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Effects of monocular viewing and eye dominance on spatial attention

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Summary

Observations in primates and patients with unilateral spatial neglect have suggested that patching of the eye ipsilateral to the injury and contralateral to the neglected space can sometimes improve attention to the neglected space. Investigators have generally attributed the effects of monocular eye patching to activation of subcortical centers that interact with cortical attentional systems. Eye patching is thought to produce preferential activation of attentional systems contralateral to the viewing eye. In this study we examined the effect of monocular eye patching on attentional biases in normal subjects. When normal subjects bisect vertical (radial) lines using both eyes, they demonstrate a far attentional bias, misbisecting lines away from their body. In a monocular viewing experiment, we found that the majority of subjects, who were right eye dominant, had relatively nearer bisections and a diminished far bias when they used their right eye (left eye covered) compared with when they used their left eye (right eye covered). The smaller group of subjects who were left eye dominant had relatively nearer bisections and a diminished far bias when they used their left eye compared with when they used their right eye. In the hemispatial placement experiment, we directly manipulated hemispheric engagement by having subjects perform the same task in right and left hemispace. We found that right eye dominant subjects had a diminished far bias in right hemispace relative to left hemispace. Left eye dominant subjects showed the opposite pattern and had a diminished far bias in left hemispace. For both groups, spatial presentation affected performance more for the non-dominant eye. The results suggest that monocular viewing is associated with preferential activation of attentional systems in the contralateral hemisphere, and that the right hemisphere (at least in right eye dominant subjects) is biased towards far space. Finally, the results suggest that the poorly understood phenomenon of eye dominance may be related to hemispheric specialization for visual attention.

Keywords: attention; eye dominance; hemispheric asymmetry; monocular; spatial bias

Introduction

Hemispheric injury may induce an attentional bias and a failure to orient, respond or report meaningful stimuli in the contralesional space, which is termed unilateral spatial neglect (Heilman, 1979*a*). Lesions in various subcortical and cortical structures, including the hypothalamus, thalamus, basal ganglia, intralaminar nuclei, midbrain tegmentum, cingulate gyrus, prefrontal cortex, parietal cortex and occipital cortex, can all cause unilateral spatial neglect (Heilman *et al*., 1993*b*; Mesulam, 1999). Some studies have focused on the role of the superior colliculi in the generation of neglect. When one superior colliculus is cooled or destroyed, animals exhibit a contralesional spatial neglect similar to the neglect caused by cortical lesions or cortical cooling (Sprague, 1966; Payne *et al*., 1996). Combined injury to cortical areas and the superior colliculus on the same side of the brain causes more severe neglect than when cortical or collicular areas are damaged alone (Sprague, 1966; Sherman, 1977; Wallace *et al*., 1989, 1990).

Investigators have attempted to modify the superior colliculus's activity in order to reverse or decrease unilateral spatial neglect. When an animal has a cortical lesion that produces neglect, metabolic studies show that the superior colliculus on the same side as the cortical lesion has markedly depressed oxidative metabolism (Hovda and Villablanca, 1990). The collicular depression ipsilateral to the cortical lesion is thought to be caused by loss of direct excitatory input from the ipsilateral cortex (Palmer *et al*., 1972; Sprague, 1975; Benson and McIlwain, 1983) as well as loss of cortical disinhibition of the tectum mediated by a cortico-striato-nigro-tectal loop (McHaffie *et al*., 1993; Sprague, 1996).

Because each superior colliculus appears to be important for spatially directing attention to contralateral space, depressed ipsilesional collicular activity would be expected to compound the neglect caused by the cortical lesion and to reduce attention to contralesional space further. Attempts to restore activity of the ipsilesional colliculus in animals, either by targeted pharmacological injections into subcortical structures or by surgical interventions that reduce inhibitory input to the colliculus, have resulted in improved attention to contralateral space (Sprague, 1966; Wallace *et al*., 1989, 1990; Ciaramitaro *et al*., 1997).

Another approach to treating neglect in animals has been to deactivate homotopic anatomical regions in the hemisphere opposite the injured hemisphere. Neglect caused by cooling deactivation of the superior colliculus on one side can be reduced when the colliculus of the opposite side is deactivated (Lomber and Payne, 1996). Likewise, neglect caused by deactivation of cortical regions in one hemisphere can be largely reversed by cooling the corresponding cortical region in the opposite hemisphere (Lomber and Payne, 1996).

Surgical intervention and regional brain cooling are not feasible approaches for treating neglect in human patients. However, Posner and Rafal (1987) proposed that because each superior colliculus receives input predominantly from the contralateral eye and each colliculus interacts with the hemisphere on the same side, one might be able to modulate activity of the contralesional colliculus and the corresponding hemisphere in a non-invasive manner by patching the ipsilesional eye. Patching the ipsilesional eye in patients with neglect should reduce activity of the contralesional colliculus as well as the activity of the contralesional hemisphere. Reducing activity of the contralesional colliculus and hemisphere could potentially help restore the balance of attention and reduce the severity of neglect. Stimulation from the eye that remains open (the contralesional eye) should result in relatively increased activation of the ipsilesional hemisphere.

Studies examining monocular eye patching as a treatment for visuospatial neglect have yielded mixed results; however, selected patients seem to respond to the treatment. Butter and Kirsch examined the effect of eye patching on five different spatial tasks in patients with neglect (Butter and Kirsch, 1992). They found improvement with ipsilesional eye patching, but the effect was consistent only in the line bisection task. Beis and colleagues examined the effect of ipsilesional eye patching as well as hemi-field eye patching on a functional independence measurement battery and a quantitative assessment of eye movement in a spatial reading task (Beis *et al*., 1999). The functional independence measure and the amount of time spent looking into the left side of space improved with both types of treatment, but the improvement was significant (when compared with a non-treated control group) only for patients with hemi-field eye patches. Walker and colleagues (Walker *et al*., 1996) compared the effect of right eye patching and left eye patching, and they did not find consistent effects of eye patching across five visuospatial tasks in patients with visuospatial neglect. They also found that some patients in whom performance was improved when the right eye was patched also demonstrated improved performance when the left eye was patched. Barrett and colleagues and Serfaty and colleagues found that contralesional rather than ipsilesional eye patching helped some patients with neglect (Serfaty *et al*., 1995; Barrett *et al*., 2001). The findings of Walker and colleagues (Walker *et al*., 1996) raise a question about the specificity of the effect of eye patching. The findings of Barrett and colleagues and Serfaty and colleagues are opposite to those predicted by Posner's and Rafal's collicular hypothesis (Serfaty *et al*., 1995; Barrett *et al*., 2001).

Most studies examining the effect of monocular patching on attentional biases have been performed in patients or animals with hemi-inattention caused by hemispheric injury (Deuel, 1985; Butter and Kirsch, 1992; Serfaty *et al*., 1995; Walker *et al*., 1996; Beis *et al*., 1999; Barrett *et al*., 2001). Subjects with lesions may have variable results because of the heterogeneity of the lesion locations. To determine whether monocular eye patching can systematically influence attentional bias we studied a more uniform population of young, normal adult subjects. If monocular patching can influence activation of lateralized attentional systems, we should be able to induce opposite hemispheric asymmetries by patching alternative eyes. The prediction would be that attentional systems contralateral to the viewing eye would be relatively activated compared with attentional systems contralateral to the patched eye.

Heilman and colleagues suggested that the left hemisphere may be attentionally biased towards close and lower space, and the right hemisphere may be more biased towards far and upper space (Heilman *et al*., 1993*a*). Behavioral studies as well as a recent PET imaging study have provided support for this distinction (Heilman *et al*., 1993*a*; Weiss *et al*., 2000). In order to test the effects of monocular viewing on attentional biases, we asked normal subjects to bisect radial lines (intersection of sagittal and transverse planes) with either one or the other eye patched.

We chose to have normal subjects bisect radial lines because normal subjects have a consistent and robust bias when they bisect radial lines (which is in the far or upward direction), whereas they have a more variable and lesser bias when they bisect horizontal lines (which in meta-analyses is to the left of centre). Having normal subjects bisect radial lines makes it less likely that their performance will reach ceiling levels that could mask the effects of attentional variables. In addition, the extents of the monocular horizontal fields are different for the two eyes, whereas the extents of the vertical fields are identical. Monocular viewing of radial lines is therefore less likely to be affected by monocular retinal field factors compared with monocular viewing of horizontal lines. Patient studies have mostly focused on attentional biases in the horizontal dimension, but patients can also have attentional biases in the radial dimension (Halligan and

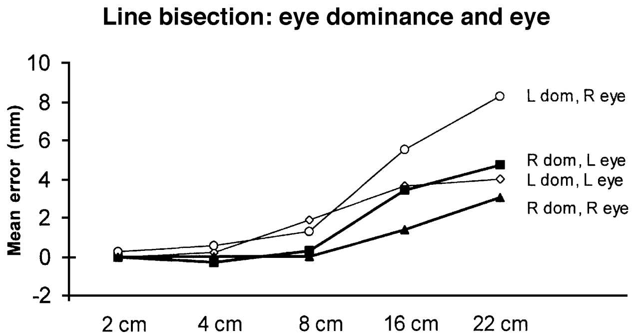

Fig. 1 Mean line bisection errors for the radial line bisection task under monocular viewing conditions in central space. Subjects make increasing errors with increasing line length. Right eye dominant subjects have smaller errors and bisect closer to their body when using the right eye compared with when they use the left eye. Left eye dominant subjects have smaller errors, and bisect closer towards their body when using the left eye compared with when they use the right eye.

Marshall, 1989; Shelton *et al*., 1990; Mennemeier *et al*., 1992).

On the basis of the proposed hemispheric specialization to near and far space, we predicted that when subjects bisect radial lines, relative activation of left hemisphere attentional systems (with patching of the left eye and viewing with the right eye) should result in a bias directed more towards close and lower space, whereas relative activation of right hemisphere attentional systems (with patching of the right eye and viewing with the left eye) should result in a bias directed more towards far or upper space. If consistent differences between the effects of right eye patching and left eye patching such as these are found in normal subjects, it would support the view that eye patching produces asymmetric activation of the hemispheres. Eye dominance laterality was also assessed to determine if monocular effects on attentional bias interact with visual laterality preferences.

Monocular viewing experiment

Subjects

Nineteen undergraduate college student volunteers from the University of Florida participated in the study. All subjects were native speakers of English and were screened for history of brain injury and learning disorders. Sighting eye dominance was determined for each subject using a variation of the Porta test (Porta, 1593; Crovitz and Zener, 1962; Gronwall and Sampson, 1971) and a ‘hole in the hand test’, a variation on the Miles test (Miles, 1930). For the Porta test variant, subjects were asked to extend one arm and align the pointer finger of the extended hand vertically with the corner of the room, with both eyes open. Subjects then closed one eye or the other alternately and reported which eye closure caused the largest alignment change. The dominant eye was recorded as the eye that when closed caused more change. For the ‘hole in the hand test’, subjects were asked to make a small hole between both their outstretched hands and sight a small object. Subjects were then instructed to move their hands towards their face without losing sight of the object. The eye to which they brought their hands back without losing sight of the object was recorded as the dominant eye.

Subjects were classified as right eye dominant if they were recorded as right eye dominant on both eye tests, and classified as left eye dominant if they were recorded as left eye dominant on both tests. Subjects with inconsistent results on the two tests were classified as showing mixed eye dominance and were excluded from the study. Of the nineteen subjects, 12 were right eye dominant, five were left eye dominant and two were mixed eye dominant; therefore, 17 subjects were included in the study. Subjects were also classified as left handed or right handed for writing, and completed a handedness questionnaire derived from that of Raczkowski and colleagues (Raczkowski *et al*., 1974).

After a discussion of the risks and benefits of the proposed research, informed consent was obtained from all subjects. The study was approved by the Institutional Review Board for the Health Science Center at the University of Florida.

Materials

Lines of 2.5 mm width were printed on 216 × 280 mm white paper, one line per sheet. Lines were oriented parallel to the long axis of the paper and were centred on the page, both horizontally and vertically. Lines were of five different line lengths (2, 4, 8, 16 and 22 cm). A black opaque eye patch was used to occlude vision in one eye.

Procedure

Subjects were seated at a table and were asked to bisect lines placed in front of them. Lines were oriented in the vertical (radial) direction in the transverse plane.

Each subject bisected 25 lines with each eye. One set of 25 lines consisted of five exemplars of each line length intermixed in a pseudo-randomized fashion. Subjects bisected the first set of 25 lines while wearing an eye patch on one eye, and the second set while wearing an eye patch on the other eye. The order of eye patching was counterbalanced across subjects, so that half the subjects bisected the lines with their right eye first, and the other half with their left eye first.

Results

Line bisection error was measured to an accuracy of 0.5 mm from true midpoint. Errors that were distal or beyond the midpoint were arbitrarily assigned a positive value, and errors that were proximal to the midpoint were given a negative value. The means and standard deviations were calculated for each line length and eye condition for each subject. A repeated measures ANOVA (analysis of variance) was performed on the data. The within subject factors were the mean errors made at each line length (2, 4, 8, 16 and 22 cm), and the eye used (left or right). The between subjects factor was eye dominance group (left or right eye dominant subjects). The analysis revealed a significant main effect of line, indicating that subjects made increasingly positive errors with increasing sizes of lines, as expected for radial line bisections in normal subjects [$F(4,12) = 6.64$, $P = 0.005$; see Fig. 1]. The analysis did not reveal a main effect of eye, indicating that the monocular patching, independent of eye preference, did not change the error bias in a consistent manner. There was, however, a significant eye by group interaction [$F(4,12) = 7.32$, $P = 0.003$]. This interaction indicated that subjects who were left eye dominant performed better, making smaller positive errors and bisecting the line relatively nearer to their body when using their left eye, and subjects who were right eye dominant performed better, making smaller errors and bisecting the line relatively nearer to their body when using their right eye. The robustness of the effect of eye dominance was apparent on review of the individual data. All the individuals who made much greater far errors when viewing from the right eye relative to the left eye, belonged to the left eye dominant group. Figure 1 depicts the performance for the left and right eyes for each eye dominance group.

Discussion

Previous studies in normal subjects tested under binocular viewing conditions have shown that normal subjects have a consistent attentional bias on the radial line bisection task, marking the centre of the line as higher, or, if the line is placed on a desk in the transverse plane before the subject, farther away than true centre (Scarisbrick *et al*., 1987; Shelton *et al*., 1990). The effect is proportional to line length such that greater absolute errors towards the far end of the line are made with increasing line lengths. The portion of a line to which greater attention is allocated appears longer than an equal length of line to which attention is not directed (Milner *et al*., 1992). When subjects bisect toward the far end of the line, therefore, they are likely to be attending more to the far end of the line and overestimating its length (or conversely attending less to the near end of the line and underestimating its length). Our findings replicate these general findings of previous studies in normal subjects. Our normal subjects consistently bisected radial lines farther away from true centre, and were presumably allocating greater attention to the far portion of the line compared with the near portions of the line.

Our results showed that monocular viewing systematically influenced bias on the radial line bisection task and that the direction of the effect was dependent on eye dominance. As discussed, monocular viewing may induce activation of the contralateral colliculus and hemispheric attentional systems. Evidence from prior studies suggests that in most people the left hemisphere is biased towards proximal peripersonal space and the right hemisphere towards distal space (Heilman *et al*., 1993*a*; Weiss *et al*., 2000). Based on this we had expected that subjects using their right eye would be relatively biased toward near space and that subjects using the left eye would be relatively biased toward far space. Consistent with this, we found that right eye dominant subjects had a greater far bias using the left eye (presumably preferentially activating the far biased right hemisphere) and a relatively nearer bias using the right eye (presumably activating the near biased left hemisphere). In contrast, left eye dominant subjects showed a reversal of this pattern, demonstrating a greater far bias using their right eye than left eye. The reversal of the bias in left eye dominant subjects may indicate that they have a hemispheric organization for spatial attention to near and far space that is the opposite of that in right eye dominant subjects.

Differences in performance under conditions of using the dominant compared with the non-dominant eye have been observed in other studies. In certain visuo-motor coordination tasks, subjects are more accurate using their dominant eye (Lund, 1932; Freeman and Chapman, 1935; Coren, 1999). Images can appear clearer and more salient (Porac and Coren, 1984) and larger (Coren and Porac, 1976) when viewed by the dominant eye as compared with images viewed with the non-dominant eye. Such differences have not been found to be related to differences in refractive index or retinal differences, and are thought to be related to central processing factors.

In our study we used an attentional task in which performance was expected to change depending on hemispheric activation. Because eye use may activate contralateral attentional systems preferentially, this differential hemispheric activation may account for the differences we observed between different eyes used in this task. Alternatively, the difference in performance between use of the dominant and non-dominant eye may be related to differences in the processing characteristics of dominant and non-dominant eyes, independent of differential hemispheric activation of attentional systems. To determine if the eye dependent performance asymmetries we found in the monocular viewing experiment are related to differences in hemispheric activation, we designed a second experiment. In this second experiment, radial lines for bisection were placed in right or left hemispace rather than being placed directly in front of the subject. Stimuli presented in left hemispace engage attentional systems differently from stimuli presented in right hemispace (Bowers *et al*., 1981). In general, stimuli presented in right hemispace, even under free viewing conditions, are thought to preferentially engage left hemisphere systems, and stimuli presented in left hemispace preferentially engage right hemisphere systems. Consistent with this selective engagement postulate is the finding that brain-damaged subjects with either left or right hemispheric damage perform more poorly when stimuli are presented in the space contralateral to the injured hemisphere (Coslett *et al*., 1993; Coslett, 1999). Functional imaging studies have also shown that the responsivity of many hemispheric

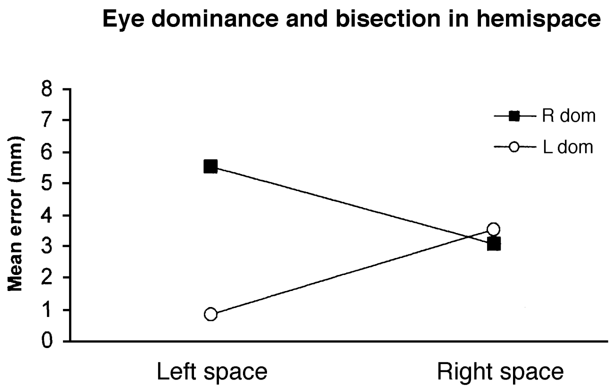

Fig. 2 Radial line bisection errors for each eye dominance group when bisections are performed in right or left hemispace. Right eye dominant subjects make smaller errors and bisect closer to their bodies in right hemispace compared with left hemispace. There is a trend for left eye dominant subjects to make smaller errors and bisect closer to their bodies in left hemispace compared with right hemispace. Bisection errors are different for the two groups in left hemispace, but not in right hemispace.

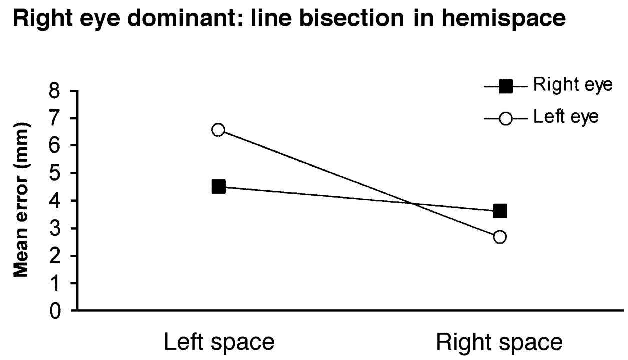

Fig. 3 Radial line bisection errors in right and left hemispace for right eye dominant subjects separated by monocular viewing condition. Right eye dominant subjects make smaller errors and bisect closer to their bodies in right compared with left hemispace when they view with their non-dominant left eye. Bisections are not significantly different for the two spaces when they view with the dominant right eye.

components for spatial attention are biased toward contralateral stimuli (Perry and Zeki, 2000).

In the second experiment we studied the hemispatial placement of radial lines to determine whether the eye effect found in the first experiment was related to selective hemispheric activation. If both monocular viewing and hemispatial placement induce selective hemispheric activation, we would expect that the hemispatial placement of radial lines would produce parallel results to that of the first experiment. Not obtaining parallel results in the hemispatial placement experiment would support the postulate that the effects of eye use found in the first experiment are independent of underlying changes in hemispheric attentional activation, and might be related to processing efficiency of the dominant eye relative to the non-dominant eye.

Hemispatial placement experiment

Subjects

College undergraduate volunteers from the University of Florida participated in the experiment. Subjects were screened to ensure that English was their native language and that they did not have neurological injury or a learning disability. Subjects were given the two tests of eye dominance described for the first experiment, and categorized accordingly into groups of right-eye and left-eye dominant subjects. Subjects with inconsistent results for the test of eye dominance were not included in the study. Twenty-seven subjects (17 right eye dominant, 10 left eye dominant) were included in the experiment. All subjects were classified according to dominant writing hand and given a handedness questionnaire derived from that of Raczkowski and colleagues (Raczkowski *et al.*, 1974).

After a discussion of the risks and benefits of the study, all subjects provided informed consent for the research. The study was approved by the Institutional Review Board for the Health Science Center at the University of Florida.

Materials

Stimuli consisted of 20 single black lines of 2.5 mm width and 22 cm length, centred on 216 × 280 mm white paper. A black opaque eye patch was used for eye occlusion.

Procedure

Subjects were seated at a table and lines were placed in the vertical (radial) direction in the transverse plane on the table. Lines were placed in either the right or left hemispace position. In the right hemispace position the medial edge of the page was aligned 25 cm to the right of the subjects' midsagittal plane and in left hemispace the medial edge of the page was aligned 25 cm to the left of the subjects' midsagittal plane. Subjects bisected the first 10 lines with one eye occluded, followed by the second 10 lines with the other eye occluded. The first five lines in each eye condition were bisected in one hemispace, and the second five lines were bisected in the other hemispace. During the task subjects were not required to hold eye fixation and were allowed to move their heads freely. The order of eye occlusion and hemispace was counterbalanced across subjects.

Results

Bisection errors were measured as in the monocular viewing experiment. A mean bisection error for each subject was calculated for each hemispace and eye viewing condition. A repeated measures ANOVA was performed to analyse mean bisection errors. The between subject factor was group (right

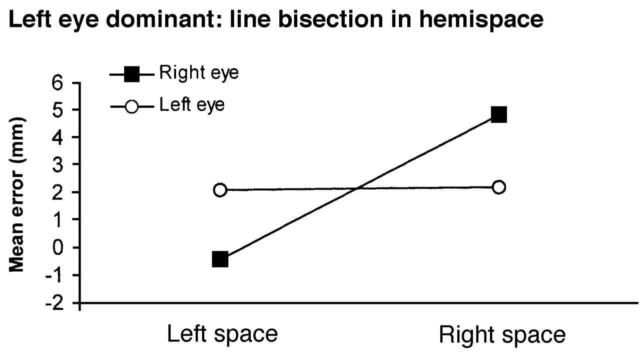

Fig. 4 Radial line bisection errors in right and left hemispace for left eye dominant subjects separated by monocular viewing conditions. Subjects make smaller errors and bisect closer to their bodies in left compared with right hemispace when they view with their non-dominant right eye. Bisections are not significantly different for the two spaces when they view with their dominant left eye.

eye dominant, left eye dominant), and the within subject factors were viewing eye (dominant eye, non-dominant eye) and hemispace (right hemispace, left hemispace). All pairwise comparisons were made using *t*-tests, with a significance level of $P < 0.05$. Comparisons of means in each space and for each eye were planned because we expected to test for differences in means for these factors.

While the analysis did not reveal any main effects of group, viewing eye or hemispace, there was a significant group–space interaction [$F(1,25) = 10.5$, $P = 0.003$; see Fig. 2] and group–space–eye interaction [$F(1,25) = 24.6$, $P < 0.001$; see Figs 3 and 4].

In order to investigate the source of the three-way interaction between group, eye and space, separate two-way ANOVAs, including the factors of eye and hemispace, were calculated for each group. The analysis of the right eye dominant subjects revealed that they made relatively nearer bisections when they bisected lines in right hemispace compared with left hemispace [$F(1,16) = 7.53$, $P = 0.014$, main effect of space]. In addition, while there was no overall difference in performance for right eye dominant subjects based on eye use across all conditions (no main effect of eye), there was a significant interaction between eye and hemispace [$F(1,16) = 8.72$, $P = 0.009$; see Fig. 3]. Follow-up comparisons of the means for performance with each eye showed that the space of presentation affected performance in the non-dominant left eye ($t = 3.72$, $P = 0.002$), but not in the dominant right eye ($t = 0.973$, $P = 0.345$). As shown in Fig. 3, right eye dominant subjects using the left eye had a farther bias on bisections in left space and a nearer bias on bisections in right space. In contrast, bisections produced by the right eye were not significantly different in the two spaces.

In contrast to right eye dominant subjects for whom bisections in right hemispace were nearer than bisections in left hemispace, an ANOVA of left eye dominant subjects revealed a trend for left eye dominant subjects to make nearer bisections when they bisected lines in left compared with right hemispace [$F(1,9) = 3.64$, $P = 0.089$]. While performance did not differ by eye use across all conditions (no main effect of eye), there was a significant interaction between eye and hemispace [$F(1,9) = 16.27$, $P = 0.003$; see Fig. 4]. Follow-up comparisons of the means showed that the space affected performance in the non-dominant right eye [$t = 3.55$, $P = 0.006$), but not in the dominant left eye ($t = 0.06$, $P = 0.954$). As shown in Fig. 4, subjects using the right eye had a farther bias on bisections in right space and a nearer bias on bisections in left space. In contrast, bisections produced by the left eye were not significantly different in the two spaces.

Based on these analyses it is apparent that the three-way interaction found in the overall ANOVA that included both groups can be derived from the differences in the interaction between eye and hemispace found for each group. For both groups the non-dominant eye and not the dominant eye differed as a function of hemispace, but in each group the effect of hemispace in the non-dominant eye was in the opposite direction. This results in a difference between these groups in relation to the interaction between eye and hemispace. In addition, there is a main effect of space in the right eye dominant group that is in the opposite direction to the effect of space that approaches significance for the left eye dominant group, indicating that these groups differ with respect to how performance is affected by space.

In the overall ANOVA that included both groups the difference in performance between the groups in relation to space was indicated by the group by space interaction. Follow-up comparison of means for this two-way interaction showed that the mean bisection errors for right eye dominant subjects were smaller in right space compared with left space ($t = 2.74$, $P = 0.014$), and there was a trend for mean bisection errors for left eye dominant subjects to be smaller in left space compared with right space ($t = 1.91$, $P = 0.089$). Comparison of means in each space indicated that bisections in left space were significantly different for the two groups ($t = 3.32$, $P = 0.009$), whereas bisections in right space were not ($t = 0.31$, $P = 0.767$).

Discussion

The hemispatial placement experiment was designed to provide a further test of the hypothesis that nearer or farther bisections on the radial line bisection task are the result of differential engagement of the hemispheres. If hemispheric engagement is driving the differences in line bisection performance seen with the first monocular viewing experiment, then systematic differences in performance should also be apparent with hemispatial presentations in the hemispatial placement experiment, which engage the hemispheres differentially. The results of the hemispatial placement experiment show that both groups systematically change their attentional bias depending on the space of stimulus presentation. Although the change in performance in relation to space is found predominantly when subjects are using their non-dominant eye, we will first discuss the main effects of space for each group overall. The explanation for why the non-dominant eye is affected more by changes in space follows, and depends on the asymmetric hemispheric participation in spatial attention.

The results of the hemispatial placement experiment provide further evidence that differences in near and far spatial biases may be mediated by differential hemispheric engagement, because in both right eye dominant and in left eye dominant subjects, hemispatial placement of stimuli systematically affected line bisection bias (albeit only significantly when the non-dominant eye was used). Right eye dominant subjects reduced their far attentional bias when lines were placed in the right hemispace (main effect of space). We had predicted that right eye dominant subjects should make nearer bisections in right hemispace because we postulated that the left hemisphere is more biased toward near space, and the left hemisphere should be relatively more engaged in attentional processing of stimuli in right hemispace compared with left hemispace. The reduction of far bias, or increased attention to near space for bisections in right space, is consistent with the hypothesis that engagement of the left hemisphere in right eye dominant subjects results in a relatively nearer bias, whereas engagement of the right hemisphere results in a relatively farther bias. Thus, the results support the hypothesis that the attentional bias in the bisection of radial lines can be modulated by altering hemispheric engagement.

Whereas the right eye dominant group's bisections were nearer in right than left space, the left eye dominant group's bisections tended to be nearer in left than right space. Although not as robust, the difference in performance with respect to hemispace for left eye dominant subjects is in the direction that supports the hypothesis that left eye dominant subjects, when compared with right eye dominant subjects, may have a reversal of the hemispheric organization of spatial biases to near and far space. In left eye dominant subjects, selective right hemisphere engagement by stimuli in left hemispace and a right hemispheric bias towards near space may explain the nearer bisections in left space.

We have assumed that the right hemisphere becomes more activated when stimuli are placed in left space and the left hemisphere is more activated when stimuli are placed in right space. But there is also evidence to suggest that one hemisphere may be 'dominant' for spatial attention, such that it attends to some degree to stimuli in both hemispaces, while the other hemisphere attends more exclusively to stimuli in contralateral space. For example, studies in hemispheric specialization of attentional processing have suggested that attentional activation in the hemispheres may normally be dominated by the right hemisphere (Heilman and Valenstein, 1979*b*; Weintraub and Mesulam, 1987). Physiological studies using PET, EEG and event-related fMRI have shown that specific components of the right hemisphere attentional system can be activated with presentation of stimuli in either right or left space, whereas these components of left hemispheric attentional systems are activated primarily when stimuli are presented in right space (Heilman and Van Den Abell, 1980; Corbetta *et al*., 1993; Perry and Zeki, 2000). Consistent with this hypothesis is the observation that hemispatial neglect is less common following left than right hemisphere injury, presumably because a remaining healthy right hemisphere may attend to both hemispaces.

The effects of hemispace on line bisection performance may also be explained by positing the dominance of attention of one hemisphere for both spaces. In this case, in right eye dominant subjects, attentional systems in the right hemisphere may be activated to some degree by presentation of stimuli in either hemispaces, whereas attentional systems in the left hemisphere are activated primarily by stimuli presented in right space. Since the right hemispheric attentional systems are activated by stimuli in either hemispace, any effects of space should mainly be due to the differential participation of the left hemisphere. According to the postulate that the left hemisphere is attentionally biased toward near space, bisections should be nearer in right hemispace where the left hemisphere (and right hemisphere) is engaged, compared with bisections performed in left hemispace where only the right hemisphere is engaged. If the hemispheric organization of spatial attention is reversed in left eye dominant subjects, their left hemisphere may be able to attend to both sides of space while the right attends primarily to left space. We have hypothesized that in left eye dominant subjects, the right hemisphere is biased toward near space. In left eye dominant subjects, therefore, bisections should be nearer in left space when the right hemisphere is engaged, compared with right space where primarily the left hemisphere is engaged. These expectations are consistent with the results in the hemispace experiment.

In both eye dominance groups, the hemispatial placement of the stimuli influenced line bisection performance primarily when the non-dominant eye was used. The differences between dominant and non-dominant eye performance as a function of hemispace may also be related to hemispheric asymmetries in the allocation of spatial attention. For example, in right eye dominant people, whereas the left hemisphere primarily attends to right hemispace, the right hemisphere attends to both hemispatial fields. The opposite would be the case for people with left eye dominance. We have postulated that each eye preferentially interacts with the opposite hemisphere. The finding that when the dominant eye (e.g. right) is used during bisection performance there are minimal right-left hemispatial asymmetries can be explained by the asymmetrical hemispheric distribution of spatial attention, because the hemisphere contralateral to the dominant eye (e.g. left hemisphere) attends primarily to contralateral (e.g. right) hemispace, but the hemisphere ipsilateral (e.g. right) to the dominant eye is capable of attending to both hemispatial fields. Thus, when one is bisecting lines using the dominant eye, the hemisphere contralateral to the dominant eye will be activated by virtue of the fact that the dominant eye is being used, and the ipsilateral hemisphere will be activated because it can be activated in either space. Since both hemispheres are activated in both spaces, there will be little difference in performance when using the dominant eye. When, however, a subject is viewing the stimuli with the non-dominant (e.g. left) eye in the ipsilateral (e.g. left) hemispace, only the opposite hemisphere (e.g. right hemisphere) is activated because the non-dominant eye activates the contralateral (e.g. right) hemisphere, and the ipsilateral (e.g. left) space activates the contralateral (e.g. right) hemisphere. When using the non-dominant eye, therefore, a greater distal bias will be produced in ipsilateral (e.g. left) space, when only the contralateral (e.g. right) hemisphere is activated. In contrast, a relatively nearer bias will be produced when the stimulus is in contralateral (e.g. right) hemispace, when both the left and right hemispheres are activated.

The results of the first monocular viewing experiment might suggest that the dominant eye always produces nearer bisections compared with the non-dominant eye. But the hemispatial placement experiment shows that the dominant eye, relative to the non-dominant eye, produces relatively farther bisections in the ipsilateral side of space, even though in contralateral space it produces relatively nearer bisections. The hemispatial placement experiment also demonstrates that the dominant eye does not always produce the most accurate performance on the bisection task. For both eye dominance groups, in one hemispace the non-dominant eye produces bisections that are closer to the actual midpoint than the dominant eye, while in the other hemispace the dominant eye produces the bisection that is closer to the true midpoint (cf. Figs 3 and 4). These findings suggest that the relationship between eye dominance and spatial bias is not simply one of the dominant eye possessing a particular characteristic bias or performing more accurately. Our experiments were originally designed to test the hypothesis that each eye may engage attentional systems of the contralateral hemisphere preferentially. The differences found for near and far biases in the hemispaces in the dominant and non-dominant eyes in the hemispatial placement experiment are consistent with predictions based on this hypothesis. Therefore we suggest that the differences in dominant and non-dominant eye performances are related to differences in their engagement of the respective contralateral hemispheres as discussed above, rather than optical features.

The main effects of hemispace on line bisection biases for the right- and left-eye dominant groups appear to be opposite, and we have attributed this difference to a possible reversal of hemispheric specialization in left eye dominant subjects for near and far space. The effect of space in relation to viewing with the dominant and non-dominant eyes also shows a reversed pattern of near and far biases (cf. Figs 3 and 4). Although in both groups the non-dominant eye is more affected than the dominant eye by hemispatial placement (this forms the main basis for the significant interaction of eye and space in the separate analyses of each group), the effects on the non-dominant eye relative to space are in the opposite direction for each group. In left eye dominant subjects, the bias for the non-dominant eye is nearer in left space and farther in right space, whereas in the right eye dominant group, the bias for the non-dominant eye is nearer in right space and farther in left space.

Finally, it should be noted that the differences in bisection performance in the right versus left hemispace under monocular viewing conditions are not due to a spatial compatibility effect, where performance is superior when the stimulus is placed on the same side as the eye being used. In right eye dominant subjects, for example, the condition in which eye and space are ipsilateral but on the left side results in the greatest line bisection errors.

Concluding remarks

It has been known since the time of Paul Broca (Broca, 1861) and Marc Dax (Dax, 1865) that the right and left hemispheres are specialized for performing different functions. In the domain of visual spatial processing, it has been found that the left hemisphere more effectively processes local aspects of stimuli, features with high visuospatial frequency, and categorical spatial relationships, whereas the right hemisphere more effectively processes global aspects of stimuli, features with a low visuospatial frequency, and coordinates spatial relationships (Sergent, 1985; Delis *et al*., 1986; Kosslyn *et al*., 1989; Van Kleeck, 1989; Kitterle and Christman, 1991). The hemispheres are also specialized with respect to how they attend to stimuli in space. In most right-handed people the left hemisphere attends primarily to right hemispace, whereas the right hemisphere attends to stimuli in both hemispaces. Of particular relevance to this study, the left hemisphere may be more attentive to activity in peripersonal or near space, and the right hemisphere to stimuli in extrapersonal or far space (Heilman *et al*., 1993*a*; Weiss *et al*., 2000). That the left hemisphere is biased more towards near space and the right hemisphere towards far space is consistent with the specialized activities mediated by these hemispheres. For example, the visually mediated cognitive activities performed by the left hemisphere, such as reading, writing, praxis, or the analysis of fine details are performed close to the body in peripersonal space. In contrast, most of the visual cognitive activities performed by the right hemisphere, such as facial and emotional recognition, route finding, and the analysis of lower spatio-temporal frequency and global relationships, take place away from the body in extrapersonal space.

Neurophysiological findings in primates have supported the distinction between near and far extrapersonal space, and have suggested that attentional processes mediate the distinction. A population of multi-modal neurones in the parietal cortex in area 7b was found, the activity of which is enhanced only by visual targets that approach the cutaneous field or by stationary stimuli within 5–10 cm of it (Leinonen and Nyman, 1979; Leinonen *et al*., 1979). Subsequent studies have shown that a region of the arcuate sulcus to which neurones in area 7b project also have properties of responding to stimuli depending on the distance away from the cutaneous field (Rizzolatti *et al*., 1981*a*, *b*).

Our study was designed to test whether monocular viewing could preferentially activate attentional systems of the contralateral hemisphere, and we expected that activation of the left hemisphere would produce a more peripersonal bias on radial line bisection tests than activation of the right hemisphere. The first monocular viewing experiment showed that right eye dominant subjects bisected radial lines relatively closer to their body when they used the right eye, and relatively farther away from their body when they used the left eye. These results provided support for the postulate that monocular viewing may preferentially activate attentional systems contralateral to the eye being used, and that whereas the left hemisphere has a proximal attentional bias, the right has a distal bias. Confirmation that the difference in bias induced by monocular viewing was mediated by increased attentional activation of the contralateral hemisphere was provided by the second experiment, which showed that right eye dominant subjects had changes in bisection bias when radial lines were placed in right and left hemispaces that were in the direction that would be predicted by hemispheric activation in the respective spaces.

The changes found with monocular viewing are thought to be related to asymmetries of retino-tectal pathways. As discussed in the Introduction, information entering one eye preferentially activates the contralateral colliculus, and since the contralateral colliculus is associated with attentional hemispheric systems on the same side, input from one eye may also result in increased activation of the contralateral hemisphere.

In addition to the crossed retino-tectal projections, there are asymmetries in the retino-geniculate system that might also contribute to the effects of monocular viewing. Studies in cats and primates have shown that the fibres from the nasal retina, which project contralaterally, outnumber the fibres from the temporal retina, which project ipsilaterally (Hubel and Wiesel, 1962; Perry *et al*., 1984). The difference in the number of fibres between the nasal and temporal retina is not completely attributable to the larger temporal field (of the nasal retina), which includes the monocular temporal crescent, because these nasal versus temporal differences are still present at small deviations from the vertical meridian. For example, within a circle of 5 mm radius around the fovea in the primate, there are 6% more fibres arising from the nasal retina than from the temporal retina (Perry *et al*., 1984). The nasal retina also has an increased density of fibres compared with the temporal retina (Østerberg, 1935; Stone and Johnston, 1981; Perry *et al*., 1984; Curcio *et al*., 1987). The increased density of fibres allows for the perceptive field centre sizes in the nasal retina to be slightly smaller than those in the temporal retina (Oehler, 1985; Spillmann *et al*., 1987). Consistent with these anatomic asymmetries, greater acuity at equal eccentricities from the fovea has been shown for the nasal retina compared with the temporal retina (Wertheim, 1894; Oehler, 1985; Spillmann *et al*., 1987; Merigan and Katz, 1990; Courage and Adams, 1996). Finally, nasal retina fibre diameters are also larger than temporal retinal fibre diameters and this could allow for faster transmission times (Bishop *et al*., 1953). In the behavioral domain, studies have shown that reaction times to suprathreshhold flashes of light are consistently quicker for nasal hemiretina (Poffenberger, 1912; Rains, 1963). If the nasal hemiretinal fibres outnumber, are faster, and produce finer spatial resolution images than the temporal hemiretinal fibres, when only one eye is used to view a stimulus, independent of the retinal position of the viewed stimulus, the hemisphere contralateral to the viewing eye may be preferentially activated and have a processing advantage. Providing further support for this possibility, a recent fMRI study showed that contralateral occipital cortex was more activated than the ipsilateral cortex when subjects viewed flashing lights with one eye (Toosy *et al*., 2001).

In the hemispatial placement experiment, when right eye dominant subjects performed radial bisections in either right or left hemispace, we found that the difference in performance between right space and left space was greater with left- than right-eye viewing. Other studies have found similar interactions in monocular viewing experiments, reporting that performance can differ much more depending on space of presentation for the left eye than for the right eye. In general these studies did not evaluate for eye dominance, but the majority of subjects were likely to have been right eye dominant since they are more common in the population. Overton and Wiener (1966) asked subjects to orally report briefly flashed words that were presented to either the right or left visual half fields under monocular viewing conditions. With the right eye, performance was the same for both fields of presentation, but with the left eye performance was superior for right field presentation compared with left field presentation. More recently, Zackon and colleagues examined the interaction between eye use and field of presentation using a task designed to investigate spatial attentional asymmetries (Zackon *et al*., 1997). They found that an effect of illusory motion changed with the laterality of cue presentation when the left eye was used, but not when the right eye was used.

In this study we suggest that interactions found between spatial placement and viewing eye (right versus left) can be explained by an asymmetry of the spatial distribution of the right and left hemispheres' attentional systems combined with the effect of monocular viewing on hemisphere engagement. For right eye dominant subjects, when stimuli are presented in right space or field, attentional processing may engage both hemispheres, whereas when stimuli are presented in the left space or field, attentional processing engages primarily the right hemisphere. In addition, the use of the right eye preferentially engages the left hemisphere, whereas use of the left eye preferentially engages the right hemisphere. Thus, in right eye dominant subjects, if activity of the left hemisphere provides a critical advantage in a task, poorest performance should be found under monocular viewing conditions with the left eye and with left-sided stimulus presentations. In this condition the left hemisphere is not engaged by either spatial attentional or eye engagement conditions, and the right hemisphere's bias should become most manifest.

An additional finding of this study was that eye dominance predicted whether subjects would have a relatively nearer bias with the left eye, or a relatively nearer bias with the right eye for stimuli in central space. Because the second experiment supported the conclusion that monocular viewing activates attentional systems of the hemisphere contralateral to the viewing eye, the differences between eye dominance groups are less likely to be related to peripheral (optical) differences between the dominant and non-dominant eye. Instead the results suggest that differences in performance between eye dominance groups may indicate that these groups have different hemispheric specialization for spatial attention. The hemispatial placement experiment also tested the hypothesis that left eye dominant subjects might have a reversal of hemispheric attentional bias to near and far space more directly, by having left eye dominant subjects perform radial bisections in left and right hemispace. Although further studies are needed to confirm this finding, the results suggest that the right hemisphere of left eye dominant subjects is biased toward near space and the left hemisphere is biased toward far space.

Eye dominance, like handedness, has a dextral population bias (65–70% of people are right eye dominant), and the preference for sighting eye is highly reliable within individuals (on repeated testing, 97% of subjects consistently use the same eye) (Porac and Coren, 1976, 1981). Although eye dominance has been thought to reflect a higher CNS processing bias because it is not related to simple differences in visual acuity (Crovitz, 1961; Coren and Kaplan, 1973; Coren and Porac, 1977), it has not been definitively linked with hemispheric dominance or hemispheric specialization of neuropsychological functions (Hayashi and Bryden, 1967; Kirssin and Harcum 1967; Sampson, 1969). The anatomic finding that each eye sends projections to both hemispheres is often cited as a possible explanation for why eye dominance has not been found to be related to hemispheric specialization and dominance. One of the few indications that a relationship between eye dominance and hemispheric functions might exist comes from studies of monkeys who prefer to sight with the eye opposite the remaining hemisphere after one of their hemispheres has been removed (Kruper *et al.*, 1967, 1971; Ettlinger and Dawson, 1969; Lehman, 1970).

Our study was different from previous studies that examined the relationship between eye dominance and cerebral hemispheric specialization, because previous studies measured cognitive processes that involved language whereas we measured non-verbal attentional processes. In our study, differences in eye dominance were associated with differences in attentional biases and the biases appeared to be associated with differences in hemispheric activation.

In summary, this investigation into the effects of monocular viewing on attentional biases in normal subjects demonstrated that normal subjects perform differently on the radial line bisection task depending on which eye they use. For those subjects with right eye dominance, there is a greater far bias and presumably greater allocation of attention to far extrapersonal space when subjects use the left eye compared with when they use the right eye. The attentional bias resulting from eye use is most likely mediated by preferential activation of attentional systems of the contralateral hemisphere. Our results are consistent with the view that the right hemisphere has a relative bias toward far space in the majority of people. The difference between differing eye dominance groups suggests that left eye dominant subjects may have a reversal of hemispheric attentional biases, such that in these subjects the left hemisphere may be dominant for attention to far space, and the right hemisphere for near space.

Few studies have previously systematically evaluated whether attentional systems are activated differently by the different eyes. Studies in the rehabilitation of spatial neglect have tested the possibility indirectly by attempting to treat patients suffering from neglect with eye patches designed to preferentially activate the hemisphere that was damaged, but not all of these studies have found the treatment effective. Our study found consistent differences in attentional bias depending on which eye is used to perform a task. These results suggest that approaches to rehabilitation using monocular viewing have potential merit, but that eye dominance differences may modify the effect in particular individuals.

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