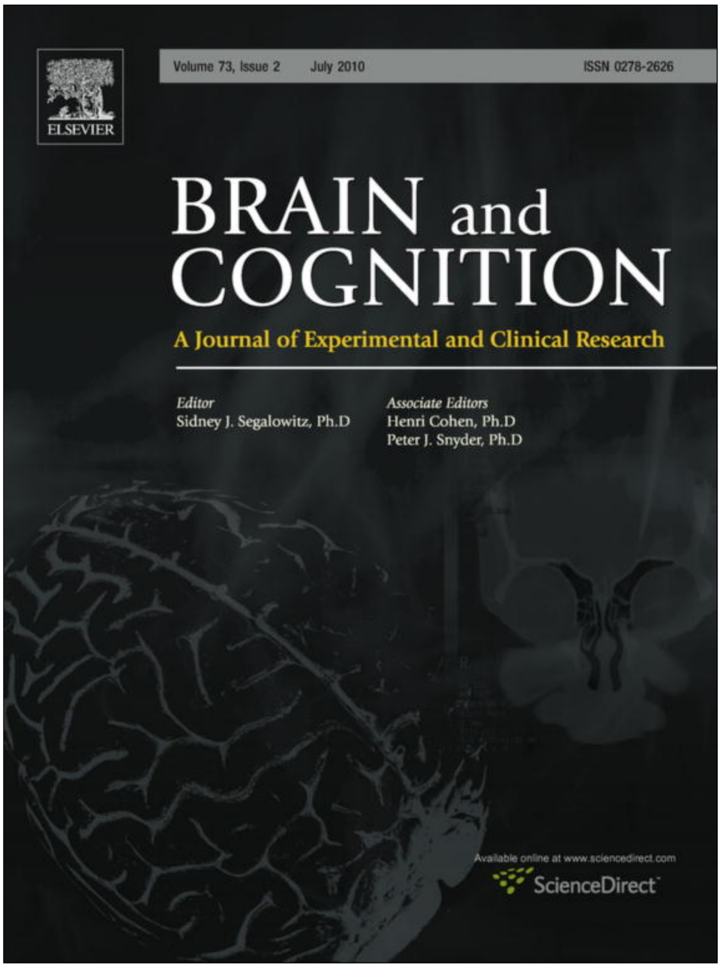
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Bilateral saccades increase intrahemispheric processing but not interhemispheric interaction: Implications for saccade-induced retrieval enhancement ☆

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Retrieval of memories is enhanced when bilateral saccades are made immediately before attempting retrieval. One hypothesis is that saccades enhance retrieval by increasing interaction of the brain hemispheres. To test this, subjects viewed arrays of lateralized letters and indicated whether target letters matched either of two probe letters. Matching targets and probes were presented to either the same hemisphere (within-hemisphere trials) or separate hemispheres (across-hemisphere trials). Match detection requires interhemispheric interaction on across-hemisphere trials but primarily intrahemispheric processing on within-hemisphere trials. Subjects performed letter matching following saccades and a fixation control condition. Saccades increased match-detection accuracy on within-hemisphere trials only, suggesting that, counter to the hypothesis, saccades enhance intrahemispheric processing but not interhemispheric interaction. Across-hemisphere accuracy was higher, however, for subjects who were not strongly right-handed, versus those who were, and the absence of strong right-handedness may reflect greater interhemispheric interaction. We discuss implications for accounts of saccade-induced retrieval enhancement.

1. Introduction

Several laboratories have recently reported a remarkable finding: Making alternating bilateral (i.e., left–right) saccades to follow a flashing dot for 30 s immediately before the retrieval phase of a memory test enhances subsequent retrieval compared to maintaining fixation on a stationary dot. Saccade-induced retrieval enhancement (SIRE) occurs across a range of test types and stimuli. For example, saccades increase recall of studied words (while decreasing false recall of non-studied words, e.g., Lyle, Logan, & Roediger, 2008, Experiment 1), discrimination between target words and lures on recognition tests (e.g., Christman, Garvey, Propper, & Phaneuf, 2003, Experiment 1; Lyle, Logan, et al., 2008, Experiment 2; Parker & Dagnall, 2007), recall of autobiographical events (Christman et al., 2003, Experiment 2), and recognition of objects in their correct spatial locations (Brunyé, Mahoney, Augustyn, & Taylor, 2009). Lyle, Logan, et al. (Experiment 2) found enhanced retrieval compared not only to the standard fixation control condition, but also to a condition in which subjects were allowed to do whatever they wanted—and thus move their eyes freely—while getting ready for an upcoming memory test. Hence, saccades apparently enhance retrieval beyond what people would naturally achieve, suggesting they may be a potential means of enhancing memory in real-world settings.

SIRE is an increasingly well-documented empirical phenomenon, but its cause remains mysterious. Why does making saccades affect the subsequent retrieval of episodic memories? In the first published report of SIRE, Christman et al. (2003) hypothesized that alternating bilateral saccades enhance retrieval by temporarily enhancing interaction of the left and right brain hemispheres. More specifically, Christman et al. based their hypothesis on three assumptions: one, that saccades equalize activation levels of the two hemispheres; two, that equalization of hemispheric activation levels allows the hemispheres to work together, or interact, more efficiently; and, three, that enhanced interhemispheric interaction facilitates episodic retrieval because retrieval is a task that depends on such interaction, at least to some extent. All three assumptions can be questioned on the grounds that what is meant by "equalization of activation levels" and "interhemispheric interaction" is underspecified, and because there is little evidence establishing causal relationships between saccades and changes in the relative activation of the two hemispheres, between equalization of across-hemisphere activation and enhanced interhemispheric interaction, or between enhanced interhemispheric interaction and episodic retrieval. Despite these limitations, all subsequent researchers (including the first author, in Lyle, Logan, et al., 2008) have

☆ This research was conducted for an undergraduate honors thesis by Jessica M. Martin.

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featured the interhemispheric interaction hypothesis prominently when contemplating SIRE's cause.

One reason the interhemispheric interaction hypothesis may seem at least plausible is that there are correlational data suggesting a positive association between degree of interhemispheric interaction (as indexed by interhemispheric connectivity) and episodic retrieval. One source of these data is research with split-brain patients, in whom the corpus callosum—the major pathway of interhemispheric connectivity and hence interaction—has been surgically severed. Split-brain patients show moderate deficits on some tests of episodic memory (e.g., Cronin-Golomb, Gabrieli, & Keane, 1996; Phelps, Hirst, & Gazzaniga, 1991). Other studies that more tenuously imply a positive correlation between interhemispheric interaction and retrieval are those showing that individuals who are strongly right-handed (SR) perform more poorly than individuals who are not (nSR; i.e., left- or weakly right-handed) on memory tests believed to involve interhemispheric interaction during retrieval (e.g., Lyle, McCabe, & Roediger, 2008; Propper, Christman, & Phaneuf, 2005). This finding relates to the role of interhemispheric interaction in retrieval because some studies (e.g., Cowell, Kertesz, & Denenberg, 1993; Witelson, 1985), although not others (e.g., Welcome et al., 2009), have found that some regions of the corpus callosum are smaller in SR than nSR individuals. Hence, a possible explanation for SR individuals' poorer memory performance is that they have less interhemispheric interaction than nSR individuals. It also bears noting that, in Lyle, Logan, et al. (2008) and Brunyé et al. (2009), SIRE occurred for SR but not nSR individuals (also, in Christman, Propper, & Brown, 2006, the effect of saccades, while statistically indistinguishable for the two groups, was noticeably larger for SR than nSR individuals). This is broadly consistent with an account of SIRE in terms of interhemispheric interaction because, if saccades affect interhemispheric interaction, they may be expected to have different effects on individuals with putatively different baseline degrees of interaction.

Even assuming some forms of retrieval do depend, to some extent, on interhemispheric interaction, as we have argued elsewhere (Lyle, McCabe, et al., 2008), there is no direct evidence that making saccades causes an increase in interaction (but see Propper, Pierce, Bellorado, Geisler, & Christman, 2007, for EEG evidence that saccades *alter* interaction in some way). However, certain neural correlates of saccades (either consequences or antecedents) are fairly well established. Among the best documented of these is that making saccades to orient attention to visual stimuli in the environment, such as the spatially alternating dots in SIRE studies, is associated with increased activity bilaterally in the intraparietal sulci (e.g., de Haan, Morgan, & Rorden, 2008; Moon et al., 2007; see also Corbetta, 1998, for a review of earlier research). While one could speculate that saccade-related bilateral recruitment of intraparietal sulcus (and other regions; see, e.g., Petit, Clark, Ingeholm, & Haxby, 1997, Fig. 1) equalizes across-hemisphere activation levels and/or enhances interhemispheric interaction, it seems possible to us that activating intraparietal sulcus affects subsequent memory retrieval without assuming anything about altered interhemispheric dynamics. This is so because there is growing appreciation that intraparietal sulcus may be involved in retrieval of episodic memories (Cabeza, 2008; Ciaramelli, Grady, & Moscovitch, 2008). Perhaps recruiting intraparietal sulcus during the saccade activity in SIRE studies promotes or increases the region's functional contribution to subsequent retrieval tasks.

Although other explanations for SIRE are possible, the interhemispheric interaction account has been by far the most prominent to date. Therefore, in the present study, we sought to test as directly as possible the core assumption of the account, which is that making saccades increases interhemispheric interaction. We examined the effect of saccades on a simple letter-matching task that can be performed under conditions that either do or do not require interhemispheric interaction (Banich & Belger, 1990). In the version of the task used here, three letters are briefly flashed on a computer screen around a central fixation cross (see Fig. 1 for examples). A lowercase target letter is presented below and to either the left or right of fixation. Two uppercase probe letters are presented above and to the left and right of fixation. Subjects' task is to press a key as quickly as possible if the name of the lowercase target letter matches the name of either of the uppercase probe letters. If the target and a matching probe are presented in the same visual field (within-hemisphere trials), then the two letters are processed within the same hemisphere and interhemispheric interaction is not necessary to detect the match. In contrast, if the target and a matching probe are presented in different visual fields (across-hemisphere trials), they are processed in different hemispheres and interhemispheric interaction is necessary for match detection. Split-brain patients can detect letter-name matches under conditions approximating those of within- but not across-hemisphere trials (Eviatar & Zaidel, 1994), supporting a greater role for interhemispheric interaction in the latter than the former. Uppercase probes and lowercase targets were used in the present study because, when probes and targets appear in the same case in this task, accuracy is nearly perfect (e.g., Compton & Mintzer, 2001; Reuter-Lorenz & Stanczak, 2000; Reuter-Lorenz, Stanczak, & Miller, 1999) and we sought to avoid a potential ceiling effect when testing whether bilateral saccades increase accuracy in this task (see below).

If saccades increase interhemispheric interaction, a straightforward prediction is that, relative to fixation, saccades should enhance performance (accuracy, response time, or both) on across-hemisphere trials. Furthermore, if one assumes, as discussed above, that increased interaction results from increased activity within each hemisphere (Christman et al., 2003), one might expect saccades to increase intrahemispheric processing, as well, and therefore also enhance performance on within-hemisphere trials.

An alternative prediction about the effect of saccades on letter matching arises from the observation that visually-guided saccades are associated with activation of regions within the intraparietal sulci. Intraparietal sulcus is involved in attentional processing (Corbetta & Shulman, 2002), although the exact nature of its involvement is, as yet, undetermined. Banich (1998) argued that within-hemisphere letter matching imposes greater attentional demands on the hemisphere that must detect the match than across-hemisphere letter matching imposes on either

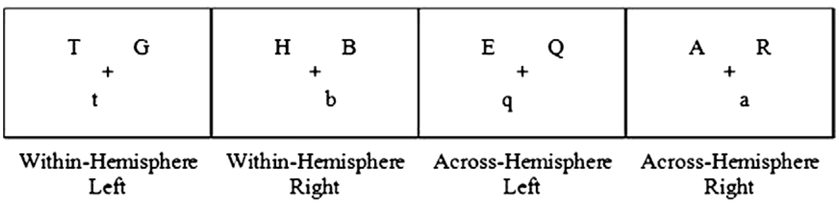

Fig. 1. Examples of stimulus arrays in the letter-matching task. Left or right refers to the target visual field.

hemisphere individually. Banich's logic was that, on within-hemisphere trials, a single hemisphere must process both the target and the matching probe before a match can be detected, while, on across-hemisphere trials, processing of the target and the matching probe is divided between the two hemispheres. If making a series of saccades promotes or increases the functional contribution of intraparietal sulcus to attentional processing in letter matching, the effect may be more apparent on more attentionally demanding within-hemisphere trials than on less demanding across-hemisphere trials.

We examined letter-matching performance as a function not only of saccades but of handedness (SR versus nSR). One reason for this is because saccades may differentially affect SR and nSR individuals on letter matching, as they sometimes do on retrieval (Brunyé et al., 2009; Lyle, Logan, et al., 2008). Another reason is because it provided a test of the hypothesis that interhemispheric interaction is greater in nSR than SR individuals. If correct, nSR subjects should outperform SR subjects on across-hemisphere trials. A previous investigation (Cherbuin & Brinkman, 2006) used a somewhat different letter-matching procedure than in the present study and, although the primary comparison was between left- and right-handers, ancillary analyses yielded some evidence of greater interhemispheric interaction in nSR than SR individuals.

2. Methods

2.1. Subjects

Eighty-four undergraduates aged 18–30 received credit in Psychology courses for participating. Based on scores on a handedness inventory (see below), subjects were classified as SR ($n = 48$, 38 females) or nSR ($n = 36$, 24 females).

2.2. Design

The experiment had a 2 (handedness: SR or nSR) × 2 (pre-matching task: saccades or fixation) × 2 (match arrangement: within- versus across-hemisphere) × 2 (target visual field: left or right) × 2 (letter-matching block: first or second) mixed factorial design in which handedness was between-subjects and all other factors were within-subjects.

2.3. Materials

Handedness was assessed by a variant of Oldfield's (1971) Edinburgh Handedness Inventory (see Lyle, McCabe, et al., 2008, for details) which yields scores ranging from −100 (exclusive left-handedness) to +100 (exclusive right-handedness). In two previous samples of undergraduates in our laboratory (Lyle, Logan, et al., 2008), the median score was +80 and individuals who scored +80 or higher were affected differently by saccades than individuals who scored lower. Therefore, in the present study, we classified subjects a priori as SR if they scored +80 or higher and nSR if they scored lower.

Stimulus arrays for the letter-matching task were modeled after those used by Compton and Mintzer (2001) in their name identity task. Arrays consisted of two uppercase letters (probes) above a central fixation cross and one lowercase letter (target) below the cross. Both probes, one on either side of the fixation point, were 1.4° above the fixation point and 2.8° lateral from the midline. The probes always differed from each other. The target was 1.4° below the fixation point and 1.4° to either the left or right of the midline. The target matched the probe in the same visual field (within-hemisphere trials), the probe in the contralateral visual field (across-hemisphere trials), or neither probe (no-match trials). For each trial type, the target was equally likely to be left or right of fixation. Each of eight letters (*a*, *b*, *e*, *g*, *h*, *q*, *r*, and *t*) served as the target equally often. Non-matching probes were randomly selected. Both targets and probes subtended approximately 0.6° vertically and 0.4° horizontally.

Trials were compiled into four blocks. Each block consisted of a different pseudo-random sequence of 56 match trials (28 within- and 28 across-hemisphere) and 56 no-match trials. The same four blocks were presented in the same order for all subjects.

The stimulus for the saccades task was a computerized sequence showing a black circle on a white background. The circle alternated between 13.5° left and 13.5° right of the vertical midline every 500 ms for 30 s. For the fixation task, the circle flashed in the center of the screen (500 ms on, 500 ms off) for 30 s.

2.4. Procedure

One to five subjects participated at a time. Upon arrival at the laboratory, subjects provided consent and filled out the handedness inventory. Subjects then received instructions for the letter-matching task. Subjects were told to maintain fixation on the central cross and press the "h" key as quickly as possible whenever the identity of the bottom letter matched that of one of the top letters. Subjects then completed 28 practice trials. A chinrest positioned 61 cm from the computer screen was used to maintain viewing distance. After practice subjects completed four experimental blocks of letter-matching trials. Two of the blocks were immediately preceded by the fixation task and two by the saccades task. The two blocks preceded by the same task were performed consecutively. A 15-min break separated the blocks preceded by different tasks; during the break subjects filled out questionnaires unrelated to the present investigation. Order of pre-matching task was counterbalanced within each handedness group.

In the letter-matching task, stimulus arrays were presented for 200 ms followed by a 2000-ms response window during which the word "Match?" appeared on the screen. Response time was recorded from the onset of the stimulus array. A central fixation cross was presented for 200 ms between trials.

For the saccades task, subjects moved their eyes to follow the circle that alternated between the left and right sides of the screen. For the fixation task, subjects fixated the stationary flashing circle without moving their eyes. The experimenter monitored compliance with instructions on these tasks.

3. Results

For ease of exposition, only significant effects involving pre-matching task or handedness are reported. A complete report of all significant effects is available upon request. Alpha was set at .05.

3.1. Accuracy on match trials

Proportion correct on match trials was submitted to an ANOVA with the design given above.[1] Fig. 2 shows that accuracy on within-hemisphere trials was greater following saccades ($M = .90$) than fixation ($M = .88$) but accuracy on across-hemisphere trials was the same following both tasks ($M = .91$). The pre-matching task × match arrangement interaction was significant, $F(1, 82) = 4.17$, $MSE = .006$, $p = .044$, $\eta_p^2 = .05$, as was the enhancing effect of saccades on within-hemisphere accuracy, $t(83) = 2.67$, $p = .009$.

[1] A similar analysis (minus the factor of match arrangement) was conducted on proportion correct on no-match trials. No effects involving pre-matching task or handedness were significant. Of greatest relevance, the main effects of pre-matching task and handedness were not significant, $F < 1$. Overall, accuracy was high ($M = .92$).

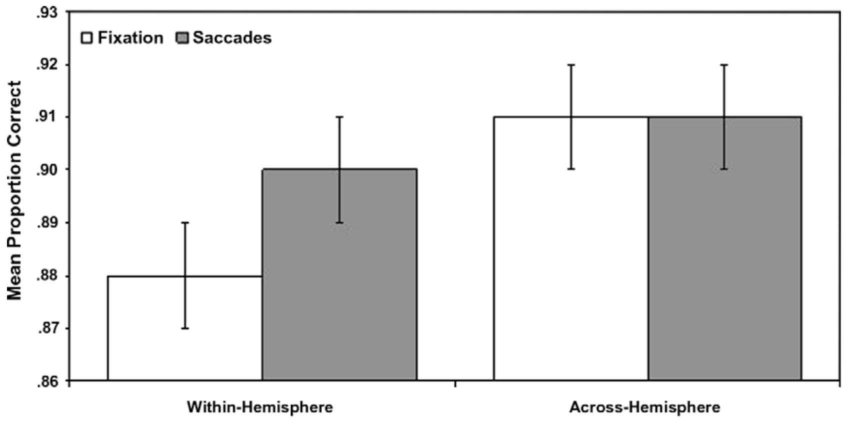

Fig. 2. Mean proportion correct on match trials. Errors bars indicate ±1 *SEM*.

The main effect of handedness was also significant: nSR subjects ($M = .92$) were more accurate than SR subjects ($M = .88$), $F(1, 82) = 5.61$, $MSE = .10$, $p = .02$, $\eta_p^2 = .06$. As seen in Fig. 3, this effect did not interact with match arrangement, $F < 1$, and was individually significant for both across- and within-hemisphere trials, smallest $t(82) = 2.31$, $p = .024$.

3.2. Response time (RT)

Mean RT for correct responses on match trials was analyzed in the same manner as proportion correct. The only conventionally significant effect was the interaction between pre-matching task and target visual field, $F(1, 82) = 7.63$, $MSE = 3372.37$, $p = .007$, $\eta_p^2 = .09$. However, these factors furthermore interacted marginally with match arrangement, $F(1, 82) = 3.38$, $MSE = 3757.33$, $p = .069$, $\eta_p^2 = .04$, and we focus on this more informative three-way interaction. As seen in Fig. 4, on across- but not within-hemisphere trials, RT was faster when the target was in the right visual field than the left and this was true regardless of pre-matching task. An interaction with task existed, however, because the size of this difference (left minus right) was significantly larger following saccades ($M = 88.2$ ms) than fixation ($M = 58.3$ ms), $t(83) = 3.52$, $p = .001$. More important for present purposes is that, whether considering the two visual fields separately or combined, RT was not significantly different following saccades versus fixation on either within- or across-hemisphere trials. Also important is that RT did not significantly differ between SR ($M = 808$ ms) and nSR subjects ($M = 784$ ms), $F < 1$.

4. Discussion

This study produced no evidence that bilateral saccades increase interhemispheric interaction. On across-hemisphere trials, which required comparison of two letters presented separately to the two hemispheres, match detection was neither more accurate nor faster following saccades than fixation. Although accuracy on across-hemisphere trials was high, as is typical in this procedure, a ceiling effect cannot explain the null effect in accuracy, at least for SR subjects: If SR subjects were at ceiling, we would not have detected significantly greater accuracy among nSR subjects. The null effect among SR subjects is especially important because hypothesized saccade-induced increases in interhemispheric interaction are expected to be most robust for these individuals (Lyle, Logan, et al., 2008).

There was one result from the present study that might be taken as evidence that saccades in some way alter, without necessarily enhancing, interhemispheric interaction. Namely, saccades altered performance on across-hemisphere trials by increasing, compared to the fixation condition, the effect whereby matches were detected faster when targets were in the right versus the left visual field. Other studies have also found faster match detection when targets were in the right visual field on across-hemisphere trials (e.g., Fecteau & Enns, 2005; Weissman & Banich, 2000), but, in those studies, unlike the present one, the same effect of target visual field (right faster than left) also occurred on within-hemisphere trials. Given this inconsistency between the present and previous data, and given that the cause of the effect is controversial in any event (Fecteau & Enns, 2005), we consider it beyond the

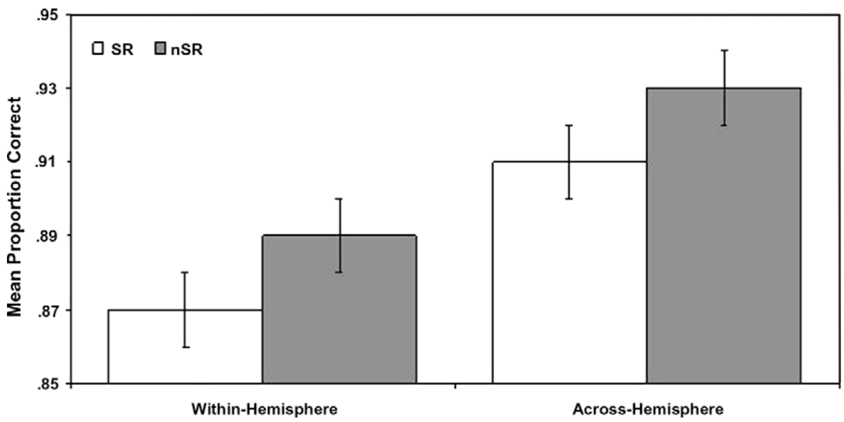

Fig. 3. Mean proportion correct on match trials. Errors bars indicate ±1 *SEM*.

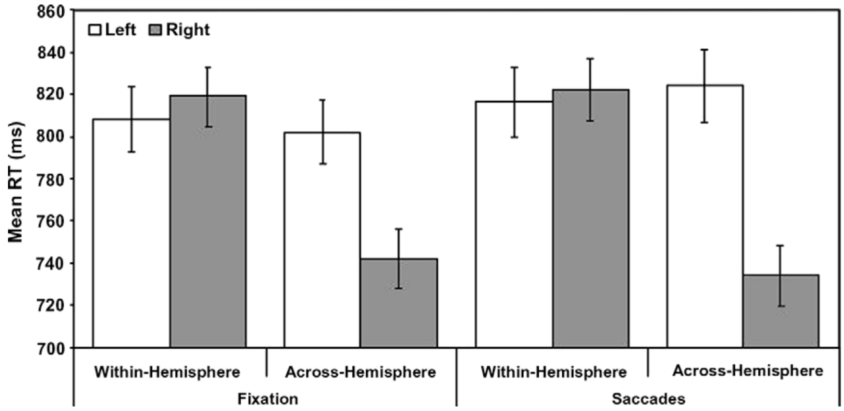

Fig. 4. Mean RT (in ms) on correct match trials. Left or right refers to the target visual field. Errors bars indicate ±1 *SEM*.

scope of this paper to speculate about why saccades magnified the target visual field difference on across-hemisphere trials. More important, we believe, to evaluating the interhemispheric interaction account of SIRE is that saccades did not significantly speed up match detection on across-hemisphere trials, no matter which visual field the target was in.

The failure of saccades to enhance performance on a measure of interhemispheric interaction in the letter-matching task challenges the interhemispheric interaction account of SIRE but does not necessitate abandoning it because interhemispheric interaction need not be considered a monolithic construct. It could be that saccades increase some type or component of interaction that is involved in retrieving memories but is not involved in letter matching. If the interhemispheric interaction hypothesis were to be developed along these lines, it would be necessary to characterize the effects of saccades on interhemispheric interaction more precisely. It would also be necessary to distinguish between the effect of saccades on interhemispheric interaction and the effect of handedness on the same. Saccades have been found to enhance performance on some of the same memory tests on which nSR individuals outperform SR individuals. Specifically, Christman, Propper, and Dion (2004) found that, after studying lists of words, all of which converge semantically on a single non-presented critical word (Deese, 1959; Roediger & McDermott, 1995), nSR individuals were less likely to false recall the critical word and saccades reduced false recall for SR individuals. Similarly, Lyle, Logan, et al. (2008, Experiment 1) found that, after studying a list of random words, nSR individuals falsely recalled fewer non-presented words and saccades reduced false recall for SR individuals. Finally, in Christman et al.'s (2006) Experiment 1, nSR individuals recalled putatively earlier childhood memories than did SR individuals and, in Experiment 2, both SR and nSR individuals recalled putatively earlier memories following saccades versus fixation. Consequently, saccades and handedness have been conceptualized as affecting interhemispheric interaction in comparable ways (Christman et al., 2004, 2006). But here handedness affected a measure of interhemispheric interaction (nSR subjects outperformed SR subjects on across-hemisphere trials) while saccades did not. Dissociations between handedness and saccade effects have also been documented on memory tests. For example, we (Lyle, Logan, et al., 2008, Experiment 2) found SIRE on a recognition test for a word list (i.e., significantly higher d' scores for SR subjects following saccades), but we did not find a significant nSR advantage in d' (also compare Christman et al., 2003, and Propper & Christman, 2004). On the basis of these dissociations, at least two hypotheses are possible. Assuming that nSR handedness is a marker for greater interhemispheric interaction, one hypothesis is that saccades simply do not increase interhemispheric interaction. Another hypothesis is that interhemispheric interaction is influenced by both saccades and handedness but in different ways. If the latter is correct, the precise nature of the difference remains a matter for future research.

Although the interhemispheric interaction hypothesis might be developed and further pursued, the saccade-induced increase in accuracy on within-hemisphere trials in the present study suggests that researchers should also consider the possibility that saccades enhance retrieval by altering processing within each hemisphere, without necessarily altering interhemispheric dynamics. What might be the nature of the affected processing? Given that attentional processes are thought to partially determine success on letter matching (Banich, 1998; Reuter-Lorenz & Stanczak, 2000), and that within-hemisphere letter matching is thought to be more attentionally demanding than across-hemisphere matching (Banich, 1998), one possibility is that saccades enhance attentional processing within each hemisphere. A possible neural basis for such enhancement is saccade-related activation of bilateral frontal eye field and/or intraparietal sulcus (Corbetta, 1998). These regions are involved in the allocation of attention (Corbetta & Shulman, 2002) and intraparietal sulcus, in particular, has been implicated in letter matching when the letters differ in case (Pollman, Zaidel, & von Cramon, 2003). By this account, saccades may affect, not only attentionally demanding within-hemisphere letter matching, but also memory retrieval by enhancing attentional processing during subsequent retrieval attempts. For example, a recent theory is that intraparietal sulcus contributes to the top-down allocation of attention during retrieval (Cabeza, 2008; Ciaramelli et al., 2008). Therefore, we suggest saccades may enhance retrieval by temporarily increasing top-down attentional control.

Consistent with the idea that saccades enhance retrieval by increasing top-down attentional control is the observation that the retrieval tasks on which SIRE has been obtained are ones that, by and large, can be conceptualized as having high demand for top-down attentional control. These tasks include free recall of word lists (Christman et al., 2004, Experiment 2; Lyle, Logan, et al., 2008, Experiment 1) and of autobiographical events recorded in a journal 2 weeks prior to testing (Christman et al., 2003, Experiment 2); sequential old/new recognition requiring discrimination of studied words (Lyle, Logan, et al., 2008, Experiment 2; Parker & Dagnall, 2007), word pairs (Parker, Relph, & Dagnall, 2008, Experiment 1), or aerial maps (Brunyé et al., 2009) from similar, related, or rearranged (and hence highly distracting) new items; recall of the color and location of words (Parker, Relph, et al., 2008, Experiment 2); and an eyewitness misinformation task in which subjects viewed a series of pictures depicting various objects, then read misleading descriptions of some of the objects, and finally had to discriminate between accurate descriptions of objects and inaccurate descriptions based on the post-viewing misinformation (Parker, Buckley, & Dagnall, 2008). In contrast, the only two retrieval tasks reported to date on which SIRE has not been obtained are less clearly demanding of top-down attentional control. One of these tasks was two-alternative forced-choice recognition of aerial maps (Brunyé et al., 2009), in which studied items and new ones were presented side by side and responses therefore were more likely than in sequential recognition to be based on bottom-up differences in familiarity. The other task was an implicit word-fragment completion task (Christman et al., 2003, Experiment 1). On that task, subjects saw word fragments that they could (and sometimes did) complete with previously studied words, but they were not required to attend to the old/new status of the words used to complete fragments.

Although we have focused in this paper on bilateral, or horizontal, saccades, it bears noting in relation to our just-advanced hypothesis that there is evidence that up–down, or vertical, saccades are also correlated with activity in frontal eye field (e.g., Pflugshaupt, Nyffeler, von Wartburg, Hess, & Müri, 2008) and intraparietal sulcus (e.g., Barash, Bracewell, Fogassi, Gnadt, & Andersen, 1991). Our hypothesis therefore predicts that vertical saccades may also produce SIRE. Supporting this prediction, Lyle, Logan, et al. (2008, Experiment 2) found that vertical saccades enhanced discrimination (d') between studied and new words on a recognition test to the same extent as did horizontal saccades (enhancement was specific to SR individuals for both saccade types). Converging, but weaker, support comes from Parker, Relph, et al. (2008, Experiment 1), who found that vertical saccades only marginally significantly increased d' on a word recognition test ($p = .07$), while horizontal saccades produced a significant increase. Also, in Christman et al. (2003, Experiment 1), d' scores on a word recognition test following vertical saccades were higher than following fixation but lower than following horizontal saccades and did not differ significantly from either. These findings suggest, more or less strongly, that vertical saccades may produce SIRE. In contrast, in several other experiments involving tasks other than word recognition, retrieval enhancement was clearly specific to horizontal, and not vertical, saccades (Brunyé et al., 2009; Parker, Buckley, et al., 2008; Parker & Dagnall, 2007; Parker, Relph, et al., 2008). More research directly comparing both the behavioral effects, and the neural correlates, of vertical and horizontal saccades is needed for a complete empirical understanding of SIRE and for theorizing about SIRE's causation.

Somewhat related to our hypothesis that saccades may impact subsequent cognition by activating frontal and parietal attentional regions, Parker, Buckley, et al. (2008) suggested that saccades may enable more efficient engagement between prefrontal and posterior regions. Parker and colleagues reasoned, partially on the basis of EEG data indicating that functional coupling between frontal and parietal regions increases during memory retrieval (Summerfield & Mangels, 2005), that more efficient anterior–posterior interactions would enhance retrieval.

Finally, the greater across-hemisphere accuracy of nSR versus SR subjects supports the idea of greater interhemispheric interaction in the former (see also Cherbuin & Brinkman, 2006). In turn, this supports the viability of interhemispheric interaction as the factor underlying superior memory in nSR individuals (Lyle, McCabe, et al., 2008; Propper et al., 2005). nSR subjects were also more accurate on within-hemisphere trials. This was not predicted but may be seen as consistent with Kinsbourne's (2003) theory that excitatory interhemispheric connections maintain the preparedness of each hemisphere to respond to stimuli. Whatever its cause, nSR individuals' greater baseline intrahemispheric processing, along with the finding that saccades increase intrahemispheric processing, advances our understanding of SIRE in two ways. One, the reason SIRE is less reliable for nSR than SR individuals (Brunyé et al., 2009; Lyle, Logan, et al., 2008) may be that the former have a smaller margin for increase in intrahemispheric processing. Two, the reason there are both parallels and dissociations between SIRE and handedness effects, as described above, may be that saccades produce the greater intrahemispheric processing that naturally occurs in nSR individuals but not the greater interhemispheric interaction.

4.1. Limitations

A limitation of this study is that we did not track subjects' eye movements during either the letter-matching task or the pre-matching activities (fixation or saccades). The same limitation applies to all previous SIRE studies and many studies using versions of the letter-matching task. Therefore, we cannot rule out the possibility that there was less than complete compliance with saccade or fixation-maintenance instructions during all phases of the experiment. Future research may seek to confirm that similar results are obtained when eye tracking is incorporated.

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