several previous psychophysical and neurophysiological studies have demonstrated chromatic (red/green) input to motion processing, the nature of this input is still a matter of debate. In particular, there exists controversy as to whether chromatic motion processing is mediated by low-level motion mechanisms versus higher-level, attention- or salience-based mechanisms. To address the role of attention, in Experiment 1, we asked whether spatial attention exerts larger effects on chromatic (red/green), as compared to achromatic, motion. To this end, we employed a motion after-effect (MAE) paradigm, and measured attention effects by comparing MAE duration between conditions where subjects attended to the adapting moving grating stimulus versus ignored that stimulus because they were required to perform an attentionally demanding vowel detection task at the center of gaze. The results from these experiments revealed equal effects of spatial attention on chromatic and achromatic motion processing, which were essentially constant (roughly 1.4-fold) across a wide range of stimulus contrasts (3.2–25% cone contrast). These findings suggest that chromatic motion processing is not affected disproportionally by higher-level spatial attention mechanisms. To address the role of salience, in Experiment 2, we investigated the effects of bottom–up salience cues on the strength of chromatic and achromatic motion, as measured with the MAE. Salience was manipulated by varying the relationship between the moving gratings and the background color. The results of these experiments revealed small and insignificant effects of salience cues on chromatic and achromatic motion processing. These findings suggest that mechanisms sensitive to feature salience do not influence low-level chromatic motion mechanisms mediating the motion after-effect.
© 2007 Elsevier Ltd. All rights reserved.

Keywords: Attention; Motion; Motion after-effect (MAE); Chromatic; Achromatic

1. Introduction

Numerous psychophysical studies have demonstrated that the primate motion system can use chromatic (red/green) information to discern direction of motion (see Cropper & Wuerger, 2005; Dobkins & Albright, 2003; Gegenfurtner & Hawken, 1996a for reviews). However, the mechanisms underlying chromatic motion processing are still under debate, with some researchers suggesting contribution from low-level motion mechanisms, and others suggesting contribution and/or reliance on higher-level mechanisms. Perhaps the strongest psychophysical evidence for mediation by low-level mechanisms comes from studies demonstrating a clear *motion after-effect (MAE)* for isoluminant chromatic (red/green) gratings (Cavanagh & Favreau, 1985; Derrington & Badcock, 1985; Mullen & Baker, 1985; Webster, Day, & Cassell, 1992). Because the MAE is thought to be mediated by adaptation in low-level motion areas, specifically in neurons of the middle temporal (MT) area or earlier (see Kohn & Movshon, 2003; Tootell et al., 1995; Van Wezel & Britten,

---
* Corresponding author.
  E-mail address: kdobkins@ucsd.edu (K.R. Dobkins).

2002 for evidence obtained using achromatic stimuli), these chromatic MAE results suggest mediation of chromatic motion by low-level mechanisms. In addition to demonstrating a chromatic MAE, some of the above-mentioned studies tested for and found cross-adaptation between chromatic (red/green) and achromatic (light/dark) gratings, i.e., adaptation to a moving chromatic grating can produce an MAE when the test grating is achromatic, and vice versa. These cross-adaptation findings suggest a *common* low-level mechanism for chromatic and achromatic motion. This suggestion is further supported by studies showing that performance on chromatic motion, but not on chromatic detection, tasks is impaired when chromatic stimuli are masked by achromatic noise (Cropper, 2005; Mullen, Yoshizawa, & Baker, 2003; Yoshizawa, Mullen, & Baker, 2003).

In addition to the evidence for low-level contribution, there also exists evidence that, compared to achromatic motion processing, chromatic motion processing relies more on higher-level processes, including (1) attentive tracking of select features and/or (2) motion correspondence based on salience differences. Evidence for chromatic motion relying on attentive feature tracking comes from a study by Cavanagh (1992), in which subjects were required to attentively track moving features in an "opposed motion stimulus", consisting of two radial gratings—one red/green chromatic, the other achromatic—superimposed and moving in opposite directions. When subjects were required to track the position of a red or green stripe in the moving chromatic grating, they could do so with ease, even under conditions when the *global* percept of motion was in the opposite direction (i.e., in the direction of the achromatic grating). By contrast, subjects were poor at tracking the position of a light or dark stripe in the moving achromatic grating that dominated the global percept. These results led Cavanagh to conclude that motion of achromatic gratings is mediated by low-level (presumably pre-attentive) mechanisms, while motion of chromatic gratings is mediated by higher-level, attentional tracking of select local features. In further support of this notion, a recent review of the chromatic motion literature (Cropper & Wuerger, 2005) concludes that chromatic motion is easiest to detect under conditions in which the stimulus features can potentially be attentively tracked; for example, when stimuli are presented foveally, at slow speeds, low spatial frequencies, and/or for long durations. This notion makes ecological sense since color is an object feature that can be used effectively for tracking object position over time. By contrast, because objects move in and out of shadows, lightness is a relatively unreliable featural cue for tracking object position.

The other high-level account of chromatic motion processing has come from work by Lu, Lesmes, and Sperling (1999a, 1999b), who suggest that chromatic motion is mediated by a "feature-salience" mechanism. Although salience is somewhat difficult to define, features perceived as foreground are typically considered of higher salience than the background (and in complementary fashion, features of higher salience tend to be perceived as foreground). According to the "feature-salience" model, motion correspondences are made between features of similar salience value (i.e. high versus low salience), without regard for the features themselves. Lu et al. argue that chromatic (red/green) motion is detected exclusively by this higher-level feature-salience mechanism. Accordingly, they propose that chromatic motion is best detected under conditions in which the red and green stripes differ in salience. In support of this notion, it has been shown that chromatic motion strength is enhanced substantially when salience differences are obtained by (1) *bottom–up* differences in salience between the red and green stripes of the grating, which can be created by presenting red/green gratings on a green background, thereby making the red stripes appear as foreground, and thus more salient than the green stripes (Lu et al., 1999a) or (2) *top–down* differences in salience between the red and green stripes of the grating, which can be attained by asking subjects to attend to "red" (Blaser, Sperling, & Lu, 1999). In sum, the results of these studies suggest that feature salience may play an important role in chromatic motion processing.

To investigate the mechanisms underlying chromatic motion further, in the current study we asked whether the effects of top–down attention (Experiment 1) and bottom–up salience cues (Experiment 2) were relatively greater for chromatic, than for achromatic, motion. In Experiment 1, we measured *spatial* attention effects by employing a motion after-effect (MAE) paradigm, and comparing MAE duration between two conditions: *full-attention*, subjects were instructed to pay attention to the adapting moving grating stimulus, and *poor-attention*, subjects were required to perform a difficult vowel detection task at the center of gaze and therefore largely ignore the adapting motion stimulus. We (Rezec, Krekelberg, & Dobkins, 2004) and others (Chaudhuri, 1990; Lankheet & Verstraten, 1995; Shulman, 1993) have used this MAE paradigm to investigate the effects of attention on achromatic motion, whereas the current study compared attention effects between achromatic and chromatic motion. In addition, the current study investigated the effects of attention across a wide range of stimulus contrasts. The MAE paradigm of the current study is critically different from the motion nulling paradigm we previously employed to test the effects of spatial attention on chromatic versus achromatic motion (Thiele, Rezec, & Dobkins, 2002). In this previous study, we found that "equivalent luminance contrast (EqLC)", i.e., the amount of luminance contrast in an achromatic grating needed to null the motion of a chromatic grating, was the same under full versus poor attention conditions, a result suggesting equal effects of spatial attention on chromatic and achromatic motion. Unfortunately, this motion nulling paradigm was limited by the fact that (1) it did not allow the effects of attention on chromatic and achromatic motion to be tested separately, and (2) the

effects of attention could not be tested as a function of stimulus contrast.

In Experiment 2, we used the MAE paradigm to measure effects of bottom–up salience cues on the strength of chromatic and achromatic motion. These experiments were designed to test the "feature-salience" model of Lu et al. (1999a, 1999b). Salience effects were measured by comparing MAE duration between a condition where the two stripes in a grating were of equal salience, and thus neither was seen as foreground versus a condition where the relationship between the grating and the background was manipulated to create a salience difference between the two stripes, such that one was perceived as foreground.

The results of our attention experiments revealed equal attention effects on chromatic and achromatic motion processing, which were essentially constant (roughly 1.4-fold) across a wide range of stimulus contrasts. By comparison, our salience experiments revealed negligible effects of salience cues on chromatic or achromatic motion processing.

2. Methods

Two main experiments were conducted, both of which used the duration of the *motion after-effect (MAE)* as a measure of the strength of motion processing (see Pantle, 1998). In Experiment 1, we investigated the effects of *spatial attention* on MAE duration. In Experiment 2, we investigated the effects of *bottom–up salience cues* on MAE duration. We first describe the methods that were common to both experiments, and then the details that differed between the two.

2.1. Apparatus

Visual stimuli were generated with in-house OpenGL software using an ATI Radeon 8500 graphics board (1280×1024 pixel resolution) residing in an AMD Athlon processor based PC. The stimuli were displayed on a 20″ analog RGB monitor (Sony GDM 2000TC, 75 Hz, non-interlaced). The voltage/luminance relationship was linearized independently for each of the three guns in the monitor using a PR-650 photometer (PhotoResearch), using a square patch of the same size and at the same position as the stimuli in the experiments. The PR-650 was also used for photometric measurements to standardize to V_λ isoluminance, as well as for spectroradiometric measurements to compute long-wavelength-selective (L) and medium-wavelength-selective (M) cone contrasts produced by our visual stimuli.

2.2. Stimuli

Stimuli consisted of horizontal sinusoidal gratings, with a spatial frequency of 0.4 cpd, and a temporal frequency of 2.5 Hz. Gratings either moved (at 6.2°/s) or counterphase-reversed (in a temporal sinusoidal fashion). The gratings subtended $10° \times 10°$, and were centered on a black fixation square ($0.9° \times 0.9°$). Gratings were one of three types: (1) "Achromatic", which varied in luminance only. These were created by sinusoidally modulating the red and green guns in phase. The individual red and green sinusoids that made up the achromatic grating were of the same mean luminance and of equal luminance contrast. (2) "Chromatic", which varied in red/green chromaticity only, i.e., were "isoluminant". These stimuli were identical to the achromatic gratings, except that the red and green guns were modulated 180° out of phase. (3) "Mixed", which varied in both chromaticity and luminance. Here, the individual red and green sinusoids were 180° out of phase, but of *unequal* luminance contrast [Note that achromatic and chromatic stimuli are some-

times referred to as L + M (i.e., producing in phase modulation of L- and M-cones) and L − M (i.e., producing out of phase modulation of L- and M-cones), respectively (e.g., Gunther & Dobkins, 2002).]. The mean luminance of all gratings was 7.0 cd/m². With the exception of one condition in Experiment 2B (see below), the mean chromaticity of all gratings had CIE coordinates[1] of $x = 0.44$, $y = 0.40$. The background was either the same mean luminance/chromaticity as the gratings (*Experiment 1: Effects of Spatial Attention*) or different (*Experiment 2: Effects of Salience*).

For all stimuli, contrast is specified in terms of L- and M-cone contrast, which describes the percent response modulation in the L- and M-cone photoreceptors produced by the grating stimulus. Because our stimuli produced negligible S-cone activation, cone contrast calculations did not consider S-cones[1]. The benefit of converting to a cone contrast metric is that it standardizes across apparatus and laboratories, and allows for the expression of chromatic and luminance contrast in comparable units (e.g., Chaparro, Stromeyer, Huang, Kronauer, & Eskew, 1993; Lennie & D'Zmura, 1988; Mullen, 1985). For *chromatic* and *mixed* gratings, cone modulations were computed by determining L- and M- cone excitations produced by the "red" and "green" peaks of the chromatic gratings, which were obtained by integrating the cross-product of stimulus spectral output of these stimuli by the Stockman and Sharpe (2000) cone fundamentals (see Gunther & Dobkins, 2002 for details). As a final step, root mean square cone contrast was determined (r.m.s. = sqrt $\{((\Delta M/M)^2 + (\Delta L/L)^2)/2\}$). In our set-up, a maximum value of 25% cone contrast was attainable for chromatic gratings at photometric (V_λ) isoluminance. For *achromatic* gratings, r.m.s. cone contrast values directly correspond to the conventional Michelson contrast: $[(\mathrm{Lum}_{max} - \mathrm{Lum}_{min})/(\mathrm{Lum}_{max} + \mathrm{Lum}_{min})]$.

2.3. Determining red/green isoluminance

Before beginning our MAE experiments, for each subject, red/green isoluminance in the chromatic gratings was determined via a minimal motion technique, which relies on the fact that motion is impoverished, slow or jerky at subjective isoluminance (Cavanagh, Tyler, & Favreau, 1984; Dobkins & Teller, 1996; Moreland, 1982). Subjects were tested in a dark room, viewed the video display binocularly from a chin rest 57 cm away, and were instructed to maintain fixation on the central fixation square. On each trial, a moving red/green grating producing 25% cone contrast appeared centered on the fixation square. This grating had the same size, spatial and temporal frequency as in the MAE experiments. The subject adjusted the relative luminance between the red and the green phases until the perceived motion strength was minimal. The isoluminance point was determined from the mean setting across 20 trials. These isoluminance settings were used in the main experiment so that each subject was tested at his/her individual isoluminance point.

Note that in Experiment 2A and 2B, where red/green gratings were presented on different background colors, we obtained isoluminance points for the different background conditions (yellow, red, green, see below). Data from our five subjects showed that while isoluminance points varied across subjects, within each subject, isoluminance points varied negligibly across the different background conditions (1-factor ANOVA, $p = .86$). For this reason, for each subject we averaged the isoluminance values across the different background conditions and used that mean value for all conditions in the MAE experiments. This lack of a background color effect on isoluminance points may seem surprising, as previous studies have demonstrated that background colors can alter the

---

[1] The purpose of modulating through yellow (rather than white) was two-fold. First, it allowed us to test higher cone contrasts in long-wavelength-selective (L) and medium-wavelength-selective (M) cones. Second, stimuli modulated through yellow produce extremely low short-wavelength-selective (S) cone activation (approximately 0.001 units in MacLeod-Boynton, MacLeod & Boynton (1979). Chromaticity diagram showing cone excitation by stimuli of equal luminance. *Journal of the Optical Society of America, 69*(8), 1183–1186. chromaticity space), and thus the contribution of S-cones to our results is expected to be negligible.

adaptation state, and in turn the relative weightings, of the L- and M-cones (see Eisner & Macleod, 1981; Stromeyer, Chaparro, Tolias, & Kronauer, 1997). An important difference, however, is that the "background" in these previous studies was physically *added* on top of the test stimuli, whereas the "background" of the current study only surrounded the test stimuli (and thus presumably had negligible effects on adaptation state).

2.4. Motion after-effect (MAE) paradigm

Subjects were instructed to maintain fixation on the central fixation square. They began each trial with a key press, after which a moving grating stimulus, the "adaptation" stimulus, appeared for 30 s. The grating moved either upward or downward (randomized across trials). After the adaptation phase, the "test" stimulus appeared. It consisted of a grating whose parameters were identical to those of the adaptation stimulus (i.e., same stimulus type, same contrast, same spatial and temporal frequency) except that it counterphase-reversed (in a temporal sinusoidal fashion) rather than moved. Note that we employed counterphase test gratings because in pilot studies we found that most subjects were able to perceive a chromatic MAE when the test stimulus was counterphased, but not when it was static. This lack of a chromatic MAE for static test stimuli might be explained by the fact that counterphase gratings have more positional uncertainty than static gratings (see Cropper & Hammett, 1997 and see Nishida, Ashida, & Sato, 1997 for results demonstrating differences in the characteristics of the achromatic MAE for static versus dynamic test stimuli). Also, note that our reason for keeping the contrast of the adapting and test stimuli the same (as we have done previously, Rezec et al., 2004) is based on evidence that perceived speed varies with contrast and stimulus type (Thompson, Kossut, & Blakemore, 1983; Hawken, Gegenfurtner, & Tang, 1994; Gegenfurtner & Hawken, 1996b). In addition, keeping the adapting and test contrast the same is expected to maximize the duration/strength of the MAE (see Nishida et al., 1997).

During the test phase, subjects perceived an MAE, i.e., the test stimulus appeared to move in the direction opposite to that of the adaptation stimulus. Subjects were required to signal (with a key press) when the MAE ended. Subjects were also given the option of reporting "no MAE" with a separate key press. Each trial was followed by a 20 second period in which subjects rested and were allowed to move their eyes. This period also allowed motion mechanisms to return to a pre-MAE baseline level of activity (e.g., van der Smagt & Stoner, 2002). A timeline depicting the course of a single trial is presented in Fig. 1.

2.5. Monitoring eye position

For each subject, eye position was monitored using an infrared camera with variable focus (12.5–75 mm) lens (Model #Fc62, Image Sensor), focused on the left eye of the subject. The subject's face was lit with an infrared illuminator and an enlarged image of the eye was viewed on a 12″ monitor outside the testing room. Before beginning each block of trials, subjects were instructed to fixate a black fixation square ($0.9° \times 0.9°$) in the center of the video display, and the outline of the pupil was drawn on transparency film that covered the monitor. Previous experiments in our laboratory have shown that this set-up allows for the easy detection of saccadic eye movements and eye drift within ±2 degrees of fixation (Dobkins & Bosworth, 2001). Subjects were instructed to maintain fixation throughout the experiment and were informed that the experiment would be temporarily interrupted if eye movements or eye drift were detected. Thus, subjects were highly discouraged from breaking fixation, and the experiment never needed to be interrupted.

2.6. Data analysis

For each subject, mean MAE durations were obtained by averaging data across trials, separately for the different stimulus conditions. For trials in which a subject reported "no MAE", the MAE duration was set to a value of 0 s before averaging across trials. This "no MAE" response was relatively rare, occurring on 2.3% and 9% of trials in Experiments 1 and 2, respectively (averaged across all subjects). We then took the logarithm of individual subject means to be used in all statistical analyses and data plots. The reason for using logs is that subject data conform to normal distributions when log-transformed. In addition, the use of logs allows for easy visual comparison and interpretation of MAE duration data plotted for different conditions, as the linear distance between the means of different conditions represents the ratio of MAE duration for one condition versus another. However, in all figures, we plot the linear equivalent of the log mean, i.e., the geometric mean, because linear values of duration are easier to understand.

2.7. Experiment 1: Effects of spatial attention

In this experiment, we tested the effects of spatial attention on the MAE duration. In Experiment 1A, we examined attention effects on moving chromatic and achromatic gratings across a range of cone contrasts. In Experiment 1B, we examined attention effects on moving chromatic, achromatic, and mixed gratings presented at a single contrast.

2.7.1. Subjects

In Experiment 1A, a total of seven subjects participated (age range = 20 to 28 years). In Experiment 1B, a total of five subjects participated (age range = 18 to 20 years), and these were the same five subjects who participated in Experiment 2B (below). All had normal or corrected-to-normal vision, normal color vision (as assessed by the Ishihara color
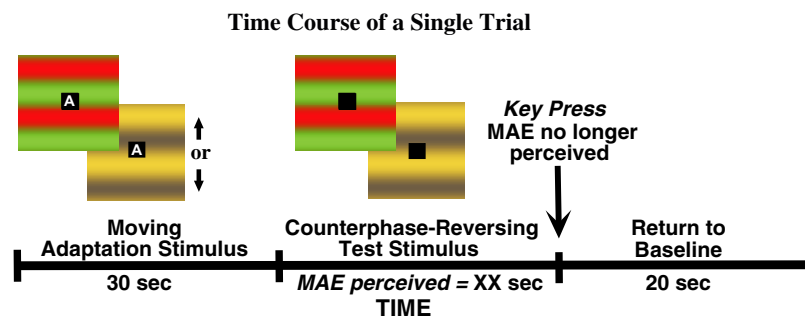
Time Course of a Single Trial

Fig. 1. Time course of a single trial. Subjects began each trial with a key press, after which the moving adaptation stimulus appeared for 30 s (moving upward or downward). This was followed by the presentation of the counterphase-reversing test stimulus, during which the motion after-effect (MAE) was perceived, i.e., motion in the direction opposite to that of the adaptation direction. Subjects were required to signal (with a key press) when the MAE ended (labeled XX sec). This was followed by a 20 s rest/recovery period. The adaptation and test stimulus were of the same type (i.e., chromatic or achromatic) and contrast. To study attention effects (Experiments 1A and 1B), an RSVP stimulus consisting of letters appeared on the central black fixation square during the adaptation phase (only one letter shown here). In our studies of salience effects (Experiments 2A and 2B) the RSVP stimulus was not present. See text for further details.

plates) and no family history of color abnormalities. With the exception of one subject (the second author), all were naïve to the purpose of the experiment.

2.7.2. Stimuli and paradigm

In Experiment 1A, moving chromatic and achromatic gratings were presented at eight cone contrasts, ranging in equal log steps from 3.22% to 25.0%. In Experiment 1B, we likewise investigated the effects of attention on moving chromatic and achromatic gratings, but in addition, compared these effects to those observed for a third stimulus, mixed gratings. Our reason for adding this mixed grating condition was based on our previous findings obtained using an equivalent luminance contrast (EqLC) motion nulling paradigm (Thiele et al., 2002, see Section 1). In that study we found that attention effects differed between conditions that employed mixed gratings (i.e., red/green gratings containing 25% luminance contrast) versus chromatic (isoluminant) red/green gratings. The three stimulus types were tested at a single cone contrast, which was roughly the same across the stimulus types (25% - 30%), as follows. Chromatic gratings were set to 25% cone contrast. Mixed gratings were created by adding 25% luminance contrast to the chromatic gratings (such that red was more luminous than green). Note that, based on inter-subject differences in red/green isoluminance points, this made for small differences in the cone contrast produced by the mixed grating stimulus across subjects (ranging from 27.2% to 30.3%). Achromatic gratings were created to produce the same amount of cone contrast as the mixed gratings. In both Experiment 1A and 1B, the mean luminance and chromaticity of the gratings were identical to the background.

MAE duration was obtained under "full" versus "poor" attention conditions. In both conditions, a rapid serial visual presentation (RSVP) of white letters (subtending $0.6° \times 0.6°$) was presented within the fixation square during the adaptation phase. A total of 160 letters was presented with the letter changing every 0.08 s. All letters of the alphabet were presented. The frequency of a vowel appearing (A, E, I, O, U) was set to ~10% (~15 to 20 out of 160). The RSVP stimuli disappeared during the test phase. In the "full-attention" condition, subjects were instructed to simply attend to the moving stimulus in the 30 s adaptation phase, ignoring the (irrelevant) stream of letters at the center of gaze. Note that, as in our previous study measuring the effects of attention on the achromatic MAE (Rezec et al., 2004), we did not explicitly monitor attention in the full-attention condition. Although this could result in variation across trials (or subjects) in the amount of attention devoted to the moving adapting stimulus, such variation (if it existed) would not affect comparisons made between the different stimulus types or contrasts, since stimulus conditions were carefully randomized across trials (see below). In the "poor-attention" condition, subjects attended away from the motion stimulus during the adaptation phase, because they were required to perform an attentionally demanding task on the RSVP stimuli appearing at the fixation spot; they were required to press a key each time a vowel appeared. Note that, in both the full- and poor-attention conditions, subjects were required to fully attend to the test stimulus since they were required to report the duration of the MAE produced by this test stimulus.

The two attention conditions were interleaved in blocks of eight trials, with the different stimulus types and contrasts varied randomly across trials within each block. The purpose of interleaving was to avoid differential practice/criterion effects in reporting the duration of MAE between the two attention conditions. In Experiment 1A, there were 32 total conditions: 2 attention conditions (full versus poor), 2 stimulus types (chromatic versus achromatic), 8 contrasts, and 10 trials were obtained for each (total trials = 320). In Experiment 1B, there were 6 total conditions: 2 attention conditions (full versus poor), 3 stimulus types (chromatic, achromatic, mixed), and 10 trials were obtained for each (total trials = 60).

After each poor-attention block, subjects were provided with feedback regarding their RSVP performance on that block. Performance was computed as the percentage of correct detections minus the percentage of false alarms, with a correct detection considered a key press within 0.8 seconds after a vowel presentation and a false alarm considered any key press outside this time window. Before beginning this experiment, subjects received ample practice on the vowel-task alone

and were required to reach asymptotic performance before commencing the main experiment. Note that the overall RSVP performance (averaged across all stimulus types/conditions) was at least as high during the MAE experiment (Experiment 1A: $78.8\% \pm 9.1\%$, Experiment 1B: $78.2 \pm 6.9\%$) as during the last practice session (Experiment 1A: $62.4 \pm 12.7\%$, Experiment 1B: $71.5 \pm 7.8\%$), and there was no significant difference between the two (Experiment 1A: $p = .20$, Experiment 1B, $p = .16$, two-tailed correlated t-tests). This confirms that, in the main experiment, the presence of the motion stimulus did not lessen the amount of attention paid to the RSVP task, and thus we can be assured that subjects adequately ignored the motion stimulus in the poor-attention condition. In addition to computing overall performance on the RSVP task, we also computed performance separately for each stimulus type (Experiment 1A: chromatic and achromatic, Experiment 1B: chromatic, achromatic, mixed). And, in experiment 1A, performance was analyzed for the different contrasts employed. In experiment 1A, a 2-factor ANOVA (stimulus type × contrast) revealed no effect of stimulus type (chromatic versus achromatic) or contrast ($p = .77$) on RSVP task performance. Likewise, in experiment 1B, there was no effect of stimulus type on RSVP task performance ($p = .99$). This suggests that any observed difference in MAE duration across the different stimulus types/contrasts in the poor-attention condition cannot be attributed to variations in the amount of attention placed on the RSVP task.

2.8. Experiment 2: Effects of salience

Although salience is not a straightforward property to define, it is generally believed that features perceived as foreground are more salient than the background (and in complementary fashion, that salient features tend to be perceived as foreground). In Experiment 2, we investigated the effects of bottom–up salience cues on MAE duration. After Lu et al., 1999a, 1999b, we attempted to make one of the two stripes in a grating (for example, the green stripes in a red/green chromatic grating) appear as foreground (and therefore more salient than the other stripe), by varying the relationship between the grating and its background color. In Experiment 2A, this was achieved by keeping the grating stimulus the same, but varying the background color. In Experiment 2B, we compared this with a salience manipulation in which the background was kept the same, but one of the stripe colors in the grating was changed (after Lu et al., 1999a). In both Experiment 2A and 2B, the grating stimulus appeared as stripes of only one color that moved across a background. It was our subjective experience, as well as that of our subjects, that these stripes appeared as foreground and had a higher salience than the background (and thus we refer to this stimulus as "enhanced salience"). By comparison, for gratings where the two stripe colors were equally different in chromaticity from the background, the two grating stripes appeared equally salient with one another, and thus neither stripe appeared as foreground (and thus we refer to this stimulus as "isosalient"). Note that salience is unrelated to the contrast of the stimulus; even at high contrasts, if the two stripes are equally different from the background, the stimulus is considered "isosalient". Table 1 presents all the conditions used in both Experiments 2A and 2B.

Table 1
Stimuli used to measure the effects of salience in Experiments 2A and 2B

Grating	Background color			
	R	G	Y	Light-Y
Chromatic: red/green	G > R	R > G	R = G	
Achromatic: light/dark			D = L	D > L
Chromatic: red/yellow			R > Y	

Shown are the different grating stimuli that were presented on different background colors. The resulting percepts for the different combinations are labeled in each cell. The symbol '=' denotes isosalience and ">" denotes enhanced salience, with one stripe containing higher salience than the other. R, red; G, green; Y, yellow; D, dark; L, light.

2.8.1. Subjects

In Experiment 2A, a total of five subjects (two of whom were also in Experiment 1A) participated (age range = 21 to 27 years). One subject did not experience an MAE for chromatic stimuli under any condition, and thus her data were not included. In Experiment 2B, a total of five subjects participated (age range = 18 to 20 years), and these were the same five subjects who participated in Experiment 1B (above). All had normal or corrected-to-normal vision, normal color vision (as assessed by the Ishihara color plates) and no family history of color abnormalities. All were naïve to the purpose of the experiment.

2.8.2. Stimuli and paradigm

All data were obtained under full-attention conditions (no RSVP stimuli were presented). In Experiment 2A, MAE data were obtained for chromatic and achromatic gratings at three different cone contrasts (4.3%, 10.4%, and 25.0%),[2]. Chromatic gratings were presented on three different backgrounds. The first was a *yellow background* that matched the mean luminance and chromaticity of the chromatic grating (as in Experiment 1A and 1B). We refer to this as the "isosalience-chromatic" condition, or 'R = G' for short. The second was a *red background* that had the same chromaticity and luminance as the peak of the red stripe in the chromatic grating. Here, the grating no longer appeared to have any red stripes, only green foreground stripes on a red background. We refer to this as the 'G > R' condition. Note that the '>' sign in this notation refers to the salience, not the luminance: all chromatic stimuli were isoluminant. The third was a *green background* that had the same chromaticity and luminance as the peak of the green stripe in the chromatic grating. Here, the grating no longer appeared to have any green stripes, only red foreground stripes on a green background. We refer to this as the 'R > G' condition.

For *achromatic* gratings, we used two backgrounds to manipulate the salience. The first was a *mean yellow background* that matched the mean luminance and chromaticity of the achromatic grating (as employed in Experiment 1A and 1B). We refer to this as the "isosalience-achromatic" condition, or 'D = L' for short. The second was a *light yellow background* that had the same luminance and chromaticity as the peak of the light stripe in the achromatic grating. Here, the grating no longer appeared to have any light stripes, only dark foreground stripes on a light background. This condition is referred to as 'D > L'.

In Experiment 2B, we asked whether salience effects differ between conditions where enhanced salience is created by keeping the grating stimulus constant but changing the background color (as in Experiment 2A) and conditions where enhanced salience is created by keeping the background constant but changing the makeup of the grating stimulus (as in Lu et al., 1999a, 1999b). To this end, MAE data were obtained for three different chromatic stimulus conditions. The first two, R = G, and R > G (cone contrast of gratings = 25%), were identical to the conditions employed in Experiment 2A. In the third condition, which was modeled after the stimuli used by Lu et al. (1999a), the grating was red/yellow (cone contrast = 14.8%) presented on a yellow background. This condition was created by modulating the green gun from 0 to 0.5 and the red gun from 0.5 to 1, where the gun activity is expressed in fractions of the total luminance of a given monitor gun. In this stimulus, the green gun contribution was reduced to the point where the grating no longer appeared to have any green stripes, only red foreground stripes on a yellow background. This condition is referred to as 'R > Y'.

The different stimulus types, contrasts and backgrounds were varied randomly across trials within a block. In Experiment 2A, there were 15 total conditions. Nine of these were chromatic conditions: three background colors (yellow, red, green) by three contrasts. Six of these were achromatic conditions: two backgrounds (mean yellow, light yellow) by three contrasts. Six trials were obtained per condition (total trials = 90). In Experiment 2B, there were 3 conditions, and 10 trials obtained per condition (total trials = 30).

---

[2] One subject was tested over a slightly different range of chromatic contrasts (13.9%, 18.7%, 25.0% since she had trouble perceiving an MAE at low chromatic contrasts.

3. Results

3.1. Experiment 1: Effects of spatial attention

3.1.1. Experiment 1A

Fig. 2 presents data from Experiment 1A, in which MAE duration (seconds, s) was measured for *achromatic* gratings (a and c) and *chromatic* gratings (b and d), under both full-attention (*filled squares, solid curve*) and poor-attention (*open squares, dashed curve*) conditions, across a range of cone contrasts. The upper panels (a and b) present data from one representative subject (CY). The bottom panels (c and d) present group mean data ($n = 7$). For both achromatic and chromatic gratings, mean MAE durations were found to be significantly greater than 0 for all contrasts and both attention conditions (achromatic: $p < .0001$ for all conditions, chromatic: $p < .018$ for all conditions). With respect to *contrast effects*, for achromatic gratings, MAE duration was found to increase with increasing contrast, asymptoting at roughly 6–8% (in both attention conditions). Over the contrast range tested, this increase in MAE duration was roughly 1.4-fold. This effect of contrast was confirmed statistically in a 2-factor ANOVA (attention condition × stimulus contrast), which revealed a significant main effect of contrast ($p = .003$), and is in line with results from previous MAE studies (Nishida et al., 1997; Rezec et al., 2004). Unlike the achromatic stimuli, there was no main effect of contrast on MAE duration for chromatic stimuli ($p = .5$). However, there was a tendency for the chromatic MAE duration to increase, then decrease, with increasing contrast. The decrease at high contrast, which is particularly evident in the example data of subject CY, was also observed in Experiment 2A (see below).

These data also allow us to address whether MAE duration is longer for achromatic or chromatic gratings when the two stimulus types are equated for cone contrast. The results of a 3-factor ANOVA (stimulus type × attention condition × stimulus contrast), revealed a main effect of stimulus type ($p = .05$), with longer MAE durations for the achromatic condition.

To more directly examine attention effects, for each subject, we obtained the log ratio of MAE duration in the full-attention condition divided by that in the poor-attention condition, and then averaged across subjects ($n = 7$). Group mean attention ratios are plotted as a function of cone contrast in Fig. 3, for achromatic gratings (*open squares*) and chromatic gratings (*open circles*). For both the achromatic and chromatic data, there was an effect of attention on the MAE; MAE was longer in the full- versus the poor-attention condition. This was confirmed in the results of the 2-factor ANOVAs (above), which revealed a significant main effect of attention condition for the achromatic data ($p = .007$), and a marginally significant effect for the chromatic condition ($p = .075$). We believe the marginal statistic for the chromatic data is a result of MAE duration data being somewhat noisy.
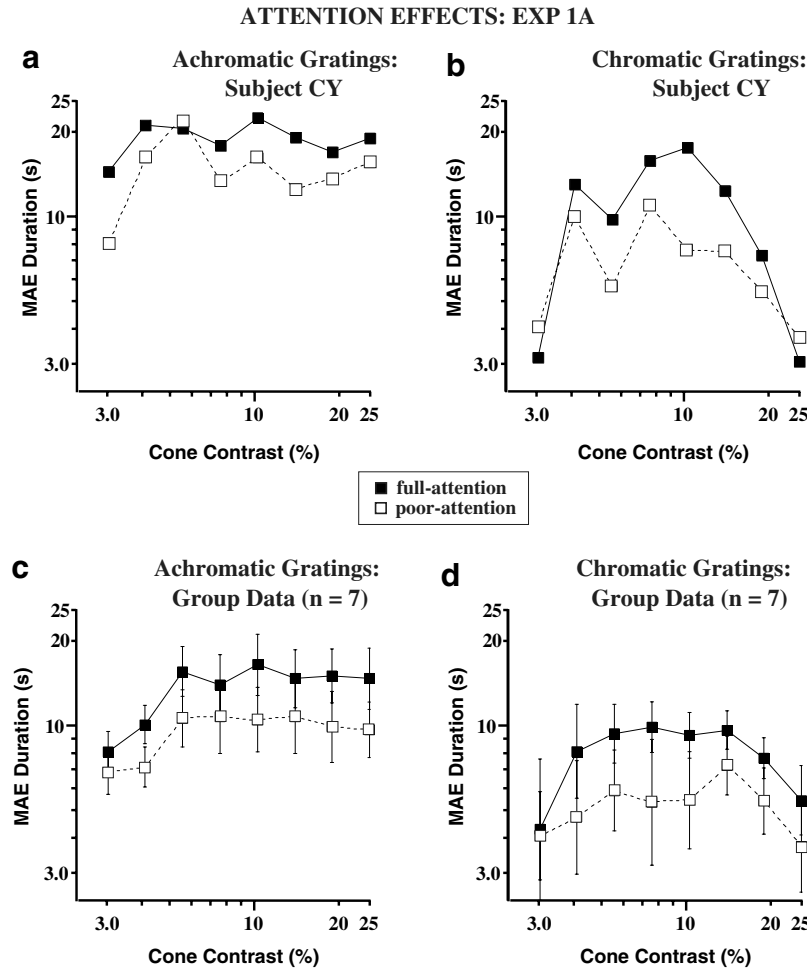
ATTENTION EFFECTS: EXP 1A

Fig. 2. Attention effects: Experiment 1A. MAE duration data plotted as a function of cone contrast for (a and c) achromatic (light/dark) gratings and (b and d) chromatic (red/green) gratings, under both full-attention (*filled squares, solid curve*) and poor-attention (*open squares, dashed curve*) conditions. The upper panels (a and b) present data from one representative subject (CY). The bottom panels (c and d) present group mean data (*n* = 7). For achromatic gratings, MAE duration asymptoted by 10% contrast. For chromatic gratings, there was a tendency for MAE duration to increase, and then decrease, as contrast increased. MAEs were significantly longer for achromatic than for chromatic stimuli. Error bars denote standard errors of the means.
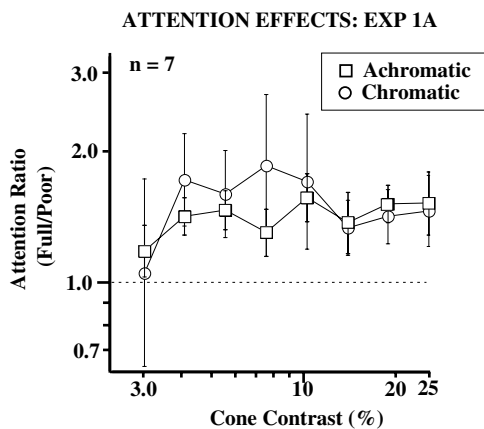

Fig. 3. Attention effects: Experiment 1A. Group mean attention ratios (full-divided by poor-attention) plotted as a function of stimulus contrast for achromatic gratings (*open squares*) and chromatic gratings (*open circles*). The attention effect was equal for chromatic and achromatic gratings and roughly constant across the range of contrasts tested. At all contrasts except the lowest tested, the attention effect was significantly greater than 1.0 (see text for details). Error bars denote standard errors of the means.

The attention ratios of Fig. 3 also reveal a constant effect of attention across a wide range of cone contrasts (3.22–25.0%), which includes contrasts where MAE duration had asymptoted (achromatic data) or peaked (chromatic data). This is supported statistically by 1-factor ANOVAs showing no effect of contrast on attention ratios (achromatic: $p = .57$, chromatic, $p = .81$). However, the effect of contrast should not be considered entirely constant, since for the lowest contrast tested (3.22%), the attention ratio was not different from 1.0 (chromatic = 1.05, $p = .46$, achromatic = 1.17, $p = .13$, one-tailed correlated t-test). Averaged across all contrasts, attention ratios were 1.39 and 1.48 for the achromatic and chromatic conditions, respectively.

Last, the data in Fig. 3 also reveal markedly similar attention ratios for achromatic and chromatic gratings, across all cone contrasts. This was confirmed statistically in a 2-factor ANOVA (contrast × stimulus type), where the main effect of stimulus type on attention ratios was not significant ($p = .64$). And, as expected from the ANO-VAs performed separately on chromatic and achromatic
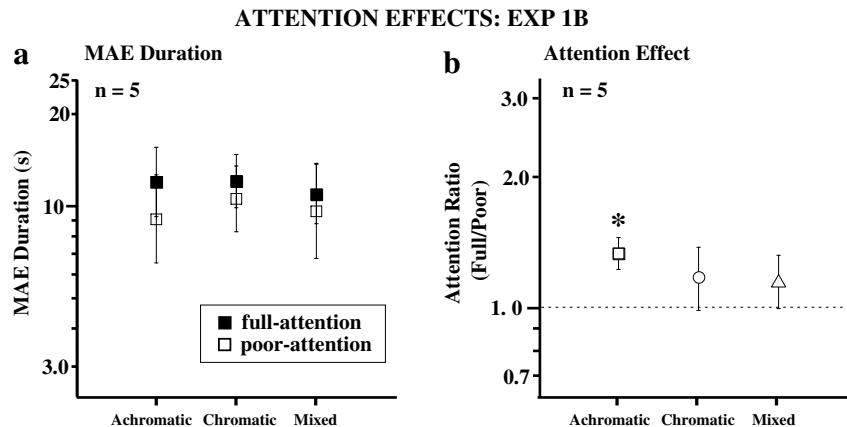
ATTENTION EFFECTS: EXP 1B

Fig. 4. Attention effects: Experiment 1B. Data obtained for achromatic, chromatic and mixed gratings, all of which produced between 27–30% cone contrast (see Section 2). (a) Group mean MAE duration plotted for full-attention (*filled squares*) and poor-attention (*open squares*) conditions. (b) Group mean attention ratios (full- divided by poor-attention) for the three stimulus types: achromatic (*open square*), chromatic (*open circle*) and mixed (*open triangle*). The attention effect was not significantly different across the three conditions, although only for the achromatic condition was the attention effect significantly greater than 1.0 (∗). Error bars denote standard errors of the means.

data, the 2-factor ANOVA revealed no main effect of contrast on attention ratios ($p = .63$). These results thus suggest that spatial attention has nearly identical effects on achromatic and chromatic motion processing across a wide range of cone contrasts.

3.1.2. Experiment 1B

Data from Experiment 1B are presented in Fig. 4. Plotted in Fig. 4a are group mean MAE durations for *achromatic*, *chromatic* and *mixed* gratings (all of which produced between 27–30% cone contrast, see Section 2) for both the full-attention (*filled squares*) and poor-attention (*open squares*) conditions ($n = 5$). The results of a 2-factor ANOVA (stimulus type × attention condition) revealed a marginally significant main effect of attention condition ($p = .10$) and there was no significant interaction ($p = .65$), i.e., the attention effect did not vary across the three stimulus types. Group mean attention ratios for the three different conditions are plotted in Fig. 4b. As can be seen in this figure, the attention ratio was highest for the *achromatic* condition, and only for the achromatic condition was the log attention ratio significantly greater than 1.0 (achromatic = 1.31, $p = .014$, chromatic = 1.14, $p = .23$, mixed = 1.13, $p = .20$, one-tailed correlated *t*-tests). We note that the small and insignificant attention effect for the chromatic gratings in Experiment 1B is a bit surprising given that in Experiment 1A chromatic gratings of the same cone contrast (25%) yielded a significant ($p = .046$) and larger (1.44-fold) attention effect (see Fig. 3, *open circles*). We assume that this difference between Experiment 1A and 1B is due to the fact that different subjects participated in the two experiments (as well as due to noise in the data). More importantly, the results of Experiment 1B clearly suggest that attention effects for the mixed condition are no greater than that observed for the chromatic and/or achromatic conditions; if anything, the mixed gratings yielded *smaller* attention effects. This finding is

somewhat contradictory to that observed in our previous study (Thiele et al., 2002). Using a motion nulling paradigm, we found that attention boosted the strength of chromatic motion processing more so for mixed gratings than for isoluminant chromatic gratings. We return to a possible explanation for the discrepancy between studies in Section 4.

3.2. Experiment 2: Effects of salience

3.2.1. Experiment 2A

Group mean MAE durations from Experiment 2A, in which salience differences between the stripes of the moving grating were created by keeping the grating stimulus the same but varying the background color, are presented in Fig. 5 ($n = 4$). Plotted are data for (A) *achromatic* gratings and (B) *chromatic* (red/green) gratings, at three different cone contrasts (4.3%, 10.4% and 25%), for both the enhanced salience (*filled squares, solid curve*) and isosalience (*open squares, dashed curve*) conditions (see Section 2 and Table 1 for details of stimulus conditions). Because the data for the two different "enhanced salience-chromatic" conditions (R > G and G > R) were not significantly different from one another ($p = .28$), data for the two were collapsed into one "enhanced salience-chromatic" condition. The results of a 2-factor ANOVA (salience condition × contrast) revealed no effects of salience condition for either chromatic gratings ($p = .63$) or achromatic gratings ($p = .13$). In fact, for achromatic gratings, there was a trend for results in the direction opposite to that predicted, i.e., MAE duration was slightly longer in the isosalience condition.

With regard to *contrast effects*, only for the chromatic data did MAE duration vary significantly with contrast (*chromatic:* $p = .006$; *achromatic,* $p = .68$). This effect of contrast for the chromatic condition was driven by the decrease in MAE duration at the highest cone contrast

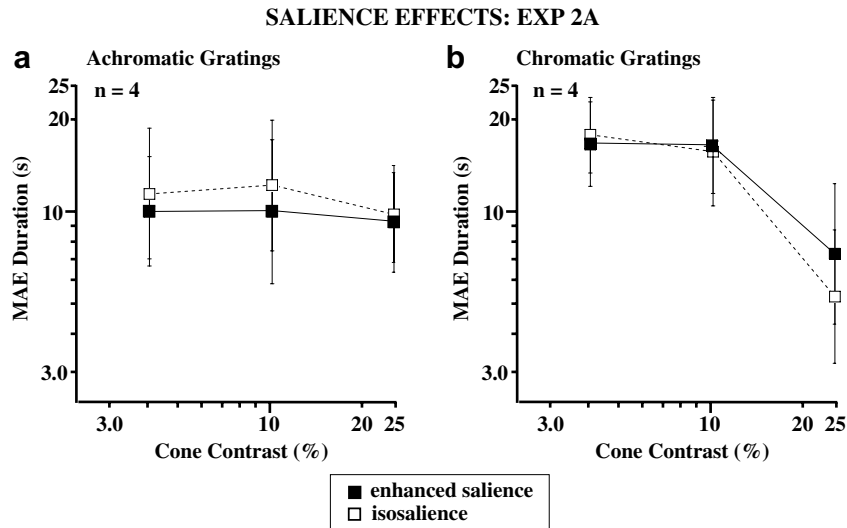**SALIENCE EFFECTS: EXP 2A**

Fig. 5. Salience effects: Experiment 2A. Group mean MAE duration data plotted as a function of contrast for (a) achromatic gratings and (b) chromatic gratings. Data are shown for both the enhanced salience (*filled squares, solid curve*) and isosalience (*open squares, dashed curve*) conditions. For chromatic gratings, there was a clear decrease in MAE duration at high contrast. Error bars denote standard errors of the means.

tested, 25%, which mirrors the trend observed in the chromatic data of Experiment 1A (see Fig. 2). This adverse effect of increasing chromatic contrast is reminiscent of previous results demonstrating that adding chromatic contrast to a moving achromatic grating slows perceived motion (Cavanagh et al., 1984) and lessens the effectiveness of the MAE (Cavanagh & Favreau, 1985). These previous findings and those of the current study might be explained by greater contribution of color-opponent mechanisms at high chromatic contrast, since color-opponent mechanisms have been suggested to hamper motion correspondence because of potential mismatches between color selectivity of inputs to motion detectors (see Derrington & Badcock, 1985 for discussion).

In sum, the data from Experiment 2A demonstrate small and insignificant salience effects on MAE duration across a wide range of cone contrasts. One could argue that this null result reflects a failure to create a strong enough salience cue rather than a failure to show effects of salience on motion *per se*. However, it was our subjective impression, as well as that of our subjects, that placing red/green gratings on a green or red background did, in fact, create a clear salience difference between the red and green stripes. Still, our null result is surprising given that Lu et al. (1999a, 1999b) have previously employed a similar manipulation to create a salience difference between the stripes in a chromatic grating and reported positive findings, i.e., increased motion strength. There are at least two reasons for the differences between the Lu et al. results and ours. First, Lu et al. used subjective ratings of motion strength, while we used MAE duration to quantify motion strength. It may be that our MAE duration paradigm is either too noisy to pick up salience effects, or that salience effects, by virtue of working at a higher-level, do not affect the MAE, which presumably

relies on low-level motion mechanisms. The second possibility concerns an obvious stimulus difference between the two studies; our Experiment 2A kept the grating stimulus constant and changed the background, while Lu et al. kept the background constant and changed the grating stimulus. To address whether this stimulus difference could explain the different results between the two studies, Experiment 2B was conducted.

3.2.2. Experiment 2B

In this experiment, we compared the MAE duration produced by isosalient red/green gratings (25% cone contrast) on a yellow background (R = G) with two different enhanced salience conditions (see Section 2 and Table 1). One enhanced salience condition used red/green gratings (25% cone contrast) on a green background (i.e., R > G, as in Experiment 2A), the other used red/yellow gratings (14.8% cone contrast) on a yellow background (R > Y, modeled after Lu et al., 1999b). Group mean MAE durations from this experiment are presented in Fig. 6 ($n = 5$). The results from this experiment revealed no difference in MAE duration between the R > G and R = G conditions ($p = .48$, one-tailed correlated t-test), thus confirming the results of Experiment 2A. By contrast, the MAE duration in the R > Y condition was significantly longer (on average, by 1.24-fold) than that in the R = G condition ($p = .01$, one-tailed correlated t-test).

To more directly examine the influence of salience on MAE duration in Experiments 2A and 2B, for each subject we obtained a salience ratio, MAE duration in the enhanced salience condition divided by that in the isosalience condition, and then averaged across subjects. Group mean salience ratios are plotted in Fig. 7 as a function of cone contrast, for achromatic gratings (Experiment 2A, D > L condition; *open squares*) and red/green chromatic
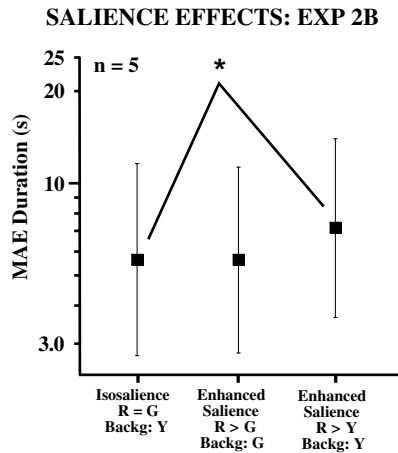
Fig. 6. Salience effects: Experiment 2B. Group mean MAE duration data plotted for three conditions: Isosalience (R = G), enhanced salience (R > G) and enhanced salience (R > Y). The R = G and R > G stimuli were identical to those used in Experiment 2A. The R > Y condition was modeled after the stimulus conditions of Lu et al. (1999a, 1999b). MAE duration was significantly longer (1.24-fold) in the R > Y condition as compared to the R = G condition (∗). Error bars denote standard errors of the means.
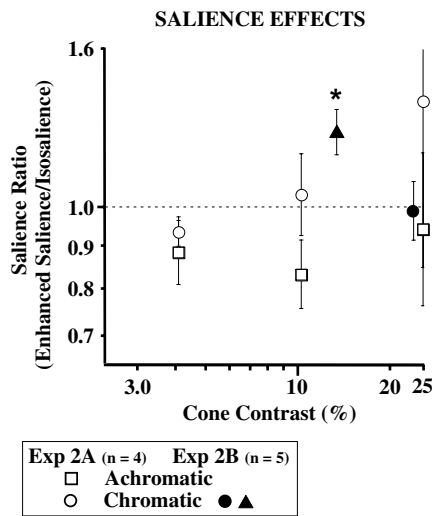

Fig. 7. Salience Ratios from Experiment 2A and 2B. Group mean salience ratios (enhanced salience divided by isosalience) plotted as a function of cone contrast, for achromatic gratings (Experiment 2A, D > L condition; *open squares*) and red/green chromatic gratings (Experiment 2A, R > G and G > R conditions combined; *open circles*, Experiment 2B, R > G condition; *filled circle*). The *filled triangle* represents the salience ratio for the R > Y chromatic grating condition of Experiment 2B, modeled after Lu et al. (1999a, 1999b). Note that the contrast at which this R > Y data point is plotted (14.8%) is somewhat arbitrary, since the cone contrast of the red/yellow grating in the enhanced salience condition was 14.8%, while that of the red/green grating in the isosalience condition was 25%. We address the relevance of this difference in cone contrast in Section 4. Values greater than 1.0 reflect longer MAE durations for conditions of enhanced salience. Significant salience effects were found only for the R > Y stimulus condition of Lu et al. (∗). Error bars denote standard errors of the means.

gratings (Experiment 2A, R > G and G > R conditions combined; *open circles*, Experiment 2B, R > G condition; *filled circle*). The *filled triangle* represents the salience ratio

for the R > Y chromatic grating condition of Experiment 2B, modeled after Lu et al. As would be expected based on the MAE data presented in Figs. 5 and 6, the salience ratio was significantly above 1.0 only when enhanced salience was created in the R > Y condition. These results show that our MAE duration paradigm is sensitive enough to measure the effects reported by Lu et al. What remains to be explained, however, is the discrepancy in results for the case where salience is manipulated by changing only the background versus changing only the grating stimulus, which we address in Section 4.

4. Discussion

The results of our study demonstrate equal effects of spatial attention on chromatic and achromatic motion processing (assessed by measuring the duration of the motion after-effect, MAE), and the attention effects are relatively constant across a wide range of cone contrasts (3.22 – 25%). In this discussion, we first address the psychophysical evidence for chromatic motion processing being mediated, at least in part, by low-level motion mechanisms, as well as discuss potential neural substrates. Second, we discuss whether chromatic motion processing relies more on attentional mechanisms than does achromatic motion processing. We argue that while featural attention may favor chromatic motion, spatial attention does not. Third, we discuss whether salience cues affect chromatic motion processing, addressing the discrepancy between results obtained in the current versus previous studies.

4.1. Evidence for mediation of chromatic motion processing by low-level mechanisms

As discussed in Section 1, because the MAE is thought to be mediated by adaptation in low-level motion mechanisms, the finding that moving chromatic gratings produce an MAE (observed in the current and previous studies) suggests mediation by low-level mechanisms. There are several reasons to believe that the MAE reflects low-level motion processes. First, in the MAE paradigm, subjects passively view the moving adaptation stimulus (i.e., there is no task), and thus the motion of this stimulus is unlikely to be processed by higher-level attentive tracking mechanisms. This is in contrast to motion paradigms that require subjects to actively report the direction of a moving stimulus; here, it is far more likely that attentive tracking mechanisms are involved. Second, monkey neurophysiological studies in area MT, which is considered a low-level motion area, have demonstrated adaptation effects that are likely to underlie the MAE (Van Wezel & Britten, 2002; Kohn & Movshon, 2003; Krekelberg, Boynton, & van Wezel, 2006; see Krekelberg, van Wezel, & Albright, 2006 for review). To some extent, the MAE may, in fact, originate as early as in primary visual cortex (V1), which feeds area MT. This notion is supported by the lack of spatial transfer of adaptation at the scale of an MT receptive field (Kohn &

Movshon, 2003). Although the above-mentioned adaptation studies in MT employed achromatic stimuli, it is likely that moving chromatic stimuli would produce the same pattern of results, since it is well documented that area MT neurons respond to moving chromatic stimuli (see Dobkins & Albright, 2003 for review).

The current study demonstrated significant chromatic MAEs (i.e., MAE durations significantly greater than 0 s) when subjects ignored the adapting motion stimulus because they were required to perform an RSVP task at the center of gaze. This finding in the poor-attention condition is in line with that of our previous study (Thiele et al., 2002), which measured the strength of chromatic motion using an equivalent luminance contrast (EqLC) motion nulling paradigm and demonstrated strong chromatic motion processing in the poor-attention condition. These previous and current findings of substantial chromatic motion processing in the near absence of spatial attention thus support the notion that chromatic motion is mediated, at least in part, by low-level (pre-attentive) mechanisms.

In another one of our previous studies, which examined the effects of spatial attention on the duration of the achromatic MAE only (Rezec et al., 2004), like the current study, we found constant effects of attention across a wide range of contrasts (3% – 80%). We accounted for these results by proposing that attention directly enhances adaptation, by a mechanism we referred to as "adaptation gain". Specifically, our results suggested that attending to an adapting motion stimulus shifts the C_{50} of the contrast response function of directionally selective mechanisms roughly 1.4-fold more to the right than does ignoring that same stimulus. Note that because attention effects were observed even at contrasts where MAE duration had asymptoted (seen in both the current and previous study), the results reject an alternative hypothesis supposing that attention increases effective contrast, which in turn, leads to greater adaptation effects (see Ling & Carrasco, 2006). The results of the current study, which show constant effects of attention across contrast for both chromatic and achromatic stimuli, therefore suggest that adaptation gain mechanisms exist, and are of equal magnitude, for both chromatic and achromatic motion.

On a related note, there is reason to believe that the low-level mechanisms involved in processing chromatic motion overlap with those involved in processing achromatic motion. As described in Section 1, this notion comes from psychophysical studies showing cross-adaptation effects in the MAE paradigm between chromatic and achromatic gratings and from studies showing that performance on chromatic motion, but not on chromatic detection, tasks is impaired when chromatic stimuli are masked by achromatic noise. We would further suggest that the finding of equal effects of attention on chromatic and achromatic motion observed in the current study is also consistent with the notion of a common mechanism for the two.

With regard to potential neural substrates for a common mechanism, we have in the past argued that the signals for both chromatic and achromatic motion processing may originate within the magnocellular (M) subcortical division of the visual system (Dobkins & Albright, 1994; Thiele, Dobkins, & Albright, 1999). This argument is based on the finding that M neurons respond to both red/green chromatic and achromatic contrast (although they are more sensitive to the latter, see Lee, Martin, & Valberg, 1989b; Lee, Pokorny, Smith, Martin, & Valberg, 1990; Lee, Martin, Valberg, & Kremers, 1993), in conjunction with the fact that the M division is known to provide strong input to motion area MT (Maunsell, Nealey, & DePriest, 1990). The red/green chromatic response in M neurons has been attributed to a non-linearity in, and/or phase shifts between, the L- and M-cone inputs to this pathway (Lee, Martin, & Valberg, 1989a; Stromeyer, Kronauer, Ryu, Chaparro, & Eskew, 1995). However, neurons of the parvocellular (P) subcortical division also respond to both red/green chromatic and achromatic contrast (although they are more sensitive to the former, see Lee et al., 1989b; Lee et al., 1990; Lee et al., 1993). And, recently, it has been demonstrated that the P division may supply substantial input to motion processing areas like MT (see Nassi, Lyon, & Callaway, 2006). This leaves open the possibility that the neural substrate for the common mechanism for chromatic and achromatic motion processing originates within the P division. An alternative possibility is that the common mechanism is created within MT itself, with the P division providing the chromatic signal, and the M division providing the achromatic signal.

4.2. Does attention favor chromatic motion processing?

Although our current and previous studies have shown that spatial attention affects chromatic and achromatic motion processing equally, results from other studies suggest that chromatic motion might rely more on *feature* attention than does achromatic motion. Using the "opposed motion stimulus", Cavanagh (1992) showed that subjects were much better at attentively tracking the position of a red or green stripe in the moving chromatic grating than a light or dark stripe in the moving achromatic grating, even when the achromatic grating dominated the global motion percept. Such findings suggest that attentional tracking of selected features favors chromatic stimuli. In a similar vein, Blaser et al. (1999) showed that the strength of the motion percept produced by a chromatic grating is significantly increased by having subjects simply attend to a feature, namely one of the two colors (red or green) of the grating. These authors explained their results by suggesting that attention increases the salience of the attended feature, creating a salience difference between the stripes in the grating, which is then used to establish motion correspondence by a "feature-salience" mechanism (sometimes referred to as a third-order motion mechanism, see Lu & Sperling, 2001).

The degree to which chromatic motion processing relies on feature tracking is likely to depend on how trackable the chromatic stimulus is (see Section 1) as well as the task at hand (i.e., a task that requires reporting direction is more likely to invoke tracking mechanisms than is the MAE paradigm where subjects passively view and adapt to a moving stimulus). Differences in task might account for the discrepant results obtained with *mixed* gratings in the current study versus our previous study (Thiele et al., 2002). In Experiment 1B of the current study, we observed equal effects of spatial attention on all three stimulus types; chromatic, achromatic and mixed moving gratings. This result is not surprising given that chromatic and achromatic motion are processed by a common mechanism. However, in Thiele et al., which employed an EqLC motion nulling task (see above), we found that attention boosted chromatic motion strength more so for mixed gratings than for isoluminant chromatic gratings or achromatic gratings. As discussed in Thiele et al., this could arise from subjects using attentive feature tracking to report direction in the EqLC task, in conjunction with the possibility that mixed stimuli are particularly easy to track. Tracking would not be expected in the current study, where subjects passively viewed the adapting motion stimulus.

In sum, the results of the current and previous studies suggest that while attentive tracking may favor chromatic motion (and perhaps even more so when chromatic stimuli contain luminance contrast), *spatial* attention amplifies motion signals in a cue-invariant fashion.

4.3. Effects of salience cues on chromatic motion processing

As described above, Blaser et al. (1999) hypothesized that attending to red in a moving red/green grating increases the salience of the red stripes, thus creating a salience difference between the red and green stripes that can be used as a correspondence cue within a "feature-salience" motion mechanism. In addition to creating "top–down" salience differences, in a different set of studies this research group created salience differences in a "bottom–up" fashion, by making one of the two colors in a chromatic grating appear as foreground and thus have higher salience (Lu et al., 1999a, 1999b). To test bottom–up salience effects, they compared subjective ratings of motion strength between two conditions: *Isosalience* Red/green chromatic gratings presented on a grey background. *Enhanced salience* Red/grey gratings presented on the same grey background. Lu et al. reported that perceived motion strength was greater in the enhanced salience condition, which they attributed to this condition providing a strong bottom–up signal to their proposed feature-salience mechanism.

In the current MAE study, we likewise investigated the possible effects of salience by making one of the two colors in the chromatic grating appear as foreground and thus have higher salience. We created enhanced salience condi-

tions in two ways. (1) We kept the red/green grating unaltered, but replaced the yellow background with the color of either the green or red stripes, referred to as 'R > G' or 'G > R'. This salience manipulation did not affect the duration of the MAE (see salience ratios in Fig. 7, *open and filled circles*). (2) Following Lu et al. (1999a, 1999b), we changed the red/green grating stimulus, replacing the green stripes with the yellow background, which produced red/yellow gratings on a yellow background, referred to as 'R > Y'. In this R > Y condition, we replicated Lu et al. by finding stronger MAEs (see Fig. 7, *filled triangle*). If salience—defined as the propensity of a feature to be associated with the foreground—determined the motion strength of these stimuli, then *both* the R > Y and the R > G enhanced salience conditions should have yielded a stronger motion signal, and hence longer MAE duration, than the isosalience condition (R = G).

We believe there might be a simple explanation for the different findings. In the conditions corresponding to those of Lu et al., the cone contrast produced by the red/yellow gratings in the enhanced salience condition (R > Y) will necessarily be substantially lower than that produced by the red/green gratings in the isosalience condition (R = G). In the current study, the cone contrast for the two gratings was 25% and 14.8%, respectively. While a larger cone contrast might be expected to produce a greater motion signal, our chromatic MAE data reveal the opposite trend. That is, MAE durations were found to decrease at cone contrasts past $\sim$10% (see Figs. 2 and 5). This adverse effect of higher chromatic contrast could explain why enhanced salience gratings (R > Y) produced a stronger MAE than isosalience (R = G) gratings. In other words, the strength of the motion signal in the R > Y condition increased not because of a salience difference between the red and yellow stripes, but because the cone contrast of the grating was reduced to a value that is more optimal for chromatic motion processing. This contrast explanation for the positive results obtained in the R > Y condition, in conjunction with the null results obtained in the R > G and G > R conditions, leads us to suggest that bottom–up salience cues do not alter the strength of motion signals within low-level chromatic motion mechanisms. This need not challenge the existence of a feature-salience mechanism, *per se*; it may be that such a mechanism receives only top–down inputs, and/or that this mechanism exists at a relatively high level of motion processing (i.e., past the level that mediates motion adaptation effects).

In conclusion, the psychophysical data of the current study show that attention increases the motion aftereffect duration equally (by about a factor of 1.4) for both chromatic and achromatic stimuli, and that the effect is independent of contrast. Such findings suggest that chromatic motion processing is not affected disproportionally by higher-level spatial attention mechanisms. Our salience studies suggest negligible effects of salience on the strength

of motion signals within low-level motion mechanisms, for either chromatic or achromatic motion.

Acknowledgments

References

Blaser, E., Sperling, G., & Lu, Z. L. (1999). Measuring the amplification of attention. *Proceedings of the National Academy of Sciences of the United States of America, 96*(20), 11681–11686.

Cavanagh, P. (1992). Attention-based motion perception. *Science, 257*(5076), 1563–1565.

Cavanagh, P., & Favreau, O. E. (1985). Color and luminance share a common motion pathway. *Vision Research, 25*(11), 1595–1601.

Cavanagh, P., Tyler, C. W., & Favreau, O. E. (1984). Perceived velocity of moving chromatic gratings. *Journal of the Optical Society of America [a], 1*(8), 893–899.

Chaparro, A., Stromeyer, C. F. I., Huang, E. P., Kronauer, R. E., & Eskew, R. T. J. (1993). Colour is what the eye sees best. *Nature, 361*(6410), 348–350.

Chaudhuri, A. (1990). Modulation of the motion aftereffect by selective attention. *Nature, 344*(6261), 60–62.

Cropper, S. J. (2005). The detection of motion in chromatic stimuli: first-order and second-order spatial structure. *Vision Research, 45*(7), 865–880.

Cropper, S. J., & Hammett, S. T. (1997). Adaptation to motion of a second-order pattern: the motion aftereffect is not a general result. *Vision Research, 37*(16), 2247–2259.

Cropper, S. J., & Wuerger, S. M. (2005). The perception of motion in chromatic stimuli. *Behavioral and Cognitive Neurosciences Reviews, 4*(3), 1–26.

Derrington, A. M., & Badcock, D. R. (1985). The low level motion system has both chromatic and luminance inputs. *Vision Research, 25*(12), 1879–1884.

Dobkins, K. R., & Albright, T. D. (1994). What happens if it changes color when it moves?: The nature of chromatic input to macaque visual area MT. *The Journal of Neuroscience, 14*(8), 4854–4870.

Dobkins, K. R., & Albright, T. D. (2003). Merging processing streams: color cues for motion detection and interpretation. In L. Chalupa & J. S. Werner (Eds.), *The Visual Neurosciences* (pp. 1217–1228). Cambridge: MIT Press.

Dobkins, K. R., & Bosworth, R. G. (2001). Effects of set-size and selective spatial attention on motion processing. *Vision Research, 41*, 1501–1517.

Dobkins, K. R., & Teller, D. Y. (1996). Infant motion:detection (M:D) ratios for chromatic-defined and luminance-defined moving stimuli. *Vision Research, 36*(20), 3293–3310.

Eisner, A., & Macleod, D. I. (1981). Flicker photometric study of chromatic adaptation: selective suppression of cone inputs by colored backgrounds. *Journal of the Optical Society of America, 71*(6), 705–718.

Gegenfurtner, K. R., & Hawken, M. J. (1996a). Interaction of motion and color in the visual pathways. *Trends in Neurosciences, 19*(9), 394–401.

Gegenfurtner, K. R., & Hawken, M. J. (1996b). Perceived velocity of luminance, chromatic and non-Fourier stimuli: Influence of contrast and temporal frequency. *Vision Research, 36*(9).

Gunther, K. L., & Dobkins, K. R. (2002). Individual differences in chromatic (red/green) contrast sensitivity are constrained by the relative number of L- versus M-cones in the eye. *Vision Research, 42*(11), 1367–1378.

Hawken, M. J., Gegenfurtner, K. R., & Tang, C. (1994). Contrast dependence of colour and luminance motion mechanisms in human vision. *Nature, 367*(6460), 268–270.

Kohn, A., & Movshon, J. A. (2003). Neuronal adaptation to visual motion in area MT of the macaque. *Neuron, 39*(4), 681–691.

Krekelberg, B., Boynton, G. M., & van Wezel, R. J. (2006). Adaptation: from single cells to BOLD signals. *Trends in Neuroscience, 29*(5), 250–256.

Krekelberg, B., van Wezel, R. J., & Albright, T. D. (2006). Adaptation in Macaque MT reduces perceived speed and improves speed discrimination. *Journal of Neurophysiology, 95*, 255–270.

Lankheet, M. J. M., & Verstraten, F. A. J. (1995). Attentional modulation of adaptation to two-component transparent motion. *Vision Research, 35*(10), 1401–1412.

Lee, B. B., Martin, P. R., & Valberg, A. (1989a). Nonlinear summation of M- and L-cone inputs to phasic retinal ganglion cells of the macaque. *Journal of Neuroscience, 9*(4), 1433–1442.

Lee, B. B., Martin, P. R., & Valberg, A. (1989b). Sensitivity of macaque retinal ganglion cells to chromatic and luminance flicker. *Journal of Physiology (London), 414*, 223–243.

Lee, B. B., Martin, P. R., Valberg, A., & Kremers, J. (1993). Physiological mechanisms underlying psychophysical sensitivity to combined luminance and chromatic modulation. *Journal of the Optical Society of America [a], 10*(6), 1403–1412.

Lee, B. B., Pokorny, J., Smith, V. C., Martin, P. R., & Valberg, A. (1990). Luminance and chromatic modulation sensitivity of macaque ganglion cells and human observers. *Journal of the Optical Society of America [a], 7*(12), 2223–2236.

Lennie, P., & D'Zmura, M. (1988). Mechanisms of color vision. *Critical Reviews in Neurobiology, 3*, 333–400.

Ling, S., & Carrasco, M. (2006). When sustained attention impairs perception. *Nature Neuroscience, 9*, 1243–1245.

Lu, Z. L., Lesmes, L. A., & Sperling, G. (1999a). The mechanism of isoluminant chromatic motion perception [see comments]. *Proceedings of the National Academy of Sciences of the United States of America, 96*(14), 8289–8294.

Lu, Z. L., Lesmes, L. A., & Sperling, G. (1999b). Perceptual motion standstill in rapidly moving chromatic displays. *Proceedings of the National Academy of Sciences of the United States of America, 96*(26), 15374–15379.

Lu, Z. L., & Sperling, G. (2001). Three-systems theory of human visual motion perception: review and update. *Journal of the Optical Society of America A Optical, Image Science, and Vision, 18*(9), 2331–2370.

MacLeod, D. I., & Boynton, R. M. (1979). Chromaticity diagram showing cone excitation by stimuli of equal luminance. *Journal of the Optical Society of America, 69*(8), 1183–1186.

Maunsell, J. H., Nealey, T. A., & DePriest, D. D. (1990). Magnocellular and parvocellular contributions to responses in the middle temporal visual area (MT) of the macaque monkey. *Journal of Neuroscience, 10*(10), 3323–3334.

Moreland, J. D. (1982). Spectral sensitivity measured by motion photometry. *Documenta Ohthalmologica Proceedings Series, 33*, 61–66.

Mullen, K. T. (1985). The contrast sensitivity of human colour vision to red–green and blue–yellow chromatic gratings. *Journal of Physiology (Lond), 359*, 381–400.

Mullen, K. T., & Baker, C. J. (1985). A motion aftereffect from an isoluminant stimulus. *Vision Research, 25*(5), 685–688.

Mullen, K. T., Yoshizawa, T., & Baker, C. L. Jr., (2003). Luminance mechanisms mediate the motion of red–green isoluminant gratings: the role of "temporal chromatic aberration. *Vision Research, 43*(11), 1235–1247.

Nassi, J. J., Lyon, D. C., & Callaway, E. M. (2006). The parvocellular LGN provides a robust disynaptic input to the visual motion area MT. *Neuron, 50*(2), 319–327.

Nishida, S. y., Ashida, H., & Sato, T. (1997). Contrast dependencies of two types of motion aftereffect. *Vision Research, 37*(5), 553–563.

Pantle, A. (1998). How do measures of the motion after-effect measure up? In G. Mather, F. Verstraten, & S. Anstis (Eds.), *The motion aftereffect: A modern perspective* (pp. 25–39). Cambridge, MA: MIT Press.

Rezec, A., Krekelberg, B., & Dobkins, K. R. (2004). Attention enhances adaptability: evidence from motion adaptation experiments. *Vision Res, 44*(26), 3035–3044.

Shulman, G. L. (1993). Attentional effects of adaptation of rotary motion in the plane. *Perception, 22*(8), 947–961.

Stockman, A., & Sharpe, L. T. (2000). The spectral sensitivities of the middle- and long-wavelength-sensitive cones derived from measurements in observers of known genotype. *Vision Res, 40*(13), 1711–1737.

Stromeyer, C. F. I., Chaparro, A., Tolias, A. S., & Kronauer, R. E. (1997). Colour adaptation modifies the long-wave versus middle-wave cone weights and temporal phases in human luminance (but not red–green) mechanism. *Journal of Physiology (London), 499*(Pt. 1), 227–254.

Stromeyer, C. F., III., Kronauer, R. E., Ryu, A., Chaparro, A., & Eskew, R. T. J. (1995). Contributions of human long-wave and middle-wave cones to motion detection. *Journal of Physiology (London), 485*(Pt 1), 221–243.

Thiele, A., Dobkins, K. R., & Albright, T. D. (1999). The contribution of color to motion processing in MT. *Journal of Neuroscience, 19*(15), 6571–6587.

Thiele, A., Rezec, A. A., & Dobkins, K. R. (2002). Chromatic input to motion processing in the absence of attention. *Vision Research, 42*(11), 1395–1401.

Thompson, I. D., Kossut, M., & Blakemore, C. (1983). Development of orientation columns in cat striate cortex revealed by 2-deoxyglucose autoradiography. *Nature, 301*(5902), 712–715.

Tootell, R. B., Reppas, J. B., Dale, A. M., Look, R. B., Sereno, M. I., Malach, R., et al. (1995). Visual motion aftereffect in human cortical area MT revealed by functional magnetic resonance imaging [see comments]. *Nature, 375*(6527), 139–141.

van der Smagt, M. J., & Stoner, G. R. (2002). Context and the motion aftereffect: occlusion cues in the test pattern alter perceived direction. *Perception, 31*(1), 39–50.

Van Wezel, R. J., & Britten, K. H. (2002). Motion adaptation in area MT. *Journal of Neurophysiology, 88*(6), 3469–3476.

Webster, W. R., Day, R. H., & Cassell, J. F. (1992). Two movement aftereffects: evidence for luminance- and color-movement pathways. *Vision Research, 32*(11), 2187–2189.

Yoshizawa, T., Mullen, K. T., & Baker, C. L. Jr., (2003). Failure of signed chromatic apparent motion with luminance masking. *Vision Research, 43*(7), 751–759.