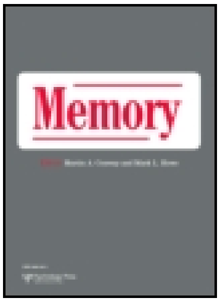

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Why does saccade execution increase episodic memory retrieval? A test of the top-down attentional control hypothesis

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Why does saccade execution increase episodic memory retrieval? A test of the top-down attentional control hypothesis

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Making repetitive saccadic eye movements has been found to increase subsequent episodic memory retrieval and also to increase subsequent top-down attentional control. We theorise that these effects are related such that saccade-induced changes in attentional processing facilitate memory retrieval. We tested this idea by examining the effect of saccade execution on retrieval conditions that differed in relative ease of consciously accessing episodic memories. Based on recent theories of episodic retrieval, we reasoned that there is a larger role for top-down attention when memories are more difficult to access. Consequently, we expected saccade execution to have a greater facilitative effect on retrieval when memories were more difficult to access. We obtained the expected result in a recall procedure in Experiment 1 and in a recognition procedure in Experiment 2. We also examined an individual difference factor—consistency of handedness—as a possible moderator of saccade execution effects on retrieval. We discuss how our top-down attentional control hypothesis can be extended to explain beneficial effects of saccade execution on other types of cognition, as well as negative effects on retrieval in some cases.

Keywords: Memory enhancement; Attentional control; Handedness consistency; Saccadic eye movements.

Beginning with Christman, Garvey, Propper, and Phaneuf (2003), many studies have shown that retrieval of episodic memories can be increased simply by making a series of rapid saccadic eye movements immediately before the retrieval attempt. In these studies, subjects make saccades to a visual target that alternates between two locations, usually left and right of centre, resulting in repetitive horizontal eye movements (we discuss vertical eye movements later). Compared to freely moving one's eyes or maintaining fixation on a stationary point, saccade execution has been found to increase correct retrieval on an impressive variety of episodic memory measures. These include free recall (Lyle, Logan, & Roediger, 2008, Experiment 1; Samara, Elzinga, Slagter, & Nieuwenhuis, 2011), old/new recognition (Lyle, Logan et al., 2008, Experiment 2; Parker & Dagnall, 2007), associative recognition (Brunyé, Mahoney, Augustyn, & Taylor, 2009; Lyle, Hanaver-Torrez, Häcklander, & Edlin, 2012; Parker, Relph, & Dagnall, 2008, Experiment 1), and a test of context/source memory (Parker Relph et al., 2008, Experiment 2). Our lab dubbed

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this effect saccade-induced retrieval enhancement (SIRE; Lyle & Martin, 2010).

In addition to the practical interest of a simple intervention that allows people to remember more about the past, SIRE is interesting because theories of episodic retrieval must be able to explain the influence of a preceding and wholly unrelated visuomotor task. SIRE joins other findings in indicating a relationship between episodic retrieval and eye movements. For example, when retrieving recently learned factual information, people move their eyes to the location they were looking at during initial encoding (Richardson & Spivey, 2000). Also, when encoding is not associated with looking at any particular location, subsequent retrieval increases the rate at which people make random saccadic eye movements (for a review, see Ehrlichman & Micic, 2012). SIRE is unique, however, in raising the question: What is happening during episodic retrieval that can be affected by, and indeed facilitated by, an act of saccade execution that has already been completed?

Our lab has been pursuing the idea that SIRE provides insights into the operation of top-down attentional processes during episodic retrieval. We (Edlin & Lyle, 2013) have proposed that the saccades task used in SIRE studies constitutes a minimal attentional control exercise. In this task (see the Method section for details), the visual target is a black circle that alternates between two fixed locations at a constant pace against a white background. With these parameters, the target is not intrinsically interesting and is unlikely to capture attention in bottom-up fashion. Instead, we assume that subjects must exert a modest amount of top-down attentional control to maintain their focus on the target. Supporting this assumption, neuroimaging studies have revealed that repetitive saccade execution is associated with activation of a frontoparietal network that is hypothesised to subserve top-down attentional control and, more specifically, selection of target stimuli in accordance with goals and agendas (Corbetta & Shulman, 2002). This network includes the frontal eye fields and regions of the intraparietal sulci and superior parietal lobes. Similar regions of parietal cortex are also activated during certain episodic retrieval tasks (for reviews and commentaries, see Ciaramelli, Grady, & Moscovitch, 2008; Vilberg & Rugg, 2008; Wagner, Shannon, Kahn, & Buckner, 2005).

The functional significance of intraparietal and superior parietal activity during episodic retrieval is a matter of debate, but one hypothesis is that it reflects top-down attentional processes involved in shifting attention to, or maintaining attention on, mnemonic representations (Cabeza, 2008; Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Wagner et al., 2005). Top-down attention may help to make mnemonic representations consciously accessible when bottom-up influences are insufficient. We hypothesise that SIRE occurs because briefly exercising top-down attentional control processes on the saccades task potentiates the operation of those processes on subsequent episodic retrieval tasks.

The logic of our hypothesis is similar to one made in the long-term cognitive training literature, albeit on a much shorter timescale: Exercising cognitive processes on one task can improve performance on a similar task (for reviews, see Klingberg, 2010; Morrison & Chein, 2011). Furthermore, the idea that episodic retrieval shares underlying processes with a function as superficially different as voluntary eye movements is consistent with component process frameworks of memory (Cabeza & Moscovitch, 2013; Johnson & Hirst, 1993). In such frameworks, complex memory processes, including episodic retrieval, arise from the operation of simpler component processes, which may contribute to memory and nonmemory functions alike. For example, retrieving episodic memories and visually orienting to perceptual stimuli may rely on a common process of selection that brings either mnemonic or perceptual representations into consciousness. Finally, from a neural perspective, our account aligns with recent theorising that ongoing neural processing (e.g., during retrieval) is partially determined by preceding neural states (e.g., those evoked by saccade execution), as well as by current stimuli and task goals (Peigneux et al., 2006; Waites, Stanislavsky, Abbott, & Jackson, 2005).

Supporting our top-down attentional control hypothesis, we (Edlin & Lyle, 2013) recently obtained critical evidence that performance of the saccades task from SIRE studies increases subsequent top-down attentional control. We had subjects either perform the saccades task or maintain stationary fixation immediately before taking the revised attention network test (Fan et al., 2009). On some trials of this test, subjects must indicate the direction of a target arrow in the presence of flankers pointing in the opposite direction. Because attentional control is needed to overcome the misleading influence of incongruent flankers, faster responding indicates greater attentional control. We found that performing the saccades task decreased response times compared to maintaining stationary fixation. On other test trials, flankers were response congruent (i.e., pointing in the same direction as the target), but the target's location was invalidly cued. Faster responding under these conditions also indicates greater attentional control because control is needed to overcome the influence of invalid spatial cues. We found that saccade execution also decreased response times on these trials. In contrast, saccade execution did *not* decrease response times on trial types that required relatively little attentional control, such as when flankers were response congruent and target locations were validly cued. Collectively, these findings support the conclusion that saccade execution increases subsequent attentional control.

In the context of episodic retrieval, we have theorised that the specific consequence of saccade-induced increases in top-down attentional processing is to facilitate bringing mnemonic representations into consciousness or maintaining them there (Lyle & Orsborn, 2011). We see this as analogous to the effect of saccade execution on the attention network test (Edlin & Lyle, 2013): Saccades potentiated attentional processes that brought the representation of the target arrow (or the target-congruent response) into consciousness, despite the presence of distractors. The idea that top-down attention helps to bring information into consciousness is well established in perception (e.g., Kastner & Ungerleider, 2001; Mack & Rock, 1998). The proposal that something similar occurs in memory is supported by a recent study showing that attending to representations in working memory can restore them to consciousness when they would otherwise be lost (Murray, Nobre, Clark, Cravo, & Stokes, 2013). We build on this to posit that the allocation of top-down attention to representations in long-term episodic memory increases their conscious accessibility. Our account therefore predicts that SIRE should occur primarily when successful retrieval requires the contribution of top-down attention to make episodic memories consciously accessible. When episodic memories are relatively easy to access on the basis of bottom-up influences alone, and retrieval involves little top-down attention, SIRE should be less likely. We sought to test this prediction in the current research.

It bears noting that previous SIRE studies have tended to employ procedures that may have required top-down attention to memory. Some of these studies have involved free recall, in which there are no retrieval cues to provide bottom-up activation of specific target memories (Lyle, Logan et al., 2008, Experiment 1; Samara et al., 2011). Other studies have involved recognition with related/similar lures (Lyle et al., 2012; Lyle, Logan et al., 2008, Experiment 2; Parker & Dagnall, 2007), or lures that were the subject of misinformation (Lyle & Jacobs, 2010; Parker, Buckley, & Dagnall, 2008). In such procedures, targets and lures are difficult to discriminate. Top-down attention may assist by increasing access to features of target memories that are diagnostic of source, but which receive little bottom-up activation (e.g., visual features). SIRE was also found on a test of recall for contextual details (Parker, Relph et al., 2008). In this study, subjects studied many different words in just two different visual contexts (colours or locations), so both contexts may have been strongly activated at test. When subjects attempted to retrieve the specific context for any single word, top-down attention may have assisted by increasing access to one context over the other. While our account would lead us to expect SIRE on tasks like these, what is needed is direct comparisons of retrieval conditions that differ in presumed involvement of top-down attention.

The only study that provided a relevant comparison is Brunyé, Mahoney, Augustyn, and Taylor (2009), in which separate groups of subjects were administered two different tests of associative recognition. Associative recognition involves discriminating targets from similar lures and may require top-down attention to memory, as discussed above. However, one of the tests was two-alternative forced-choice (2AFC) and the other was sequential old/new recognition. We would expect the need for top-down attention to memory to be less on 2AFC, where the differential familiarity of targets and lures (Speer & Curran, 2007) is driven in bottom-up fashion and can provide a basis for subjects' memory judgments. Therefore, our account would predict a more pronounced SIRE effect on the sequential old/new test than on the 2AFC test. Brunyé et al. obtained exactly that pattern: A significant SIRE effect was obtained on the sequential old/new test but not the 2AFC. This finding is encouraging, but more research is needed, especially because we cannot say for certain that it was the difference in top-down attentional requirements that caused saccade execution to affect 2AFC and sequential old/new recognition tests differently. It may have been some other difference between the two test types (including that different groups of subjects took the tests) that caused only one to show an effect.

In the present experiments, we examined the effect of saccade execution on conditions that differed in relative ease of consciously accessing episodic memories. We used a recall procedure in Experiment 1 and a recognition procedure in Experiment 2. In each experiment, ease-of-access was manipulated within the same retrieval task and within-subjects, allowing for more straightforward comparisons between conditions than was possible in Brunyé et al. (2009). In Experiment 1, we used a version of the procedure popularised for studying retrieval-induced forgetting (Anderson, Bjork, & Bjork, 1994). In this procedure, subjects study exemplars of several categories (e.g., fruits). After study, subjects practice retrieving half of the exemplars from some of the categories (e.g., orange), but do not practice retrieving any exemplars from other categories. This yields three item types, each with its own shorthand designation: practiced exemplars (*Rp*+), nonpracticed exemplars from practiced categories (*Rp*−), and nonpracticed exemplars from nonpracticed categories (*Nrp*). After the retrieval practice phase, subjects are tested on their memory for all item types. Unsurprisingly, subjects are more likely to retrieve *Rp*+ items on the final test than either type of nonpracticed item (i.e., the testing effect, Gates, 1917; Roediger & Karpicke, 2006). More important, though, is that nonpracticed items are especially difficult to retrieve if other exemplars from the same category were practiced earlier. That is, recall of *Rp*− items is lower than recall of *Nrp* items. This impairment, which is known as retrieval-induced forgetting, is caused by multiple factors. One is that subjects tend to retrieve *Rp*+ items before *Rp*− items, which produces output interference (Smith, 1971). A second factor is often identified as inhibition of *Rp*− items (for a recent review, see Storm & Levy, 2012), but other possibilities exist (Raaijmakers & Jakab, 2013).

Whatever the exact mechanisms of retrieval-induced forgetting, theories of episodic retrieval suggest that top-down attentional control processes should be more involved in retrieving *Rp*− items than *Nrp* items. Cabeza's (2008) dual attentional processes hypothesis and Ciaramelli, Grady, and Moscovitch's (2008) attention-to-memory hypothesis both stipulate that certain retrieval conditions trigger the involvement of top-down attention. Cabeza characterises those conditions as being when memory performance is low, including when memories are endorsed with low confidence, and when retrieval effort is high. Ciaramelli et al. also identify low confidence as a sign that top-down attention may be involved. Selective retrieval practice obviously results in low memory performance for *Rp*− items and it has been described as reducing general memory strength for those items (Spitzer & Bäuml, 2007). Selective retrieval practice also reduces confidence in *Rp*− items, at least in some cases (Stone, Luminet, & Hirst, 2013). Therefore, we predicted that saccade execution would increase retrieval of *Rp*− items more than it increased retrieval of *Nrp* items thereby reducing retrieval-induced forgetting.

In Experiment 2, we manipulated ease of accessing memories by dividing an old/new recognition test into two halves and assessing retrieval separately in each half. As recognition tests proceed, and more probes are presented, episodic memories become harder to access. Targets are less likely to be recognised when they appear in later test positions versus earlier ones (Criss, Malmberg, & Shiffrin, 2011; Malmberg, Criss, Gangwani, & Shiffrin, 2012). As in recall, this is the phenomenon of output interference. In the early stages of recognition tests, we assume that the bottom-up influence of test probes is largely sufficient to yield conscious access to target memories. In this situation, neuroimaging data indicate that recognition involves an attentional network distinct from the one that subserves top-down attention to memory (Burianová, Ciaramelli, Grady, & Moscovitch, 2012). However, we assume that, in later stages of recognition tests, top-down attentional modulation assists in overcoming interference and making memories accessible. Again, this follows from Cabeza's (2008) hypothesis that top-down attention in retrieval is involved when memory performance is low and retrieval effort is high. We therefore predicted that saccade execution would increase target recognition specifically on the second half of the test thereby reducing output interference.

In both experiments, we measured an individual difference factor known as handedness consistency, which is the degree to which a single preferred hand (left or right) is consistently used to perform unimanual tasks (e.g., writing, brushing teeth). Laterality researchers have long recognised that most individuals are highly consistent, but a minority is relatively inconsistent, making greater use of both hands (e.g., Annett, 1970; Oldfield, 1971; Peters & Murphy, 1992). Consistency is a less well-known dimension of handedness than the distinction between left- and right-handedness. Nonetheless, consistency is at least as important an individual difference factor as left/right direction of dominance, if not a more important one (Prichard, Propper, & Christman, 2013). Differences in consistency are apparent within the first two years of life (Nelson, Campbell, & Michel, 2013) and may stem from genetic variation (Arning et al., 2013). Multiple neuroanatomical studies have shown that some regions of the corpus callosum are larger in inconsistent-handers than consistent-handers (Cowell, Kertesz, & Denenberg, 1993; Habib et al., 1991; Luders et al., 2010; Witelson, 1985). Although some studies have not found these structural differences (Jäncke & Steinmetz, 2003; Welcome et al., 2009), behavioural studies have indicated that interhemispheric interaction is greater in inconsistent-handers than consistent-handers (Chase & Seidler, 2008; Lyle & Martin, 2010; Potter & Graves, 1988). Neurofunctional differences between the groups also exist. For example, although many people are familiar with the idea that left-handed individuals sometimes exhibit right-lateralised language processing, consistency is also an important factor, with inconsistently right-handed individuals being more likely than consistently right-handed individuals to exhibit right lateralization (Knecht et al., 2000).

Given the plethora of neurally grounded differences between inconsistent and consistent individuals, cognitive differences are also to be expected. Indeed, we measure consistency in our lab because consistent and inconsistent individuals perform differently on many memory tests. These differences appear to be independent of left/right direction of handedness (Lyle et al., 2012) and may be a consequence of differences in interhemispheric interaction (Lyle, McCabe, & Roediger, 2008; Propper, Christman, & Phaneuf, 2005; but see also Lyle & Orsborn, 2011). To date, the differences have always favoured inconsistent individuals, who have exhibited advantages including greater paired associate recall and recall of contextual details (Lyle, McCabe et al., 2008), greater correct recall from word lists (Propper et al., 2005), less false recall from word lists (Lyle, Logan et al., 2008), and fewer false alarms in associative recognition (Lyle et al., 2012).

Consistent and inconsistent individuals are also differentially affected by saccade execution. SIRE occurs reliably for consistent individuals, but not inconsistent ones. The effect of saccade execution on inconsistent individuals is highly variable. While one study found SIRE for inconsistent-handers (Lyle & Jacobs, 2010), another found a null effect (Brunyé et al., 2009), and still others have found significant *negative* effects of saccade execution (Lyle et al., 2012; Lyle, Logan et al., 2008). Negative effects took the form of increased false retrieval without any effect on correct retrieval. It is not yet known why consistency moderates the effect of saccade execution, but one possibility is that saccade-induced increases in top-down attention control interact with the differing baseline neuro-cognitive states of consistent and inconsistent individuals (Lyle et al., 2012). Given this complexity, and because consistency-based differences were not the focus of this research, we did not formulate predictions about how inconsistent-handers would perform relative to consistent-handers in the present experiments. However, we thought it possible that our previously tendered predictions might be borne out only among consistent-handers. To reiterate, though, consistent-handers are the majority of the population. To foreshadow, some consistency-based differences were obtained, especially in Experiment 2, and we discuss them where appropriate.

METHOD

Subjects

Subjects were University of Louisville undergraduates aged 18–30 who received credit in psychology courses for participating. Subjects were classified (see below) as consistently handed (n = 98) or inconsistently handed (n = 52). Among consistently handed subjects, 48 (M absolute handedness score = 92.6; 16 males) were randomly assigned to the saccades activity and 48 (M absolute handedness score = 91.9; 12 males) to the fixation activity. Among inconsistently handed subjects, corresponding numbers were 24 (M absolute handedness score = 54.4; 9 males) and 28 (M absolute handedness score = 53.6.; 10 males). Data from two additional subjects were excluded due in one case to responding incorrectly on 60% of the retrieval practice trials and in the other case for producing a number of intrusions on the final test that was more than 5.9 SD above the mean.

Materials

We used a modified version of the Edinburgh Handedness Inventory (Oldfield, 1971) described in Lyle, McCabe, and Roediger (2008), which queries direction and consistency of handedness for 10 everyday activities. Scores range from 100 (exclusive left-handedness) to +100 (exclusive right-handedness) in five-point intervals.

Study materials consisted of six exemplars from each of 10 categories. Eight categories and their exemplars were taken from Anderson, Bjork, and Bjork (1994). Associative strength between exemplars and corresponding category was strong for four categories and weak for four categories. We also created two filler categories (birds and furniture). The study list contained one presentation of each exemplar paired with its category name (e.g., fruits—orange). Presentation order was pseudorandom with the constraint that one exemplar from each category was presented before a category was repeated.

Retrieval practice materials consisted of three exemplars from each of two strong categories, two weak categories, and one filler category. The retrieval practice list contained three presentations of the first two letters of each exemplar, paired with its category name (e.g., fruits—or). Presentation order was pseudorandom with the constraint that all of the category-exemplars pairs were presented before one were repeated. Assignment of categories and exemplars to the retrieval practice list was counterbalanced.

The final test consisted of the names of the 10 categories. Names were presented individually in the same order for all subjects. The first and last names were the filler categories. The remaining category names were presented in a single random order.

The stimulus for the saccade execution task was a computerised sequence showing a black circle on a white background. At a viewing distance of 24 inches, the circle alternated between 13.5° left and 13.5° right of the vertical midline every 500 ms for 30 s. For the fixation task, the circle flashed in the centre of the screen (500 ms on, 500 ms off) for 30 s.

Procedure

Subjects first completed the handedness inventory. As in previous studies (Lyle, Chapman, & Hatton, 2013; Lyle et al., 2012; Lyle & Grillo, 2014), we classified subjects with an absolute handedness score of 80 or higher as consistently handed and a score below 80 as inconsistently handed.

The memory procedure consisted of three phases (study, retrieval practice, and test) and was modelled after Anderson et al. (1994, Experiment 1). During the study phase, category-exemplar pairs appeared in the centre of a computer screen for 5 s each with a 1-s interstimulus interval. Subjects were instructed to study the pairs by relating each exemplar to its category. The retrieval practice phase began immediately after the last study pair was presented. During this phase, subjects were presented with a category and the first two letters of an exemplar from that category. Subjects were instructed to type the name of an exemplar from the study phase that fit the two-letter cue. Subjects had 12 s to respond. Following the retrieval practice phase, there was a 10-min break during which subjects completed an unrelated questionnaire. Immediately after the break, subjects were randomly assigned to perform either the saccade execution task or the fixation task. In the saccade execution task, subjects were instructed to move their eyes to maintain fixation on the circle without moving their heads. In the fixation task, subjects were instructed to maintain fixation on the stationary circle without moving their eyes. The experimenter monitored compliance with instructions. In the test phase, each category name was presented one at a time at the top of the screen and subjects were instructed to type all the exemplars from the study phase that belonged to that category. The test was self-paced.

RESULTS

Alpha was set at .05 in all analyses. Except where noted, any effects that did not reach this level are not reported. We submitted proportion recall of nonpracticed items to a 2 (category composition: strong or weak) × 2 (item type: *Rp*− or *Nrp*) × 2 (handedness: consistent or inconsistent) × 2 (pretest activity: saccade execution or fixation) mixed-design analysis of variance (ANOVA). The first two factors were within-subjects and the second two were between-subjects. There was a relatively uninteresting main effect of category composition,

$F(1, 144) = 45.01$, $p < .001$, $\eta_p^2 = .238$. More items were recalled from strong categories ($M = .46$) than weak ones ($M = .37$). There was also a main effect of item type, $F(1, 144) = 24.58$, $p < .001$, $\eta_p^2 = .146$. As expected, more *Nrp* items were recalled ($M = .44$) than *Rp−* items ($M = .39$). Of greatest importance, however, this main effect was qualified by a significant interaction with pretest activity, $F(1, 144) = 4.88$, $p = .029$, $\eta_p^2 = .033$. Figure 1 depicts the interaction and reveals the predicted result. Although *Rp−* items were less likely to be recalled than *Nrp* items following both pretest activities, the difference was smaller after saccades ($M_{\text{difference}} = .03$) than after fixation ($M_{\text{difference}} = .08$). This reduction in retrieval-induced forgetting was due entirely to recall of *Rp−* items being higher following saccades ($M = .41$) than fixation ($M = .36$), $t(146) = 1.78$, $p = .078$. Recall of *Nrp* items was identical following both activities ($M = .44$).

Intrusions were uncommon, but we also submitted the number of falsely recalled words to an ANOVA with the same design as above. The only significant effect was of pretest activity, $F(1, 144) = 6.03$, $p = .015$. Intrusions were more common following saccade execution ($M = 1.5$) than following fixation ($M = .98$).

Finally, although not of primary interest, we also submitted proportion recall of *Rp+* items to an ANOVA with the same design as in the preceding analyses, except omitting the factor of item type. The only significant effect was of category composition, $F(1, 144) = 45.43$, $p < .001$, $\eta_p^2 = .240$. As was true of nonpracticed items, more items were recalled from strong categories ($M = .77$) than weak ones ($M = .64$). Unsurprisingly, these recall rates were much higher overall than for nonpracticed items. Recall of practiced items was almost identical following saccades ($M = .71$) as following fixation ($M = .70$).

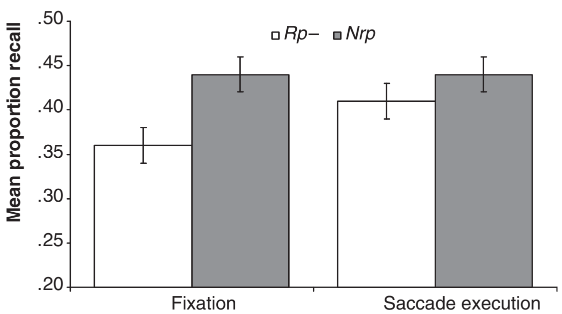

Figure 1. Mean proportion recall as a function of pretest activity and item type. Errors bars indicate ±1 *SEM*.

No effect involving handedness reached significance in any of these ANOVAs, but, in the analysis of nonpracticed items, the interaction between item type and handedness approached significance, $F(1, 144) = 3.32$, $p = .071$, $\eta_p^2 = .023$. *Rp−* items were less likely to be recalled than *Nrp* items for consistent- and inconsistent-handers alike, but the difference for consistent-handers ($M_{\text{difference}} = .03$) was smaller than for inconsistent-handers ($M_{\text{difference}} = .08$). Recall of *Rp−* items was about the same for inconsistent-handers ($M = .38$) and consistent-handers ($M = .39$), but inconsistent-handers had somewhat greater recall of *Nrp* items than did consistent-handers (*M*s = .46 and .42, respectively), $t(146) = 1.64$, $p = .103$.

DISCUSSION

As predicted, saccade execution specifically increased retrieval of those episodic memories that were, as a class, most difficult to access (i.e., memories of *Rp−* items). Saccade execution had no effect on retrieval of easier-to-access memories for *Nrp* items. Consequently, saccade execution reduced the typical retrieval-induced forgetting effect. It is worth noting that saccade execution also did not affect retrieval of memories for *Rp+* items, which were easiest of all to access. What can account for this highly specific SIRE effect? It was not the result of a ceiling effect, because, although we deemed *Nrp* (and *Rp+*) items "easy" to retrieve compared to *Rp−* items, retrieval of the former was far from perfect. Instead, we propose that saccade execution potentiated top-down attentional control processes (Edlin & Lyle, 2013), which were mobilised primarily when episodic memories were difficult to access.

In the Introduction, we provided theoretical reasons to expect the involvement of top-down attention in retrieval of *Rp−* items. We also note that, in Kuhl, Kahn, Dudkovic, and Wagner (2008), successful retrieval of *Rp−* items was associated with greater neural activity in intraparietal and superior parietal brain regions compared to retrieval of *Rp+* items. Because those regions are implicated in top-down attention (Corbetta & Shulman, 2002), it bolsters our belief that retrieval of the most difficult to access memories in our experiment involved top-down attention to a greater extent than did retrieval of easier-to-access memories.

We have said that we believe that saccade execution affects the top-down processes that bring mnemonic representations into consciousness or maintain them in consciousness. As we see it, the selection and/or maintenance of mnemonic representations can be achieved via the operation of at least one of two possible processes: Increasing activation of a target memory or decreasing activation of competing memories. We theorise that saccade execution enhances one or both of these facets of attentional modulation (see also Edlin & Lyle, 2013).

While target upmodulation is theoretically dissociable from competitor downmodulation, the two processes are difficult to disentangle empirically because they lead to the same outcome (increased target salience relative to competitors) and may operate in conjunction. Nonetheless, we see the results of this experiment as more consistent with an effect of saccade execution on an upmodulatory mechanism. There are two reasons for this. First, saccade execution increased retrieval of *Rp*− items without affecting retrieval of the type of item that was most obviously in competition with them (i.e., *Rp*+ items). If saccade execution increased retrieval of difficult-to-access memories by decreasing activation of easier-to-access memories, one might have expected saccade execution to decrease retrieval of *Rp*+ items. Second, saccade execution increased false recall of nonpresented exemplars. While nonpresented exemplars did not have episodic representations from the study phase of the experiment, they have semantic representations that could have competed with target representations. The fact that intrusions were more likely following saccade execution is at odds with the possibility of competitor downmodulation.

The saccade-induced increase in false recall of nonpresented exemplars in this experiment is not particularly surprising for inconsistently handed individuals. Saccades have previously been shown to increase false recall and recognition of words for inconsistent-handers (Lyle et al., 2012; Lyle, Logan et al., 2008). However, saccade execution has never previously been found to increase false retrieval for consistent-handers. On the contrary, multiple studies have found that SIRE can involve significant *decreases* in false retrieval (Brunyé et al., 2009; Christman, Propper, & Dion, 2004; Lyle, Logan et al., 2008; Parker & Dagnall, 2007). We provide a possible explanation for the atypical finding in this experiment in the General Discussion, after examining whether there was an effect of saccade execution on false retrieval in Experiment 2.

The only effect of handedness consistency that even approached significance in Experiment 1 was the interaction whereby retrieval-induced forgetting was greater for inconsistent-handers than consistent-handers ($p = .07$). Although the effect was weak, it bears mentioning because inconsistent-handers have been shown to possess episodic memory advantages (e.g., Lyle, McCabe et al., 2008; Propper et al., 2005), and it has been proposed that inhibition of nontarget memories facilitates retrieval of target memories (Storm, 2011). If inconsistent-handers are better able to inhibit nontarget memories, it could be a causal factor in their memory advantages. Another reason to give this effect some consideration is because inconsistent-handers have been found to have more diffuse semantic associations (Sontam & Christman, 2012). If to-be-retrieved words are embedded in richer semantic networks, successful retrieval might require greater inhibition to suppress more numerous or more strongly activated competitors. This could lead to greater retrieval-induced forgetting. These possibilities may warrant future research.

EXPERIMENT 2

Experiment 2 extends the present research to a recognition memory paradigm. An old/new recognition memory test was divided into two halves with the expectation that episodic memories would be more difficult to access on the second half than the first (i.e., output interference). If top-down attentional modulation of mnemonic representations is necessary to overcome output interference on the second half of the test, but is not so necessary on the first half, then saccade execution should enhance recognition memory specifically on the second half.

Experiment 2 also extends the research to alternating up-down (or vertical) saccades, as opposed to left-right (or horizontal) saccades in Experiment 1. Lyle, Logan, and Roediger (2008) previously found that horizontal and vertical saccades produced similar SIRE effects. In contrast, several other studies have shown that only horizontal saccades produce significant SIRE (Brunyé et al., 2009; Christman, Garvey, Propper, & Phaneuf, 2003; Parker, Relph et al., 2008). A methodological limitation of those studies is that they did not measure subjects' consistency of handedness. Because inconsistent-handers do not benefit from saccade execution as reliably as consistent-handers, fair comparisons of horizontal and vertical conditions require equal assignment of inconsistent-handers to both conditions. There is no way to know whether equal assignment was achieved in studies that did not measure handedness. Our top-down attentional control account of SIRE predicts that vertical saccades, like horizontal ones, will produce SIRE because vertical and horizontal saccades presumably require similar levels of attentional control. Moreover, saccade execution in various directions is associated with activation of the same frontoparietal network (de Haan, Morgan, & Rorden, 2008).

METHOD

Subjects

Subjects were undergraduates aged 18–30 at Washington University in Saint Louis and the University of Louisville who received credit in psychology courses for participating. Due to experimenter error, sex information was not collected on a subject-by-subject basis. As in Experiment 1, subjects were classified as consistently-handed ($n = 40$) or inconsistently handed ($n = 28$). Among consistently handed subjects, 18 (M absolute handedness score = 92.2) were randomly assigned to the saccades activity and 22 (M absolute handedness score = 91.4) to the fixation activity. Among inconsistently handed subjects, corresponding numbers were 12 (M absolute handedness score = 61.3) and 16 (M absolute handedness score = 52.8).

Materials

The handedness inventory was the same as in Experiment 1.

For the study phase, 30 coloured line drawings of common objects (e.g., chair, truck, pen) were downloaded from the Internet.[1] The name of the object appeared in all caps directly beneath the drawing. A single random ordering of these items (drawing plus name) was created for a study list. Items were presented on a computer monitor.

For the test phase, two test lists were created. The names of 15 randomly selected studied objects were assigned to each list, along with the names of 15 nonstudied objects which served as lures. Targets and lures that appeared on one list did not appear on the other. Targets and lures were pseudo-randomly intermixed in each list with the constraint that the two item types were evenly distributed throughout the list. On each list, the name of the object appeared next to the response options *Picture* or *New*. Test lists were administered with paper and pencil.

Stimuli for the saccade execution and fixation tasks were the same as in Experiment 1 with the exception that, for the saccades task, the circle alternated between 13.5° above and 13.5° below the horizontal midline of the computer screen.

Procedure

In the study phase, items were presented one at a time for 3 s each and subjects were instructed to pay attention because they would take an unspecified memory test later. After study there was 5-min retention interval during which subjects performed an unrelated task. Then subjects were randomly assigned to perform either the saccade execution task or the fixation task. The experimenter monitored compliance with instructions. Immediately thereafter, subjects were administered one of the test lists. Subjects were instructed to circle *Picture* if they had seen a picture of the object or *New* if they had not. After completing the test list, subjects performed the same pretest activity they had performed before the first list. Then subjects were administered the second test list in the same manner as the first. Completion of both test lists was self-paced. Critically, the order in which subjects completed the two test lists was counterbalanced within each cell of the pretest activity × handedness crossing. Consequently, if performance in any condition was worse on the second list than the first, we could attribute the impairment to output interference rather than between-list item differences.

RESULTS

Alpha was set at .05 in all analyses. Except where noted, any effects that did not reach this level are not reported. We initially analysed all dependent

[1] We tested colour memory in this procedure, in addition to item memory. Analysis revealed that none of the independent variables, we examined (list, pretest activity, or handedness) had a significant effect on colour memory. Therefore, we do not consider colour memory further.

variables using 2 (test list: first or second) × 2 (handedness: consistent or inconsistent) × 2 (pretest activity: saccade execution or fixation) mixed-design ANOVAs in which the first factor was within-subjects and the latter two were between-subjects.

Discrimination

To measure subjects' ability to discriminate between targets and lures, we calculated *A*, which is a nonparametric index of sensitivity (Zhang & Mueller, 2005). Higher *A* scores indicate greater discrimination. There was a main effect of handedness, $F(1, 64) = 9.26$, $p = .003$, $\eta_p^2 = .126$. Consistent-handers exhibited greater discrimination ($M = .89$) than inconsistent-handers ($M = .84$) and Figure 2 shows that this held in almost every condition. More relevant to the present research, there was also a significant three-way interaction between test list, handedness, and pretest activity, $F(1, 64) = 5.77$, $p = .019$. As seen in Figure 2, the predicted pattern clearly emerged for consistent-handers. Following fixation, consistent-handers exhibited lower discrimination on the second test list ($M = .85$) than the first ($M = .89$), $t(21) = 2.46$, $p = .023$, $\eta_p^2 = .083$. Following saccade execution, however, there was no reduction across lists whatsoever. On average, consistently handed subjects performed identically on both lists ($M = .91$). Saccade execution produced significantly higher discrimination than fixation on the second list, $t(38) = 2.69$, $p = .011$, but not the first, $t(38) = .71$, $p = .483$. The three-way interaction with handedness arose because, for inconsistent-handers, discrimination did not decrease across test lists following either pretest activity, fixation $t(15) = .70$, $p = .496$, saccade execution $t(11) = 1.32$, $p = .213$. Because there was no output interference in the fixation condition for inconsistent-handers, there obviously could be no saccade-induced amelioration of interference.

Hits and false alarms

To explore how saccade execution and handedness influenced discrimination, we analysed hits and false alarms separately. For hits, only the main effect of test list reached conventional significance, $F(1, 64) = 7.53$, $p = .008$, $\eta_p^2 = .105$. As would be expected, given output interference, the proportion of hits was lower on the second list ($M = .72$) than the first ($M = .77$). For false alarms, only the main effect of handedness was significant, $F(1, 64) = 11.72$, $p = .001$, $\eta_p^2 = .155$. False alarms were more common for inconsistent-handers ($M = .20$) than consistent-handers ($M = .10$). Hence, these analyses reveal that inconsistent-handers' lower discrimination relative to consistent-handers was driven primarily a higher false alarm rate, as opposed to a lower hit rate. Because pretest activity was not a significant factor in either analysis, it is possible that saccade execution improved consistent-handers' discrimination via a combination of somewhat increasing their hit rate and somewhat decreasing their false alarm rate, as in previous SIRE studies (Lyle & Jacobs, 2010; Lyle, Logan et al., 2008). This was confirmed by

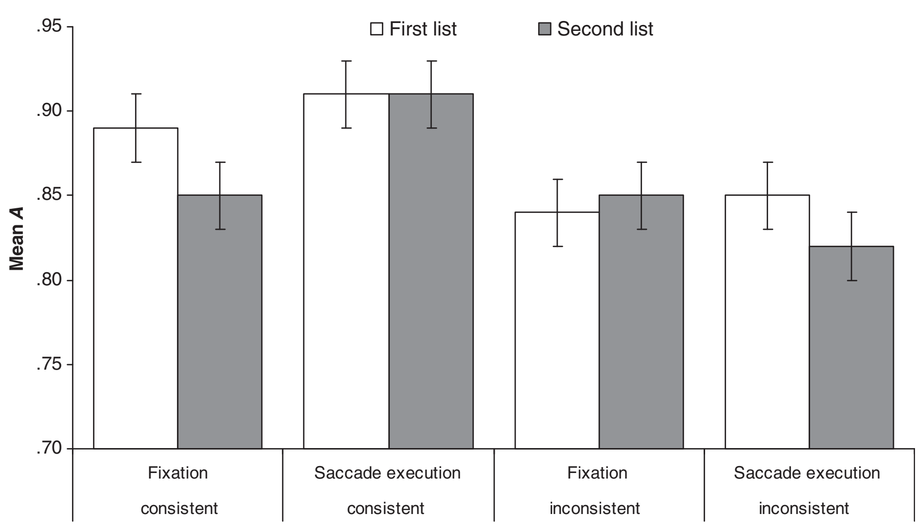

Figure 2. Mean *A* as a function of handedness, pretest activity, and test list. Error bars indicate ±1 *SEM*.

visual inspection of mean hit and false alarm rates on the second list. Following saccade execution, consistent-handers' hit rate was higher (*M* = .78) and their false alarm rate was lower (*M* = .07) than following fixation (*M*s = .65 and .11, respectively).

DISCUSSION

For consistently handed subjects, our predictions were fully supported. First, we established in the fixation condition that, when probes were presented on the second list versus the first, episodic memories were more difficult to access. This was reflected in a significant between-list reduction in overall discrimination and in the hit rate. Second, we found that saccades significantly increased discrimination relative to fixation on the second list but not the first. Third, saccade execution reduced the retrieval deficit for memories probed on the second list, rendering it nonsignificant. As in Experiment 1, we are left to explain the specificity of SIRE, which occurred on the second list but not the first. It was not due to a ceiling effect on the first list, because, although performance was superior on the first list than the second, it was far from perfect (e.g., the hit rate on the first list was only .77 in the fixation condition). Rather, we assume that top-down attentional control processes were mobilised to help overcome output interference on the second list but were less involved, if at all, on the first list. It was these processes that were potentiated by saccade execution, which consequently only affected retrieval on the second list. It is not possible to say with certainty whether saccade execution affected a process whereby target mnemonic representations were strengthened or whereby competing representations were weakened. However, if an inhibitory process had been potentiated, one might have expected a saccade-induced reduction in false alarms, which did not occur. Therefore, these results, like those of Experiment 1, more strongly implicate target upmodulation.

As just stated, saccade execution did not reduce false alarms, but neither did it increase them. Hence, for consistent-handers, saccade execution increased correct retrieval (on the second list) without increasing false retrieval. This is the pattern (sometimes featuring reduced false retrieval) obtained for consistent-handers in all previous SIRE studies, except the present Experiment 1, where an increase in false retrieval occurred. We attempt to reconcile this difference between experiments in the General Discussion.

Vertical saccades in this experiment produced SIRE for consistent-handers. Lyle, Logan et al. (2008) found the same when they directly compared horizontal and vertical saccades. From our theoretical perspective, vertical saccades should produce SIRE in the same manner as horizontal saccades because, to our knowledge, there is no reason to believe that vertical saccades activate the frontoparietal attentional-control network differently than do horizontal saccades. While other studies have failed to find that vertical saccades produce SIRE (Brunyé et al., 2009; Christman et al., 2003; Parker, Relph et al., 2008), those studies did not measure subjects' handedness consistency. It is possible that null effects in vertical conditions occurred because disproportionate numbers of inconsistent-handers were inadvertently assigned to those conditions.

We did not have specific predictions about how handedness consistency would affect the results of this experiment, but we found that inconsistent subjects differed from consistent subjects in three ways. Inconsistent-handers (1) did not exhibit output interference in the fixation condition, (2) did not exhibit SIRE on the second test list, and (3) had a significantly higher false alarm rate and lower discrimination. These findings should be interpreted with caution because the number of inconsistent subjects in this sample was smaller than that in other studies documenting consistency-based memory differences. Nonetheless, two points bear making. First, if inconsistent-handers are less susceptible to output interference, it may be considered yet another episodic memory advantage for that group, among many others previously documented (e.g., Lyle, McCabe et al., 2008; Propper et al., 2005). Second, the finding that inconsistent-handers had a higher false alarm rate than consistent-handers is, to our knowledge, the first indication that consistent-handers may have a memory advantage under certain conditions. Consistent- and inconsistent-handers have previously been compared on recognition memory (Lyle, Logan et al., 2008; Propper & Christman, 2004) but no consistent-hander advantage was observed. One aspect of the present procedure that differentiates it from previous ones is the use of object names and pictures as stimuli. Given that consistent- and inconsistent-handers are distinguished by how they manually interact with objects, it is interesting to speculate that their cognitive processing of object stimuli may also differ. Recent research has shown that individuals' ability to access conceptual information about objects is affected by their history of manual interaction with them (Yee, Chrysikou, Hoffman, & Thompson-Schill, 2013). It is an open and interesting question whether this has implications for memory.

GENERAL DISCUSSION

Recent theories of episodic retrieval posit a role for top-down attention (Cabeza, 2008; Ciaramelli et al., 2008). Intriguingly, prior research has shown that saccade execution increases subsequent episodic retrieval (e.g., Christman et al., 2003; Lyle, Logan et al., 2008) and increases subsequent top-down attentional control (Edlin & Lyle, 2013). We theorise that these effects are not independent but rather that saccade-induced increases in top-down attentional processing cause SIRE. Support for our theory would come from finding larger SIRE effects under retrieval conditions that require greater top-down attention. In two experiments, we obtained exactly that pattern, as did one previous study (Brunyé et al., 2009).

At the same time that our findings support our top-down attentional control hypothesis of SIRE, they present a challenge to a prominent alternative hypothesis, first put forth by Christman et al. (2003). We have discussed this alternative account in detail elsewhere (Lyle, Logan et al., 2008; Lyle & Martin, 2010; Lyle & Orsborn, 2011) and here provide only the briefest of outlines. The account assumes that executing horizontal saccades increases the functional coordination of the left and right brain hemispheres, with the former being relatively specialised for the encoding of episodic memories and the latter for retrieval. The hypothesised increase in coordination with encoding regions is thought to enhance retrieval. Christman et al. argued that the account predicts an effect of saccade execution on episodic, but not implicit, retrieval. However, the account has never specified particular episodic retrieval conditions that should be more likely than others to reveal SIRE, and therefore it cannot accommodate the current findings. Moreover, the account stipulates that only *horizontal* saccades increase interhemispheric coordination, and therefore only them, and not vertical saccades, should produce SIRE. This assertion was contradicted by our Experiment 2.

Returning to our own hypothesis, although we have focused in this paper on top-down attentional modulation of episodic mnemonic representations, we do not assume that saccade execution affects attentional processes that only operate on mnemonic representations. Rather, we assume these processes are domain-general and may operate on perceptual representations, as in Edlin and Lyle (2013), as well as on nonepisodic reflective representations, such as representations of information in working memory or semantic memory. This assumption is important because it allows us to explain effects of saccade execution on cognition beyond episodic retrieval. Several such effects have been documented. One example comes from Lyle and Orsborn (2011), where subjects had to classify faces as famous or novel. The task was nontrivial because faces were presented for only 150 ms. For consistently handed subjects, saccade execution increased classification accuracy. We theorise that saccade execution potentiated attentional modulation of face representations in working memory. This led to more strongly activated representations and hence higher-fidelity or longer-lasting internally maintained images. Given recent evidence that attention can not only maintain representations in working memory but restore them after they have dropped out (Murray et al., 2013; see also Sergent et al., 2013), it is also possible that saccade execution increased subjects' ability to bring faces back into visual working memory after initially losing access to them.

An even more recent example of saccade-induced enhancement beyond episodic retrieval comes from Di Noto, Uta, and DeSouza's (2013) study of performance on a rapid serial visual presentation task. In this task, subjects had to detect and sometimes identify target letters that appeared at various intervals between 50 ms and 382 ms after another target. The detection rate was lower when the interval between the preceding target and the current one was shorter (i.e., attentional blink; Raymond, Shapiro, & Arnell, 1992). Subjects performed the task before and after either executing saccades or maintaining stationary fixation. The saccades activity was much longer than in SIRE studies (18.5 min) and involved making saccades in multiple directions, but it was similar to the standard SIRE activity in that the only requirement was the execution of saccades to a simple visual stimulus. Subjects were better able to detect and identify targets after making saccades than before (i.e., reduced attentional blink). The control activity produced no such improvement. We would explain this finding in terms of saccade-induced strengthening of the representations of target letters. A similar mechanism could explain Lyle and Martin's (2010) finding that saccade execution increased subjects' ability to detect identity matches between simultaneously presented letters (e.g., *a-A*).

Although saccade execution can enhance cognition, it can also have negative effects. Specifically, saccade execution can increase false recall and false recognition (Lyle, Logan et al., 2008; Lyle et al., 2012). An important question is whether our account can explain these negative effects, and explain why they appear to be more common for inconsistent-handers. In Experiment 1, saccade execution increased false recall of nonpresented exemplars and, for the first time, did so for consistent-handers, as well as inconsistent-handers. This negative effect was in addition to increasing correct recall of *Rp*− items. The two item types that were affected by saccade execution—nonpresented items and presented but difficult-to-access items—are also the two item types that were least likely to be strongly activated by the bottom-up influence of the retrieval cue alone (i.e., the category name). Nonetheless, we can assume that there was some weak activation of these items. This would certainly be true for presented items and might well be true for nonpresented items, given that category-cued recall procedures are known to activate nonpresented exemplars (e.g., Smith, Tindell, Pierce, Gilliland, & Gerkens, 2001). It may be that top-down attentional modulation is triggered by the presence of weakly activated mnemonic representations, regardless of whether they are episodic representations of presented items or semantic representations of nonpresented items. If so, saccade execution could increase the likelihood that either type of representation would enter consciousness by increasing the potency of upmodulatory attentional signals. Once brought to mind, the represented items would be candidates for identification (rightly or wrongly) as episodic memories from the study phase. Source-monitoring failures for nonpresented exemplars would not be surprising given the general plausibility that they appeared on a list of category exemplars (Johnson, Hashtroudi, & Lindsay, 1993).

In other experiments, saccade execution has not increased false retrieval for consistent-handers and has only sometimes done so for inconsistent-handers. For example, in the present Experiment 2, neither handedness group exhibited increased false recognition. If our explanation for increased false recall in Experiment 1 is correct, then saccade-induced increases in false retrieval may depend on nonpresented items being sufficiently activated at some weak level and posing a source-monitoring challenge. This is unlikely to have been the case in Experiment 2, where there was no obvious source of bottom-up activation for the visual features of lures (recall that this was a test of picture memory). Nor would it be the case in certain other procedures used in SIRE studies. Free recall of random word lists is an interesting example. Studying a random word list does not produce much activation of nonpresented items, and, as would therefore be expected, saccade execution has not been found to increase false recall for consistent-handers (Lyle, Logan et al., 2008; Samara et al., 2011). However, Lyle, Logan et al. found that saccade execution *did* increase false recall among inconsistent-handers. Differences between the handedness groups may stem from differential patterns of semantic activation. Inconsistent-handers have more diffuse semantic networks than consistent-handers (Sontam & Christman, 2012) and may also differ in language lateralisation (Knecht et al., 2000). These ideas are speculative, but they provide a needed basis for testable predictions about when retrieval-induced impairment will and will not occur.

Going forward, it will be important to test our top-down attentional control hypothesis even more rigorously. One avenue would be to obtain more direct evidence that retrieval conditions differ in top-down attentional control requirements before assessing the effect of saccade execution. This could be done by dividing attention during retrieval. The condition in which retrieval suffers more from dividing attention should be the one in which a stronger SIRE effect occurs.

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