



Horizontal saccadic eye movements enhance the retrieval of landmark shape and location information

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ABSTRACT

Recent work has demonstrated that horizontal saccadic eye movements enhance verbal episodic memory retrieval, particularly in strongly right-handed individuals. The present experiments test three primary assumptions derived from this research. First, horizontal eye movements should facilitate episodic memory for both verbal and non-verbal information. Second, the benefits of horizontal eye movements should only be seen when they immediately precede tasks that demand right and left-hemisphere processing towards successful performance. Third, the benefits of horizontal eye movements should be most pronounced in the strongly right-handed. Two experiments confirmed these hypotheses: horizontal eye movements increased recognition sensitivity and decreased response times during a spatial memory test relative to both vertical eye movements and fixation. These effects were only seen when horizontal eye movements preceded episodic memory retrieval, and not when they preceded encoding (Experiment 1). Further, when eye movements preceded retrieval, they were only beneficial with recognition tests demanding a high degree of right and left-hemisphere activity (Experiment 2). In both experiments the beneficial effects of horizontal eye movements were greatest for strongly right-handed individuals. These results support recent work suggesting increased interhemispheric brain activity induced by bilateral horizontal eye movements, and extend this literature to the encoding and retrieval of landmark shape and location information.

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1. Introduction

A rich understanding of geographic information requires knowledge of both the characteristics of landmarks and their unique locations in space (e.g., Brown & Kosslyn, 1995; Brunyé & Taylor, 2008a, 2008b; Hegarty & Kozhevnikov, 1999). Indeed knowing the visual characteristics of Checkpoint Charlie is of minimal use to navigation without understanding its location within Berlin. Conversely, knowing which city area contains a phone booth is only useful when one complements this knowledge with the booth's unique shape, color, and size. Given the practical importance of accurately recalling memories for landmark characteristics and location, it is of interest to better understand how the brain accomplishes this feat and how it might be improved. Several decades of work in cognitive neuroscience demonstrate the importance of bilateral brain activity during the successful retrieval of landmark feature and location information (e.g., Aguirre & D'Esposito, 1997; Kohler, Moscovitch, Winocur, Houle, & McIntosh, 1998; Owen, Milner, Petrides, & Evans, 1996b; for a review, see Cabeza & Nyberg,

2000). The present study capitalizes on this work and examines whether facilitating the interactivity of right and left brain hemispheres through horizontal saccadic eye movements can enhance the retrieval of spatial (location) and non-spatial (shape) information.

Interaction between the right and left cerebral hemispheres is essential to the performance of many complex cognitive tasks, including old/new recognition in episodic memory paradigms (i.e., Nolde, Johnson, & Raye, 1998). Recent research suggests that one way to increase baseline interhemispheric brain interaction is via repetitive bilateral horizontal saccades (for a review, see Propper & Christman, 2008). These saccades involve repetitively moving one's eyes from side to side in response to a visual cue (e.g., Propper, Pierce, Bellorado, Geisler, & Christman, 2007). A number of recent studies incorporating a variety of verbal learning paradigms have demonstrated that such eye movements can improve episodic memory (e.g., Christman, Garvey, Propper, & Phaneuf, 2003; Christman, Propper, & Dion, 2004; Lyle, Logan, & Roediger, 2008; Parker & Dagnall, 2007). Further, some work suggests that these horizontal saccadic eye movements can enhance the retrieval of non-verbal episodic memories, such as memory for word color and location (Parker, Relph, & Dagnall, 2008), intentionally-encoded object color (Lyle, 2008), and memory for visual details gathered from a slide show (Parker, Buckley, & Dagnall, 2009).

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The present studies test three primary assumptions derived from this work. First, increased interhemispheric interaction should benefit performance on a non-verbal object shape and spatial location episodic memory task. Second, individuals with low baseline interhemispheric interaction such as strong right-handers (e.g., Habib et al., 1991; Lyle, Logan, & Roediger, 2008; Lyle, McCabe, & Roediger, 2008; Witelson, 1985) should particularly benefit from horizontal saccadic eye movements (e.g., Christman, Propper, & Brown, 2006; Lyle, Logan, & Roediger, 2008; Lyle, McCabe, & Roediger, 2008). Finally, these eye movements should only improve performance when they precede a task necessitating a high degree of interhemispheric interaction (Christman et al., 2003, 2004, 2006). We begin by reviewing the literature demonstrating the positive effects of eye movements on episodic memory, then detail the motivation and hypotheses of our first study.

1.1. Eye movements and memory

The effects of rapid eye movements on episodic memory have attracted the attention of researchers for several decades, most notably (and controversially) as a potential treatment for post-traumatic stress disorder (EMDR; for a review see Shapiro, 2002). Recent work has examined rapid eye movements in non-clinical and carefully controlled experimental settings in an attempt to identify the mechanisms that might be responsible for their beneficial effects on episodic memory. In 2003, Christman and colleagues demonstrated that participants showed higher sensitivity on a recognition test when they performed horizontal saccadic eye movements (relative to vertical or no movements) immediately prior to retrieval. Overall, participants were better able to discriminate old versus new items after performing horizontal relative to vertical or fixated eye movements. In a second study, the authors applied the eye movement procedure to the retrieval of autobiographical memories. Participants kept journals of unusual personal events for a period of six days, and then two weeks later they were tested for their memory of the recorded events. Half of the participants performed horizontal eye movements immediately prior to retrieval, and half watched a dot change colors at the center of a computer monitor. Horizontal eye movements nearly doubled participants' sensitivity (d') on the retrieval test by increasing hit rates and decreasing false alarms.

Three later studies supported these results using verbal false memory paradigms, demonstrating lower false alarm rates and higher sensitivity following horizontal relative to fixated (Lyle, Logan, & Roediger, 2008; Lyle, McCabe, & Roediger, 2008) and vertical eye movements (Christman et al., 2004; Parker & Dagnall, 2007). In each study, the authors attributed the change in recognition sensitivity to an increase in interhemispheric communication between the left and right prefrontal cortices. Three primary neuroimaging findings support this idea. First, saccadic eye movements to the left are associated with increased brain activity in the contralateral hemisphere, providing some suggestion that bilateral saccades may increase bilateral brain activity (Bakan & Svorad, 1969). Second, bilateral horizontal eye movements alter prefrontal coherence (across hemispheres) in the Gamma frequency range while measuring brain activity with electro-encephalography (Propper et al., 2007). Finally, bilateral brain activity (particularly prefrontal activity) is implicated in episodic memory retrieval, particularly with demanding recognition tasks (Nolde, Johnson, & D'Esposito, 1998; Nolde, Johnson, & Raye, 1998). Taken together, these findings suggest that horizontal eye movements increase interhemispheric brain activity, and by doing so facilitate episodic memory retrieval and increase sensitivity during recognition tests.

Few studies, however, have examined the utility of eye movements in non-verbal memory paradigms (Lyle, 2008; Parker et al., 2008, 2009); if the memory advantages seen with verbal

materials can be attributed to increased interhemispheric activity then this effect should be seen across information formats. Like verbal episodic memory retrieval, the retrieval of object shape and spatial location information has also been shown to demand bilateral brain activity, particularly during sequential old/new recognition tests (e.g., Kohler et al., 1998; Nolde, Johnson, & D'Esposito, 1998; Nolde, Johnson, & Raye, 1998). The present studies test whether memory for landmark shape and spatial location information is improved following horizontal relative to vertical or fixated eye movements.

Another finding from the eye movement literature is that the benefits of horizontal eye movements are most evident in strongly right-handed individuals (Lyle, Logan, & Roediger, 2008; Lyle, McCabe, & Roediger, 2008). This finding is most likely attributable to right-handers having relatively low baseline interhemispheric brain interactivity (Christman et al., 2003, 2004; Christman et al., 2006), as evidenced by both neuroimaging (Nielsen, Abel, Lorrain, & Montplaisir, 1990) and behavioral studies (Christman, 1993; Hellige, 1993), and smaller overall corpus callosum sizes relative to mixed- and left-handed individuals (Clarke & Zaidel, 1994; Cowell, Kertesz, & Denenberg, 1993; Witelson, 1985). The notion is that given their lower baseline hemispheric interactivity and smaller corpus callosum size, strongly right-handed individuals are better suited to benefit from horizontal eye movements than those who are left-handed or only moderately right-handed. Further, given previous reports of inferior episodic memory in strongly right-handed individuals relative to the non-right-handed (e.g., Propper, Christman, & Phaneuf, 2005), the former individuals may be particularly suited to benefit from measures designed to improve episodic memory retrieval.

1.2. Interhemispheric activity during encoding and retrieval

The hemispheric encoding/retrieval asymmetry (HERA) model states that episodic encoding and retrieval processes involve predominantly left and right prefrontal activity, respectively (Habib, Nyberg, & Tulving, 2003; Nyberg, Cabeza, & Tulving, 1996; Tulving, Kapur, Craik, Moscovitch, & Houle, 1994). For instance, Owen and colleagues used positron emissions tomography (PET) to record brain activity during the encoding of object features and locations. In two studies, they found that object feature (Owen, Milner, Petrides, & Evans, 1996a) and location (Owen et al., 1996b) encoding were both left-lateralized in the frontal, parietal, and temporal lobes. In contrast, these same studies showed that retrieval of object feature and location information was right-lateralized across frontal brain regions. Similarly, Haxby et al. (1996) used PET to examine the encoding and retrieval of human faces, and found left- and right-lateralized frontal activity during memory encoding and retrieval, respectively. In all of the above work, the authors used two-alternative forced-choice recognition tasks.

Some work, in contrast, has demonstrated that unlike with forced-choice tests, relatively demanding recognition tasks elicit activity in both right and left prefrontal hemispheres during episodic memory retrieval (Nolde, Johnson, & D'Esposito, 1998; Nolde, Johnson, & Raye, 1998). For instance, whereas simple forced-choice recognition tasks appear to primarily activate the left prefrontal cortex, relatively complex sequential old/new recognition tasks appear to activate both right and left prefrontal cortices (i.e., Buckner, Koutstaal, Schacter, Wagner, & Rosen, 1998). The 'cortical asymmetry of reflective activity' (CARA) hypothesis summarizes several decades worth of data and extends the HERA model by stating that whereas encoding activity is primarily left-hemisphere dependent, in certain circumstances retrieval activity is bilateral (Nolde, Johnson, & D'Esposito, 1998; Nolde, Johnson, & Raye, 1998). It is likely the case that memory tasks requiring relatively complex reflective processes elicit involvement from the bilateral, rather

than unilateral right, prefrontal cortex. According to the CARA hypothesis, these processes are active during deliberate reflection, maintenance, and the self-cuing process involved in deliberately retrieving additional information in order to solve a retrieval task (Johnson, 1997; Nolde, Johnson, & D'Esposito, 1998; Nolde, Johnson, & Raye, 1998). This notion is in line with dual-process models of recognition memory, which state that the brain activity and cognitive processes involved during retrieval vary as a function of the demands imposed at test (Gardiner, 1988; Jacoby, 1991; Mandler, 1980). It is also in line with research showing that naïve versus repeated episodic retrieval tasks tend to elicit bilateral (versus right unilateral) activity in the prefrontal cortex, further suggesting that the inherent processing complexity of a task is positively associated with the extent of bilateral prefrontal brain activity (Wagner et al., 1997).

As mentioned above, the encoding of episodic memories is generally accepted as primarily left-hemisphere dependent, eliciting little right-hemisphere activity. This finding holds across a variety of stimulus types and experimental paradigms (for a review, see Cabeza & Nyberg, 2000). Recent work examining bilateral horizontal eye movements in episodic memory paradigms has consistently required participants to perform eye movements between episodic encoding and retrieval (Christman et al., 2003, 2004; Christman et al., 2006; Lyle, Logan, & Roediger, 2008; Lyle, McCabe, & Roediger, 2008). Because some episodic retrieval tasks appear to involve both left and right cortices, and horizontal eye movements seem to increase interactivity between these two hemispheres, participants show reliably increased task performance following horizontal relative to vertical or fixated eye movements. Our first experiment tests whether eye movements placed immediately prior to encoding versus prior to test would differentially affect memory performance on a sequential old/new recognition test. We expect that horizontal eye movements placed prior to retrieval will enhance memory for landmark shape and location information. In contrast, when these same eye movements are placed prior to encoding we do not expect them to enhance memory. These hypotheses are based on research demonstrating that the retrieval (i.e., Aguirre & D'Esposito, 1997; Kohler et al., 1998; for a review, see Cabeza & Nyberg, 2000), but not encoding (i.e., Kelley et al., 1998; Owen et al., 1996a), of landmark shape and location information demands activation of the bilateral prefrontal cortex.¹

2. Experiment 1

We used a non-verbal object appearance and spatial location memory task that has been shown to recruit primarily unilateral prefrontal brain regions during encoding but bilateral regions during retrieval (e.g., Aguirre & D'Esposito, 1997; Kohler et al., 1998). Participants learned an array of uniquely-shaped objects and then completed a yes/no recognition task. Either horizontal, vertical, or fixated eye movements were done immediately prior to or following encoding. The recognition task differentially tested memory for object shape and location information. We used this task to assess whether the results found with verbal materials can be generalized to non-verbal materials, and to assess whether eye movements can enhance memory when they are placed prior to versus following encoding. According to earlier work, it should be the case that horizontal eye movements do not enhance the integration of object location and shape information during encoding (given the unilateral basis of this process), but do facilitate the retrieval of these information types for application during a complex old/new recog-

ognition test (given the bilateral basis of this process). We also tested whether any performance changes introduced by horizontal eye movements are modulated by participant handedness. Recent work suggests that episodic memory enhancements due to horizontal eye movements are particularly pronounced in strongly right-handed individuals (Lyle, Logan, & Roediger, 2008; Lyle, McCabe, & Roediger, 2008).

2.1. Method

2.1.1. Participants and design

A total of 72 right-handed Tufts University undergraduates (38 female; mean age 19.12) were recruited to participate for monetary compensation. We used a mixed 3 (eye movement: horizontal saccade, vertical saccade, fixation) \times 2 (timing: eye movements before learning or before testing) design, with eye movement varied within- and timing between-participants. The order of the three eye movement conditions, as well as which of three stimulus sets was associated with each condition, were counterbalanced in a Latin square design across participants. Half of the participants performed eye movements immediately prior to learning ($n = 36$, 20 female), and half immediately prior to testing ($n = 36$, 19 female). Memory was tested using an object shape and spatial location old/new recognition test. All procedures were jointly approved by the Tufts University Institutional Review Board and the U.S. Army Research Institute of Environmental Medicine Human Use Review Committee.

2.1.2. Materials

2.1.2.1. Edinburgh handedness index. We used a modified version of the Edinburgh index (Schachter, 1994) to determine the extent of participant handedness on a continuum from left to right. Handedness scores can range from -100 (strongly left) to $+100$ (strongly right).

2.1.2.2. Maps. Four arrays of spatial (object location) and non-spatial (object shape) information were developed using satellite images of environments from industrial areas of Albany, NY, Pittsburgh, PA, Phoenix, AZ, and Atlanta, GA. Each array showed a brown and green land background surface with multiple low-elevation buildings. Each array was 1048×624 pixels, and was digitally-manipulated to conform to the following constraints: twelve uniquely-shaped landmarks (buildings), equal area occupied by landmarks relative to background, and pseudo-randomly placed landmarks with at least 3° visual angle separation from one another.

2.1.2.3. Eye movement stimuli. Three eye movement tasks were constructed. The horizontal saccade task depicted a single black dot subtending approximately 4° of visual angle, sequentially appearing in left and right vertically-centered positions on the computer monitor at 27° apart; the vertical saccade task was analogous to this, but appeared in top and bottom horizontally-centered positions (Christman et al., 2003; Lyle, Logan, & Roediger, 2008; Lyle, McCabe, & Roediger, 2008; Parker & Dagnall, 2007). The non-saccade task depicted a single colored dot subtending 4° of visual angle, sequentially appearing in the center position in six different colors (red, orange, yellow, green, blue, and purple) (Christman et al., 2006).

2.1.2.4. Recognition test. Four recognition tests were developed, one for each stimulus set. Each task contained 18 trials and tested for object shape and location memory by presenting a single test image for yes/no verification. Test images were created by using the original background image and digitally manipulating the presence and absence of particular landmarks. On each trial, a single old

¹ While not specifically considered here, object shape and location information are also generally considered to be processed in the ventral (what) and dorsal (where) pathways, respectively (i.e., Brown & Kosslyn, 1995; Goodale & Milner, 1992).

(previously studied) or new (previously unstudied) object appeared in either an old or new location against the otherwise object-free background. In this way we tested for shape and location memory in a 2×2 factorial design, crossing whether the object was old or new, and whether the location was old or new. The four trial types are as follows: old objects in their old locations (nine trials), old objects in new but previously-occupied locations (three trials), new objects in previously-occupied locations (three trials), and new objects in previously-unoccupied locations (three trials). Half of the trials were thus correct and half incorrect. Fig. 1 depicts a recognition trial comprised of an old object in an old location.

2.1.3. Procedure

Following informed consent, participants completed the Edinburgh Handedness Index, and were then seated at a 19" monitor connected to a Macintosh computer running SuperLab 4.0 (Cedrus Corporation., 2008). Participants completed four blocks: one practice and three experimental. The practice block involved a learning period and then recognition test, precisely matching the experimental block procedures but without an eye movement task. Each experimental block involved one of the three eye movement conditions (horizontal saccade, vertical saccade, and central fixation) placed either immediately prior to learning or testing, as a function of random group assignment.

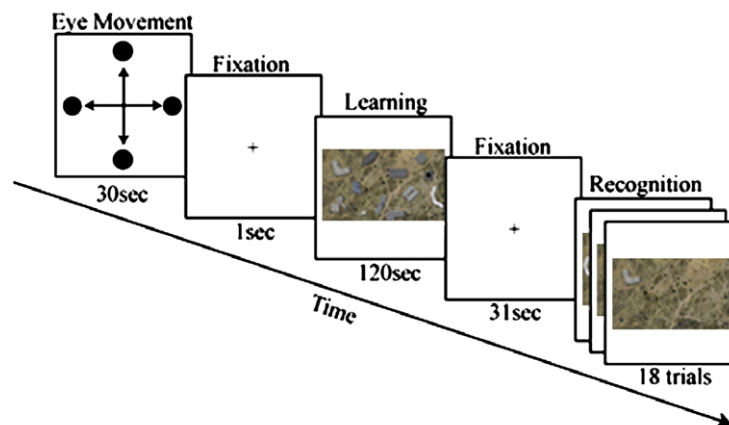
In the horizontal eye movement condition, participants watched a black dot move successively between left and right

positions at a rate of 500 ms per position, for a total of 30 s. The vertical eye movement condition was identical to this, but the dot moved successively between upper and lower positions. The non-saccade condition involved monitoring a central dot that rotated through a 6-color sequence for a total of 30 s. The experimenter confirmed that each participant was indeed tracking the dot position. When eye movement preceded learning, a 31-s fixation followed map study to equate the study-test intervals across the two participant groups (see Fig. 1). The spatial arrays were presented centered on the monitor for 120 s, and participants were instructed to learn everything they could about the array.

The old/new recognition test presented 18 trials in random order, and participants responded true or false via keys labeled as such (C and M, respectively). Each test trial timed out after 5 s without a response. Response times and accuracy were automatically recorded for each trial. Overall, the recognition test took approximately 30 s for participants to complete.

Participants took a 10-min break between each experimental block to mitigate carry-over effects. During this time participants walked around the building, talked to others, etc. We note that, to our knowledge, this is the first reported study that varies eye movement conditions within-participants. The duration of any eye movement effects on brain activity is unknown; we thus chose a large enough time period to allow participants to engage in activities entirely unrelated to the experimental paradigm. The 10-min time period is also outside of the typical duration of increased neural excitability induced by transcranial magnetic stimulation of the

Group 1: Eye movement before learning



Group 2: Eye movement before testing

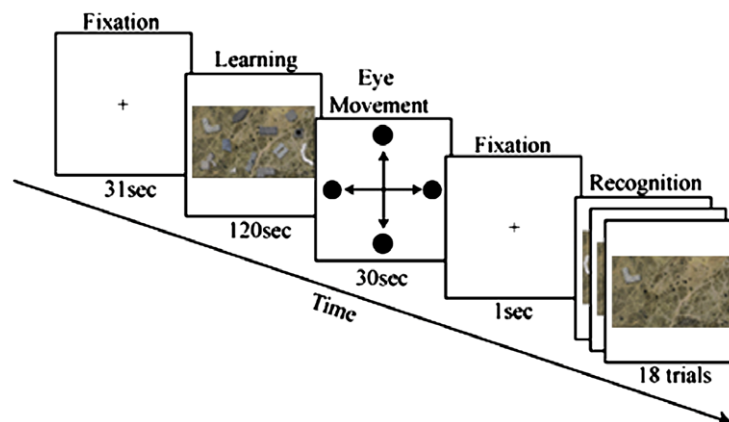


Fig. 1. Experiment 1 procedure for administering eye movement, encoding, and testing, for each of the two timing groups.

Table 1
Experiment 1 hit and false alarm rates.

Timing group and eye movement condition	Hit rate		False alarm rate	
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
<i>Pre-encoding</i>				
Horizontal	.84	.15	.10	.20
Vertical	.83	.13	.10	.19
Fixation	.84	.13	.10	.19
<i>Post-encoding</i>				
Horizontal	.90	.11	.04	.11
Vertical	.87	.13	.10	.21
Fixation	.86	.17	.10	.18

human cortex (i.e., 3–4 min; Pasqual-Leone, Valls-Solé, Wassermann, & Hallett, 1994); one might expect that saccadic eye movements could produce similar-duration effects in the prefrontal cortex, but this question remains unexplored.

2.2. Results

2.2.1. Handedness

Participant handedness ranged from +50 to +100, with a median of 80 ($SD = 15$); handedness scores were approximately evenly distributed about the mean (Shapiro-Wilk's $W = .94$, $p < .05$).

2.2.2. Eye movements and memory: sensitivity

Table 1 details hit and averaged false alarm rates for the three eye movement and two timing conditions. We used d -prime (d') as a composite measure of recognition sensitivity², and report Cohen's d as a measure of effect size. A 3 (eye movement: horizontal saccade, vertical saccade, fixation) \times 2 (timing: eye movements before learning or before testing) mixed-model analysis of variance (ANOVA) confirmed an effect of Eye Movement, $F(2, 140) = 3.44$, $p < .05$, $\eta^2 = .04$. Paired t -tests revealed higher sensitivity following horizontal eye movements relative to both vertical movements, $t(71) = 2.26$, $p < .05$, $d = .27$, and fixation, $t(71) = 2.16$, $p < .05$, $d = .25$ (vertical and fixation did not differ, $t(71) = .06$, $p = .95$).

The effect of eye movement interacted with timing, $F(2, 140) = 3.2$, $p < .05$, $\eta^2 = .04$. As depicted in Fig. 2, sensitivity following horizontal eye movements only increased when eye movements preceded test; this effect was confirmed by an independent-samples t -test comparing the two timing groups for relative sensitivity in the horizontal eye movement condition, $t(70) = 2.41$, $p < .05$, $d = .57$.

Overall, false alarm rates were low ($M = .09$, $SD = .18$), particularly on recognition trials containing a new landmark in a new location ($M = .06$, $SD = .16$). Recall that there were three possible false alarm types: old objects in incorrect locations ("location error"), new objects in previously-occupied locations ("shape error"), and new objects in previously-unoccupied locations ("total error"). In general, these three false alarm types were lower in the horizontal eye movement condition (location error: $M = .09$, $SD = .19$; shape error: $M = .05$, $SD = .12$; total error: $M = .05$, $SD = .16$) relative to the vertical (location error: $M = .16$, $SD = .24$; shape error: $M = .09$, $SD = .18$; total error: $M = .06$, $SD = .16$) and fixated (location error: $M = .12$, $SD = .20$; shape error: $M = .10$, $SD = .18$; total error: $M = .07$, $SD = .16$) conditions. A marginal effect of eye movement supported this pattern in a 3 (eye movement) \times 2 (timing) \times 3 (false alarm type) ANOVA, $F(2, 140) = 2.66$, $p < .10$, $\eta^2 = .04$. This pattern did not interact with false alarm type, $F(4, 280) = 1.03$, $p = .39$, but did interact marginally with timing, $F(2, 140) = 2.57$, $p < .10$, $\eta^2 = .03$, suggesting that the above differ-

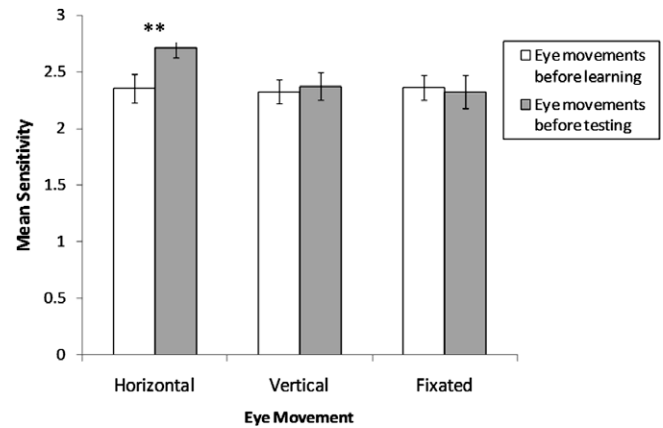


Fig. 2. Experiment 1 mean sensitivity and standard error on the recognition test for the three eye movement conditions and two timing groups. Asterisks indicate significant between-groups differences: ** = $p < .05$.

ences in false alarm rates were only present when eye movements preceded test.

In general, response bias (using c , Macmillan & Creelman, 1991; overall $M = .08$, $SD = .25$) did not vary as a function of eye movement, $F(2, 140) = .86$, $p > .10$, $\eta^2 = .01$, or timing group, $F(1, 70) = 2.4$, $p > .10$, $\eta^2 = .03$, and these two variables did not interact, $F(2, 140) = 1.29$, $p > .10$, $\eta^2 = .01$.

2.2.3. Eye movements and memory: response time (for HITS)

There were no main effects of eye movement or timing. As with sensitivity, eye movement interacted with timing, $F(2, 140) = 4.59$, $p < .05$, $\eta^2 = .06$. As depicted in Fig. 3, response times were fastest following horizontal eye movements, but only when the movements preceded test rather than study; this effect was confirmed in an independent-samples t -test, $t(70) = 2.28$, $p < .05$, $d = .54$. The two timing groups did not differ for vertical eye movements, $t(70) = .89$, $p = .38$, or fixation, $t(70) = .38$, $p = .71$.

2.2.4. Handedness and eye movements

To test whether strongly right-handed individuals were better able to benefit from eye movements, we conducted two analysis types: regression, and median split. Our first set of analyses tested whether handedness scores on the Edinburgh index could predict difference scores between the horizontal and fixated eye movement conditions (horizontal–fixated). Higher difference scores thus represent larger differences between an individual participant's

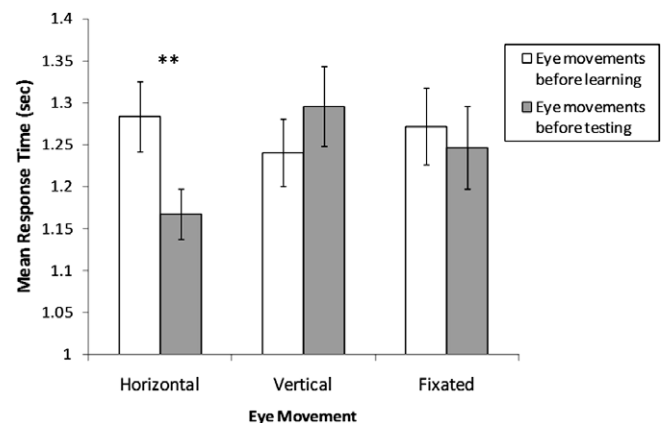


Fig. 3. Experiment 1 mean response time (to HITS) and standard error on the recognition test for the three eye movement conditions and two timing groups. Asterisks indicate significant between-groups differences: ** = $p < .05$.

² In cases where $FA = 0$ or $HIT = 1$, we used a standard correction of $1/(2N)$ for FA where N is the number of noise trials (9), and $1 - 1/(2N)$ for HIT where N is the number of signal trials (9). Further, sensitivity was calculated by collapsing across the three possible false alarm types (which are later considered separately).

sensitivity following horizontal relative to fixated eye movements. Higher scores on the Edinburgh index indicate stronger right-handedness. When eye movements preceded testing, right-handedness was a significant predictor of sensitivity difference scores; the association was positive, with higher Edinburgh scores predicting higher difference scores, $\beta = .22$, $t(35) = 1.97$, $p < .05$. This effect was marginal when using horizontal–vertical difference scores, $\beta = .22$, $t(35) = 1.89$, $p = .06$. No effects were found when these analyses were done on data from when eye movements preceded learning (all p 's $> .10$). These effects did not approach significance when examining response times.

Our second set of analyses was performed using a median split based on Edinburgh handedness scores. In the present data, handedness scores ranged from 50 to 100, with a median of 80; a median split produced a group of what we will label *strong right-handers* ($n = 33$) and *mixed right-handers* ($n = 39$); those participants with a handedness score of 80 were considered *mixed right-handers*. Within the pre-encoding timing group, there were 18 strong and 18 mixed right-handers; within the post-encoding timing group, there were 15 strong and 21 mixed right-handers. Within the pre-encoding timing group, we examined sensitivity and response time measures between the strong and mixed right-handers, and between the three eye movement conditions: a 2 (right-handedness: strong, mixed) \times 3 (eye movement: horizontal saccade, vertical saccade, fixation) mixed-model ANOVA on sensitivity data revealed no main or interactive effects of right-handedness or eye movement (all F 's < 1). The same was found when examining response times. Within the post-encoding timing group, however, sensitivity analyses revealed a marginal interaction between right-handedness and eye movement condition, $F(2,68) = 2.65$, $p = .07$, $\eta^2 = .06$. To follow-up on this effect, paired t -tests comparing fixated versus horizontal eye movements in each of the two groups revealed that the strongly right-handed benefitted from horizontal eye movements (fixated $M = 2.32$, $SD = .88$; horizontal $M = 2.69$, $SD = .51$), $t(14) = 2.98$, $p < .01$, $d = .77$, whereas the mixed right-handed did not (fixated $M = 2.36$, $SD = .67$; horizontal $M = 2.35$, $SD = .74$), $t(20) = 1.55$, $p > .10$, $d = .34$. Similar results were found when comparing vertical versus horizontal eye movements in each of the two groups: strong (vertical $M = 2.37$, $SD = .74$; horizontal $M = 2.69$, $SD = .51$), $t(14) = 3.30$, $p < .01$, $d = .85$, and mixed (vertical $M = 2.32$, $SD = .64$; horizontal $M = 2.35$, $SD = .74$), $t(14) = .99$, $p > .10$, $d = .22$. Response time analyses did not show a significant interaction ($F < 1$).

2.3. Discussion

The present study confirmed three assumptions derived from research on eye movements and interhemispheric communication in the brain. First, we tested whether an old/new non-verbal episodic memory task would benefit from horizontal eye movements much like what has been found with verbal tasks, and more recently non-verbal tasks (i.e., Christman et al., 2003, 2004; Lyle, 2008; Lyle, Logan, & Roediger, 2008; Lyle, McCabe, & Roediger, 2008; Parker & Dagnall, 2007; Parker et al., 2008, 2009). We extend recent research by uniquely demonstrating enhanced retrieval of landmark shape and location information as a result of horizontal eye movements. Indeed we found higher sensitivity, lower false alarms, and faster response times when participants performed horizontal eye movements prior to a sequential old/new recognition test requiring precise knowledge of what landmarks looked like (shape) and where they were located (spatial location).

Second, we examined whether individuals with low baseline interhemispheric interaction, as measured through handedness (Clarke & Zaidel, 1994; Habib et al., 1991; Nielsen et al., 1990; Witelson, 1985), would particularly benefit from horizontal eye

movements. In line with recent work demonstrating the pronounced effectiveness of horizontal eye movements in the strongly right-handed (Lyle, Logan, & Roediger, 2008; Lyle, McCabe, & Roediger, 2008), both regression and median-split analyses reveal that those with stronger right biases tend to show larger benefits of horizontal eye movements.

Third, we examined whether horizontal eye movements could enhance memory when they preceded the learning of landmark shape and location information. The idea was that if horizontal eye movements increase interhemispheric interactivity in the prefrontal cortex, the beneficial effects of these movements should only be seen when the task that immediately follows eye movement demands such interactivity. The encoding of shape and spatial location information in episodic memory appears to be predominantly left-lateralized in the prefrontal cortex (e.g., Buckner et al., 1998; Owen et al., 1996a, 1996b). As such, we did not expect that the acquisition of these information types would benefit from horizontal eye movements prior to encoding. This hypothesis was borne out, with this group of participants showing no performance changes with horizontal eye movements relative to fixation or vertical eye movements. It remains to be seen, of course, whether horizontal eye movements may enhance encoding when bilateral brain activity is demanded by the encoding task.

3. Experiment 2

Our second experiment examines whether the effects seen at retrieval in Experiment 1 can be modulated by the extent to which the retrieval task demands right and left prefrontal activity. The CARA hypothesis posits that the hemispheric basis of activity in the prefrontal cortex is contingent upon the reflective demands of a retrieval task (Nolde, Johnson, & D'Esposito, 1998; Nolde, Johnson, & Raye, 1998). One consistent finding is that relatively simple recognition tests, such as two-alternative forced-choice, primarily rely upon the right prefrontal cortex (e.g., Haxby et al., 1996; Moscovitch, Kapur, Kohler, & Houle, 1995; Owen et al., 1996b); in contrast, relatively complex sequential old/new recognition tests rely upon both prefrontal cortices (i.e., Buckner et al., 1998; Rugg, Fletcher, Frith, Frackowiak, & Dolan, 1996; Tulving, Markowitsch, Craik, Habib, & Houle, 1996). The latter was used in Experiment 1, and showed beneficial effects of horizontal eye movements when it immediately preceded recognition.

The second experiment attempts to replicate the effect of horizontal eye movements on old/new recognition performance and specifically compare it with a forced-choice recognition test. Old/new recognition tasks involve more elaborate recollective processing relative to forced-choice recognition tests, which are thought to be more dependent on familiarity (i.e., Aggleton & Shaw, 1996; Bastin & Van der Linden, 2003). Recent work suggests that eye movements (Parker et al., 2008) and mixed handedness (Propper & Christman, 2004) may enhance recollection by increasing hit rates and reducing false alarms during recognition. One explanation for these findings is that increased bilateral brain activity leads to increased performance on recognition tests that place demands on relatively associative and recollective memory processes (Parker et al., 2008). If this is the case, then horizontal eye movements should be particularly effective at enhancing performance when they precede old/new but not forced-choice recognition tests.

3.1. Method

3.1.1. Participants and design

A total of 72 right-handed Tufts University undergraduates (38 female; mean age 19.12) were recruited to participate for monetary compensation. We used a mixed 3 (eye movement: horizontal saccade, vertical saccade, fixation) \times 2 (test type: forced-choice,

old/new) design, with eye movement varied within- and test type between-participants. The order of the three eye movement conditions, as well as which of three stimulus sets was associated with each condition, were counterbalanced in a Latin square across participants. Half of the participants performed the forced-choice recognition test ($n = 36$, 20 female) and half the sequential old/new recognition test ($n = 36$, 18 female).

3.1.2. Materials

3.1.2.1. Edinburgh handedness index. As in Experiment 1, we used a modified version of the Edinburgh index to assess participant handedness (Schachter, 1994).

3.1.2.2. Maps and eye movement stimuli. We used the same maps and eye movement stimuli as in Experiment 1.

3.1.2.3. Recognition tests. The sequential old/new recognition test matched that used in Experiment 1. The forced-choice recognition test used a two-alternative configuration. The task contained 12 trials which tested for object shape and location memory. On each trial, two stimulus arrays were presented to the left and right of center. Each map depicted a single old (previously studied) or new (previously unstudied) object presented in either an old or new location against the otherwise object-free background. Half of the trials depicted the target (old) stimulus on the left, and half on the right. A second version of each test reversed the location of the correct stimulus (left to right, right to left), across participants.

3.1.3. Procedure

The procedure followed that of Experiment 1 when eye movements preceded testing, with the addition of the forced-choice recognition test. The forced-choice recognition test presented trials in random order, and participants selected which of two stimuli displayed to the left and right of center was correct (old). Participants responded 'left' or 'right' via keys labeled as such (C and M, respectively). As in Experiment 1, each test trial timed out after 5 s without a response, and response times and accuracy were automatically recorded.

3.2. Results

3.2.1. Handedness

Participant handedness ranged from +40 to +100, with a median of 80 ($SD = 16$); handedness scores were approximately evenly distributed about the mean (Shapiro-Wilk's $W = .94$, $p < .05$).

3.2.2. Eye movements and memory: sensitivity

Table 2 details hit rates and averaged false alarm rates for the three eye movement and two timing conditions. As in Experiment 1, we used d -prime (d') as a composite measure of recognition sensitivity, and report Cohen's d as a measure of effect size. A 3 (eye movement: horizontal saccade, vertical saccade, fixation) \times 2 (test type: forced-choice, old/new) mixed-model analysis of variance (ANOVA) confirmed an eye movement by test type interaction, $F(2, 140) = 3.35$, $p < .05$, $\eta^2 = .05$. Within the old/new test group, paired t -tests revealed higher sensitivity following horizontal eye movements relative to both vertical movements, $t(35) = 2.29$, $p < .05$, $d = .38$, and fixation, $t(35) = 2.51$, $p < .05$, $d = .41$ (vertical and fixation did not differ, $t(35) = .42$, $p = .68$). These effects were not found in the forced-choice group (all t 's < 1). As depicted in Fig. 4, sensitivity following horizontal eye movements only increased on the old/new test type; this effect was confirmed by an independent-samples t -test comparing the two test type groups for relative sensitivity in the horizontal eye movement condition, $t(70) = 2.25$, $p < .05$, $d = .53$.

Table 2

Experiment 2 hit and false alarm rates.

Test type group and eye movement condition	Hit rate		False alarm rate	
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
<i>2AFC test</i>				
Horizontal	.93	.09	.08	.15
Vertical	.89	.12	.11	.16
Fixation	.93	.09	.09	.16
<i>Old/new test</i>				
Horizontal	.86	.09	.06	.15
Vertical	.80	.12	.11	.16
Fixation	.80	.09	.11	.16

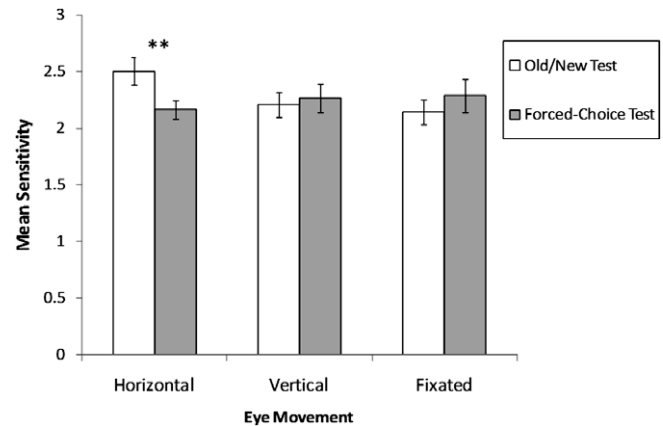


Fig. 4. Experiment 2 mean sensitivity and standard error on the recognition test for the three eye movement conditions and two test type groups. Asterisks indicate significant between-groups differences: ** = $p < .05$.

Overall, false alarm rates were low ($M = .09$, $SD = .03$), particularly on recognition trials containing a new landmark in a new location ($M = .07$, $SD = .02$). Replicating Experiment 1, the three false alarm types were generally lower in the horizontal eye movement condition (location error: $M = .06$, $SD = .15$; shape error: $M = .08$, $SD = .14$; total error: $M = .05$, $SD = .19$) relative to the vertical (location error: $M = .12$, $SD = .18$; shape error: $M = .10$, $SD = .18$; total error: $M = .09$, $SD = .19$) and fixated (location error: $M = .11$, $SD = .20$; shape error: $M = .10$, $SD = .20$; total error: $M = .09$, $SD = .18$) conditions. A marginal effect of eye movement supported this pattern in a 3 (eye movement) \times 2 (test type) \times 3 (false alarm type) ANOVA, $F(2, 140) = 2.81$, $p < .10$, $\eta^2 = .04$. This pattern did not interact with false alarm type, $F(4, 280) = .43$, $p = .79$, but did interact marginally with test type, $F(2, 140) = 2.63$, $p < .10$, $\eta^2 = .02$, suggesting that the above differences in false alarm rates were only present with the old/new and not the forced-choice test.

3.2.3. Eye movements and memory: response time (for HITS)

A main effect of test type revealed overall faster response times on the old/new test ($M = 1.28$, $SE = .03$) relative to the forced-choice test ($M = 1.91$, $SE = .03$), $F(2, 140) = 7.21$, $p < .01$, $\eta^2 = .72^3$. As with sensitivity, eye movement interacted with test type, $F(2, 140) = 5.42$, $p < .05$, $\eta^2 = .07$. In the old/new test group, response

³ Note that this effect runs counter to the notion that old/new tests are more demanding than forced-choice tests (i.e., Yonelinas, 2002). However, we note that with the forced-choice test, participants must study two arrays (rather than one) in order to make an accurate determination. Further, it is debated whether response time measures can accurately index the "difficulty" of component processes involved in task completion; for instance, time taken to complete two familiarity judgments may exceed that taken to perform a single recollective judgment, despite the relative complexity of the latter (see also, Dewhurst, Holmes, Brandt, & Dean, 2006; Gardiner, Konstantinou, Karayianni, & Gregg, 2005; Nolde et al., 1998).

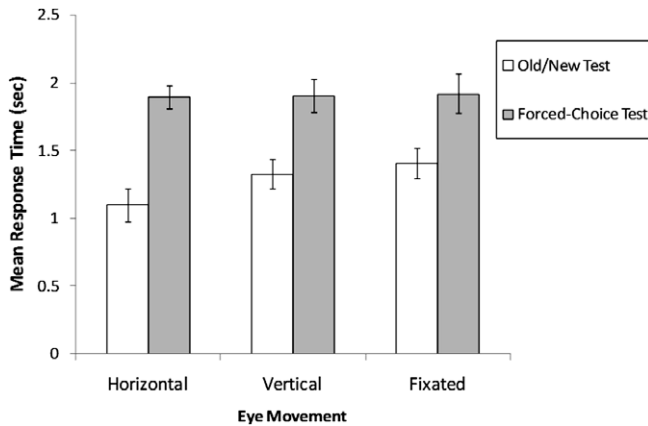


Fig. 5. Experiment 2 mean response time (to HITS) and standard error on the recognition test for the three eye movement conditions and two test groups.

times were fastest following horizontal eye movements relative to vertical, $t(35) = 3.23$, $p < .01$, $d = .54$, and fixated, $t(35) = 4.49$, $p < .01$, $d = .75$, eye movements (see Fig. 5). This was not the case with the forced-choice test (all t 's < 1).

3.2.4. Handedness and eye movements: sensitivity

As in Experiment 1, we tested whether strongly right-handed individuals were better able to benefit from eye movements, by using two analysis types: regression, and median split. Regression analyses revealed that within the old/new test type, right-handedness was a significant predictor of sensitivity difference (horizontal–fixation) scores; the association was positive, with higher Edinburgh scores predicting higher difference scores, $\beta = .64$, $t(35) = 4.81$, $p < .01$. This effect was also evident when using horizontal–vertical difference scores, $\beta = .42$, $t(35) = 2.71$, $p < .01$. No effects were found when performing these analyses with difference scores from the forced-choice test (all p 's $> .10$).

Our second set of analyses was performed using a median split based on Edinburgh handedness scores. In the present data, handedness scores ranged from 40 to 100, with a median of 80; a median split produced a group of what we will label *strong right-handers* ($n = 38$) and *mixed right-handers* ($n = 34$); those participants with a handedness score of 80 were considered *mixed right-handers*. Within the forced-choice test type group, there were 18 strong and 18 mixed right-handers; within the old/new test type group, there were 20 strong and 16 mixed right-handers. Within the forced-choice test type group, we examined sensitivity and response time measures between the strong and mixed right-handers, and between the three eye movement conditions: a 2 (right-handedness: strong, mixed) \times 3 (eye movement: horizontal saccade, vertical saccade, fixation) mixed-model ANOVA on sensitivity data revealed no main or interactive effects of Right-handedness or eye movement (all p 's $> .10$). The same was found when examining response times. Within the old/new test type group, however, sensitivity analyses revealed an interaction between Right-handedness and eye movement condition, $F(2,68) = 5.67$, $p < .01$, $\eta^2 = .13$. To follow-up on this effect, paired t -tests comparing fixated versus horizontal eye movements in each of the two handedness groups revealed that the strongly right-handed benefitted from horizontal eye movements (fixated $M = 2.14$, $SD = .81$; horizontal $M = 2.50$, $SD = .59$), $t(19) = 4.47$, $p < .01$, $d = 1.0$, whereas the mixed right-handed did not (fixated $M = 2.29$, $SD = .50$; horizontal $M = 2.17$, $SD = .68$), $t(15) = .77$, $p > .10$, $d = .19$. Similar results were found when comparing vertical versus horizontal eye movements in each of the two groups: strong (vertical $M = 2.21$, $SD = .74$; horizontal $M = 2.50$, $SD = .59$), $t(19) = 2.50$, $p < .05$,

$d = .56$, and mixed (vertical $M = 2.26$, $SD = .54$; horizontal $M = 2.17$, $SD = .68$), $t(15) = .62$, $p > .10$, $d = .15$, respectively. Response time analyses did not show a significant interaction ($F < 1$).

In general, response bias (overall $M = .08$, $SD = .28$) did not vary as a function of eye movement, $F(2,140) = .26$, $p > .10$, $\eta^2 < .01$, or timing group, $F(1,70) = .4$, $p > .10$, $\eta^2 < .01$, and these two variables did not interact, $F(2,140) = .13$, $p > .10$, $\eta^2 < .01$.

3.3. Discussion

As hypothesized, we replicated Experiment 1 results demonstrating increased old/new recognition sensitivity following horizontal relative to vertical or fixated eye movements; with the forced-choice test, however, performance did not vary as a function of eye movements. These results converge with a dual-process model of recognition memory, suggesting that forced-choice tasks are served by familiarity and old/new tasks are potentially served by both familiarity and relatively complex recollective processes (Bastin & Van der Linden, 2003; Gardiner, 1988; Jacoby, 1991; Mandler, 1980). Recent work posits that success in recollection is related to both frontal executive function (Anderson et al., 2008) and the extent of prefrontal brain activity as measured by fMRI (for a review, see Skinner and Fernandes, 2007). These same results do not hold for tests of familiarity. These findings suggest that recollection and familiarity are supported by or require dissociated patterns of brain activity, particularly in the frontal lobes. Results of the present studies suggest that recollective (but not familiarity-based) processes that are the locus of the prefrontal cortex might be particularly enhanced by horizontal saccadic eye movements. Finally, we support the results of Experiment 1, in that strongly right-handed individuals benefitted most from these eye movements; again, this effect only occurred on the old/new and not the forced-choice recognition test.

4. General discussion

Given the work demonstrating a high degree of bilateral prefrontal brain activity during the retrieval of shape and location memory during sequential old/new recognition tests (e.g., Buckner et al., 1998; Kohler et al., 1998; Nolde, Johnson, & D'Esposito, 1998; Nolde, Johnson, & Raye, 1998), the present results support the notion that horizontal relative to vertical or fixated eye movements enhance interhemispheric interactivity and benefit episodic memory retrieval. Unilateral saccades increase prefrontal brain activity in the contralateral hemisphere (Bakan & Svorad, 1969). When eye movements are done bilaterally, this effect may lead to increased interactivity between the two prefrontal hemispheres; indeed recent work finds altered EEG coherence in these brain areas following horizontal eye movements (Propper et al., 2007). Hemispheric interactivity may help integrate activities that are typically the locus of left (production of information, monitoring specific memory characteristics; Cabeza, Locantore, & Anderson, 2003) and right (monitoring of general or undifferentiated information; Mitchell, Johnson, Raye, & Greene, 2004) prefrontal cortices.

Relatively complex old/new recognition tests involve bilateral prefrontal activation for successful performance (see the CARA hypothesis; Nolde, Johnson, & D'Esposito, 1998; Nolde, Johnson, & Raye, 1998). The old/new task reliably elicited effects of horizontal eye movements across both experiments, unlike the relatively simple forced-choice test. It appears to be the case that horizontal saccadic eye movements do not benefit performance on all episodic memory tasks, but rather only those that demand bilateral brain activity. Our results support the notion that horizontal eye movements facilitate interhemispheric communication, and provide further support for the CARA hypothesis. In a general sense,

horizontal eye movements increased sensitivity and decreased response times on old/new recognition tests. To our knowledge, this is the first evidence that horizontal eye movements might improve response times on recognition tests involving the recollection of item-specific (i.e., shape) and contextual (i.e., location) information. It could be the case that an increase in bilateral activity in the prefrontal cortex enhances the retrieval of associated landmark location and shape information, and thus cueing a single object property at test quickly activates memory for the “missing” object property (i.e., shape or location). Evidence for such a process comes from work demonstrating that relatively rapid recollection can occur in cases where test items are designed to cue contextual details about an item (Dewhurst et al., 2006; Gardiner et al., 2005). In any case, more research is needed to specifically associate interhemispheric interactivity in the prefrontal cortex to the types of benefits seen in the present study.

In both experiments we found evidence that strongly right-handed individuals stand to benefit more from horizontal eye movements relative to those without strong right-handedness. This finding further supports the theory that horizontal eye movements enhance interhemispheric activity, as it posits that the effectiveness of these eye movements should be predicted by the degree of participant right-handedness (Christman et al., 2003; Propper & Christman, 2004). It seems to be the case that individuals with lower baseline interhemispheric interactivity (the strongly right-handed) benefit more from horizontal eye movements than those with relatively high baseline activity. In fact, recent work suggests that those with mixed handedness may actually suffer on episodic memory tests relative to the strongly right-handed following horizontal eye movements (see Lyle, Logan, & Roediger, 2008; Lyle, McCabe, & Roediger, 2008 for an explanation of this effect).

Additional research is needed, including the examination of the distinct neural areas that may be differentially activated by retrieval tasks following horizontal versus vertical or fixated eye movements. At present, it appears to be the case that horizontal eye movements can benefit episodic memory retrieval for not only verbal information, but also spatial information that requires the recollection of associated landmark shape and location. This effect is only found when the memory task demands bilateral brain activity, and appears to be particularly true for strongly right-handed individuals. These findings hold promise for enhanced spatial learning and navigation performance in individuals with low baseline interhemispheric activation. Horizontal eye movements may be one way to facilitate optimal binding of spatial and non-spatial information prior to the retrieval and application of knowledge to complex spatial tasks.

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