Dorsal Stream Contributions to Perceptual Asymmetries

Nicole A. Thomas,[1] Oliver Schneider,[2] Carl Gutwin,[3] AND Lorin J. Elias[4]

[1]School of Psychology, Flinders University, Adelaide, Australia
[2]Department of Computer Science, University of British Colombia, Vancouver, British Columbia
[3]Department of Computer Science, University of Saskatchewan, Saskatoon, Saskatchewan
[4]Department of Psychology, University of Saskatchewan, Saskatoon, Saskatchewan

Abstract

Neurologically normal individuals show a bias toward the left side of space, referred to as pseudoneglect due to its similarity to clinical hemispatial neglect. The left bias appears to be stronger in the lower visual field during free-viewing, which could result from preferential dorsal stream processing. The current experiments used modified greyscales tasks, incorporating motion and isoluminant color, to explore whether targeting dorsal or ventral stream processing influenced the strength of the left bias. It was expected that the left bias would be stronger on the motion task than on a task incorporating isoluminant color. In Study 1, similar left biases were observed during prolonged viewing for luminance, motion and red, but not green color. The unexpected finding of a leftward bias for red under prolonged viewing was replicated in Study 2. A leftward bias for motion was also evident during 150 ms viewing in Study 2. In Study 3, the left bias was not apparent when using a blue/yellow condition, suggesting the left bias for red under prolonged viewing was likely unique to red. Furthermore, the leftward bias for red disappeared under brief viewing conditions. It is suggested that dorsal stream processing likely underlies visual field differences in pseudoneglect. (*JINS*, 2011, *18*, 1–9)

Keywords: Visuospatial attention, Global motion, Isoluminant color, Presentation time, Pseudoneglect

INTRODUCTION

Neurologically normal individuals demonstrate a leftward spatial bias, referred to as pseudoneglect due to its similarity to hemispatial neglect (Bowers & Heilman, 1980; Jewell & McCourt, 2000; McCourt & Jewell, 1999). On manual line bisection, participants use a stylus to bisect lines and typically show a bias to the left of center (Luh, 1995). On perceptual line bisection, participants view pre-transected lines and tend to indicate the transection mark is located to the left of centre (e.g., McCourt & Jewell, 1999). Another method of examining pseudoneglect is the greyscales task (Nicholls, Bradshaw, & Mattingley, 1999), where participants view a pair of mirror-reversed luminance gradients. Each rectangle is dark on one side and gradually becomes brighter on the opposing side. Although the images are equiluminant, participants tend to select the image that is dark on the left as being darker overall.

The strength of the leftward attentional bias varies in the upper and lower visual fields. On a tachistoscopic perceptual line bisection task, participants viewed lines presented at 3.6° and 5.8° visual angle above or below the midline and showed a stronger left bias when lines were in the upper visual field (UVF; McCourt & Garlinghouse, 2000; McCourt & Jewell, 1999). In contrast, Barrett, Crosson, Crucian, and Heilman (2000) used free-viewing manual line bisection at 40.5 cm either above or below the horizontal plane and found a stronger left bias in the lower visual field (LVF). Using a free-viewing greyscales task, Thomas and Elias (2010) also found a stronger leftward bias in the LVF.

As prior research was methodologically different, Thomas and Elias (2011) examined the influence of presentation time on visual field differences on the greyscales task. They found an interaction consistent with prior results wherein a stronger left bias occurred in the UVF during 150-ms presentation and in the LVF during free-viewing. This suggests processing differences influence the strength of the left bias differently in the upper and lower visual fields (Thomas & Elias, 2011).

Thomas and Elias (2010b) further examined spatial location by using a greyscales task wherein one rectangle in each pair was shifted toward the left or the right side. Although one might expect the leftward bias to be stronger for all left-shifted images, this was only true for images in the LVF. Thomas and Elias (2010b) conducted another study to examine whether object-based coordinates would be more dominant if actual objects were used. Participants viewed pairs of everyday objects with

opposing directions of luminosity and chose which appeared to be brighter. Objects were located diagonally from one another, in the top right and lower left, or top left and lower right quadrants. Again a strong LVF bias occurred as significant leftward biases were seen for all conditions where the LVF image exhibited at least one leftward characteristic (brighter on the left or located on the left). When the LVF image was lit from the right and located on the right no significant bias was seen, suggesting that the LVF bias is quite dominant and mediates the bias toward the left.

Visual field differences have been consistently observed for various tasks, with most showing a LVF performance advantage. For example, the LVF has better attentional resolution (He, Cavanagh, & Intriligator, 1996), is advantaged in motion processing and displays superior contrast sensitivity at low spatial frequencies (see Christman & Niebauer, 1997, for review). It has also been shown that the lower and left visual fields show similar advantages, whereas the upper and right visual fields are related (Christman & Niebauer, 1997). As a similar relation is seen in hemispatial neglect where neglect is most pronounced in the lower and left visual fields (Rubens, 1985), a better understanding of visual field differences in pseudoneglect would benefit both clinical and healthy populations.

The left bias appears to result from right hemisphere posterior parietal cortex activation during visuospatial attention, with attention being preferentially directed toward the left (Corbetta, Shulman, Miezin, & Petersen, 1995; Niemeier, Stojanoski, Singh, & Chu, 2008; Posner & Rothbart, 2007). Neuroimaging data support this, as proposed visuospatial attention networks are more activated by left visual field information (Siman-Tov et al., 2007) and the right hemisphere shows more activation during line bisection and landmark tasks (Bjoertomt, Cowey, & Walsh, 2002; Çiçek, Deouell, & Knight, 2009; Fink et al., 2000; Fink, Marshall, Weiss, & Zilles, 2001; Foxe, McCourt, & Javitt, 2003). Although this explanation has received much support, it cannot explain why upper and lower visual field differences occur.

Previc (1990, 1998) proposed that, from an evolutionary perspective, stimuli in the UVF are more likely to be located in extrapersonal space, whereas those in the LVF are more likely to be in peripersonal space. When stimuli in extrapersonal space are brought into peripersonal space, a similar transition from the UVF to the LVF occurs. In extrapersonal space, an UVF advantage has been observed for accuracy and reaction time on random dot stereogram discrimination (Previc, Breitmeyer, & Weinstein, 1995) and reaction time on visual search (Previc & Blume, 1993). As performance was most impaired in the lower left quadrant, Previc et al. (1995) suggested the LVF is linked to peripersonal space. Previc (1990, 1998) has further suggested that the LVF and peripersonal space are processed by the dorsal stream, whereas the UVF and extrapersonal space are processed by the ventral stream. Neuroimaging studies partially support this suggestion as greater dorsal stream activity is observed during line bisection in peripersonal space and ventral stream activation is greater when performing in extrapersonal space (Bjoertomt et al., 2002; Weiss et al., 2000).

In addition, lesion studies show differential deficits depending on whether the dorsal or the ventral stream is damaged.

Ventral stream lesions lead to facial and object agnosias (Bauer & Demery, 2003), whereas dorsal stream lesions disrupt spatial localization as in optic ataxia (Perenin & Vighetto, 1988). Of interest, simultanagnosia can result from either dorsal (bilateral occipitoparietal lesions) or ventral (left occipital lesion) stream damage. In dorsal simultanagnosia, patients experience difficulty in spatial localization as they only perceive one object at a time (Bálint & Harvey, 1995; Duncan et al., 2003; Luria, 1959). In contrast, ventral stimultanagnosia patients can perceive several objects, but cannot make sense of an entire scene (Duncan et al., 2003; Kinsbourne & Warrington, 1962). Early primate research (Mishkin, Lewis, & Ungerleider, 1982) and subsequent neuroimaging studies (e.g., Haxby et al., 1991; James, Culham, Humphrey, Milner, & Goodale, 2003; Kastner & Ungerleider, 2000) support the existence of dual visual processing systems.

The dorsal and ventral streams are specialized in performing specific tasks. The dorsal "where" pathway plays a role in action, determining location and processing motion. In contrast, the ventral "what" pathway is involved in object recognition and in processing color and local details (Goodale & Milner, 1992; Livingstone & Hubel, 1988). These processing differences simply indicate relative advantages as the visual streams are only partially segregated beyond the lateral geniculate nucleus and interact with one another as they project to the cortex (Goodale & Westwood, 2004; Nieuwenhuis, Jepma, La Fors, & Olivers, 2008). However, they do provide an initial means of exploring upper and lower visual field differences.

The current study used the greyscales task, and modified greyscales tasks, incorporating either motion or isoluminant color, to examine visual stream processing differences. In modifying the greyscales, the tasks maintained their spatial nature, but each task targeted a particular processing advantage. In doing so, the demands of each task were similar, but it was possible to explore how engaging the dorsal or ventral stream to a greater (or lesser) extent subsequently influenced performance. It has been suggested that the horizontal allocation of visuospatial attention is more influenced by the dorsal than the ventral stream (Drago, Crucian, Pisani, & Heilman, 2006), which would be consistent with a stronger left bias in the LVF (Barrett et al., 2000; Thomas & Elias, 2010a, 2010b, 2011). A strong left bias was expected on the motion task, with a similar but slightly weaker bias on the greyscales task. No significant bias was expected for the isoluminant color task; however, as color information is minimally accessible during guided reaching (White, Kerzel, & Gegenfurtner, 2006), which is a dorsal stream task, a weak left bias might occur.

STUDY 1. GREYSCALES, MOTION, AND RED/GREEN TASKS UNDER PROLONGED VIEWING CONDITIONS

Method

Participants

Eighty-nine undergraduate Psychology students (25 males; $M_{age} = 20.26$; $SD = 4.94$) at the University of Saskatchewan

participated. Students received course credit in exchange for participation. Based upon self-report (Elias, Bryden, & Bulman-Fleming, 1998), eight participants were left-handed and all participants had normal or corrected-to-normal vision. The Behavioral Research Ethics Board at the University of Saskatchewan granted ethical approval and the study was performed in accordance with the ethical standards of the 1964 Declaration of Helsinki.

Materials

An IBM clone computer (PIV 2.6 GHz) interfaced with a 19″ LCD monitor running at 1024 × 768 resolution was used. A chin rest minimized head movement and distance to the screen was 711 mm. A fixation cross preceded each trial and stimulus pairs were presented in the centre of the visual field, one directly above the other. Participants were free to scan the images as all presentations were free-viewing and visible for a maximum of 5 s. Responses were made using the number pad keys 8 and 2. As simple button press responses evoke a minimal amount of motor movement (e.g., McCourt & Olafson, 1997), responses were not confounded by motor biases.

Greyscales task. Greyscale pairs, of 4 different lengths: 132, 154, 176, and 198 mm, were administered using E-prime 1.0 software (Psychology Software Tools, Inc.; www.pstnet.com/E-prime/e-prime.htm). Length was varied to discourage standard response use (Nicholls et al., 1999; Nicholls & Roberts, 2002). Stimuli consisted of mirror-reversed luminance gradients, with one of the images being dark on the left side and the other dark on the right (see Nicholls et al., 1999). Participants identified which image appeared to be more black or more white overall (64 trials of each).

Isoluminant color tasks. Stimuli from the greyscales task were modified to be isoluminant red and green in color (see Figure 1a) by matching red and green color values using the luminance feature in Paint Shop Pro 7.0 (Jasc Software) and then using a Tektronix J6523-2 1° narrow angle luminance probe to match for isoluminance. Stimuli were not subjectively isoluminant as individual differences in isoluminance were not considered. In each pair one image was red on the left and the other was red on the right, with both transitioning to green on the other side. Participants identified which image appeared to be more red or more green overall. E-prime administered 64 trials for each judgment.

Motion Tasks. Stimuli consisted of two uniformly colored rectangles, with pixels of the opposing color moving across them (see Figure 1b for still image). The moving pixels travelled east to west in one rectangle and west to east in the other. Therefore, one rectangle was dark (or bright) on the left and the other on the right. Motion was not entirely uniform as some rogue pixels travelled randomly to avoid having participants follow the motion of any one particular pixel. Participants identified which appeared to be darker for white rectangles with black pixels and which appeared
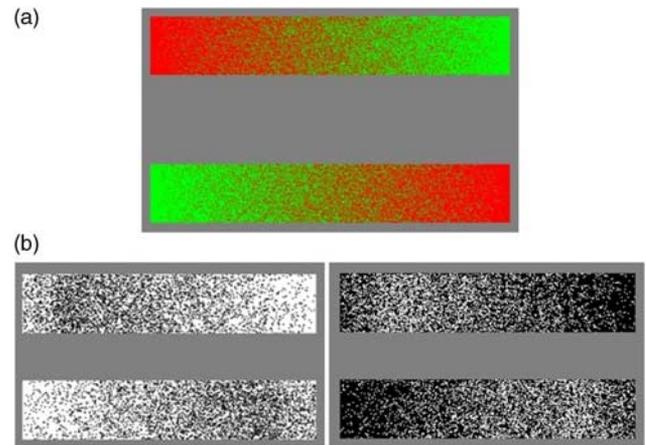

Fig. 1. Sample stimuli from the isoluminant color and the motion tasks. a: Depicts the red-green stimuli. b: Depicts still images of the motion tasks.

to be brighter for black rectangles with white pixels (128 trials each).

Supplementary Materials

To review a video of the motion tasks, please access the online-only supplementary material. Please visit journals.cambridge.org/INS, then click on the link "Supplementary Materials" at this article.

Procedure

Following informed consent, participants completed a demographic questionnaire addressing sex, age, handedness, and visual impairments (Elias et al., 1998). Participants then completed the greyscales, isoluminant color, and motion tasks. Task order was counterbalanced among participants. On each task, participants selected whether the image on the top or bottom of the pair appeared to include the target characteristic (i.e., darker, more red). Responses were scored as leftward when the image with the target characteristic on the left was chosen and as rightward when the image with the target characteristic on the right was chosen. Response bias scores were calculated by subtracting the number of leftward responses from the number of rightward responses and dividing by the total number of trials, with a negative score indicating a leftward bias (Nicholls et al., 1999).

RESULTS

A repeated-measures analysis of variance (ANOVA) was computed using within-subjects variable task (luminance, motion, color) on response bias scores. The main effect of task was not significant, $F(2,176) = 1.704$, $p = .185$, $\eta^2 = .019$. One-sample t tests were used to determine whether significant biases occurred on each task. Significant leftward biases were seen for luminance, $t(88) = -5.156$, $p < .001$, motion, $t(88) = -3.723$, $p < .001$, and color, $t(88) = -4.633$, $p < .001$ (see Figure 2).
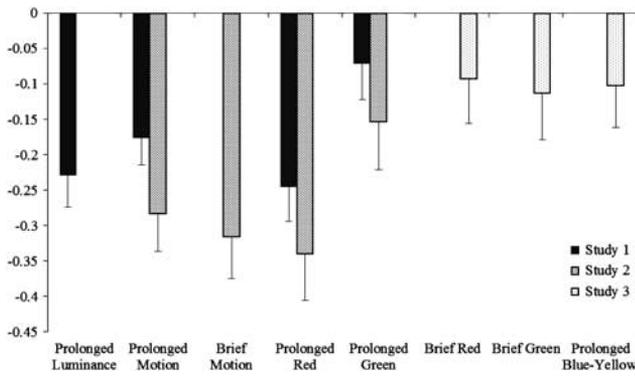
Fig. 2. Mean bias scores in Studies 1, 2, and 3. Errors bars represent the standard error of the mean.

In an effort to better understand why an unexpected bias occurred for color, a paired-samples t test compared bias scores for red and green judgments. The red and green judgments were significantly different from one another, $(t(88) = -3.310, p = .001)$, indicating the two biases were not comparable and should be kept separate. A significant bias was observed for red judgments, $t(88) = -5.026, p < .001$, whereas no bias occurred for green judgments, $t(88) = -1.391, p = .168$.

Paired-samples t tests were used to compare the strength of the bias among the tasks. A significant difference emerged between judgments for green and luminance, $t(88) = 3.539, p = .001$, and for green and motion, $t(88) = 3.065, p = .003$. Both luminance and motion exhibited stronger left biases than green judgments. No significant difference was observed between luminance and motion ($t(88) = .079; p = .937$), or between the red judgments and luminance ($t(88) = -.380; p = .705$), or motion ($t(88) = -1.390; p = .168$).

DISCUSSION

As hypothesized, a leftward bias occurred for motion, illustrating that the bias occurs when dorsal stream processing is preferential. A dorsal processing advantage is consistent with the previously observed LVF bias for visuospatial tasks (Barrett et al., 2000; Thomas & Elias, 2010a, 2010b, 2011). Notably, the bias was similar for luminance and motion, suggesting similar levels of dorsal processing for both tasks. As the greyscales task is assumed to measure visuospatial ability, the spatial nature of the task likely leads to dorsal stream activation, consistent with a dorsal influence on the horizontal allocation of spatial attention (Drago et al., 2006).

Several possible explanations exist for the unexpected findings for red color. To examine visual stream processing differences in pseudoneglect, all tasks had to be spatial. Although the spatial nature of the task might have allowed the bias to emerge, one would expect to see similar biases for red and green if the bias was simply related to this. It is also possible that the red bias was nebulous and, therefore, will not be replicable. If the bias for red is reliable, it remains possible that isoluminant color differs from luminance. Equivalent biases for luminance are observed regardless of

whether the target characteristic is "darker" or "brighter" (Nicholls et al., 1999), whereas "red" and "green" judgments were not equivalent. Furthermore, preferentially engaging the ventral stream during green judgments did not lead to the same bias as did motion.

It has previously been shown that the leftward bias persists with brief presentation (McCourt & Garlinghouse, 2000; McCourt & Jewell, 1999; Thomas & Elias, 2011), suggesting the initial leftward direction of attention influences subsequent visuospatial judgments. If similar neural mechanisms underlie the leftward biases for motion and luminance, the bias for motion should persist during brief presentation. Study 2 replicated the prolonged viewing conditions on the isoluminant color and motion tasks. In addition, the motion task was completed under 150-ms viewing.

STUDY 2: RED/GREEN TASK UNDER PROLONGED VIEWING AND MOTION TASK UNDER BRIEF AND PROLONGED VIEWING CONDITIONS

Method

Participants

Forty-one undergraduate Psychology students (10 males; $M_{age} = 20.15$; $SD = 4.87$) at the University of Saskatchewan participated. Students received course credit in exchange for participation. Based upon self-report (Elias et al., 1998), two participants were left-handed and all participants had normal or corrected-to-normal vision. The Behavioral Research Ethics Board at the University of Saskatchewan granted ethical approval and the study was performed in accordance with the ethical standards of the 1964 Declaration of Helsinki.

Materials

The prolonged motion and isoluminant color tasks were repeated, with the addition of a brief condition for the motion task. The brief condition consisted of 150-ms stimulus presentation, followed by a 5-s maximum response. There were 256 trials for brief motion (128 darker, 128 brighter).

Procedure

Following informed consent, participants completed a demographic questionnaire addressing sex, age, handedness and visual impairments (Elias et al., 1998). Participants then completed the isoluminant color and motion tasks. Task order was counterbalanced among participants, although the motion conditions with differing presentation times were not consecutive. Response bias scores were calculated as in Study 1; however, red and green scores remained separate.

RESULTS

A repeated-measures ANOVA was computed using within-subjects variable task (prolonged motion, brief motion, red,

green) on response bias scores. There was a main effect of task, $F(3,120) = 4.788$, $p = .003$, $\eta^2 = .107$. Pairwise comparisons (with a Bonferroni correction) indicated significant differences between green judgments and both brief motion ($p = .049$), and red judgments ($p = .001$).

One-sample *t* tests were used to determine whether significant biases occurred in each condition (Bonferroni corrected $p = .013$). Significant leftward biases were seen for prolonged motion ($t(40) = -5.294$; $p < .001$), brief motion ($t(40) = -5.238$; $p < .001$), and red judgments ($t(40) = -5.078$; $p < .001$). The bias score for green judgments was not significant, $t(40) = -2.266$; $p = .029$ (see Figure 2).

Paired-samples *t* tests were used to compare the strength of the bias among the tasks. The red and green judgments were significantly different, ($t(40) = -4.078$; $p < .001$). A significant difference also emerged between judgments for green and both prolonged ($t(40) = 2.377$; $p = .022$) and brief motion ($t(40) = 2.787$; $p = .008$). Both motion conditions exhibited stronger left biases than green judgments. No significant differences occurred between red and either prolonged ($t(40) = -1.095$; $p = .280$) or brief motion ($t(40) = -.403$; $p = .689$). The prolonged and brief motion conditions did not differ from one another, ($t(40) = .651$; $p = .519$).

DISCUSSION

Study 1 was replicated as a leftward bias was observed for red judgments, whereas no bias occurred for green. Results from both studies suggest the leftward bias is decreased when the ventral stream is engaged, relative to tasks that preferentially engage the dorsal stream. However, the question of why a bias occurs for red, but not green remains. Of interest, pre-existing associations with the color red potentially influenced the way in which visuospatial attention was directed during red judgments.

The color red is often associated with stop signs, warnings, and errors (e.g., Braun, Sansing, & Silver, 1994; Braun & Silver, 1995; Elliot & Maier, 2007; Elliot, Maier, Moller, Friedman, & Meinhardt, 2007; Mehta & Zhu, 2009; Moller, Elliot, & Maier, 2009), or alternatively, with emotions such as passion and love, or anger (Elliot & Niesta, 2008; Hupka, Zaleski, Otto, Reidl, & Tarabrina 1997; Kaya & Epps, 2004). These associations can lead red to capture attention differently than other colors (Bellizzi & Hite, 1992; Clynes, 1977; Lu & Zhou, 2005; Maier, Barchfeld, Elliot, & Pekrun, 2009; Tchernikov & Fallah, 2010; Wilson, 1966). If pre-existing associations with the color red unknowingly influenced how attention is directed, additional processing time would be required for these associations to be activated and influence spatial judgments. Therefore, the left bias for red judgments should be eliminated during brief viewing when judgments are based on the initial direction of attention. This would suggest that the left bias for red is not the result of ventral stream involvement in the task, but alternatively, the result of how red influences attention.

Therefore, brief presentation was used on the red-green color task to determine if the left bias would be eliminated when processing time was decreased. In addition, isoluminant blue-yellow stimuli were created. The attenuation of the leftward bias on this task would confirm that red attracts attention differently than other colors. No significant biases were expected for either task, which would demonstrate that relatively greater ventral stream involvement decreases the left bias.

STUDY 3: RED/GREEN TASK UNDER BRIEF VIEWING AND BLUE/YELLOW TASK UNDER PROLONGED VIEWING

Method

Participants

Forty undergraduate Psychology students (eight males; $M_{age} = 20.15$; $SD = 3.74$) at the University of Saskatchewan participated. Students received course credit in exchange for participation. Based upon self-report (Elias et al., 1998), four participants were left-handed and all participants had normal or corrected-to-normal vision. The Behavioral Research Ethics Board at the University of Saskatchewan granted ethical approval and the study was performed in accordance with the ethical standards of the 1964 Declaration of Helsinki.

Materials

The red-green color task was used, with each trial consisting of a 150-ms stimulus presentation, followed by a 5-s maximum response.

Blue-Yellow Isoluminant Color Task. Stimuli from the greyscales task were modified to be isoluminant blue and yellow in color (see Figure 3) by matching blue and yellow color values using the luminance feature in Paint Shop Pro 7.0 (Jasc Software) and then using a Tektronix J6523-2 1° narrow angle luminance probe to match for isoluminance. Stimuli were not subjectively isoluminant as individual differences in isoluminance were not considered. In each pair one image was blue on the left and the other was blue on the right, with both transitioning to yellow on the other side. Presentations were free-viewing and visible for a maximum of 5 s. Participants identified which image appeared to be more blue or more yellow overall. E-prime administered 64 trials for each judgment.
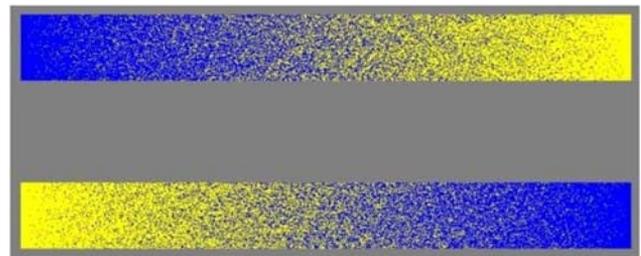

Fig. 3. Sample stimuli from the blue-yellow isoluminant color task.

Procedure

Following informed consent, participants completed a demographic questionnaire addressing sex, age, handedness, and visual impairments (Elias et al., 1998). Participants then completed both tasks in counterbalanced order. Response bias scores were calculated as in Study 1.

RESULTS

One-sample t tests were used to determine whether leftward biases occurred, with no significant biases on the blue-yellow, $t(39) = -1.713$, $p = .095$, or the red-green tasks, $t(39) = -1.759$, $p = .086$ (see Figure 2). A paired-samples t test was used to compare biases on the two tasks. Although the tasks used different presentation times, they were completed within-subjects and, therefore, performance on the two measures could be compared. No significant difference emerged, $t(39) = .002$, $p = .999$, suggesting participants did not perform the two tasks differently.

DISCUSSION

As hypothesized, no significant bias occurred for blue-yellow isoluminant color. In addition, 150-ms presentation of the red-green isoluminant color task eliminated the left bias for red judgments. This supports the suggestion that prolonged processing time is needed in order for the red bias to occur. A possible explanation for this relates to pre-existing associations with the color red, which have the potential to influence the manner in which attention was captured (e.g., Clynes, 1977; Elliot & Maier, 2007; Elliot & Niesta, 2008; Lu & Zhou, 2005; Maier et al., 2009; Mehta & Zhu, 2009; Tchernikov & Fallah, 2010; Wilson, 1966). The left bias for more red judgments only occurred when additional time would have allowed for these pre-existing associations to be activated and subsequently influence the direction of attention. This indicates the initial leftward attentional vector does not underlie the left bias for red judgments.

It should be noted that feature-based attention, such as hue processing, peaks at approximately 400 ms (e.g., Hikosaka, Miyauchi, & Shimojo, 1993). Therefore, 150-ms duration may not allow feature-based attention to be distributed appropriately. Although this is possible, this attribute renders feature-based attention inconsistent with the leftward spatial bias observed under 150-ms viewing. If feature-based attention plays a significant role in pseudoneglect, leftward biases would not occur for luminance or motion during brief viewing. As a left bias has been observed during brief viewing (Thomas & Elias, 2011; Study 2), it argues against a necessary role for feature-based attention in pseudoneglect.

Prior research has shown that the leftward bias persists on visuospatial tasks using very brief presentations (McCourt & Garlinghouse, 2000; McCourt & Jewell, 1999; Thomas & Elias, 2011). The current finding of a left bias for motion under brief viewing suggests the same neural mechanisms underlie the biases for motion and luminance, but not color.

Differential effects of presentation time would not be expected for only one characteristic (color). For this reason, we suggest that prolonged processing time led more red judgments to be influenced by pre-existing cognitive associations. The motion task, which elicited relatively greater dorsal stream activation, led to a strong left bias, whereas the color task, which encouraged relatively greater ventral stream processing, decreased the strength of the left bias.

GENERAL DISCUSSION

Various tasks, when completed in peripersonal space, show a LVF performance advantage (Christman & Niebauer, 1997; He et al., 1996). In addition, performance advantages have been shown in the UVF in extrapersonal space (Previc & Blume, 1993; Previc et al., 1995). It has been further suggested that the LVF and peripersonal space are processed primarily by the dorsal stream, whereas the ventral stream preferentially processes the UVF and extrapersonal space (Previc, 1990, 1998). Partial support for this exists as line bisection, when performed in peripersonal space, leads to dorsal stream activation and the ventral stream is activated in extrapersonal space (Bjoertomt et al., 2002; Weiss et al., 2000). This proposed relation suggests visual stream processing differences influence the horizontal allocation of visuospatial attention (Drago et al., 2006) and might underlie visual field differences.

The visual streams have specialized processing advantages such that the ventral "what" stream is superior in object recognition and in processing color and the dorsal "where" stream primarily processes motion and spatial localization (Goodale & Milner, 1992; Livingstone & Hubel, 1988; Nieuwenhuis et al., 2008). Primate studies (Mishkin et al., 1982) and neuroimaging research (Haxby et al., 1991; James et al., 2003; Kastner & Ungerleider, 2000) have both supported the existence of dual visual processing systems. Clinical studies have also increased understanding how differential deficits arise depending on whether lesions occur in the dorsal or ventral stream (e.g., Duncan et al., 2003).

It is difficult to completely isolate dorsal and ventral stream functions in the general population where both are fully functional. For instance, area MT, which is highly involved in motion, receives a large number of dorsal stream inputs, but also receives information from the ventral stream and koniocellular pathway (Skottun & Skoyles, 2006). However, the relative advantages of each visual stream can be evaluated by using tasks that preferentially engage each one.

Modified greyscales tasks, incorporating motion and isoluminant color, were used to target dorsal and ventral stream processing, respectively. The leftward bias for motion demonstrates that the bias persists when dorsal stream activation is greater than ventral stream activity. A dorsal processing advantage is also consistent with the tendency for a stronger leftward bias in the LVF (Barrett et al., 2000; Thomas & Elias, 2010a, 2010b, 2011). The left bias was decreased for green, blue, and yellow (but not red), which suggests that ventral stream processing does not lead to the same leftward bias as

does dorsal stream processing. The biases observed for motion and luminance were of comparable strength, suggesting the relative advantage of the dorsal stream in motion did not outweigh the involvement of the dorsal stream in the greyscales task. This could be because both were visuospatial measures.

The use of brief presentation clarified that the color red influences visuospatial attention differently than other colors. Prolonged viewing, and, therefore, also a longer processing time, were needed to elicit the left bias for red, suggesting the initial direction of attention differed for isoluminant color compared to motion and luminance. When 150-ms stimulus presentations have been used for luminance (Thomas & Elias, 2011) and motion (Study 2), the initial direction of visuospatial attention allows the left bias to be maintained; however, with isoluminant color, the same bias did not occur. This suggests preferential ventral stream processing did not lead to the left bias for more red judgments during free-viewing. It is possible that brief viewing lead to an inability to adequately process hue (e.g., Hikosaka et al., 1993). Alternatively, numerous pre-existing associations with the color red (e.g., Clynes, 1977; Elliot & Maier, 2007; Elliot & Niesta, 2008; Lu & Zhou, 2005; Maier et al., 2009; Mehta & Zhu, 2009; Tchernikov & Fallah, 2010; Wilson, 1966) could have influenced the way in which attention was directed, which suggests isoluminant blue and yellow are more appropriate for looking at ventral stream contributions in visuospatial attention.

It must be noted that it is difficult to achieve isoluminance, even in the best laboratory conditions (Gur & Akri, 1992) as isoluminance depends on the specific task being performed and also varies among individuals (Livingstone & Hubel, 1987; Mullen, 1985). Individual differences in isoluminance undoubtedly created additional variance in the current study; however, this would assist in preserving the left bias, as opposed to decreasing it. The observed decrease in the leftward bias for green, yellow, and blue illustrates the strength of the design to outweigh this limitation. It is expected that accounting for individual differences in isoluminance would lead the bias on the isoluminant color task to be decreased even further, providing additional evidence that dorsal stream processing influences the strength of the left bias (Drago et al., 2006; Thomas & Elias, 2010a, 2010b, 2011).

As the dorsal "where" stream plays a role in spatial localization (Goodale & Milner, 1992; Haxby et al., 1991; Livingstone & Hubel, 1988; Nieuwenhuis et al., 2008), it follows that the strength of the left bias on the greyscales task would be mediated by the dorsal stream. The current studies demonstrate that visual stream processing differences provide a potential explanation for upper and lower visual field differences in perceptual asymmetries. Future research should make use of the tasks developed here to further examine visual field differences. Presentation of these tasks to the upper and lower visual field separately would provide additional evidence that dorsal stream processing underlies visual field differences in perceptual asymmetries.

As the same neural mechanisms appear to underlie the spatial biases observed in hemispatial neglect and pseudoneglect (e.g., Jewell & McCourt, 2000; McCourt & Jewell, 1999),

future research should also examine visual field differences more closely in clinical hemispatial neglect patients. Of interest, simultanagnosia can result from damage to either visual stream and has been suggested to be a sort of "bilateral neglect" (Duncan et al., 2003). A better understanding of the differential involvement of the visual streams in visuospatial attention in healthy populations could also lead to a better understanding of simultanagnosia. This would not only increase our understanding of the relationship between these phenomena, but furthermore, would prove useful in creating a general model of visuospatial attention that adequately accounts for all phenomena.

ACKNOWLEDGMENTS

REFERENCES

Bálint, R., & Harvey, M. (1995). Psychic paralysis of gaze, optic ataxia, and spatial disorder of attention. *Cognitive Neuropsychology*, *12*, 265–281. doi:10.1080/02643299508251999

Barrett, A.M., Crosson, B., Crucian, G.P., & Heilman, K.M. (2000). Horizontal line bisections in upper and lower body space. *Journal of the International Neuropsychological Society*, *6*, 455–459. doi:10.1017/S135561770064403X

Bauer, R.M., & Demery, J.A. (2003). Agnosia. In K.M. Heilman & E. Valenstein (Eds.), *Clinical neuropsychology* (pp. 236–295). New York: Oxford University Press.

Bellizzi, J.A., & Hite, R.E. (1992). Environmental color, consumer feelings, and purchase likelihood. *Psychology and Marketing*, *9*, 347–363. doi:10.1002/mar.4220090502

Bjoertomt, O., Cowey, A., & Walsh, V. (2002). Spatial neglect in near and far space investigated by repetitive transcranial magnetic stimulation. *Brain*, *125*, 2012–2022. doi:10.1093/brain/awf211

Braun, C.C., Sansing, L., & Silver, N.C. (1994). The interaction of signal word and color on warning labels: Differences in perceived hazard. *Human Factors and Ergonomics Society Annual Meeting Proceedings*, *2*, 831–835. doi:10.1177/154193129403801407

Braun, C.C., & Silver, N.C. (1995). Interaction of signal word and colour on warning labels: Differences in perceived hazard and behavioural compliance. *Ergonomics*, *38*, 2207–2220. doi:10.1080/00140139508925263

Bowers, D., & Heilman, K.M. (1980). Pseudoneglect: Effects of hemispace on a tactile line bisection task. *Neuropsychologia*, *18*, 491–498. doi:10.1016/0028-3932(80)90151-7

Christman, S.D., & Niebauer, C.L. (1997). The relation between left-right and upper-lower visual field asymmetries (or: what goes up goes right, while what's left lays low). In S.D. Christman (Ed.), *Cerebral asymmetries in sensory and perceptual processing* (pp. 263–296). Amsterdam: Elsevier Science B. V.

Çiçek, M., Deouell, L.Y., & Knight, R.T. (2009). Brain activity during landmark and line bisection tasks. *Frontiers in Human Neuroscience*, *3*, 1–8. doi:10.3389/neuro.09.007.2009

Clynes, M. (1977). *Sentics: The touch of emotions*. Garden City, NY: Anchor Press.

Corbetta, M., Shulman, G.L., Miezin, F.M., & Petersen, S.E. (1995). Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. *Science*, *270*, 802–805. doi:10.1126/science.270.5237.802

Drago, V., Crucian, G.P., Pisani, F., & Heilman, K.M. (2006). Distribution of attention in normal people as a function of spatial location: Right-left, up-down. *Journal of the International Neuropsychological Society*, *12*, 532–537. doi:10.1017/S1355617706060681

Duncan, J., Bundesen, C., Olson, A., Humphreys, G., Ward, R., Kyllingsbaek, S., … Chavda, S. (2003). Attentional functions in dorsal and ventral simultanagnosia. *Cognitive Neuropsychology*, *20*(8), 675–701. doi:10.1080/02643290342000041

Elias, L.J., Bryden, M.P., & Bulman-Fleming, M.B. (1998). Footedness is a better predictor than is handedness of emotional lateralization. *Neuropsychologia*, *36*, 37–43. doi:10.1016/S0028-3932(97)00107-3

Elliot, A.J., & Maier, M.A. (2007). Color and psychological functioning. *Current Directions in Psychological Science*, *16*, 250–254. doi:10.1111/j.1467-8721.2007.00514.x

Elliot, A.J., Maier, M.A., Moller, A.C., Friedman, R., & Meinhardt, J. (2007). Color and psychological functioning: The effect of red on performance attainment. *Journal of Experimental Psychology: General*, *136*, 154–168. doi:10.1037/0096-3445.136.1.154

Elliot, A.J., & Niesta, D. (2008). Romantic red: Red enhances men's attraction to women. *Journal of Personality and Social Psychology*, *95*, 1150–1164. doi:10.1037/0022-3514.95.5.1150

Fink, G.R., Marshall, J.C., Shah, N.J., Weiss, P.H., Halligan, P.W., Grosse-Ruyken, M., … Freund, H.J. (2000). Line bisection judgments implicate right parietal cortex and cerebellum as assessed by fMRI. *Neurology*, *54*, 1324–1331.

Fink, G.R., Marshall, J.C., Weiss, P.H., & Zilles, K. (2001). The neural basis of vertical and horizontal line bisection judgments: An fMRI study of normal volunteers. *Neuroimage*, *14*, S59–S67. doi:10.1006/nimg.2001.0819

Foxe, J.J., McCourt, M.E., & Javitt, D.C. (2003). Right hemisphere control of visuospatial attention: Line-bisection judgments evaluated with high-density electrical mapping and source analysis. *Neuroimage*, *19*, 710–726. doi:10.1016/S1053-8119(03)00057-0

Goodale, M.A., & Milner, A.D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, *15*, 20–25. doi:10.1016/0166-2236(92)90344-8

Goodale, M.A., & Westwood, D.A. (2004). An evolving view of duplex vision: Separate but interacting cortical pathways for perception and action. *Current Opinion in Neurobiology*, *14*, 203–211. doi:10.1016/j.conb.2004.03.002

Gur, M., & Akri, V. (1992). Isoluminant stimuli may not expose the full contribution of color to visual functioning: Spatial contrast sensitivity measurements indicate interaction between color and luminance processing. *Vision Research*, *32*, 1253–1262. doi:10.1016/0042-6989(92)90220-D

Haxby, J.V., Grady, C.L., Horwitz, B., Ungerleider, L.G., Mishkin, M., Carson, R.E., … Rapoport, S.I. (1991). Dissociation of object and spatial visual processing pathways in human extrastriate cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *88*, 1621–1625. doi:10.1073/pnas.88.5.1621

He, S., Cavanagh, P., & Intriligator, J. (1996). Attentional resolution and the locus of visual awareness. *Nature*, *383*, 334–337. doi:10.1038/383334a0

Hikosaka, O., Miyauchi, S., & Shimojo, S. (1993). Voluntary and stimulus-induced attention detected as motion sensation. *Perception*, *22*, 517–526.

Hupka, R.B., Zaleski, A., Otto, J., Reidl, L., … Tarabrina, N.V. (1997). The colors of anger, envy, fear, and jealousy: A cross-cultural study. *Journal of Cross-Cultural Psychology*, *28*, 156–171. doi:10.1177/0022022197282002

James, T.W., Culham, J., Humphrey, K., Milner, A.D., & Goodale, M.A. (2003). Ventral occipital lesions impair object recognition but not object-directed grasping: An fMRI study. *Brain*, *126*, 2463–2475. doi:10.1093/brain/awg248

Jewell, G., & McCourt, M.E. (2000). Pseudoneglect: A review and meta-analysis of performance factors in line bisection tasks. *Neuropsychologia*, *38*, 93–110. doi:10.1016/S0028-3932(99)00045-7

Kastner, S., & Ungerleider, L.G. (2000). Mechanisms of visual attention in the human cortex. *Annual Review of Neuroscience*, *23*, 315–341. doi:10.1146/annurev.neuro.23.1.315

Kaya, N., & Epps, H.H. (2004). Relationship between color and emotion: A study of college students. *College Student Journal*, *38*, 396–405.

Kinsbourne, M., & Warrington, E.K. (1962). A disorder of simultaneous form perception. *Brain*, *85*, 461–486. doi:10.1093/brain/85.3.461

Livingstone, M.S., & Hubel, D.H. (1987). Psychophysical evidence for separate channels for the perception of form, color, movement, and depth. *The Journal of Neuroscience*, *7*, 3416–3468.

Livingstone, M., & Hubel, D. (1988). Segregation of form, color, movement, and depth: Anatomy, physiology, and perception. *Science*, *240*, 740–749. doi:10.1126/science.3283936

Lu, S., & Zhou, K. (2005). Stimulus-driven attentional capture by equiluminant color change. *Psychonomic Bulletin & Review*, *12*, 567–572. doi:10.3758/BF03193806

Luh, K.E. (1995). Line bisection and perceptual asymmetries in normal individuals: What you see is not what you get. *Neuropsychology*, *9*, 435–448. doi:10.1037/0894-4105.9.4.435

Luria, A.R. (1959). Disorders of "simultaneous perception" in a case of bilateral occipito-parietal brain injury. *Brain*, *82*(3), 437–449. doi:10.1093/brain/82.3.437

Maier, M.A., Barchfeld, P., Elliot, A.J., & Pekrun, R. (2009). Context specificity of implicit preferences: The case of human preference for red. *Emotion*, *9*, 734–738. doi:10.1037/a0016818

McCourt, M.E., & Garlinghouse, M. (2000). Asymmetries of visuospatial attention are modulated by viewing distance and visual field elevation: Pseudoneglect in peripersonal and extra-personal space. *Cortex*, *36*, 715–731. doi:10.1016/S0010-9452(08)70548-3

McCourt, M.E., & Jewell, G. (1999). Visuospatial attention in line bisection: Stimulus modulation of pseudoneglect. *Neuropsychologia*, *37*, 843–855. doi:10.1016/S0028-3932(98)00140-7

McCourt, M.E., & Olafson, C. (1997). Cognitive and perceptual influences on visual line bisection: Psychophysical and chronometric analyses of pseudoneglect. *Neuropsychologia*, *35*, 369–380. doi:10.1016/S0028-3932(96)00143-1

Mehta, R., & Zhu, R. (2009). Blue or red? Exploring the effect of color on cognitive task performances. *Science*, *323*, 1226–1229. doi:10.1126/science.1169144

Mishkin, M., Lewis, M.E., & Ungerleider, L.G. (1982). Equivalence of parieto-preoccipital subareas for visuospatial ability in monkeys. *Behavioral Brain Research*, *6*, 41–55. doi:10.1016/0166-4328(82)90080-8

Moller, A.C., Elliot, A.J., & Maier, M.A. (2009). Basic hue-meaning associations. *Emotion*, *9*, 898–902. doi:10.1037/a0017811

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

Nicholls, M.E., Bradshaw, J.L., & Mattingley, J.B. (1999). Free-viewing perceptual asymmetries for the judgement of brightness, numerosity and size. *Neuropsychologia*, *37*, 307–314. doi:10.1016/S0028-3932(98)00074-8

Nicholls, M.E., & Roberts, G.R. (2002). Can free-viewing perceptual asymmetries be explained by scanning pre-motor or attentional biases? *Cortex*, *38*, 113–136. doi:10.1016/S0010-9452(08)70645-2

Niemeier, M., Stojanoski, B., Singh, V.W., & Chu, E. (2008). Paradoxical cross-over due to attention to high or low spatial frequencies. *Brain and Cognition*, *67*, 115–125. doi:10.1016/j.bandc.2007.12.002

Nieuwenhuis, S., Jepma, M., La Fors, S., & Olivers, C.N. (2008). The role of the magnocellular and parvocellular pathways in the attentional blink. *Brain and Cognition*, *68*, 42–48. doi:10.1016/j.bandc.2008.02.119

Perenin, M.T., & Vighetto, A. (1988). Optic ataxia: A specific disruption in visuomotor mechanisms. *Brain*, *111*, 643–674. doi:10.1093/brain/111.3.643

Posner, M.I., & Rothbart, M.K. (2007). Research on attention networks as a model for the integration of psychological science. *Annual Review of Psychology*, *58*, 1–23. doi:10.1146/annurev.psych.58.110405.085516

Previc, F.H. (1990). Functional specialization in the lower and upper visual fields in humans: Its ecological origins and neurophysiological implications. *The Behavioral and Brain Sciences*, *13*, 519–575. doi:10.1017/S0140525X00080018

Previc, F.H. (1998). The neuropsychology of 3-D space. *Psychological Bulletin*, *124*, 123–164. doi:10.1037//0033-2909.124.2.123

Previc, F.H., & Blume, J. (1993). Visual search asymmetries in three-dimensional space. *Vision Research*, *33*, 2697–2704. doi:10.1016/0042-6989(93)90229-P

Previc, F.H., Breitmeyer, B.G., & Weinstein, L. (1995). Discriminability of random-dot stereograms in three-dimensional space. *International Journal of Neuroscience*, *80*, 247–253. doi:10.3109/00207459508986103

Rubens, A. (1985). Caloric stimulation and unilateral visual neglect. *Neurology*, *35*, 1019–1024.

Siman-Tov, T., Mendelsohn, A., Schonberg, T., Avidan, G., Podlipsky, I., Pessoa, L., … Hendler, T. (2007). Bihemispheric leftward bias in a visuospatial attention-related network. *The Journal of Neuroscience*, *27*, 11271–11278. doi:10.1523/JNEUROSCI.0599-07.2007

Skottun, B.C., & Skoyles, J.R. (2006). Is coherent motion an appropriate test for magnocellular sensitivity? *Brain and Cognition*, *61*, 172–180. doi:10.1016/j.bandc.2005.12.004

Tchernikov, I., & Fallah, M. (2010). A color hierarchy for automatic target selection. *Public Library of Science*, *5*, 1–4. doi:10.1371/journal.pone.0009338

Thomas, N.A., & Elias, L.J. (2010a). Do perceptual asymmetries differ in peripersonal and extrapersonal space? *Journal of the International Neuropsychological Society*, *16*, 210–214. doi:10.1017/S135561770999097X

Thomas, N.A., & Elias, L.J. (2010b). Perceptual asymmetries in greyscales: Object-based versus space-based influences. *Cortex* doi:10.1016/j.cortex.2010.11.015 [Epub ahead of print].

Thomas, N.A., & Elias, L.J. (2011). Upper and lower visual field differences in perceptual asymmetries. *Brain Research*, *1387*, 108–115. doi:10.1016/j.brainres.2011.02.063

Weiss, P.H., Marshall, J.C., Wunderlich, G., Tellmann, L., Halligan, P.W., Freund, H., … Fink, G.R. (2000). Neural consequences of acting in near versus far space: A physiological basis for clinical dissociations. *Brain*, *123*, 2531–2541. doi:10.1093/brain/123.12.2531

White, B.J., Kerzel, D., & Gegenfurtner, K.R. (2006). Visually guided movements to color targets. *Experimental Brain Research*, *175*, 110–126. doi:10.1007/s00221-006-0532-5

Wilson, G.D. (1966). Arousal properties of red versus green. *Perceptual and Motor Skills*, *23*, 947–949. doi:10.2466/pms.1966.23.3.947