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DECONSTRUCTING SACCADES: IDENTIFYING THE COMPONENTS OF SACCADES THAT PRODUCE SACCADE-INDUCED RETRIEVAL ENHANCEMENT.

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ABSTRACT

DECONSTRUCTING SACCADES: IDENTIFYING THE COMPONENTS OF SACCADES THAT PRODUCE SACCADE-INDUCED RETRIEVAL ENHANCEMENT.

James Matthew Edlin

November 20, 2013

Multiple studies have found that performing repetitive saccades for 30 s improves subsequent memory retrieval. Although the effect is well established, the mechanism by which saccades affect retrieval is currently unknown. Saccade-induced retrieval enhancement (SIRE) has been hypothesized to be a product of increasing: interaction between the hemispheres, interaction within the hemispheres, or attentional control. It is currently unknown which components of the saccade activity are necessary to produce SIRE. The saccade activity in previous SIRE research is similar to an orienting activity that produces predictive saccades. Predictive saccades begin as exogenous orienting to a rhythmically alternating target. After a few repetitions, the pattern is learned and saccades are endogenously guided by memory instead of by the visual onset of the target. The goal of Experiment 1 was to determine whether purely endogenous or exogenous orienting to a target without a predictable location produces SIRE on a paired-associates test. Neither type of orienting improved retrieval relative to fixating on a stationary point. Only the saccade activity used in previous research, which may have produced predictive saccades, improved performance. None of the theoretical accounts of SIRE can fully accommodate this pattern of results.

An additional component of the standard saccade activity is that attention and the eyes move simultaneously. However, attention can also be shifted covertly, without moving the eyes. The goal of Experiment 2 was to determine whether overt orienting is necessary for retrieval enhancement. Neither covert orienting nor saccades improved retrieval relative to fixation. Differences between the novel orienting activities in Experiment 1 and the standard saccade activity are discussed in relation to the cortical activity that has previously been associated with these activities. The implications of these results for the various theoretical accounts of SIRE are also discussed.

TABLE OF CONTENTS

LIST OF FIGURES

INTRODUCTION

Memory is an important aspect of cognition and normal memory failures are salient in daily life. Forgetting an important date, the items on your grocery list, or the name of the person you met yesterday can be embarrassing and disadvantageous. These types of memory failures increase with age (e.g., Small, Stern, Tang, & Mayeux, 1999), but even in youth, when memory for the average person is at its peak (Salthouse, 2009), people often desire memory improvement. Therefore, it is not surprising that interventions for memory enhancement permeate our culture, ranging from computer-based training programs with long-term commitments, such as Cognitfit or Braintrian (for review, see Jak, Seelye, & Jurick, 2013), to quick mnemonic techniques that can be applied during encoding (e.g., Roy G. Biv to remember the colors of the rainbow). Some interventions, such as memory-enhancing drugs, can have detrimental side effects (for review, see Husain & Mehta, 2011).

One little-known intervention for improving memory retrieval is rapidly shifting the eyes back and forth to fixate on a target. This type of eye movement, known as saccades, improves performance on subsequent memory tests compared to fixating on a stationary target. Saccades have an advantage over mnemonic techniques in that they are performed immediately before retrieval, and require no preparation during encoding. Also, saccades only require 30 s, which gives them an advantage over training programs and pharmacological interventions.

Saccades are also of theoretical interest because they are a simple activity that enhances performance on a subsequent memory test. Brain imaging studies have associated patterns of cortical activation with performing tasks. The effect of saccades on cognition suggests that cortical activation from one task can carry over and affect another task. This suggests that cognition can be influenced by other tasks that have just occurred.

In typical studies examining saccade-induced benefits, subjects perform saccades by moving their eyes left and right for 30 s to fixate on a black circle that alternates between the left and right side of the screen every 500 ms. Performing bilateral (left/right) saccades immediately before retrieval of episodic memories enhances old/new recognition (Christman, Garvey, Propper, & Phaneuf, 2003, Experiment 1; Lyle, Logan, & Roediger, 2008, Experiment 2), associative recognition (Lyle, Hanaver-Torrez, Häcklander, & Edlin, 2012; Parker, Relph, & Dagnall, 2008, Experiment 1), and free recall (Lyle, Logan, et al., 2008, Experiment 1; Nieuwenhuis et al., 2013, Experiment 1). However, some evidence suggests that saccade-induced benefits may be limited to retrieval that requires attentional control (Lyle & Edlin, under review).

Enhanced retrieval has manifested as greater correct retrieval of previously seen information (e.g., Lyle, Logan, et al., 2008, Experiment 2) and lesser false retrieval of previously unseen information (e.g., Christman et al., 2003, Experiment 1). In studies designed to elicit false memories of semantically primed lures, saccades have increased recognition of studied words and decreased false memory of non-studied non-lure words in adults (Parker & Dagnall, 2007, 2012). Saccades have also decreased false memories of primed lures in adults (Christman, Propper, & Dion, 2004; Parker & Dagnall, 2007, 2012), but not in children (Parker & Dagnall, 2012).

The effects of saccades are not limited to recognizing or recalling word lists, but also extend to color and spatial information (Parker et al., 2008, Experiment 2), recognition of landmark shapes and locations (Brunye, Mahoney, Augustyn, & Taylor, 2009, Experiment 1), and recognition of famous and novel faces (Lyle & Orsborn, 2011). Saccades have improved autobiographical memory by increasing the amount (Parker, Parkin, & Dagnall, 2013), accuracy (Christman et al., 2003, Experiment 2), and vividness (Parker & Dagnall, 2010) of memories recalled. In addition, saccades have decreased the age of earliest childhood memories recalled (Christman, Propper, & Brown, 2006, Experiment 2). Saccades have also improved eyewitness memory for events (Lyle & Jacobs, 2010) and protected memory against misinformation (Parker, Buckley, & Dagnall, 2009).

Most research on saccade-related benefits has focused on memory enhancement, with the effect being labeled saccade-induced retrieval enhancement (SIRE; Lyle & Martin, 2010), but other forms of cognition have also benefited from saccade-induced enhancement. Saccades have enhanced creativity by making responses more distinctive and original (Shobe, Ross, & Fleck, 2009) and increased detection of letter matches from briefly viewed arrays (Lyle & Martin, 2010). Also, saccades have decreased response times when locating invalidly-cued targets (Edlin & Lyle, 2013; Kuiken, Bears, Miall, & Smith, 2002) and responding to the direction of an arrow that is flanked by contradictory arrows (Edlin & Lyle, 2013).

Handedness Effects

An important qualification is that saccade-related benefits depend on the consistency of an individual's hand preference (e.g., Lyle et al., 2012). Most individuals consistently use one hand to perform daily activities (e.g., writing, combing hair, using a spoon), but some individuals are inconsistent in their hand use (e.g., Dragovic, 2004). Inconsistent individuals may perform some activities with one hand and other activities with the other hand, or they may use either hand to perform the same activity. A subject's handedness consistency can be quantitatively measured with a handedness inventory (see Dragovic, 2004). In previous studies, saccades have produced beneficial effects on consistently right-handed subjects, but for individuals who are not consistently right-handed, saccades have improved performance (Christman et al., 2006), decreased performance (Lyle, Logan, et al., 2008), or had no effect (Brunye et al., 2009; Lyle & Orsborn, 2011; Shobe et al., 2009). Originally, it was thought that being consistent and being right-handed were necessary for reliable saccade-induced benefits, but recent studies have shown that consistently left-handed subjects also exhibit SIRE (Lyle et al., 2012). In other words, consistent-handers gain a consistent benefit from saccades, whereas inconsistent-handers do not.

Hypotheses of Saccade-Induced Enhancement

The mechanism by which saccades affect cognition is currently unknown. Several hypotheses have been put forth to explain how saccades enhance *retrieval,* and each is described below. The attentional control hypothesis, unlike the other two hypotheses, explains how saccades enhance, not only retrieval, but also creativity and attention.

Interhemispheric interaction hypothesis.

Christman et al. (2003) proposed that if one hemisphere has less activation than the other, then the less active hemisphere will have trouble interacting with the more active hemisphere. These authors believe that saccades equalize the activity in both hemispheres because each bilateral shift of the eyes produces activity in the contralateral hemisphere. When both hemispheres have equal levels of activity, then communication between the hemispheres is less difficult and interhemispheric interaction is more efficient. If saccades increase interhemispheric interaction, then saccades may only enhance performance on tasks that involve such interaction.

Some types of retrieval appear to depend on interhemispheric interaction. Evidence for this has come from studies of epilepsy patients that have had their corpus callosum severed. Interhemispheric interaction primarily occurs through the corpus callosum. Individuals who have had their corpus callosum severed are impaired on tasks that require high levels of interhemispheric interaction (e.g., explicit memory), but not on tasks that require low levels of interaction (e.g., implicit memory) (Cronin-Golomb, Gabrieli, & Keane, 1996; Phelps, Hirst, & Gazzaniga, 1991). Even when the corpus callosum is intact, its size may influence retrieval. Some studies have suggested that the corpus callosum is larger in inconsistent-handers than consistent-handers (Cowell, Kertesz, & Denenberg, 1993; Habib et al., 1991; Luders et al., 2010; Witelson, 1985), although other studies have found no difference (Jäncke & Steinmetz, 2003; Welcome et al., 2009). If inconsistent-handers have a larger corpus callosum, and presumably greater interhemispheric interaction, this may explain why they have outperformed consistent-handers on some retrieval tests (e.g., Lyle, McCabe, & Roediger, 2008; cf. Lyle & Orsborn, 2011).

In early SIRE studies, the benefit of saccades on consistent-handers seemed to support the interhemispheric interaction hypothesis because saccades caused consistent-handers to perform similar to inconsistent-handers (e.g., Christman et al., 2003; Christman et al., 2004). For example, in a study designed to elicit false memories of semantically primed lures, inconsistent-handers exhibited fewer false memories than consistent-handers (Christman et al., 2004, Experiment 1). However, when consistent-handers performed saccades prior to the same test, their rate of false memories was lower than consistent-handers that performed fixation (Christman et al., 2004, Experiment 2).

In addition, the effects of saccades on retrieval have been unreliable for inconsistent-handers, sometimes producing benefits (Christman et al., 2006) or detriments (Lyle, Logan, et al., 2008), and sometimes having no effect (Brunye et al., 2009; Lyle & Orsborn, 2011). Lyle, Logan, et al. suggested that, if SIRE is due to increased interhemispheric interaction, then individuals with lower baseline interaction may benefit more from saccades than individuals with a higher baseline. Thus, consistent-handers benefit more from saccades than inconsistent-handers. Inconsistent-handers may already be performing at the optimal level, and increasing interaction beyond that point could lead to no improvement or even have a detrimental effect on performance.

Several pieces of evidence weigh against the interhemispheric interaction hypothesis. First, SIRE has been found in electroencephalograph studies, without any indication that saccades increased interhemispheric coherence (Samara, Elzinga, Slagter, & Nieuwenhuis, 2011). Indeed, saccades have actually been shown to decrease interhemispheric coherence (Propper, Pierce, Geisler, Christman, & Bellorado, 2007).

Second, two studies tested the interhemispheric interaction hypothesis behaviorally, and neither indicated that saccades increase interhemispheric interaction. Lyle and Martin (2010) examined performance on a letter-matching task following either saccades or fixation. In this task, subjects were presented with two uppercase letters (targets) above a fixation cross and one lowercase letter (probe) below the cross. Each target was in a different visual field, and the probe could appear in the same visual field as its uppercase counterpart or in the contralateral visual field. Subjects were required to press a key when the identity of the probe matched one of the targets. Detecting that a target and probe shared the same identity required *intra*hemispheric processing when the target and probe appeared in the same visual field and *inter*hemispheric processing when the target and probe appeared in different visual fields. Saccades enhanced accuracy on trials that required intrahemispheric processing but had no effect on trials that required interhemispheric processing.

Lyle and Orsborn (2011) examined the effect of saccades on interhemispheric interaction in the context of face memory and a phenomenon called bilateral gain. Bilateral gain is an effect whereby previously learned faces or words are more likely to be recognized when presented to both visual fields at the same time, instead of just one. There is no bilateral gain for identifying novel faces or words. If saccades increase interhemispheric interaction, then they should increase bilateral gain. Lyle and Orsborn found that saccades did not increase the magnitude of bilateral gain for famous faces, although they did improve memory overall for novel and famous faces.

The results of Lyle and Martin (2010), and Lyle and Orsborn (2011), along with the electroencephalograph data cited above, indicate that saccades do not increase interhemispheric interaction and that enhanced interhemispheric interaction is not the cause of saccade-induced enhancement.

Attentional control hypothesis.

Another hypothesis for saccade-induced enhancement is that saccades improve attentional control. Lyle and Martin (2010) proposed that saccade-induced enhancement is caused by increased activation in brain regions associated with attentional control. Saccadic eye movements activate frontoparietal regions such as the intraparietal sulci (IPS) and frontal eye fields (FEF) (e.g., Corbetta & Shulman, 1998; Moon et al., 2007), which are associated with the top-down control of attention (Corbetta & Shulman, 2002).

The IPS have been shown to mediate preparatory attention (Luks, Simpson, Dale, & Hough, 2007) by modulating the salience of a target based on behavioral goals (for review, see Bisley, Mirpour, Arcizet, & Ong, 2011). Transcranial magnetic stimulation (TMS) knockout of the IPS have disrupted subjects' ability to ignore high salience distracters during target selection (Mevorach, Hodsoll, Allen, Shalev, & Humphreys, 2010). In addition to the IPS, the FEF are also recruited during target detection and inhibitory processes. Temporarily disabling the FEF using TMS knockout has decreased inhibitory control (Muggleton, Chen, Tzeng, Hung, & Juan, 2010), and TMS facilitation of the FEF has improved target detection (Grosbras & Paus, 2002; Moore & Fallah, 2004). If saccade-induced enhancement is a product of increased activation in these frontoparietal areas, then saccades should improve target detection when the target is not salient or when distracting information is competing with the target.

Edlin and Lyle (2013) directly tested the above prediction with a cued-flanker task called the attention network test (Fan et al., 2009). In this task, the subject's goal is to determine the direction of an arrow that faces left or right. The arrow can appear on the left or right side of the screen at three different time intervals. Before the arrows appear, both possible locations can flash, providing the subject with a temporal cue of the impending stimulus, but no spatial cue for the location. Alternatively, one location may flash, which provides both temporal and spatial cues, but half of the spatial cues are invalid, because the wrong location of the stimulus is cued. Finally, on some trials there is no flash, providing no temporal or spatial information. Temporal cues alert the subject that the next target will appear, so response time is lower because the subject can prepare to orient attention. Valid spatial cues also reduce response time because the subject knows where to orient. Invalid cues produce the longest response times, because the subject must disengage attention from the invalid location before orienting to the actual location. When the target arrow appears, it is flanked by two arrows on each side that face either the same direction (congruent flankers) or the opposite direction (incongruent flankers). Incongruent flankers produce an additional increase in response time, because the subject must resist the information provided by four of the arrows and respond based on the central arrow. The differences between response times across different trial types provide a measurement of the operation of the three attentional networks originally proposed by Posner and Petersen (1990): alerting, orienting, and executive function (Fan et al., 2009). The executive function network controls attention and is measured by the difference in response times between trials with incongruent and congruent flankers. Edlin and Lyle (2013) found that saccades selectively decreased response times when incongruent flankers surrounded the target. This finding signified that saccades specifically enhanced the executive function network by improving performance on the trials that required the most attentional control. Furthermore, saccades reduced response times when the target's location was invalidly cued, which was more attentionally demanding than when the cues were valid, because it required the subject to overcome the influence of the invalid cue.

Enhanced executive control can explain previous saccade-induced benefits on other cognitive domains that have been associated with attentional control such as memory retrieval (for review, see Levy & Anderson, 2002), creativity (Groborz & Necka, 2003), and letter matching (Banich, 1998). Frontoparietal regions such as the IPS and FEF that are active during attentional control tasks are also active during memory retrieval and are thought to reflect actively attending to items in memory (Cabeza, 2008; Ciaramelli, Grady, & Moscovitch, 2008; Wagner, Shannon, Kahn, & Buckner, 2005). In fact, overlapping areas of IPS are active during visual orienting and memory orienting, with connectivity between the IPS and visual cortex increasing during visual orienting and activity between the IPS and medial temporal lobe increasing during memory orienting (Cabeza et al., 2011). Therefore, increasing activation in the IPS may lead to better detection of a target regardless of whether the target is located in memory or in a visual array.

One prediction that follows from this line of reasoning is that the retrieval benefits of saccades will be more likely on difficult tasks that require greater top-down attentional control. One method of manipulating retrieval difficulty within a single test is by having subjects learn a list of exemplars (e.g., apple, orange) from different categories (e.g., fruits, birds) and then practice retrieval of some of the words from some of the categories (e.g., fruits-orange). When memory of the original list is tested after the practice phase, retrieval is greater for practiced exemplars (e.g., fruits-orange) than exemplars from unpracticed categories (e.g., birds-robin), but retrieval is lower for unpracticed exemplars from practiced categories (e.g., fruits-apple) than exemplars from the unpracticed categories (e.g., Anderson, Bjork, & Bjork, 1994). The decrease in retrieval of unpracticed exemplars from practiced categories, known as retrieval-induced forgetting, indicates that these items are more difficult to retrieve than items from unpracticed categories (Anderson, 2003). Lyle and Edlin (under review, Experiment 1) found that saccades reduced the effects of retrieval-induced forgetting in consistent-handers by selectively increasing retrieval of unpracticed exemplars from practiced categories.

Retrieval difficulty can also be manipulated within a single test with output interference. Output interference is one consequence of repeated retrieval whereby the initial items on a test are easier to retrieve than later items, because as the number of retrieved items increases so too does the difficulty of retrieving additional items (Criss, Malmberg, & Shiffrin, 2011). Therefore, if subjects are given a list to study and then some of the items are tested on a first test and some are tested on a second, output interference should decrease retrieval of items on the second test compared to the first. In support of this, Lyle and Edlin (under review, Experiment 2) found that consistent-handers had lower retrieval on a second recognition test than a first, but only following fixation. Saccades produced equal performance on both tests.

In addition, if saccades only enhance tasks that require attentional control, this may explain the lack of saccade-induced enhancement on a word-fragment completion test (Christman et al., 2003, Experiment 1) and a two-alternative forced choice recognition test (Brunye et al., 2009), because these tests required less attentional control than the retrieval tests in other studies.

Edlin and Lyle (2013) suggested that saccades might be an attentional exercise that produces temporary benefits on tasks that require attentional control. This effect may be similar to attention-training programs that require multiple sessions over an extended period (Rueda, Rothbart, McCandliss, Saccomanno, & Posner, 2005).

Anterior-posterior interaction hypothesis.

Parker and Dagnall (2007) suggested that saccades increase interaction between anterior and posterior regions of the brain, although they did not specify how. In particular, they specified an interaction between prefrontal attentional control regions and parahippocampal gyrus where memories are stored. Functional connectivity (increase in the flow of information) between these two regions may be necessary for complex retrieval tests (for review, see Simons & Spiers, 2003).

Activation of frontal and parahippocampal gyrus during retrieval may denote the involvement of prefrontal areas during effortful retrieval and hippocampal areas during conscious recollection (see Schacter, Alpert, Savage, Rauch, & Albert, 1996).

Alternatively, hippocampal activity during retrieval may reflect encoding processes (e.g., re-encoding the presented information and encoding irrelevant background information) that must be suppressed by prefrontal regions during effortful retrieval (Reas & Brewer, 2013). Both of these interpretations suggest that increasing the functional connectivity between these regions might enhance retrieval by increasing the ability of prefrontal regions to effectively interact or suppress hippocampal regions.

This hypothesis has not been tested, but predictions based on this hypothesis are similar to predictions made by the attentional control hypothesis, with one notable exception. Increased attentional control and increased functional connectivity between attentional control and memory storage could produce saccade-induced *retrieval* enhancement, but only the attentional control hypothesis predicts that saccades will also provide a benefit on attention tasks that do not require retrieval. For example, the anterior-posterior interaction hypothesis would predict results similar to the findings in Lyle and Edlin (under review) on retrieval tests that manipulate the difficultly of to-be-retrieved items. However, a functional coupling between prefrontal cortex and the parahippocampal gyrus cannot explain the finding that saccades selectively reduced response times on trials with incongruent flankers or invalid cues in a cued-flanker task (Edlin & Lyle, 2013).

Parker and Dagnall (2007) specifically posited an anterior-posterior interaction between prefrontal regions and parahippocampal gyrus. However, the evidence they cited for interactions between anterior and posterior regions included one experiment (Summerfield & Mangels, 2005) involving a functional coupling between frontal and parietal regions. Furthermore, they referred to Lyle and Martin's (2010) proposal that saccades increase activity in the IPS and FEF as an anterior-posterior interaction (see Parker et al., 2013). If the anterior-posterior interaction hypothesis is expanded to include interaction between regions in the frontoparietal network, then it might also explain the benefit of saccades on creativity and the cued-flanker task.

Previous Variations of the Saccade Task

Previous SIRE research has primarily focused on the effect of saccades on retrieval. Relatively few studies have manipulated the saccade and fixation activities themselves, and none has attempted to compare different types of saccades in order to determine which components of the task produce SIRE. In addition to comparing saccades to the standard fixation activity (a central circle that alternates between visible or not visible for 500 ms), saccades have also been compared to smooth pursuit eye movements (Christman et al., 2003, Experiment 1), no pre-trial activity (Christman et al., 2003, Experiment 1), a fixation circle that pseudorandomly alternated between six colors (Christman et al., 2004, Experiment 2), and unconstrained free eye movements (Lyle, Logan, et al., 2008, Experiment 2). Saccades were found to improve retrieval compared to all of these activities. Vertical saccades have been compared to bilateral saccades with inconsistent findings. Vertical saccades have sometimes significantly enhanced performance (Edlin & Lyle, 2008; Lyle & Edlin, under review; Lyle, Logan, et al., Experiment 2) and other times had no effect (e.g., Brunye et al., 2009; Christman et al., 2003, Experiment 1).

Overview of Dissertation Research

Previous research has not attempted to determine which components of the saccade activity produce the subsequent cognitive benefits. Although saccades are a simple attention task, they actually contain multiple components that might cause SIRE.

The standard saccade activity involves moving the eyes left and right to orient to the target circle. Orienting can be endogenously controlled through top-down mechanisms to look at a target voluntarily, or exogenously controlled by reflexive orienting to an abrupt or salient target in the environment (for review, see McDowell, Dyckman, Austin, & Clementz, 2008). In activities like the standard saccade activity, orienting to a stimulus with a constant temporal and spatial pattern begins as exogenous orienting, but within 2 to 3 s becomes a specific type of endogenous orienting called predictive saccades (e.g., Dallos & Jones, 1963; Ross & Ross, 1987). During predictive saccades, the spatial location of targets are maintained in working memory and saccades to those locations are based on the representation in working memory instead of the visual onset of the target (Wong & Shelhamer, 2011). This is evidenced by the fact that early reflexive saccades occur approximately 200 ms after stimulus onset, which reflects the time needed to process the visual stimulus, but later predictive saccades can occur approximately 200 ms prior to visual onset (Shelhamer & Joiner, 2003). If the standard saccade activity produces predictive saccades, then the component that produces SIRE may be initial exogenous orienting, later endogenous orienting, or predictive saccades.

Additionally, the saccade activity in all published research involves overtly shifting attention between two circles, but there are two ways to shift attention. One is by overtly shifting attention, which also involves moving the eyes to focus the fovea on a target. The second involves covertly shifting attention without moving the eyes. It is unknown whether covert attentional shifts are sufficient to create SIRE, or whether the physical act of moving the eyes is a necessary component.

This dissertation attempts to deconstruct the standard saccade activity by comparing it to new orienting activities that isolate certain components. Experiment 1 will determine whether endogenous or exogenous orienting enhances retrieval. Experiment 2 will determine whether covert orienting enhances retrieval. Both studies employ a within-subjects design to examine accuracy on a paired-associates test following fixation, saccades, or one of the new orienting activities. A between-subjects comparison of the endogenous and exogenous orienting activities is also possible.

The dependent measure in these experiments is performance on a paired-associates test. In this task, the subjects study a list of unrelated word pairs (e.g., tore-walk, sag-zinc, low-grin). Later they must discriminate between pairs that were studied (e.g., tore-walk), and pairs that were not studied but are recombinations of studied pairs (e.g., sag-grin). In the past, SIRE has occurred on more attentionally demanding retrieval tests, but not less demanding ones like word-fragment completion (Christman et al., 2003, Experiment 1) or two-alternative forced choice recognition (Brunye et al., 2009).

Two studies have found SIRE on a paired-associates test (Lyle et al., 2012; Parker et al., 2008, Experiment 2). This indicates that a paired-associates test is of sufficient difficulty to produce SIRE. Furthermore, when the effects of saccades on consistent-handers and inconsistent-handers are compared on this test, saccade-induced benefits are limited to consistently-handed individuals (Lyle et al., 2012). Because the goal of the current research is to determine which components of saccades produce cognitive benefits, only consistent-handers were included in the current experiments.

Finally, because of Lyle and Edlin's (under review) finding that saccades differentially affected the first and second half of a recognition test, test half is included in the analyses as a within-subjects factor. The second half of the paired-associates test should be more difficult than the first half because of output interference. This suggests that saccades may be more beneficial on the second half of the test by reducing output interference. Alternatively, if SIRE diminishes as the test progresses then saccades may primarily enhance retrieval on the first half. In Lyle and Edlin, saccades were performed before each half so subjects began the second half of the test immediately after performing saccades. In the current experiments, subjects will only perform the orienting activities before the first half. The duration of SIRE is currently unknown, although it is thought to last 7 to 9 m (Shobe et al., 2009). Therefore, SIRE may diminish before the test is completed.

EXPERIMENT 1: ENDOGENOUS AND EXOGENOUS ORIENTING

Introduction

Experiment 1 explores the potential of two novel orienting activities to produce SIRE. One activity is a strictly endogenous task with two constant target circles instead of a single alternating one, and a background color change that cues the subject to saccade back and forth between the circles. Because the circles in this activity do not appear and disappear, there are no abrupt spatial cues to produce exogenous orienting. Another activity is an exogenous orienting task that requires saccades from a central fixation point to a random location to the left or right of the vertical midline.

Because the movements will originate from a central point on the vertical midline, instead of from a location left or right of the vertical midline, the eye movements in this activity are half the distance of those in the standard saccade activity (13.5° versus 27°, respectively). Reducing the amplitude of the saccades should not decrease the degree of frontoparietal activation produced, because activation apparently depends on the frequency of saccades and not the amplitude (Kimmig et al., 2001).

It bears noting that the exogenous activity in the current experiment and similar activities in other research are referred to as exogenous orienting, but this activity actually involves both endogenous and exogenous orienting systems. Because subjects are specifically instructed to follow a circle, a limited amount of top-down control is employed to increase the salience of that particular stimulus (see Corbetta & Shulman, 2002). A purely exogenous task would require a more salient stimulus that reflexively draws attention without instructions to attend to that stimulus. Although such a task would be interesting theoretically, it would significantly deviate from the standard saccade activity, thereby preventing the single-component analysis that is the focus of the current research.

An additional possible component of the saccade activity is that it produces predictive saccades. Predictive saccades require a temporally and spatially constant pattern that alternates faster than .3 Hz (e.g., Dallos & Jones, 1963; Shelhamer & Joiner, 2003). The standard saccade activity is a temporally (1 Hz) and spatially predictable pattern, so it may produce predictive saccades[1]. In contrast, the novel endogenous and exogenous activities do not involve a predictable alternating pattern and therefore should not produce predictive saccades (e.g, Bronstein & Kennard, 1987; Joiner & Shelhamer, 2006; Ross & Ross, 1987).

Predictive saccades are memory-guided instead of visually-guided, which makes them functionally different from the novel (endogenous and exogenous) orienting activities studied in the current experiment. Brain imaging studies have not compared predictive saccades to endogenous orienting, but predictive saccades have been compared to fixation and to exogenous activities similar to those under investigation in the current experiment (Simo, Krisky, & Sweeney, 2005). Relative to stationary fixation, predictive and exogenous orienting produce similar activation in frontoparietal regions, with the exception of the FEF, which exhibit less activation during predictive saccades than

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[1] It should be noted that saccade latencies for saccades used in SIRE studies have never been measured to determine the presence of predictive saccades. Predictive saccade latencies are much lower than visually-guided saccades (see Shelhamer & Joiner, 2003).

exogenous orienting (Simo et al.; cf. Gagnon, O'Driscoll, Petrides, & Pike, 2002)[2]. Most pertinent to the current research, Simo et al. found that only predictive saccades and not exogenous orienting produced greater activation relative to fixation in middle frontal gyri (MFG), angular gyri (AG), hippocampi, supramarginal gyri (SMG), and anterior cingulate cortices (ACC). Activation in these regions presumably reflects the memory-guided nature of predictive saccades, because these regions are also active during retrieval (e.g., Burianova, McIntosh, & Grady, 2010; Rugg & Vilberg, 2013). If increased activation in regions produced by predictive saccades is necessary for SIRE, then neither of the novel orienting activities should enhance memory.

Predictions based on the hypotheses of saccade-induced enhancement

Interhemispheric interaction hypothesis.

According to the interhemispheric interaction hypothesis, saccades produce bilateral activity that equalizes the activation in the two hemispheres (Christman et al., 2003). This hypothesis predicts that endogenous orienting, exogenous orienting, and saccades will produce SIRE because they all include bilateral saccades. However, Christman et al. claimed that smooth-pursuit eye movements do not increase interhemispheric interaction because they produce less cortical activation than saccades. Although the specific areas that exhibit less cortical activity were not indicated, the experiment these authors cited to support their claim found less bilateral activation during smooth pursuit in FEF, medial superior parietal regions, and supplementary motor area

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[2] Gagnon et al.'s (2002) results differed from Simo et al.'s (2005). However, Gagnon et al. compared predictive saccades to an exogenous task with unpredictable locations and timing. The results of Simo et al. are discussed in the current research, because these authors compared predictive saccades to an exogenous orienting task similar to the task in the current experiment (unpredictable locations and predictable timing).

(O'Driscoll et al., 1998). Unfortunately, activation produced by smooth-pursuit movements has only been compared to that produced by saccades, without distinguishing between purely exogenous or endogenous orienting. Therefore, predictions based on equal activity in specific regions are not possible until this hypothesis is developed further or additional information is provided by brain imaging studies.

Attentional control hypothesis.

The attentional control hypothesis specifically implicates the IPS and FEF (e.g., Lyle & Martin, 2010, Edlin & Lyle, 2013). Both endogenous and exogenous orienting are associated with activity in the IPS and FEF, therefore either could, by this hypothesis, produce SIRE (e.g., Corbetta & Shulman, 1998; Moon et al., 2007; Petit et al., 2009). In addition, if the level of enhancement is correlated with the level of activation in these frontoparietal regions, then endogenous orienting should produce greater cognitive enhancement than exogenous orienting, because endogenous orienting tends to produce higher levels of activation in the IPS and FEF (e.g., Mort et al., 2007; Rosen et al., 1999). Alternatively, exogenous orienting, which produces less activity in the frontoparietal regions, may not be sufficient to produce SIRE.

Anterior-posterior interaction hypothesis.

The anterior-posterior interaction hypothesis states that SIRE is due to increased interaction between anterior control networks and posterior memory storage (Parker & Dagnall, 2007). The hypothesis does not stipulate the mechanism by which saccades increase interaction, so no formal predictions can be made about which orienting activities will produce SIRE.

Method

Subjects.

Subjects were undergraduates aged 18-30 who received credit in psychology courses for participating and provided informed consent under protocols approved by the University of Louisville IRB. A modified version of Oldfield's (1971) Edinburgh Handedness Inventory was used to classify subjects as consistently-handed (score $\geq |80|$) using the procedure described below. Consistently-handed subjects were randomly assigned to either the endogenous condition ($n = 48$; M absolute handedness score = 92.3; 9 males) or the exogenous condition ($n = 48$; M absolute handedness score = 92.6; 11 males). Two subjects' data were not analyzed because one did not correctly identify any studied word pairs and one falsely identified every non-studied word pair.

Materials.

Handedness inventory.

The handedness inventory was a modified version (see Appendix A) of the Edinburg Handedness Inventory (Oldfield, 1971) that has been used in our lab and others (e.g., Christman et al., 2003; Lyle et al., 2012; Propper et al., 2007). The inventory measures hand preference for ten common activities. Response options and their associated values are Always Left (-10), Usually Left (-5), No Preference (0), Usually Right (+5), and Always Right (+10). The values are summed to produce a handedness score ranging from -100 to +100. As in previous studies (e.g., Edlin, Carris, & Lyle, 2013; Lyle et al., 2012), subjects were classified a priori as consistent-handers if the absolute value of their score was 80 or higher, or as inconsistent-handers if the absolute value of their score was lower than 80.

Paired-associates test.

The word pairs for the paired-associates test were taken from a 100 word pair list used in Parker et al. (2008) and a second 100 word pair list created by Lyle et al. (2012) to the same specifications as the Parker et al. list. Word pairs were taken from these two lists to create three new paired-associates word lists, each consisting of 60 pairs of unrelated words (see Appendix B). The new lists contained word pairs with comparable frequencies of occurrence. Word pairs on the study list were presented in a pseudorandom, pre-generated order. A pseudorandom order was chosen to prevent groupings of more than two word pairs on the study list that would later become original or new items on the upcoming test. Because the first items and last items in a list are sometimes easier to remember than items in the middle of the list (Henson, 1998), three additional word pairs (not included in the Appendix) were added at the beginning and end of each list.

The paired-associates test for each word list was created by separating the word list into three groups of 20 words. Group A pairs appeared on the test in their original form. The first word in a group B pair was combined with the second word in a group C pair to create 20 new word pairs. The test therefore consisted of 20 old pairs and 20 new pairs. Items were presented in a pseudorandomly pre-generated order with the rule that no more than two old pairs or two new pairs could occur consecutively in the list. All subjects received the same study lists and tests in the same order.

Exogenous version activities.

Exogenous orienting.

The exogenous orienting activity consisted of a central fixation cross and a black circle that appeared 13.5° to the left or right of the vertical midline on a screen with a white background (Figure 1). Trials followed a fixed pseudorandom pattern with the restriction that the target would not appear in the same visual hemifield on more than three consecutive trials. The circle was visible for 500 ms and disappeared for 500 ms. This frequency was the same as the frequency of the standard saccade activity, but produced saccades of lower amplitude. Subjects received the following instructions, "In this task you will see a cross in the center of the screen and a dot that will repeatedly appear and disappear. The dot will appear on the left or the right side of the cross. You should start with your eyes on the cross. When the dot appears, move your eyes to look at the dot. When the dot disappears, move your eyes back to the cross. Do not stop this task until you see a screen telling you that it is okay for you to stop moving your eyes. Please sit so that your chin is in line with the edge of the desk."

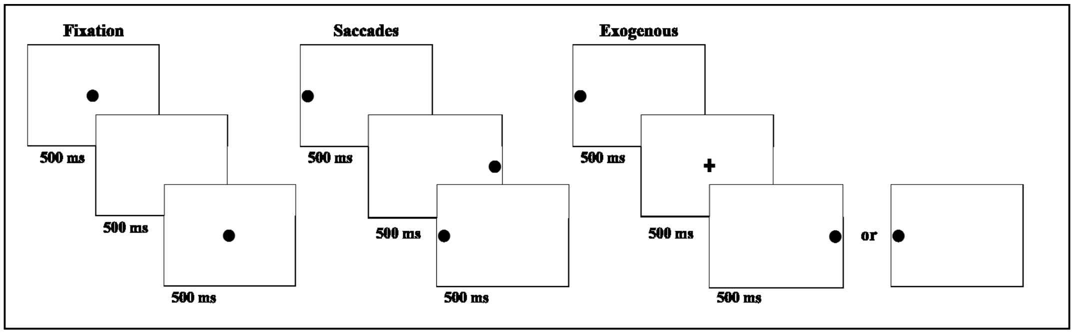

Figure 1. Orienting activities in the exogenous version.

Fixation.

The fixation activity consisted of a black circle that flashed in the center of a screen with a white background for 30 s. The circle was visible for 500 ms and disappeared for 500 ms (Figure 1). Subjects received the following instructions, "In this task you will see a dot repeatedly appear and disappear in the center of the screen. Your job is to watch the dot. Keep your eyes on the dot and do not move your eyes until you see a screen telling you that it is okay for you to move your eyes. Please sit so that your chin is in line with the edge of the desk."

Saccades.

The saccades activity consisted of a black circle that alternated between the left and right sides of a screen with a white background for 30 s. The circle alternated every 500 ms to a position on the left or right side of the screen exactly 13.5° from the vertical midline (Figure 1). Subjects received the following instructions, "In this task you will see a dot repeatedly appear and disappear. The dot will alternate between the left side of the screen and the right. First, the dot will appear on the left, then the right, then the left, then the right, and so on. Your job is to follow the dot with your eyes. Move your eyes left and right in time with the dot. Do not stop moving your eyes until you see a screen telling you that it is okay for you to stop moving your eyes. Please sit so that your chin is in line with the edge of the desk."

Endogenous version activities.

Endogenous orienting.

The endogenous orienting activity consisted of two stationary black circles located on the left and right sides of the screen exactly 13.5° from the vertical midline. Exactly 475 ms after task onset and every 500 ms thereafter, the background on the screen shifted to gray for 25 ms causing a perceptible flash (Figure 2). Subjects received the following instructions, "In this task you will see two dots, one on the left side of the screen and one on the right. You should start by looking at the dot on the left side of the screen. The screen will flash. When this happens, shift your gaze from the dot on the left to the dot on the right. When the screen flashes again you should shift your gaze back to the left dot. Your job is to continue shifting your eyes back and forth between the dots each time the screen flashes. Do not stop moving your eyes until you see a screen telling you that it is okay for you to stop moving your eyes. Please sit so that your chin is in line with the edge of the desk."

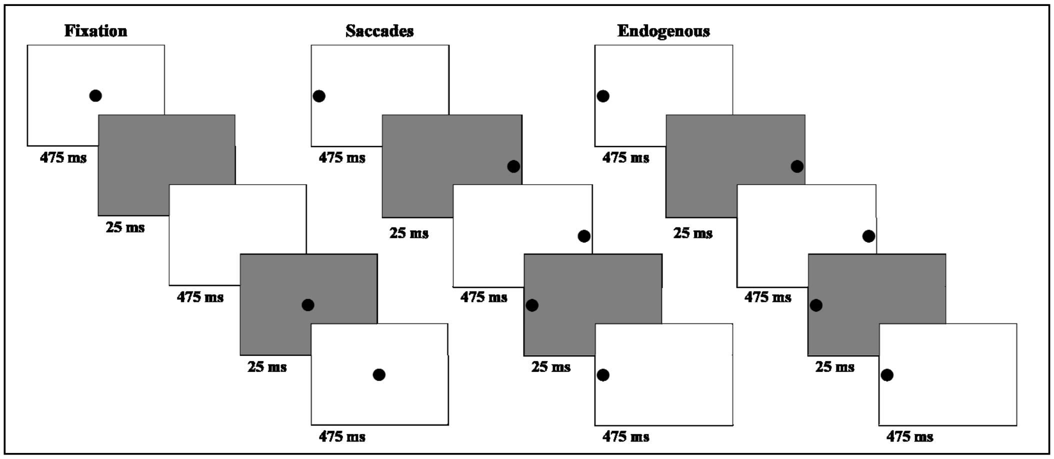

Figure 2. Orienting activities in the endogenous version.

Fixation and saccades.

The endogenous version included fixation and saccade activities similar to those in the exogenous condition. The only difference was that, exactly 475 ms after task onset and every 500 ms thereafter, the background on the screen shifted to gray for 25 ms causing a perceptible flash. This change was made to increase consistency with the endogenous orienting activity.

Procedure.

Subjects signed an informed consent document and then completed the handedness inventory. As in previous studies, subjects were classified as consistently-handed if the absolute value of their handedness score was greater than or equal to 80. Data from inconsistent-handers were not analyzed. Consistent-handers were randomly assigned to either the exogenous or the endogenous version. All additional instructions and tasks were administered on a computer. Subjects were instructed to study the list of word pairs and told that their memory would be tested later. Subjects were informed that some of the pairs would be original pairs from the study list and others would be recombinations of words from the study list that had been paired differently. Word pairs appeared in the center of the screen for 3 s with a 1 s interstimulus interval. During the test phase, pairs of words appeared in the center of the screen and subjects were instructed to press “f” if the pair had been studied or press “j” if the pair was not studied. The test was self-paced.

Subjects practiced using a 9-item paired-associates study list and a test with three old word pairs and three new word pairs. After the practice session, subjects were given a chance to ask questions to make sure they understood the nature of the task. Once the experimenter was satisfied that all subjects understood the instructions, the subjects began the first study phase. Subjects viewed all the word pairs in the first study list, performed one of the three activities associated with their assigned condition, and then completed the first test. After the test, there was a 5-min break before continuing to the second list, which followed the same process as with the first study list, except this time they performed one of the two remaining activities associated with their assigned condition before taking the second test. The process repeated for the third list and subjects performed the remaining activity before the third test. The order of study lists and tests was the same for all subjects, but the order in which subjects performed the activities was counterbalanced. After the subjects completed all three paired-associates tests, they were debriefed.

Results

Design.

All dependent variables were submitted to a 3 (activity: saccades, fixation, novel) x 2 (half: first or second) x 2 (version: endogenous or exogenous) x 6 (order: fixation-saccades-novel, fixation-novel-saccades, etc.) mixed-factorial ANOVAs with activity and half as within-subjects factors, and version and order as between-subjects factors.

Discrimination.

Subjects' ability to discriminate between intact and rearranged word pairs was measured with corrected recognition. Corrected recognition is calculated by subtracting the proportion of falsely remembered new pairs (false alarms) from the proportion of correctly remembered intact pairs (hits).

There was a main effect of half, $F(1, 84) = 26.58$, $p < .001$, $\eta_p^2 = .240$, such that discrimination was higher on the first half ($M = .37$) than the second half ($M = .28$) of each test. There was a significant three-way interaction between activity, half and order, $F(10, 168) = 2.21$, $p = .019$, $\eta_p^2 = .116$. To understand the dynamics giving rise to this complex interaction, each half was analyzed separately. On the first half of the tests, there were no significant interactions, but there was a significant main effect of activity, $F(2, 168) = 3.18$, $p = .044$, $\eta_p^2 = .037$.

As seen in Figure 3, saccades increased subjects' discrimination of intact pairs ($M = .41$) relative to either fixation ($M = .34$), $t(95) = 2.46$, $p = .016$, or the novel activities ($M = .35$), $t(95) = 1.99$, $p = .050$. Although the interaction between activity and version was not significant, $F(2, 83) = .639$, $p = .53$, $\eta_p^2 = .015$, a primary goal of this experiment was to determine whether endogenous or exogenous orienting produced SIRE. Therefore, differences between the activities were analyzed using individual paired *t* tests. In the endogenous version (which included a flashing screen during all three activities), saccades ($M = .44$) significantly increased discrimination relative to fixation ($M = .36$), $t(95) = 2.20$, $p = .033$ and endogenous orienting ($M = .34$), $t(95) = 2.13$, $p =$

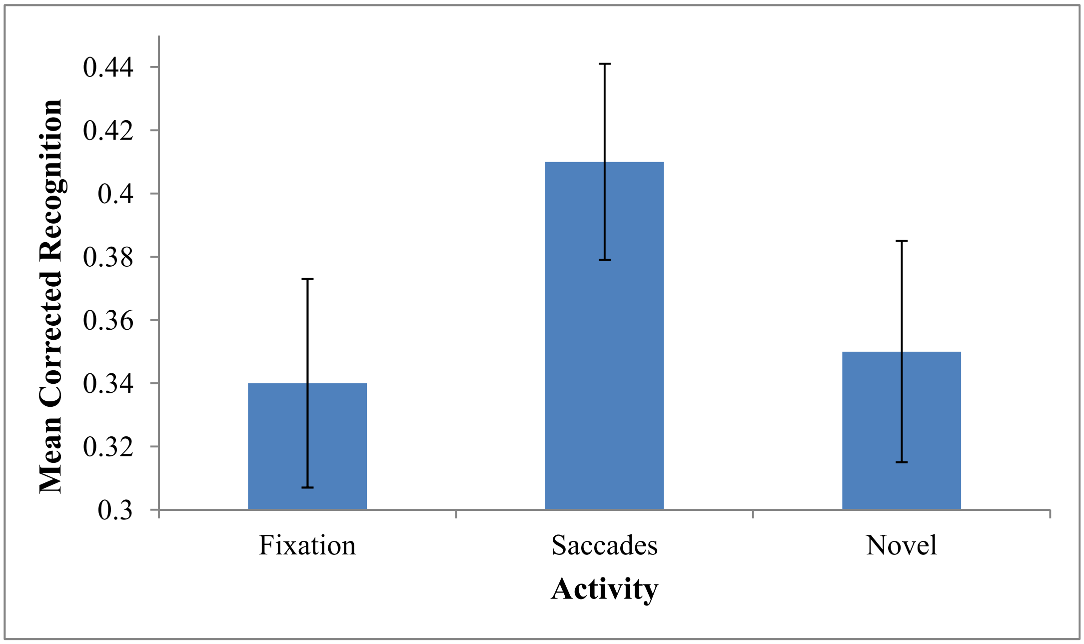

Figure 3. Mean corrected recognition as a function of activity on the first half of the tests. Error bars indicate ±1 *SEM*.

.038 (Figure 4). In the exogenous version, saccades (*M* = .38), fixation (*M* = .32), and exogenous orienting (*M* = .35) were relatively similar, largest *t*(47) = 1.40, *p* = .168. It bears noting

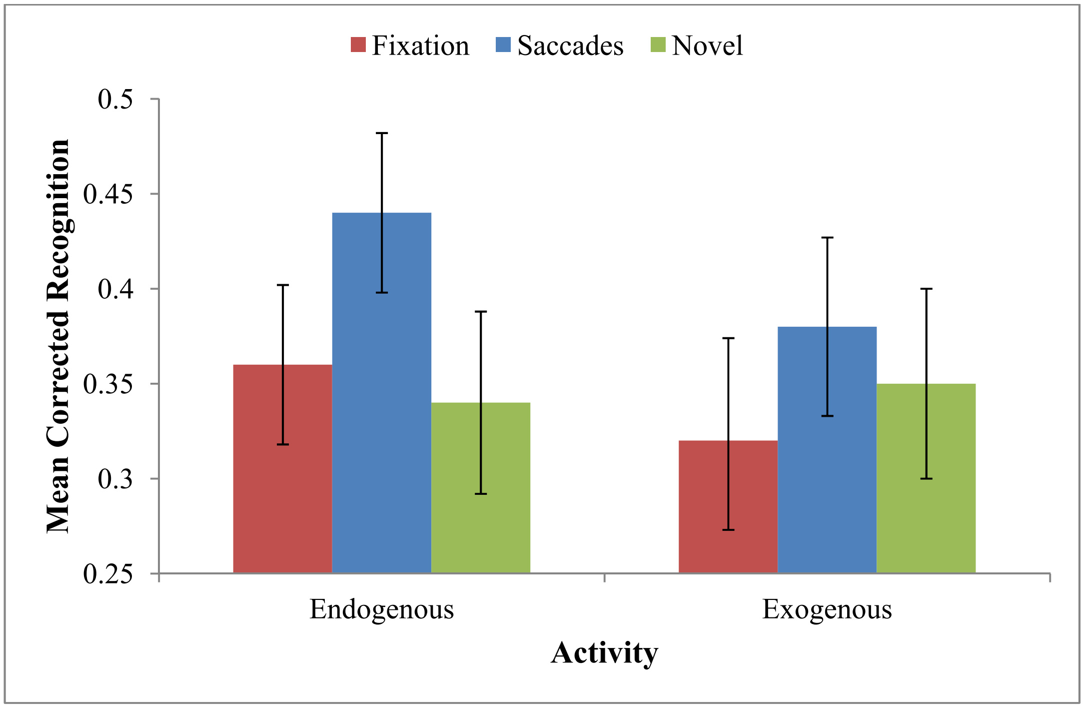

Figure 4. Mean corrected recognition of activity and version on the earlier trials in Experiment 1 and Experiment 2. Error bars indicate ±1 *SEM*.

that discrimination following the exogenous activity was in-between saccades and fixation. Previous research has found that the effects of vertical eye movements sometimes fall between these two conditions (Christman et al., 2003; Parker et al., 2013).

On the second half of the test there was an interaction between activity and order, $F(10, 168) = 2.06$, $p = .030$, $\eta_p^2 = .109$. As seen in Figure 5, this interaction was driven by lower discrimination following saccades on the third test ($M = .18$) versus the first ($M = .37$), $t(62) = 2.67$, $p = .010$. This reduction from the first to the third test did not occur following either fixation (*M*s = .28 and .32, respectively) or the novel activities (*M*s = .27 and .31, respectively), largest $t(62) = .573$, $p = .569$.

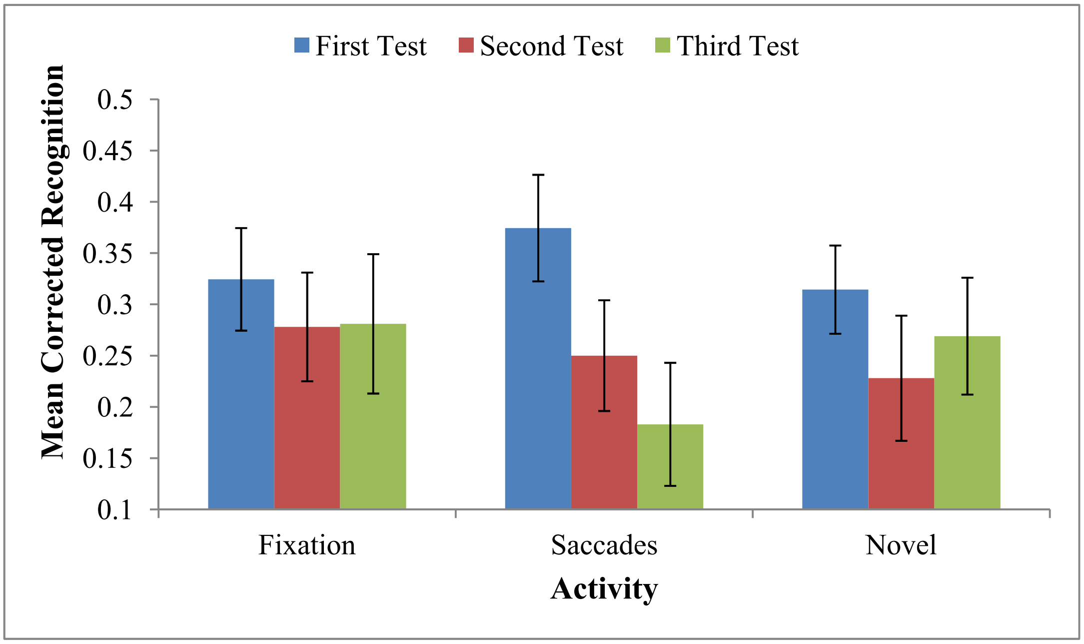

Figure 5. Mean corrected recognition as a function of test order and activity on the second half of the tests. Error bars indicate ±1 *SEM*.

Hits and false alarms.

To explore how test half and orienting activity influenced discrimination, hits and false alarms were analyzed separately.

Test half.

For test half, there was a main effect of half for both hits, $F(1, 84) = 5.82$, $p = .018$, $\eta_P^2 = .065$, and false alarms, $F(1, 84) = 22.05$, $p < .001$, $\eta_P^2 = .208$. Therefore, lower discrimination on the second half of the test was due to a lower hit rate ($M = .61$) and higher false alarm rate ($M = .34$) than on the first (Ms = .62 and .27, respectively).

Activities.

Given evidence that saccades have enhanced discrimination on a paired-associates test by increasing hits (Lyle et al., 2012) or increasing hits and decreasing false alarms (Parker et al., 2008), saccades were expected to increase hits and possibly decrease false alarms on the first half of the tests.

Hits.

There was an activity by order interaction $F(10, 168) = 3.75$, $p < .001$, $\eta_P^2 = .182$, subsumed by an interaction between activity, half, and order $F(10, 168) = 2.19$, $p = .021$, $\eta_P^2 = .115$. Therefore, as with discrimination, each half of the tests was analyzed separately. On the first half of the tests there was a significant interaction between activity and order, $F(10, 168) = 3.56$, $p < .001$, $\eta_P^2 = .175$. As shown in Figure 6a, this interaction was driven by a lower proportion of hits following the novel activities on the third test ($M = .54$) versus the first ($M = .66$), $t(62) = 2.02$, $p = .047$. This reduction did not occur following fixation (Ms = .62 and .61, respectively) or saccades (Ms = .60 and .65, respectively), largest $t(62) = 1.20$, $p = .233$. The main effect of activity was not significant, $F(2, 83) = 1.44$, $p = .244$, $\eta_P^2 = .033$, which was unexpected given that two previous studies found that saccades increased hits on a paired-associates test.

There was also a significant interaction between activity and order on the second half of the tests, $F(10, 168) = 2.67$, $p < .005$, $\eta_p^2 = .137$. As in the first half of the tests,

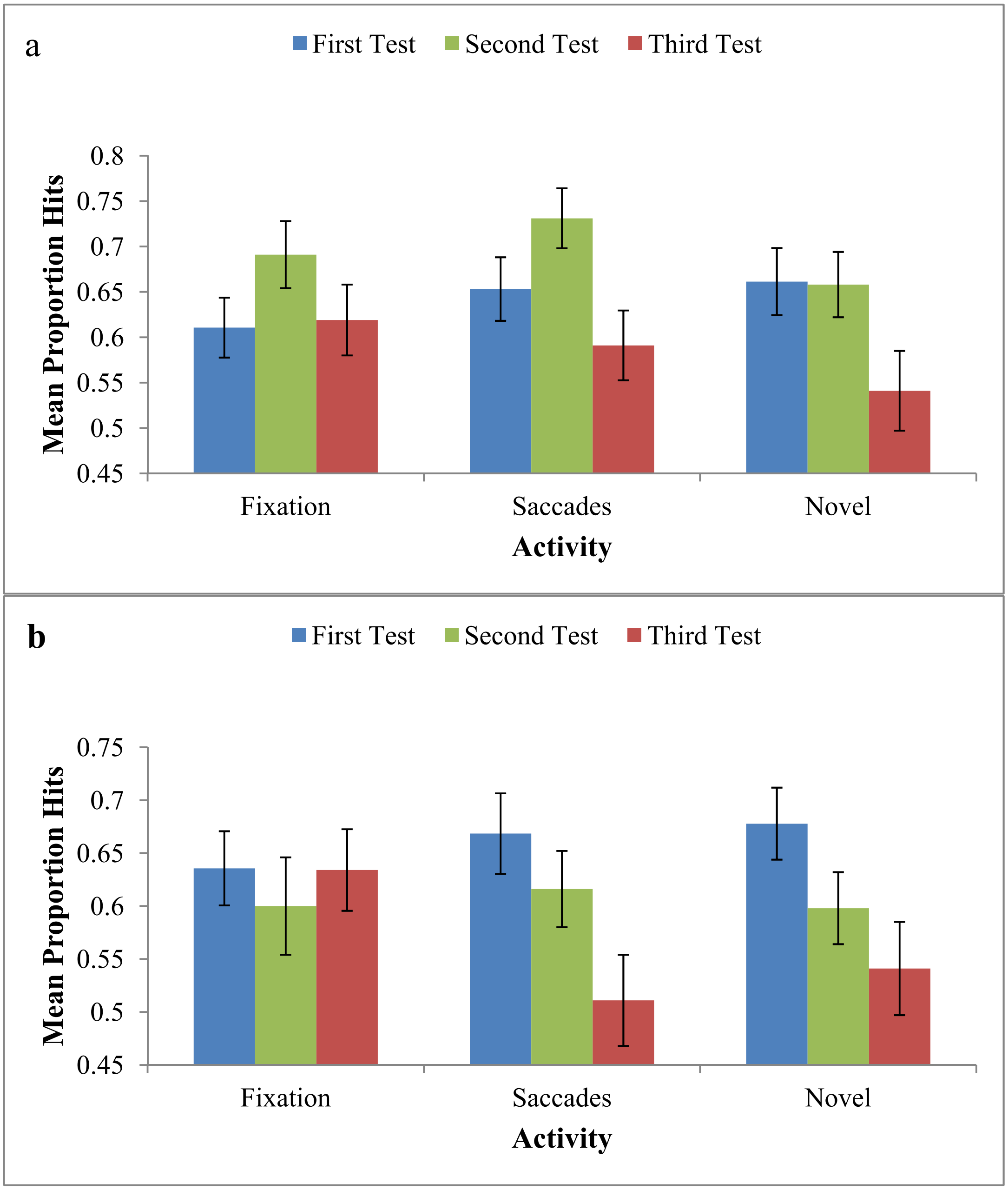

Figure 6. Mean hits as a function of test order and activity on the (a) first half and (b) second half of the tests. Error bars indicate ±1 *SEM*.

subjects had a lower proportion of hits following the novel activities on the third test (*M* = .54) versus the first (*M* = .68), *t*(62) = 2.47, *p* = .016. This reduction did not occur following fixation (*M*s = .63 and .64, respectively), *t*(62) = .024, *p* = .981. Unlike the first half of the tests, subjects also had a lower proportion of hits following saccades on the third test versus the first (*M*s = .51 and .67, respectively), *t*(62) = 2.75, *p* = .008 (Figure 6.b).

False alarms.

For false alarms, there was an interaction between activity, half, and order, *F*(10, 168) = 2.02, $p < .034$, $\eta_P^2 = .108$. As with discrimination, each half of the tests was analyzed separately. The analysis of the first half of the tests revealed a main effect of activity, *F*(2, 168) = 3.53, *p* = .031, $\eta_P^2 = .040$. As seen in Figure 7, this effect occurred

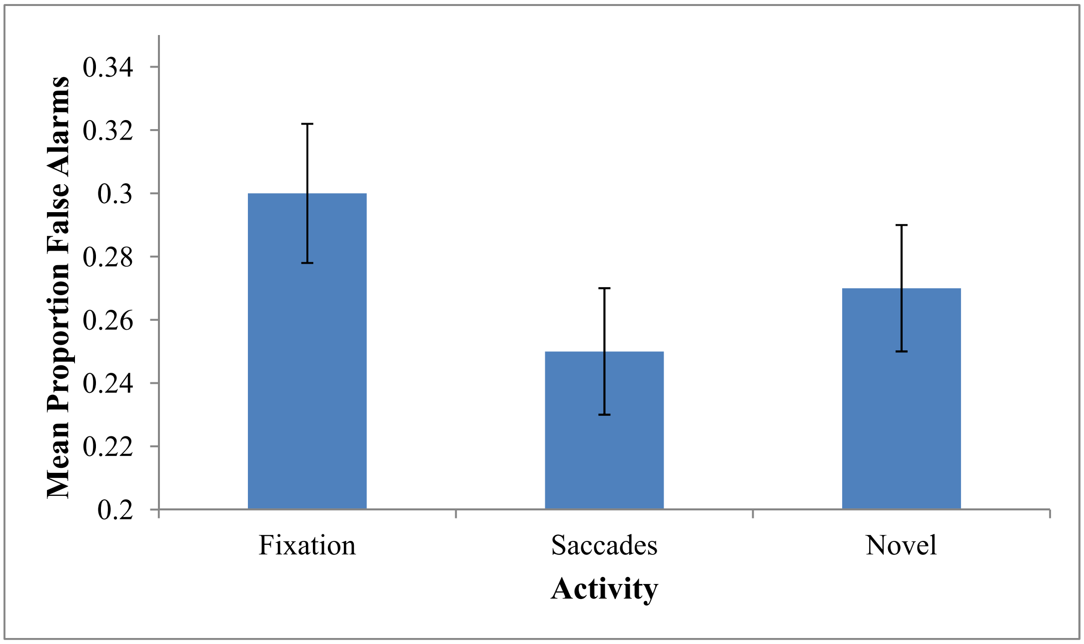

Figure 7. Mean proportion false alarms as a function of activity on the first half of the tests. Error bars indicate ±1 *SEM*.

because subjects had significantly fewer false alarms after performing saccades ($M = .25$) than after fixation ($M = .30$), $t(95) = 2.85$, $p = .005$. Although saccades numerically reduced false alarms relative to the novel activities ($M = .27$) this reduction was not significant, $t(95) = 1.18$, $p = .211$. Together, the analyses of hits and false alarms for the first half of the tests indicated that saccades improved discrimination by lowering false alarm rate.

In addition to the main effect of activity, there was also an interaction between activity and order on the first half of the tests, $F(10, 168) = 2.25$, $p = .017$, $\eta_p^2 = .118$. As Figure 8 shows, the interaction between activity and order is primarily driven by a lower proportion of false alarms following the novel activities on the third test ($M = .17$) than following the first ($M = .36$), $t(62) = 3.71$, $p < .001$. This reduction did not occur

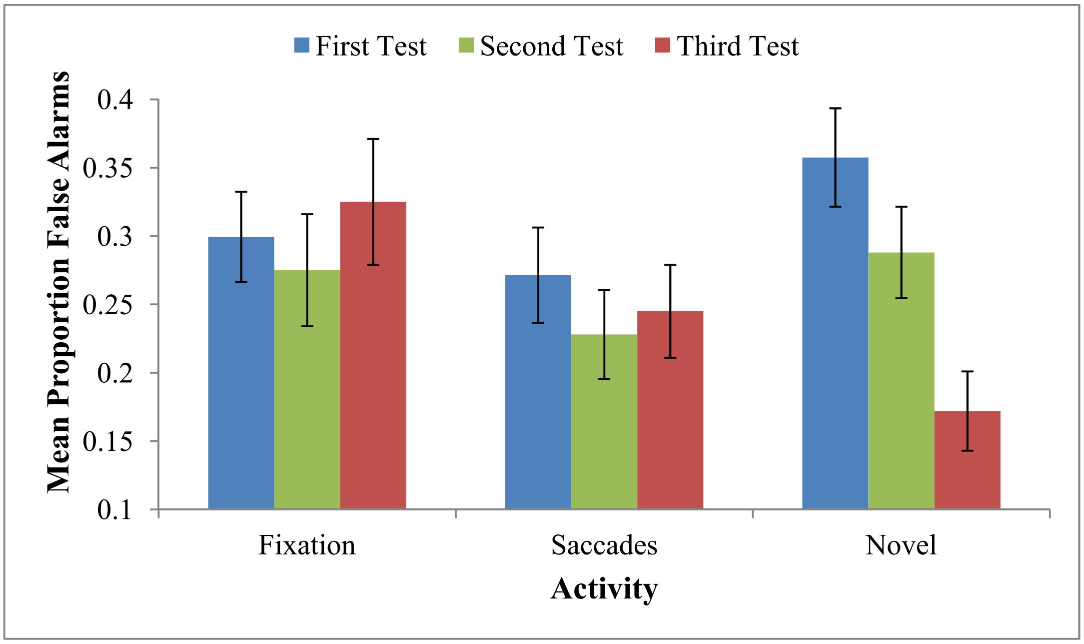

Figure 8. Mean proportion false alarms as a function of test order and activity on the first half of the tests. Error bars indicate ±1 *SEM*.

following fixation (*M*s = .32 and .30, respectively) or saccades (*M*s = .25 and .27, respectively), largest $t(62) = .535$, $p = .594$.

The interaction between activity and version was not significant on the first half of the tests, but because the new orienting activities were the focus of this experiment, individual paired *t* tests were conducted to explore any potential differences between them. In the endogenous version, saccades ($M = .22$) reduced false alarms compared to fixation ($M = .28$), $t(47) = 2.43$, $p = .019$. There was a lower false alarm rate following saccades than following endogenous orienting ($M = .27$), which approached significance, $t(47) = 1.96$, $p = .056$. In the exogenous version, saccades ($M = .28$), fixation ($M = .32$), and exogenous orienting ($M = .27$) were relatively similar, largest $t(47) = 1.63$, $p = .109$.

On the second half of the tests, the interaction between activity and order only approached significance, $F(10, 168) = 1.68$, $p = .089$, $\eta_p^2 = .091$. Together, the analyses of hits and false alarms for the second half of the tests indicated that the decrease in discrimination following saccades on the third test was primarily due to a decrease in hit rate.

Discussion

In Experiment 1, two novel orienting activities were compared to saccades and to fixation. Discrimination on the earlier trials (first half of the test) was significantly higher than on the later trials (second half). This difference was due to a greater number of hits and fewer false alarms in the earlier trials. The increased difficulty of later trials was likely a consequence of output interference from retrieving items on the earlier trials (Criss et al., 2011).

The main effect of activity was only significant on earlier trials. Because the goal of Experiment 1 was to examine differences between the orienting activities, and only the earlier trials produced a clear SIRE effect, the orienting activities are discussed in relation to these trials. The lack of SIRE in later trials of the current experiment will be discussed in more detail in the Later Trials section. The final section of this discussion explains how these findings relate to the three hypotheses described in the Introduction: interhemispheric interaction, attentional control, and anterior-posterior interaction.

Earlier trials.

Although saccades numerically increased hits when performed prior to the first and second tests, the benefit of saccades on discrimination was primarily because of a decrease in false alarms. The finding that saccades produce SIRE on a paired-associates test replicates findings from previous studies (Lyle et al., 2012; Parker et al., 2008).

Saccades improved discrimination relative to the novel orienting activities introduced in the current experiment, suggesting that neither of these activities were capable of producing SIRE. Although there was no significant interaction between activity and version (endogenous versus exogenous), these two versions were further analyzed because comparison of the novel activities was a central goal of Experiment 1. These additional analyses revealed that, in the endogenous version, discrimination following saccades was significantly higher than following the endogenous activity. In the exogenous version, saccades were only numerically higher than following the exogenous activity. Neither of the novel activities improved discrimination relative to fixation. However, discrimination following the exogenous condition was in-between discrimination following saccades and fixation. This effect was similar to that produced by vertical saccades in previous studies (e.g., Christman et al., 2003). It should be noted that vertical saccades sometimes produce an effect in-between saccades and fixation (e.g., Christman et al., 2003) and sometimes enhance retrieval (e.g., Lyle, Logan, et al., 2008). If exogenous saccades are similar to vertical saccades, then exogenous saccades may also enhance retrieval under some circumstances. It remains for future research to determine if exogenous and vertical saccades enhance performance on some types of retrieval tests.

Components necessary for SIRE.

The findings in the earlier trials provide evidence that moving the eyes back and forth is not sufficient to produce SIRE. Neither endogenous orienting to a constant target nor exogenous orienting to a random target improved recognition. Therefore, the term SIRE may not be entirely accurate because not all types of saccades enhance retrieval. This finding is theoretically important because it indicates that a specific component of the standard saccade activity must be necessary to produce SIRE.

A possibility suggested in the Introduction is that the standard saccade activity produces a specific type of saccades called predictive saccades. The two novel orienting activities studied in this experiment should not have produced predictive saccades and both failed to produce SIRE. The memory-guided nature of predictive saccades and their activation of brain regions implicated in retrieval (see Simo et al., 2005) suggest that predictive saccades may be a likely mechanism of enhancement. The potential role of these regions in memory enhancement is explained further in the General Discussion.

Later trials.

There was an interaction between activity and order for discrimination on the second half of the paired-associates tests. This interaction occurred because performance following saccades was lower on the third test relative to the first test, whereas performance following fixation or the novel orienting activities was similar across those tests.

It is unclear why saccades had no effect on later trials. Previous studies using the paired-associates test (Lyle et al., 2012; Parker et al., 2008) did not include test half as a factor, so it is unknown whether SIRE decreased on later trials in those studies. The lower recognition on later trials relative to earlier trials suggests the presence of output interference on later trials, which was eliminated by saccades in a previous experiment (Lyle & Edlin, under review, Experiment 2). However, Lyle and Edlin had subjects make saccades prior to each half of the test, unlike the current experiment, which included only one activity prior to the entire test. Therefore, SIRE might have diminished by later trials in the current experiment. Brunye et al. (2009) suggested that the duration of SIRE might be similar to the duration of TMS stimulation of cortical regions, which averages 3 to 4 m (Pascual-Leone et al., 1998). Shobe et al. (2009) estimated that the effect of saccades lasts from 7 to 9 m, but they used a test that measured multiple dimensions of creativity (fluency, originality, elaboration, categorical distinctiveness, and appropriateness) instead of a retrieval test. Their results suggested a diminishing effect of saccades over time, but a significant enhancement lasted 7 to 9 m for originality and 1-3 m for categorical distinctiveness. The exact duration of saccade-induced benefits on retrieval are unknown, but have been found to persist for at least 3 m (Parker et al., 2013). The retrieval phase in the current experiment was self-paced, and completion time was not recorded, so SIRE might have ended prior to later trials.

Another difference between the current experiment and previous experiments is the number of times the paired-associates test was administered. In previous studies, subjects completed the paired-associates test once (Parker et al., 2008) or twice (Lyle et al., 2012), but subjects in the current experiment completed the test three times. The current experiment was not designed to detect changes in SIRE during repeated testing; therefore, it is difficult to explain the exact nature of the diminishing effect of saccades in the current experiment. One disadvantage of a within-subjects design is the possibility of carryover effects. For example, subjects may develop test-taking strategies, which improve their performance on later tests. Normally, counterbalancing controls for carryover effects. However, SIRE may have long-term consequences for carryover effects. For example, subjects who performed saccades prior to the first or second test may have developed a better-test taking strategy during that test, which prevented a decline in performance on the third test compared to subjects who got saccades prior to the third test. Although this explanation alone cannot account for the lack of SIRE on the later trials in the first test, this possibility warrants further investigation if future SIRE studies continue to use a within-subjects design.

Outcome of hypotheses predictions.

In the following subsections, the results of Experiment 1 are discussed in relation to predictions made by each of the hypotheses of saccade-induced enhancement.

Interhemispheric interaction hypothesis.

The interhemispheric interaction hypothesis suggests that SIRE is due to the bilateral nature of saccades. Because all three saccade activities included bilateral movements of the eyes, all three activities should have equalized the activity across the hemispheres leading to increased interhemispheric interaction. Endogenous and exogenous orienting did not produce SIRE in the current experiment. Therefore, the results of this experiment contradict the interhemispheric interaction hypothesis.

Attentional control hypothesis.

The attentional control hypothesis predicts that all three orienting activities should have produced SIRE, because all three have been shown to produce activity in the IPS and FEF (e.g., Corbetta & Shulman, 1998; Moon et al., 2007; Petit et al., 2009). In addition, if enhancement is correlated with the level of activation in these frontoparietal regions, then endogenous orienting should have produced greater SIRE than exogenous orienting. Neither of these predictions was borne out by the results. Endogenous and exogenous orienting did not increase retrieval relative to the fixation condition, and endogenous orienting produced numerically lower retrieval than exogenous orienting. The results of Experiment 1 do not contradict the basic premise of the attentional control hypothesis—that saccades increase attentional control—but do necessitate a restructuring of the role of frontoparietal activity.

Anterior-posterior interaction hypothesis.

According to the anterior-posterior interaction hypothesis, saccades increase the interaction between anterior regions involved in attentional control and posterior regions where the memory is stored. Because Parker and Dagnall (2007) did not explain how saccades increase this interaction, no formal predictions about the two new orienting activities could be made. However, anterior regions involved in attentional control and posterior regions involved in memory are only activated during predictive saccades (see Simo et al., 2005). Endogenous and exogenous orienting activities that should not have produced predictive saccades did not produce SIRE. Only the standard saccade activity, which does produce predictive saccades, improved retrieval in the current experiment.

Summary.

In Experiment 1, only the standard saccade activity produced a benefit relative to fixation on a paired-associates test. This benefit was limited to earlier trials of the test. The endogenous and exogenous activities in Experiment 1 did not increase retrieval relative to the fixation condition on earlier or later trials. These types of saccades are visually-guided, whereas predictive saccades are memory-guided. If the standard saccade activity produces predictive saccades, then this may be the component necessary for SIRE.

Although none of the hypotheses described in the Introduction could predict the results of the current experiment, the results do provide tentative support for the anterior-posterior interaction hypothesis. According to this hypothesis, saccades increase the interaction between regions implicated in attentional control and memory storage (Parker & Dagnall, 2007). Predictive saccades have been found to produce activity in these areas (Simo et al., 2005). If the standard saccade activity involves predictive saccades, then this is the first indication that brain regions implicated by the anterior-posterior interaction hypothesis are active during saccades.

EXPERIMENT 2: COVERT AND OVERT ORIENTING

Introduction

The saccade activity in all SIRE research involves overtly shifting attention between two targets. There are two ways to shift attention. One is by overtly shifting attention, which also involves moving the eyes to focus the fovea on a target. The second involves covertly shifting attention without moving the eyes. It is unknown whether covert attentional shifts are sufficient to enhance retrieval, or if the physical act of moving the eyes is a necessary component.

Experiment 2 tests whether overt orienting is necessary for retrieval enhancement. In addition to the typical saccade and fixation conditions, subjects also performed a covert orienting activity requiring them to direct their attention to a target to the right or left, while maintaining fixation on a central fixation point. Because covert orienting requires subjects to shift their attention without moving their eyes, two components were added to the orienting activities to ensure compliance. One, a camera recorded subjects' eyes to ensure they made no eye movements during covert orienting. Two, subjects were required to indicate whether any of the targets had a white center to ensure they were covertly shifting attention.

Predictions based on the hypotheses of saccade-induced enhancement.

Interhemispheric interaction hypothesis.

According to the interhemispheric interaction hypothesis, saccades produce bilateral activity that equalizes the activation in the two hemispheres (Christman et al., 2003). Therefore, only the saccades condition should enhance retrieval because the physical eye movements are necessary for SIRE.

Attentional control hypothesis.

According to the premotor theory of attention, a covert shift of attention is equivalent to an overt shift with the physical eye movements suppressed (see Rizzolatti, Riggio, Dascola, & Umilta, 1987; cf. Smith & Schenk, 2012). Some studies have indicated that overt shifts lead to higher levels of activation in the frontoparietal network (Beauchamp, Petit, Ellmore, Ingeholm, & Haxby, 2001; de Haan, Moryan, & Rorden, 2008), whereas others have suggested that covert shifts lead to higher levels of activation (Corbetta, 1998), and still others have found no difference (Nobre, Gitelman, Dias, & Mesulam, 2000). Although there are disparate findings, all these studies agree that overt and covert shifts of attention activate the same frontoparietal network, which according to Lyle and Martin (2010) leads to SIRE. If frontoparietal activation is the component of saccades that leads to enhancement, and both types of orienting produce activation in these areas, then both should produce SIRE.

Anterior-posterior interaction hypothesis.

The anterior-posterior interaction hypothesis does not explain how saccades increase interaction between these areas, so no formal predictions can be made.

Method

Subjects.

Subjects were 24 consistently-handed undergraduates (*M* absolute handedness score = 91.2; 6 males) recruited and classified using the same methods as in Experiment 1. Subjects were removed for moving their eyes during the covert activity (*n* = 18; 2 males), not moving their eyes during the saccades activity (*n* = 1; 0 males), or failing to accurately determine the presence or absence of the white center circle during any of the activities (*n* = 4; 0 males).

Materials.

The covert orienting activity in Experiment 2 required subjects to shift their attention without moving their eyes. To ensure that subjects complied with the instructions, a 10-megapixel webcam attached to the top of the monitor recorded subjects' eyes during the experiment. All videos were recorded in 640 x 480 resolution.

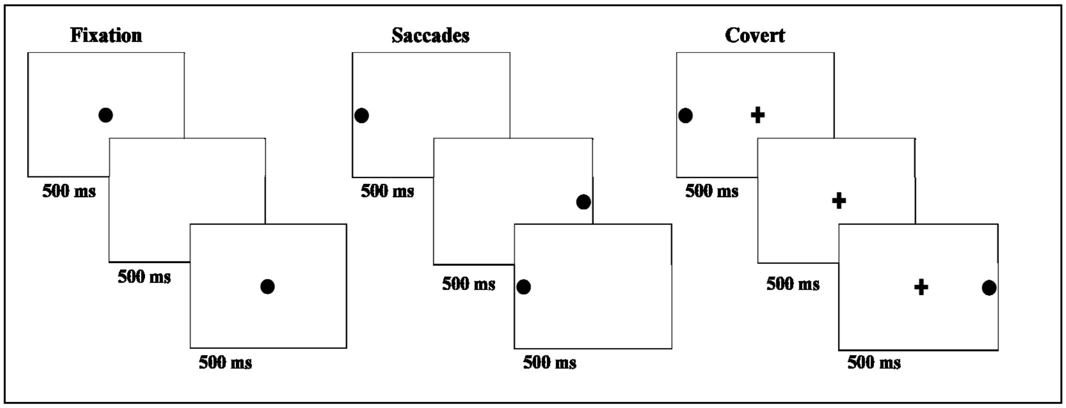

Figure 9. Orienting activities in Experiment 2.

Activities.

Covert orienting.

The covert orienting activity consisted of a central fixation cross and a black circle that alternated between the left and right sides of a screen with a white background. The circle alternated every 500 ms between the left and right side of the screen 13.5°

from the vertical midline (Figure 9). To determine whether subjects were covertly shifting their attention to follow the circle during the covert orienting activity, there was a 50% chance that one random circle during the last 15 s of each activity contained a white center that was half the size of the black circle.

Subjects were given the following instructions, “In this task you will see a dot repeatedly appear and disappear. The dot will alternate between the left side of the screen and the right. First, the dot will appear on the left, then the right, then the left, then the right, and so on. Your job is to follow the dot without moving your eyes. When the dot appears, you should try to look at it by shifting your attention, but keep your eyes on the cross. Do not move your eyes until you see a screen telling you that it is okay for you to move your eyes. After the task, you will be asked if any of the dots contained a white inner circle. Please sit so that your chin is in line with the edge of the desk. The webcam will be recording your eyes during the task”.

Fixation and saccades.

Experiment 2 included the fixation and saccades activities described in the exogenous condition of Experiment 1. For consistency across conditions, the fixation and saccades activities also included the webcam and the 50% chance that one of the circles in the last 15 s of each activity would include a white center (Figure 9). The instructions subjects received prior to performing the fixation and saccades conditions included the additional instructions, “after the task you will be asked if any of the dots contained a white inner circle”, and informed subjects the webcam would be recording their eyes during the task.

Procedure.

Experiment 2 followed the same procedure as Experiment 1, except as follows. Before the practice test, the experimenter turned on the camera and informed subjects their eye movements would be recorded during the experiment. After each of the three activities, subjects indicated whether they had seen a white center in any of the black circles by pressing “y” or “n” on the keyboard.

After subjects left the testing room, the experimenter reviewed the videos to ensure subjects complied with the instructions for each activity. Subjects who moved their eyes during the fixation activity, failed to move their eyes during the saccade activity, or made more than one accidental saccade during the covert orienting activity (typically if the circle with the white center appeared) were excluded from subsequent analyses.

In the course of data collection, it became apparent that many subjects were moving their eyes during the covert orienting condition. To ensure that all subjects followed the instructions, the experimenter told subjects to read the instructions for each task carefully before telling them that the camera would be recording their eyes during the task. This additional instruction did not increase compliance. Therefore, the experimenter also told subjects that they would perform three different types of activities with their eyes during the experiment. This instruction increased compliance, but some subjects still moved their eyes during the covert orienting condition.

Results

Design.

All dependent variables were submitted to a 3 (activity: saccades, covert orienting, fixation) x 2 (half: first or second) x 6 (order: saccades-covert-fixation, saccades-fixation-covert, etc.) mixed-factorial ANOVAs with activity and half as within-subjects factors, and order as a between-subjects factor.

Discrimination.

Subjects' ability to discriminate between intact and rearranged pairs was measured with corrected recognition. Mirroring the results of Experiment 1, there was a main effect of half, $F(1, 18) = 16.22$, $p = .001$, $\eta_P^2 = .474$, such that subjects had higher discrimination on the first half ($M = .46$) than on the second ($M = .34$).

There was no main effect of activity or any significant interactions, but the interaction between activity and half approached significance $F(2, 17) = 3.77$, $p = .068$, $\eta_P^2 = .271$. A post hoc power analysis using Gpower (Erdfelder, Faul, & Buchner, 1996) revealed that 30 subjects would be required for an 80% chance that an effect of this size would be detected at an alpha of .05. Although this interaction was not significant,

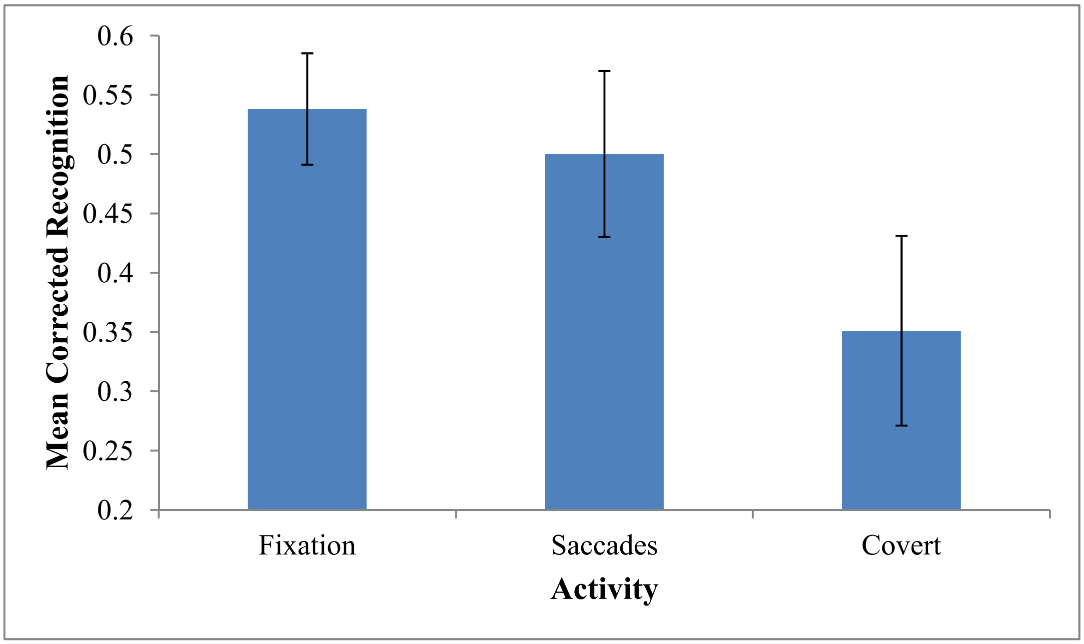

Figure 10. Mean corrected recognition as a function of activity on the first half of the tests. Error bars indicate ±1 *SEM*.

further analysis was conducted in pursuit of the experimental goal of comparing covert orienting to saccades. On the first half of the test, discrimination was significantly lower for covert orienting (*M* = .35) than fixation (*M* = .53), *t*(23) = 2.24, *p* = .035, and covert orienting was numerically lower than saccades (*M* = .50), *t*(23) = 1.20, *p* = .059 (Figure 10).

On the second half of the test, performance was similar for fixation (*M* = .37), saccades (*M* = .34), and covert orienting (*M* = .33), largest *t*(23) = .55, *p* = .58.

Hits and false alarms.

To determine how test half influenced discrimination, hits and false alarms were analyzed separately. There was a main effect of half for both hits, *F*(1, 18) = 6.3, *p* = .022, η_P^2 = .259, and false alarms, *F*(1, 18) = 10.10, *p* = .005, η_P^2 = .359, with more hits (*M* =.69) and fewer false alarms (*M* = .22) in the first half than in the second half (*M*s = .62 and .28, respectively). No other main effects or interactions approached significance.

To determine why discrimination decreased following covert orienting, hits and false alarms were analyzed separately for the first half of the test. The proportion of hits was significantly lower following covert orienting (*M* = .62) than following fixation (*M* = .72), *t*(23) = 2.18, *p* = .040, and numerically lower following covert orienting than following saccades (*M* = .72), *t*(23) = 1.79, *p* = .086.

The proportion of false alarms was numerically higher following covert orienting (*M* = .27) than following fixation (*M* = .18), *t*(23) = 2.01, *p* = .057, or saccades (*M* = .22), *t*(23) = 1.25, *p* = .224.

Removed Subjects

In the current experiment, the results of 18 subjects were excluded from analyses because these subjects made eye movements during the covert activity. To determine how removing these subjects might have affected the results of Experiment 2, corrected recognition on the first half of the tests was submitted to a 3 (activity: fixation, saccades, covert orienting) x 2 (inclusion: included or removed) mixed-factorial ANOVA with activity as a within-subjects factor, and inclusion as a between-subjects factor. There was an interaction between activity and inclusion $F(2, 80) = 3.77$, $p = .027$, $\eta_p^2 = .086$. Following fixation, the corrected recognition of included subjects ($M = .54$) was significantly higher than removed subjects ($M = .29$), $t(40) = 2.57$, $p = .014$, and numerically higher following saccades (Ms = .50 and .34, respectively), $t(40) = 1.54$, $p = .131$ (Figure 11). Following the covert activity, included subjects ($M = .35$) and removed

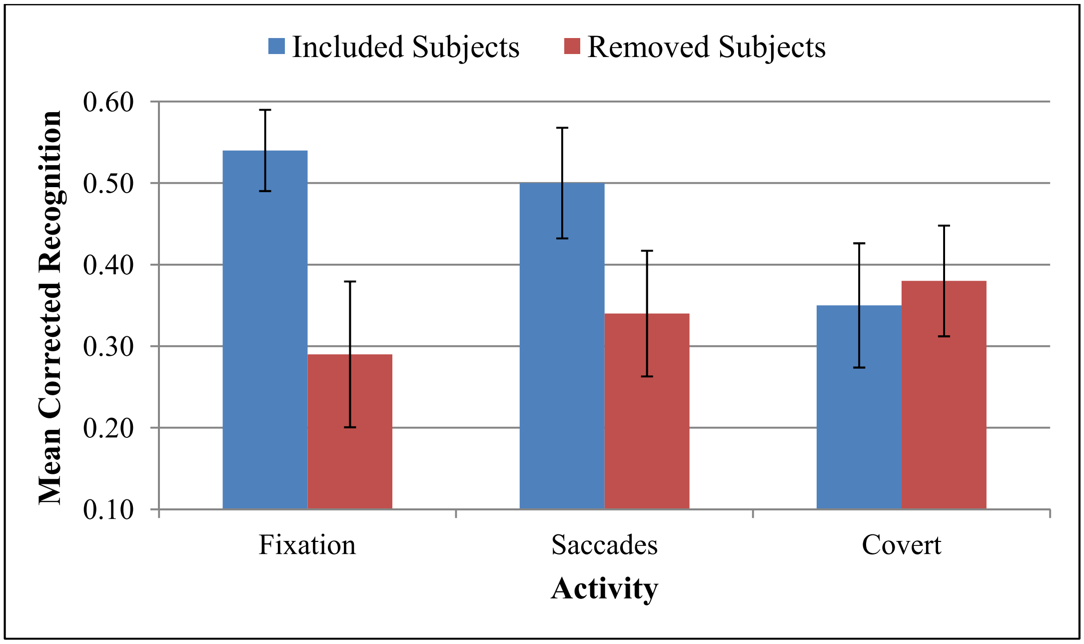

Figure 11. Mean corrected recognition as a function of activity and inclusion on the first half of the tests. Error bars indicate ±1 *SEM*.

subjects (*M* = .38) were relatively similar, *t*(40) = .24, *p* = .812, despite the fact that removed subjects did not perform the covert activity.

Discussion

Discrimination was significantly lower on the second half of the tests than the first. As stated in relation to Experiment 1, this may have been due to output interference. No other main effects or interactions in Experiment 2 were significant, however, the interaction between activity and half approached significance. On the first half of the tests, covert orienting produced lower discrimination than did fixation by decreasing hits and increasing false alarms.

Although the interaction between activity and half was not significant, the fact that covert orienting produced lower discrimination than fixation on the first half of the tests is interesting to consider when explaining why saccades did not produce SIRE. The absence of SIRE in the current experiment may have been because of Type II error, but two other theoretically interesting possibilities are suggested below based on how the results of Experiment 2 are described.

One description of these results is that, relative to fixation, saccades did not produce a beneficial effect and covert orienting had a detrimental effect. In the current experiment, subjects who moved their eyes during covert orienting were excluded from analysis. The subjects that were capable of inhibiting eye movements may have had more attentional control than the subjects that were removed. SIRE has been hypothesized to involve increases in attentional control (Lyle & Martin, 2010), but the relationship between baseline attentional control and SIRE has never been tested. It may be that individuals with lower baseline attentional control derive greater benefits from performing saccades because they have more room for improvement. Subjects that were removed had significantly lower corrected recognition following the fixation activity than included subjects did, but not following saccades. Saccades decreased the difference between these groups by slightly decreasing the performance of included subjects and increasing the performance of removed subjects. This finding suggests that SIRE may depend on baseline attentional control and warrants further investigation with a study that measures this factor. Unfortunately, no measure of attentional control was included in the current experiment and the group of removed subjects may have included subjects that were unable to perform the covert activity and subjects that failed to follow instructions.

Although the subjects in the current experiment had sufficient attentional control for covert orienting, performing the covert orienting activity may have depleted those resources. The covert orienting activity was difficult, as evidenced by the fact that 38% of subjects were excluded because of failure to perform the activity. In addition, some brain imaging studies show higher levels of frontoparietal activation during covert orienting than saccades (e.g., Corbetta, 1998), which implies that covert orienting is more taxing on the attentional network. Performing a difficult, attentionally demanding activity prior to retrieval might have depleted attentional resources (for review, see Muraven & Baumeister, 2000). Taxing attentional control on one task can decrease performance on subsequent tasks (Inzlicht & Schmeichel, 2012; Muraven & Baumeister, 2000). Depletion of attentional control may have produced the detrimental effects of covert orienting in the current experiment.

A second description of the results from Experiment 2 is that covert orienting had no effect on memory retrieval, and that both saccades and fixation produced a beneficial effect. On the first half of Experiment 2, the mean corrected recognition for saccades (*M* = .50) and fixation (*M* = .53) was higher than saccades (*M* = .41) in the first half Experiment 1, whereas covert orienting (*M* = .35) was similar to fixation (*M* = .34) in Experiment 1. In previous studies, saccades enhanced retrieval compared to fixation, but the current experiment included the additional requirement that subjects determine if any of the black circles contained a white center. Although this activity did not require saccades, it might have required sufficient attentional control to serve as an attentional control exercise. As mentioned in the Introduction of Experiment 1, exogenous orienting during saccades is not completely exogenous, because subjects must employ top-down control to increase the salience of the circles (see Corbetta & Shulman, 2002). The fixation activity in the current experiment may have represented a target detection task that required subjects to increase the salience of the circle with the white center. Edlin and Lyle (2013) posited that practicing attentional control during saccades might increase attentional control during subsequent retrieval. Similarly, practicing target detection during fixation might increase the ability to detect a target memory during subsequent retrieval. However, one problem with this interpretation is that the exogenous activity in Experiment 1 did not significantly increase corrected recognition relative to the fixation activity without a target detection task. In addition, the predictive saccade task did increase corrected recognition, but should be less reliant on target detection because the location of targets are stored in memory. A second problem with this interpretation is that the covert orienting activity also contained the target detection component but did not enhance retrieval. As stated in the paragraph above, the covert orienting activity may have depleted attentional resources and hence negated any benefit from practicing target detection. Future research is needed to determine if a fixation activity that includes target detection improves retrieval relative to a fixation activity that does not.

Summary.

In Experiment 2, neither covert orienting nor saccades enhanced retrieval relative to the fixation activity. These results indicate the possibility of a Type II error. Conversely, modifying the fixation activity or removing subjects with low attentional control may have inadvertently affected the results.

GENERAL DISCUSSION

Previous research has shown that 30 s of saccades improve memory retrieval (e.g., Brunye et al., 2009; Christman et al., 2003; Lyle, Logan, et al., 2008; Nieuwenhuis et al., 2013; Parker & Dagnall, 2007), an effect labeled SIRE (Lyle & Martin, 2010). This dissertation examined individual components of the standard saccade activity to determine which components of the activity were necessary for SIRE. The results are discussed below. Following this is a discussion of how these results relate to the three hypotheses of SIRE presented in the Introduction.

Necessary Components for SIRE

The saccade activity in previous SIRE research is similar to an orienting activity that causes predictive saccades (e.g., Ross & Ross, 1987; Shelhamer & Joiner, 2003). In predictive saccade studies, subjects orient exogenously to a target with a constant spatial and temporal pattern. After a few repetitions, the subjects predict the appearance of the target and orient endogenously to the location before the target appears. Because the standard saccade activity involves exogenous orienting and endogenous orienting, it is possible that either activity alone is the one that produces SIRE. Moreover, the standard saccade activity may involve predictive saccades, and these saccades may be necessary for SIRE. Experiment 1 was designed to determine if endogenous or exogenous orienting produced SIRE. These orienting activities, which should not have produced predictive saccades, did not produce SIRE relative to the fixation activity. Alternatively, the standard saccade activity did produce SIRE, albeit only on earlier test trials.

A second component of the saccade activity is that it involves overt orienting, or moving the eyes and attention simultaneously. Alternatively, attention can be covertly oriented without moving the eyes. Experiment 2 was designed to determine whether saccades (overt orienting) are necessary for retrieval enhancement, or whether covert attention shifts alone are sufficient. Neither saccades nor covert orienting improved retrieval relative to fixation. Potential reasons for the lack of SIRE were posited in the Discussion of Experiment 2.

Predictive saccades.

Because the results of Experiment 1 suggest that predictive saccades may be the necessary component for SIRE, they warrant further discussion. As mentioned in the Introduction, predictive saccades are guided by memory instead of by visual stimuli, and thus produce activity in regions associated with memory retrieval (see Simo et al., 2005). In addition to the activation produced by visually-guided saccades, predictive saccades also produce greater activation in ACC, MFG, SMG, AG, and the hippocampi relative to fixation (Simo et al., 2005). Individual regions are mentioned briefly below, but their potential role in SIRE is discussed afterwards in terms of attentional networks that include these regions.

Anterior cingulate cortices and medial frontal gyri.

MFG, which include dorsolateral prefrontal cortices (dlPFC), and ACC are frontal regions associated with executive control. As mentioned in the Introduction, executive control has been associated with memory retrieval (for review, see Levy & Anderson, 2002), creativity (Groborz & Necka, 2003), and letter matching (Banich, 1998). ACC and dlPFC serve different executive functions in the control of attention. The ACC are involved in error detection and conflict monitoring (see Kerns et al., 2004; cf, Mansouri, Tanaka, & Buckley, 2009), whereas dlPFC are involved in resolving conflict (e.g., Fassbender et al., 2004; Silton et al., 2010) and maintaining task goals (for review, see MacDonald, Cohen, Stenger, & Carter, 2000). During retrieval, ACC and dlPFC are more active when retrieval is more attentionally demanding (for review, see Levy & Anderson, 2002) or when confidence in a retrieved memory is low (e.g., Fleck, Daselaar, Dobbins, & Cabeza, 2006).

Furthermore, ACC and dlPFC are associated with other tasks that have shown saccade-induced benefits. On a cued-flanker task, these regions are more active during trials with incongruent flankers than congruent flankers (Fan, Flombaum, McCandliss, Thomas, & Posner, 2003). Edlin and Lyle (2013) found that saccades specifically reduce response times on trials with incongruent flankers. Also, there is activity in these regions during creativity tasks (for review, see Gonen-Yaacovi et al., 2013) similar to the alternate uses task used by Shobe et al. (2009) to show that saccades enhanced creativity.

Supramarginal gyri and angular gyri.

The AG are activated during a variety of tasks, and may relay information between different cortical regions (for review, Seghier, 2013). The AG are active during successful memory retrieval (e.g., Ciaramelli et al., 2008) and TMS knockout of the left AG is detrimental to recognition (Sestieri, Capotosto, Tosoni, Romani, & Corbetta, 2013). In addition to the AG, the SMG are also active during successful recognition (e.g., Burianova, Ciaramelli, Grady, & Moscovitch, 2012; Ciaramelli et al., 2008).

The SMG and AG constitute the inferior parietal lobule, which is activated during other tasks that have benefitted from saccades. The inferior parietal lobule is more active during incongruent trials than congruent trials on a cued-flanker task (e.g., Fan et al., 2003) and are also active during creativity tasks (for review, see Gonen-Yaacovi et al., 2013).

Hippocampi.

The hippocampi are involved in episodic, semantic, and autobiographical retrieval (see Burianova et al., 2010). They are associated with consciously remembering information as opposed to implicitly retrieving information (see Schacter et al., 1996), and are more active during retrieval of strong memories than weak ones (for review, see Bunge, Burrows, & Wagner, 2004; e.g., Wais, 2011). This structure is also active during creativity tasks that require generating ideas (e.g., Ellamil, Dobson, Beeman, & Christoff, 2012). Increasing the activity of this structure could produce retrieval benefits similar to the ones in previous studies. However, the hippocampi are not associated with attentional control (Fan et al., 2003) and therefore increased hippocampal activity cannot readily explain how saccades reduced response times for incongruent flankers on a cued-flanker task. Therefore, this structure is not discussed in relation to previous research.

Relation to Past Research

The brain is thought to have two distinct frontoparietal attentional networks (Corbetta & Shulman, 2002). The dorsolateral prefrontal cortex, along with the IPS (previously implicated in SIRE; see Lyle & Martin, 2010), is part of a dorsal attention network involved in top-down attentional control (see Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Ciaramelli et al., 2008). The ACC and inferior parietal lobule (SMG and AG) are part of a ventral attention network involved in bottom-up attentional control (see Cabeza et al., 2008; Ciaramelli et al., 2008). According to the attention to memory hypothesis (e.g., Burianova et al., 2012; Cabeza et al., 2008; Ciaramelli et al., 2008), the ventral attention network retrieves memories from the hippocampi when the memory is strong, or confidence in the memory is high. Sometimes a memory cannot be automatically retrieved because the memory is weak, or sufficient cues are not available. Other times, a memory may be retrieved, but with low confidence. In either case, the dorsal attention network initiates a search of memory storage based on retrieval goals. The dorsal attention network monitors the output of the memory search until the ventral attention network signals that a memory has been located or memory failure occurs. The potential involvement of each network in SIRE is discussed below in relation to previous studies.

Dorsal attention network.

The dorsal attention network was discussed in the Introduction in relation to the attentional control hypothesis. Although Lyle and Martin (2010) referred to the frontoparietal attention network in general, they implicated the dorsal attention network by referring to top-down attentional control. This specification seemed justified because saccades specifically increased top-down control on a cued-flanker task (Edlin & Lyle, 2013). The cued-flanker task required subjects to respond to the direction of a central arrow flanked by arrows that were either congruent or incongruent with the central arrow. Saccades specifically reduced response times on trials with incongruent flankers, suggesting that saccades improved top-down attentional control allowing subjects to focus on the target and ignore the flankers.

SIRE studies also suggest a role for top-down attentional control. Saccades have selectively enhanced performance on attentionally demanding retrieval tests, while having no effect on tests with low attentional demands. Previous SIRE studies have focused on tests that require explicit conscious retrieval of information (e.g., Christman et al., 2003; Lyle, Logan, et al., 2008), because an initial study found no effect on information implicitly retrieved without conscious effort (Christman et al., 2003, Experiment 1). Christman et al. tested implicit retrieval with a word-fragment completion test. Subjects studied a list of words and later completed word-fragments with any word that came to mind. Completion of word-fragments with studied words was taken as evidence that subjects had implicitly retrieved the words. Word-fragment completion is not attentionally demanding, as evidenced by the fact that concurrently performing another task does not decrease the number of words implicitly retrieved. (Clarke & Butler, 2008). When Christman et al. tested explicit and implicit memory for a list of words, they found SIRE only for explicitly retrieved words. Saccades did not increase the number of word-fragments completed with studied words.

Christman et al. (2003) found that saccades only enhanced explicit retrieval. However, additional evidence has indicated that saccades may only enhance certain types of explicit retrieval. For example, Brunye et al. (2009) tested the effect of saccades on recognition of spatial locations. In one condition, subjects were shown a map and asked whether they had previously seen it (old/new recognition). In another condition, subjects were shown two maps and asked which one they had previously seen (two-alternative forced choice). Saccades improved retrieval relative to fixation on the old/new recognition test, but not on the two-alternative forced choice test. Old/new recognition involves more elaborative processes and is more difficult than two-alternative forced choice recognition (e.g., Bastin & Van der Linden, 2003). Although both conditions required subjects to retrieve information, SIRE only occurred for old/new recognition, perhaps because this condition was more attentionally demanding.

Lyle and Edlin (under review) provided two examples that further support the idea that SIRE depends on attentional demands at retrieval. In their first experiment, subjects studied exemplars from different categories, and then practiced retrieving half of the exemplars in half the categories. Later, when memory for the original list was tested, there were three types of exemplars: practiced exemplars, unpracticed exemplars from practiced categories, and unpracticed exemplars from unpracticed categories. Practicing some of the exemplars in a category has been shown to increase the difficulty of retrieving unpracticed exemplars from that category at test (e.g., Anderson et al., 1994). Lyle and Edlin found that retrieval of unpracticed exemplars from practiced categories was lower than retrieval of unpracticed exemplars from unpracticed categories, but saccades reduced this effect by increasing retrieval of unpracticed exemplars from practiced categories.

In a second experiment, Lyle and Edlin (under review) examined the effect of manipulating attentional demands on SIRE by comparing two halves of a recognition memory test. One consequence of retrieving items on the first half of the test is that items on the second half are more difficult to retrieve (e.g., Criss et al., 2011). Lyle and Edlin gave subjects a list of items to remember and then tested half the items on a first test and half on a second test. Retrieval was lower on the second test than the first, but only following fixation. When saccades were performed prior to the second test, there was no decrease in performance from the first test.

The aforementioned studies are examples of how the attentional demands of the retrieval test may moderate SIRE. The role of top-down attentional control in SIRE has already been established in previous literature (see Edlin & Lyle, 2013). The current experiments may provide some insight into the cortical regions involved in SIRE. According to Lyle and Martin (2010), saccade-induced increases in attentional control are related to activation in the IPS and FEF. The results of Experiment 1 add the possibility that this top-down control could be influenced by additional regions of the dorsal attention network, such as dlPFC, that are activated by predictive saccades.

Ventral attention network.

Although there is some evidence that SIRE is related to top-down attentional control, the possibility that bottom-up attentional control also plays a role in SIRE has never been explored. The ventral attention network controls bottom-up attentional control of retrieval. This network is more active when memories are strong and subjects are highly confident about the retrieved memory. A hypothesis of SIRE based solely on the enhancement of the ventral attention network cannot explain the influence of top-down control in previous studies. However, previous SIRE research was not designed to differentiate between the attention networks, so it is impossible to determine whether enhancement of the ventral attention network is also involved in SIRE. Saccades could enhance both the dorsal attention network *and* the ventral attention network. Therefore, further discussion of the ventral attention network will focus on potential influences of this network on SIRE.

One potential influence the ventral attention network could exert during SIRE is increasing the salience of items retrieved from storage. The ventral attention network is more active when successfully labeling old items as “old” than when labeling new items as “new”, presumably because this network is associated with re-experiencing the retrieved information (e.g., Ciaramelli et al., 2008). If saccades increase the ability to re-experience old items, then SIRE should manifest as an increase in memory for old items without affecting new items. However, previous SIRE studies have not indicated that saccades selectively increase memory for old items. Even in studies using similar paired-associates tests, SIRE has manifested as increased memory for old items (Lyle et al., 2012), decreased false memories of new items (the current experiment), or both (Parker et al., 2008). A similar argument is that increased activation of this network may lead to higher confidence in retrieved memories or a tendency to retrieve higher confidence memories. The only SIRE study that has included confidence ratings found that saccades increased confidence in hits, but also decreased confidence in false memories of new items (Lyle & Jacobs, 2010).

Another potential outcome of increased functioning of the ventral attention network would be an enhancement of bottom-up attentional capture. Edlin and Lyle (2013) may have provided evidence of this type of enhancement when studying the effects of saccades on the cued-flanker task. During the cued-flanker task, some trials included a valid or invalid cue that signaled where the target and flankers would appear. Saccades reduced response times on trials that were invalidly cued, which Edlin and Lyle suggested was due to the increased difficulty of the invalidly cued trials. While this is one possible explanation, it is also possible that saccades increased bottom-up attentional capture allowing faster exogenous orienting to the invalidly cued locations. When the target appeared at the invalid location, bottom-up attention was necessary to notice the appearance of the target and shift attention to the unexpected location. Previous brain imaging studies during cued orienting activities similar to the cued-flanker task have found greater activation in the ventral attention network during invalidly cued trials than validly cued trials (e.g., Engell et al., 2010). The decrease in response times on invalidly cued trials in Edlin and Lyle's experiment may suggest enhancement of the ventral attention network following saccades.

SIRE may involve the ventral and dorsal attention networks, not only in isolation from one another, but as they interact. As mentioned earlier, the two networks work together during memory retrieval. The ventral attention network retrieves memories from the hippocampi, but when a memory cannot be automatically retrieved, the dorsal attention network initiates a search for the memory based on retrieval goals (see Cabeza et al., 2008; Ciaramelli et al., 2008). Practicing a task such as saccades, which requires the two networks to work together, may improve performance on a subsequent memory test that also requires these two networks to work together. In other words, the functional coupling of the two attention systems may be necessary for SIRE. Additional research is required to determine whether the ventral attention network or its functional connectivity with the dorsal attention network is enhanced by saccades.

Theoretical Implications

The hypotheses put forth to explain SIRE are discussed in more detail below, but briefly, saccades have been proposed to increase: interaction between the hemispheres (interhemispheric interaction; Christman et al., 2003), activation in frontoparietal areas (attentional control; Lyle & Martin, 2010), or interaction within the hemispheres (anterior-posterior interaction; Parker & Dagnall, 2007). None of the hypotheses can fully accommodate the results of the current experiment.

Interhemispheric interaction hypothesis.

According to the interhemispheric interaction hypothesis, performing saccades equalizes activation in the two hemispheres, which increases the efficiency of interhemispheric communication (Christman et al., 2003). This hypothesis implies that the movement of the eyes is necessary to produce the effect. Therefore, the two new novel orienting activities introduced in Experiment 1 should have produced SIRE, but they did not. This hypothesis also predicted that covert orienting in Experiment 2 would not produce SIRE, because of the absence of eye movements. Although the covert activity in Experiment 2 did not produce SIRE, neither was there a benefit from overt orienting. The failure to obtain SIRE on a paired-associates test in Experiment 2, unlike in Experiment 1 and other previous experiments (Lyle et al., 2012; Parker et al., 2008, Experiment 2), may have been due to a Type II error. Alternatively, novel aspects of the procedure may have reduced the benefit of saccades or increased the benefit of fixation (see Experiment 2 Discussion). Therefore, support for the interhemispheric interaction hypothesis based on the results of Experiment 2 is tenuous at best.

Attentional control hypothesis.

Lyle and Martin (2010) posited that saccades increase attentional control by activating the frontoparietal network. Because they specified IPS and FEF, the attentional control hypothesis was unable to predict the results of the current research. However, this is the only hypothesis capable of explaining previous benefits of saccades on memory, attention, and creativity.

One fundamental difference between current and past research is that past research only required a general understanding of how saccades enhanced cognition. If saccades increase top-down attentional control then the attentional control hypothesis could accurately predict the outcome of SIRE studies. However, in Experiment 1 all of the orienting activities presumably increased activation in attentional control regions. Therefore, in order to predict which activities would produce SIRE, this hypothesis needed to specify exactly which attentional control regions produce the benefit.

Lyle and Martin's focus on the IPS and FEF stemmed from the observation that visually-guided saccades produce SIRE. Lyle and colleagues' (e.g., Lyle et al., 2012; Lyle & Martin, 2010) citations for IPS activity during saccades include reviews (e.g., Corbetta & Shulman, 2002) and studies (e.g., de Haan et al., 2008; Petit, Clark, Ingeholm, & Haxby, 1997) that have focused on visually-guided saccades rather than predictive saccades. If predictive saccades produce SIRE, then brain regions that are activated by predictive saccades, but not by visually-guided saccades, may also be central to producing SIRE. The attentional control hypothesis needs to address the activity, and potential training of these previously underappreciated regions.

Anterior-posterior interaction hypothesis.

Parker and Dagnall (2007) posited that saccades increase interaction between anterior attentional control regions and posterior locations where memories are stored, but did not specify exactly how this increase was achieved. Therefore, no predictions about the activities in the current experiment were possible based on this hypothesis.

Lyle and Martin's (2010) attentional control hypothesis may provide one potential explanation for increased interaction between anterior and posterior regions. According to Lyle and Martin, saccades produce frontoparietal activation. Edlin and Lyle (2013) posited that repeatedly activating frontoparietal regions during saccades is an attentional exercise similar to attention training programs (Rueda et al., 2005). Instead of focusing on the activation in target areas, the anterior-posterior interaction hypothesis could posit that repeatedly performing a task that requires interaction between regions temporarily increases the functional connectivity between those regions. This addition to the anterior-posterior hypothesis would allow it to posit that predictive saccades temporarily increase the connectivity between dorsolateral prefrontal cortex and the hippocampi. Increased functional connectivity between these regions could explain retrieval enhancement, but not enhancement of attentional control. However, as mentioned in the Introduction, some of Parker and Dagnall's (2007) comments suggest they may also believe that SIRE is caused by increased interaction within the frontoparietal network. Therefore, for this hypothesis to account for all saccade-induced benefits, it would also need to assume that saccades increase the functional connectivity of the frontoparietal network. These changes to the anterior-posterior interaction hypothesis would make it similar to the attentional control hypothesis, with the exception that the later implicates activation in the frontoparietal network and the former implicates interaction within the frontoparietal network.

Recommendations for Future Research

Experiment 1.

An important limitation of Experiment 1 is that eye tracking was not included to measure saccade latencies during the three orienting activities. Experiment 1 was primarily designed to determine whether endogenous or exogenous orienting produced

SIRE. This experiment did not directly test the necessity of predictive saccades by measuring saccade latencies. Instead, the importance of predictive saccades was inferred from the failure of endogenous and exogenous orienting to produce SIRE. Based on previous research with predictive saccades, the endogenous and exogenous orienting activities should not have produced predictive saccades. However, additional evidence that predictive saccades produce SIRE is necessary.

In addition, prior research in this area assumed that any type of saccade was sufficient to enhance retrieval. Although this dissertation attempted to refine this assumption to a particular type of orienting, it is important to note that SIRE was measured by a single retrieval test. SIRE has been found during a variety of retrieval tests, and manifests in different ways to enhance retrieval (e.g., Lyle, Logan, et al., 2008; Christman et al., 2003). Saccades also enhance attention tasks that do not include a retrieval component (Edlin & Lyle, 2013). If similarities in activation between the orienting activity and the subsequent test are important, then some types of saccades may preferentially enhance some types of tasks. For example, predictive saccades may preferentially enhance retrieval tests that require both the dorsal and ventral attention networks, whereas endogenous saccades may preferentially enhance attention tasks that rely solely on top-down control. Therefore, if future research supports the role of predictive saccades in SIRE, then additional research should also determine if this extends to other types of saccade-induced enhancement.

Finally, the benefit of saccades relative to fixation only occurred on the earlier trials in the paired-associates test. Performance on later trials did not benefit from saccades, despite the fact that retrieval may have been more attentionally demanding on these trials due to output interference. The lack of SIRE on later trials was primarily due to lower corrected recognition following saccades on the third test compared to the first. This decrease may suggest that repeated testing modulates the effects of saccades. Although previous experiments have included repeated testing with saccades versus fixation as a within-subjects factor (e.g., Brunye et al., 2009; Lyle et al., 2012; Lyle & Orsborn, 2011), none have compared the effect of saccades on earlier versus later trials. Furthermore, previous experiments included two tests with 10-15 m between each test. The current experiment included three tests with only 5 m between each test. The extra test and shorter break between tests may have exacerbated any effects of repeated testing in the current experiment. Further research is needed to determine if practice effects and/or fatigue from repeated testing influence SIRE.

Experiment 2.

In Experiment 2, recognition following saccades did not increase relative to fixation. This result raised two theoretically important research questions. One, did adding a target detection task to the fixation activity increase recognition? Edlin and Lyle (2013) posited that practicing attentional control during saccades might increase attentional control during subsequent retrieval. Similarly, practicing target detection during fixation could increase the ability to detect a target memory during subsequent retrieval. Two, did removing subjects who could not orient covertly decrease SIRE? Although the current research did not measure attentional control, subjects who were unable to orient covertly may have had less attentional control than subjects who could. This raises the possibility that saccades may provide more benefit for subjects with lower attentional control. An experiment comparing SIRE for individuals with high and low baseline levels of attentional control should be conducted to determine whether this is the case.

Conclusions

The goal of this research was to determine which components of the saccade activity are necessary to produce SIRE. The results of Experiment 1 provide initial support for the necessity of predictive saccades in retrieval enhancement. Predictive saccades produce activity in memory-related cortical regions (Gagnon et al., 2002; Simo et al., 2005), which would provide a direct link between saccades and memory. However, the current experiment was not designed to ensure that only the saccade activity produced predictive saccades. Additional research is needed to support a link between predictive saccades and SIRE.

If the standard saccade activity produces predictive saccades, and these are necessary for SIRE, then the results of Experiment 1 have important theoretical implications. Previous hypothesizing has been based on the idea that the standard saccade activity produces visually-guided saccades instead of memory-guided saccades, and these hypotheses were unable to predict the results of Experiment 1. If predictive saccades are the only type of saccade capable of producing SIRE, then regions of the dorsal and ventral attention networks activated exclusively by predictive saccades should be considered in future hypothesizing. This is relevant to the attentional control hypothesis, which focuses on the dorsal attention network, without regarding the ventral attention network. Furthermore, predictive saccades activate the hippocampi (Simo et al., 2005). This is the first indication of a link between saccades and the posterior memory locations implicated in the anterior-posterior interaction hypothesis. However, activation in these structures does not imply increased functional connectivity. It remains for future research to determine if SIRE is a product of increased activation in memory-related brain regions, or a product of changes in the connectivity between these regions.

The results of this research suggest that SIRE requires a specific type of saccade. A practical implication of this finding is that future research exploring the effects of saccades should not deviate from the standard saccade activity. In addition, careful adherence to the standard saccade activity should be maintained if SIRE is applied to events outside the laboratory. For example, previous research has suggested that SIRE may have practical applications such as improving eyewitness memory (e.g., Lyle & Jacobs, 2010). When taking statements at the scene of a crime, the convenience of asking witnesses to endogenously saccade to two points in space instead of bringing extra equipment to elicit saccades may seem like a sufficient comprise to law enforcement officers. Therefore, officers that use saccades to improve memory should be made aware that not all saccades are sufficient to enhance retrieval.

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Appendix A

Modified Version of the Edinburg Handedness Inventory

Participant #: _______

Score: _______

Handedness Inventory

Please indicate your preference in the use of hands for each of the following activities or objects by placing a check in the appropriate column.

	Always Left	Usually Left	No Preference	Usually Right	Always Right
Writing					
Drawing					
Spoon					
Open Jars					
Toothbrush					
Throwing					
Comb Hair					
Scissors					
Knife (without fork)					
Striking a match					

Is your mother left-handed? __________
Is your father left-handed? __________
Do you have any brothers or sisters who are left-handed? __________
What is your age? __________
What is your sex (Male or Female)? __________

Appendix B

Associative Recognition Word Lists with Group Assignment

First Study List	Group	Second Study List	Group	Third Study List	Group
tore-walk	C	task-worn	C	beg-whip	A
sag-zinc	A	pat-yogi	A	lip-team	A
lump-sign	A	hall-sea	C	bend-ripe	B
low-gin	B	stay-pool	A	dig-film	A
chef-send	C	tube-ask	A	call-dark	B
rise-ace	B	car-site	A	log-mass	C
post-thin	A	cat-kill	C	met-rain	B
wash-loch	B	odd-amp	B	suit-wax	B
net-fort	A	term-bow	B	base-tips	C
grow-glad	B	fat-era	A	rule-dry	A
echo-fig	B	step-wake	B	toss-evil	C
rich-tie	C	earn-bin	B	palm-wise	A
yes-bath	B	pill-clay	C	jay-yard	B
gun-trim	A	key-role	B	sad-afar	C
self-zest	C	acid-bead	A	bed-mill	C
wish-damp	B	flow-dear	A	edge-pin	A
toy-race	C	cry-open	B	wide-tool	B
poor-shot	A	path-mood	A	roar-alit	B
pit-draw	C	poem-pie	C	lime-move	A
army-span	B	fall-corn	A	text-tub	B
flat-risk	C	dogs-soap	A	view-main	A
laws-plus	A	laid-easy	C	link-nice	C
foil-lay	A	vote-chin	A	hit-tall	B
dump-heat	C	bill-led	A	list-due	C
coin-deep	C	camp-foot	C	ship-fell	C
died-wool	B	drew-fit	B	stop-woe	A
read-vice	B	file-aunt	A	try-save	B
job-cap	C	goal-hut	B	tail-woke	A
apt-knee	B	rage-firm	C	pro-fine	C
dust-herd	A	rock-note	C	tap-mark	B
add-spot	B	navy-lift	B	wept-die	A
poet-lot	C	news-oak	B	neck-size	A
pay-fog	C	won-bit	C	hem-date	B
epic-deal	A	beef-gain	B	jury-nose	A
act-wood	B	fair-wit	C	trap-safe	A
fun-dew	C	care-ran	B	tone-bond	B
café-hole	A	wet-none	B	nap-vent	C
stem-yell	A	pain-hill	A	talk-arm	C
belt-cave	B	sum-wan	C	farm-code	A
sky-unit	B	acre-game	A	eye-jeep	C
mess-aim	A	cup-area	C	run-pink	A
hart-test	A	papa-joy	A	hear-bad	C
ale-boat	B	bold-sit	B	age-blow	B
goat-born	A	fast-wave	C	row-soil	C
trio-sat	B	wrap-lake	A	eat-zero	B
six-ice	A	gas-cook	C	toe-park	C
hour-cash	A	cast-dot	A	hate-beat	B
jazz-aid	B	wind-copy	B	push-raw	C
tin-busy	C	sun-hang	A	pale-wire	B
pip-shop	C	lost-seed	B	bale-item	A
warm-duty	A	fee-wall	A	calf-lady	C
rose-trip	C	ash-fury	C	tray-blue	A
taxi-zoo	B	inch-hook	C	ball-nut	B
sale-atom	A	mold-ton	B	bloc-song	C
east-kept	C	spur-cold	C	box-boys	A
loss-nine	C	wait-arch	C	gray-tire	C
auto-host	A	lack-toll	B	bank-lead	B
bee-hell	C	roof-plug	B	ward-bus	C
pick-lots	C	pun-wine	C	kid-rank	B
wing-buy	B	bar-oil	B	bare-hot	A

CURRICULUM VITAE

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Publications

Edlin, J.M., Carris, E.K., & Lyle, K.B. (2013). Memory for hand use depends on consistency of handedness. *Frontiers in Human Neuroscience*, *7*. doi: 10.3389/fnhum.2013.00555

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Papers Under Review

Lyle, K.B., & Edlin, J.M. Why does saccade execution increase episodic memory retrieval? A test of the top-down attentional control hypothesis. *Memory.*

Conference Presentations

Lyle, K.B. & Edlin, J.M. (2012). *Look both ways before crossing memory lane: Bilateral saccades reduce retrieval-induced forgetting*. Poster presented at the fifty-third annual meeting of the Psychonomic Society. Minneapolis, MN.

Edlin, J.M., & Lyle, K.B. (2010). *Increasing executive control with a flick of the eyes*. Poster presented at the fifty-first annual meeting of the Psychonomic Society. Saint Louis, MO.

Lyle, K.B., Edlin, J.M., Hanaver-Torrez, S.D., & Hackländer, R.P. (2010). *Consistency of hand preference, regardless of direction, predicts baseline memory performance and potential for enhancement*. Poster presented at the fifty-first annual meeting of the Psychonomic Society. Saint Louis, MO.

Edlin, J.M., & Lyle, K.B. (2008). *Repetitive vertical saccades improve procedural memory*. Poster presented at the twentieth annual meeting of the Association for Psychological Science. Chicago, Illinois.