

The effect of repetitive saccade execution on the attention network test: Enhancing executive function with a flick of the eyes

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ABSTRACT

The simple act of repeatedly looking left and right can enhance subsequent cognition, including divergent thinking, detection of matching letters from visual arrays, and memory retrieval. One hypothesis is that saccade execution enhances subsequent cognition by altering attentional control. To test this hypothesis, we compared performance following repetitive bilateral saccades or central fixation on the revised attention network test, which measures the operation of three distinct attentional networks: alerting, orienting, and executive function. The primary finding was that saccade execution increased the subsequent operation of the executive function network, which encompasses attentional control. Specifically, saccade execution decreased response time to target stimuli in the presence of response-incongruent flankers. A secondary finding was that saccade execution decreased response time to targets when an invalid location was cued prior to target onset. These findings suggest that saccades are an effective means of improving attentional control. Of greater theoretical importance, the study establishes attentional enhancement as a potential mechanism by which saccades enhance other aspects of cognition. Although some saccade execution effects have been found to depend on consistency of handedness (i.e., the consistency with which an individual uses one hand over the other), saccade-induced enhancement of attentional control occurred independently of handedness consistency.

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1. Introduction

The simple act of repeatedly looking left and right can enhance subsequent cognition. This surprising effect has been established in numerous studies that have compared cognitive performance following 30 s of repetitive bilateral saccade execution to performance following 30 s of either central fixation or spontaneous, unrestrained eye movement. Saccade execution enhances subsequent divergent thinking on the Alternate Uses Task (Shobe, Ross, & Fleck, 2009), detection of matching letters in briefly flashed arrays (Lyle & Martin, 2010), and, most commonly, memory retrieval (e.g., Christman, Garvey, Propper, & Phaneuf, 2003; Lyle, Logan, & Roediger, 2008). For example, in Lyle et al., subjects recalled more studied words, and falsely recalled fewer nonstudied words, following saccades vs. fixation. The effect of saccade execution on memory retrieval has been dubbed saccade-induced retrieval enhancement (SIRE; Lyle & Martin, 2010), but the broader phenomenon may be called saccade-induced cognitive enhancement (SICE).

Although SICE is well documented empirically, its cause is unknown. An initial hypothesis (Christman et al., 2003) that saccades

enhance cognition by increasing functional coordination of the left and right cerebral hemispheres (i.e., the interhemispheric interaction account) has received mixed support, which we now review. Lyle and Martin (2010) tested whether saccade execution would increase subjects' ability to detect an identity match between two letters that differed in case (e.g., *A* and *a*) when the two letters were briefly flashed in separate visual fields and hence were initially processed by separate hemispheres. The authors reasoned that, if saccades increase the functional coordination of the hemispheres, then they should enhance match detection under these conditions, which require interhemispheric interaction (Eviatar & Zaidel, 1994). However, saccade-induced enhancement was not obtained under these conditions. Rather, saccades increased match detection when the two letters were presented in the same visual field and hence processing of the match was primarily intrahemispheric. Subsequently, Lyle and Orsborn (2011) tested whether saccade execution would increase bilateral gain for famous faces, which is the effect whereby such faces are more quickly or accurately identified when they are initially processed by both hemispheres simultaneously (given bilateral visual presentation) vs. when they are initially processed by only a single hemisphere (given unilateral presentation). Bilateral gain is thought to depend on interhemispheric interaction (Mohr, Pulvermuller, Rayman, & Zaidel, 1994), but its magnitude was unaffected by saccades in Lyle

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and Orsborn's study. In contrast, saccades increased identification of novel faces, which do not show a bilateral gain effect. Hence, in two behavioral studies, saccades enhanced cognition (intra-hemispheric letter matching and novel-face identification) without affecting indices of interhemispheric interaction.

In addition to the behavioral data, electrophysiological findings relevant to the interhemispheric interaction account have been reported, but are inconclusive. Propper, Pierce, Geisler, Christman, and Bellorado (2007) found that saccades decreased gamma-band coherence between the hemispheres, which suggests that saccades may indeed affect interhemispheric interaction in some way, but two caveats are necessary. First, Propper et al.'s study did not have a behavioral component, and so could not reveal whether saccade-induced changes in coherence were accompanied by cognitive enhancement. Second, it is not clear whether decreased coherence represents an increase in interhemispheric interaction, as the interhemispheric interaction hypothesis stipulates, or a decrease. Following up on this finding, Samara, Elzinga, Slagter, and Nieuwenhuis (2011) conducted a combined behavioral and electrophysiological study and found that saccades increased retrieval but had no significant effect on interhemispheric coherence. From this we may conclude that, even if saccades sometimes do affect interhemispheric interaction, as suggested by Propper et al.'s finding, a change in interaction is not necessary for SICE to occur.

As an alternative to the interhemispheric interaction account, Lyle and Martin (2010) hypothesized that saccade execution might enhance subsequent cognition by altering the top-down allocation or control of attention. Top-down attentional control is theoretically vital to much of complex cognition, including those tasks that have shown SICE, as we detail next. First, multiple authors have recently suggested that attentional control may play a role in episodic memory retrieval when stimulus-driven mental events alone are insufficient for a desired memory judgment or experience (Cabeza, 2008; Ciaramelli, Grady, & Moscovitch, 2008; Wagner, Shannon, Kahn, & Buckner, 2005). These situations would include those that require multiple retrieval attempts, post-retrieval monitoring, or goal-driven maintenance or shifting of attention on or between mnemonic representations. Specific retrieval phenomena posited to involve attentional control include source recollection, rejection of related/similar lures in recognition, and correct recognition of high vs. low frequency words (Ciaramelli et al., 2008). Second, the Alternate Uses Task studied by Shobe et al. (2009), while broadly characterized as a test of creativity, is more specifically a measure of divergent thinking, which is the ability to generate diverse solutions to a problem (see Dietrich & Kanso, 2010, for discussion of separable processes in creativity). In Shobe et al.'s version of the task, subjects saw the name and one common use of 15 different objects. Subjects were instructed to list as many uses for each object as possible, other than the common use they were given, in 60 s. There is a role for episodic memory retrieval in this task, because many subjects initially produce uses by retrieving instances in which they saw the objects used in uncommon ways (Gilhooly, Fioratou, Anthony, & Wynn, 2007). This type of retrieval may require a high level of attentional control, because subjects must ignore the common use and not become fixated on uses similar or identical to previously given uses. Third and finally, Banich (1998) argued that detecting letter-identity matches intra-hemispherically is more attentionally demanding than detecting them interhemispherically. In sum, while each of the tasks on which SICE has been observed depend on multiple perceptual and cognitive processes, the top-down control of attention may be a shared process that is common to all.

In developing their attentional control hypothesis, Lyle and Martin (2010) drew on the well-established finding that making goal-directed saccades activates a frontoparietal network of brain regions, including the frontal eye field, intraparietal sulcus, and

superior parietal lobe (Corbetta & Shulman, 2002). The frontoparietal network is hypothesized to be involved in the implementation of top-down attentional control. Lyle and Martin hypothesized that, by activating brain regions involved in attentional control immediately prior to task onset, saccade execution may increase control and thereby enhance subsequent task performance. Critically, functional neuroimaging has revealed that the intraparietal sulcus and superior parietal lobe, which are activated by saccade execution, are also activated during episodic memory retrieval, and especially for retrieval tasks that require a high degree of attentional control, such as source recollection, rejection of similar/related lures, and correct recognition of high frequency words (Cabeza, 2008; Ciaramelli et al., 2008; Wagner et al., 2005). Furthermore, the intraparietal sulcus has also been implicated in detecting identity-matches between letters (Pollmann, Zaidel, & von Cramon, 2003) and the superior parietal lobe has been implicated in the Alternate Uses Task in one investigation (Abraham et al., 2012), albeit not another (Fink et al., 2010).

Lyle and Martin's (2010) attentional control hypothesis predicts that SICE should not occur for tasks that do not require a high degree of top-down attentional control. Consistent with this, Brunyé, Mahoney, Augustyn, and Taylor (2009, Experiment 2) did not find enhancement when old items (in this case, aerial maps) had to be discriminated from rearranged items in a two-alternative forced-choice procedure. Brunyé et al. posited that performance on their forced-choice task may have been driven primarily by bottom-up differences in familiarity between the two stimuli and may not have depended on executive function, which subsumes top-down attentional control. Also, Christman et al. (2003, Experiment 1) did not find enhancement on an implicit retrieval task. Subjects saw word fragments that they could (and sometimes did) complete with previously studied words, but they were not required to attend to the old/new status of the words used to complete fragments.

Lyle and Martin's (2010) idea that goal-directed saccade execution might improve attentional control is interesting in its own right, regardless of whether such improvement is actually the cause of previously documented SICE effects. Saccade execution can be conceptualized as a minimal attentional control task insofar as control is required to repetitively shift attention according to a pre-established agenda. Lyle and Martin's idea, therefore, is that exercising attentional control in the service of saccades and for as little as 30 s, may produce measurable improvement in control. Could merely exercising attentional control lead to its improvement? The answer is yes according to studies of training attention (e.g., Rueda, Rothbart, McCandliss, Saccomanno, & Posner, 2005) and the closely related construct of working memory (for reviews, see Klingberg, 2010; Morrison & Chein, 2011). Training regimens that involve the repetitive performance of tasks requiring attentional control have been found to produce improvement on other, non-trained tasks. In those studies, the improvement has occurred following hours of repetitive practice. Furthermore, the demands placed on control processes often have not been static, but rather have increased throughout training. Hence, while those studies demonstrate the possibility of improving attentional control, it is an open question whether improvement can be achieved following performance of an attentional control task that is very brief and has low and static demands, such as 30 s of saccade execution.

No previous study has directly examined possible effects of saccade execution on attentional processing. Therefore, in the present study, we compared performance following saccades or central fixation on the revised attention network test (ANT-R; Fan et al., 2009), which measures the operation of three dissociable attentional networks: alerting, orienting, and executive function (for review, see Posner & Petersen, 1990). On each trial in the ANT-R (see Fig. 1 for an example), subjects indicate the direction that a

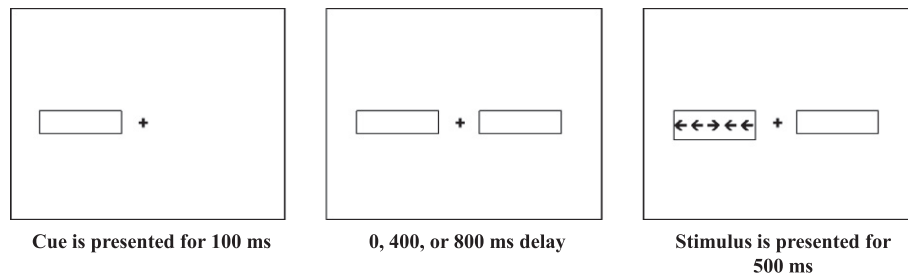


Fig. 1. An example of an ANT-R trial that includes an invalid cue with incongruent flankers.

target arrow is pointing (left or right). The primary dependent variable is RT to the target. The target arrow appears left or right of a fixation cross. Prior to target onset one of four cue types is presented: none, double, single valid, or single invalid. The alerting network prepares the attentional system for an impending stimulus and is measured by the RT difference between no cue and double cue trials. The orienting network moves and engages attention and is measured as the RT difference between trials with a double cue and a valid cue. In addition to the cue manipulation, there are arrows flanking the target arrow and the flankers' direction may be congruent or incongruent with the target. The RT difference between trials with congruent vs. incongruent flankers measures control of attention because responding quickly in the presence of incongruent flankers requires ignoring distracting stimuli. Control of attention is the domain of the executive function network. The ANT-R has been used to assess the impact of a wide range of factors on attentional processing, from subject variables such as age (Konrad et al., 2005) to training regimens such as mindfulness-based stress reduction (Jha, Krompinger, & Baime, 2007).

Given Lyle and Martin's (2010) hypothesis, which of the attentional networks would be expected to show saccade-induced enhancement? All of the networks are associated with frontoparietal activation (Fan, McCandliss, Fossella, Flombaum, & Posner, 2005). As saccade execution is also associated with frontoparietal activation, one could argue purely from the perspective of shared neural circuitry that all of the networks are possible candidates for enhancement. However, Lyle and Martin specifically posited that saccade execution may increase attentional control and, as reviewed above, saccade-induced enhancement has not been found on retrieval tasks that require low levels of attention control (Brunyé et al., 2009, Experiment 2; Christman et al., 2003, Experiment 1). In the ANT-R, responding to the target in the presence of incongruent flankers (a component of the executive function network) requires a high level of attention control, while simply responding to the target following an alerting or an orienting cue does not. Therefore, from a combined neural and behavioral perspective, the prediction would be for saccade-induced enhancement of the executive function network only.

An additional prediction might be generated from Stickgold's (2002) theorizing about the role of eye movements in the therapeutic procedure known as Eye Movement Desensitization and Reprocessing. Stickgold suggested that these eye movements replicate the rapid orienting system. This could foster the expectation that saccade execution would enhance the orienting network. Further bolstering this expectation is the fact that the saccades task involves repetitively orienting attention to one of two lateralized locations. The task therefore may be conceptualized as a minimal attentional orienting task and its repetitive practice may improve orienting.

An intriguing aspect of SICE is that it is not equally likely for all people. An important individual difference factor is the consistency with which people use one hand over the other for manual activities. Consistency is quantified with handedness inventories. These

inventories (e.g., Annett, 1970; Oldfield, 1971) query which hand (left, right, or both) is typically used to perform various activities. If one hand is preferred for an activity, some inventories further query the strength or consistency of the preference. Some people report a highly consistent tendency to use a single hand (left or right) while others are more inconsistent and make greater use of both hands. In the subset of SICE studies that have assessed consistency, consistent right-handers have unfailingly exhibited enhancement, while inconsistent-handers have improved on only some measures (Christman, Propper, & Brown, 2006; Lyle & Jacobs, 2010; Lyle & Martin, 2010). On other measures, saccades have either had no significant effect on inconsistent-handers (Brunyé et al. 2009; Lyle & Orsborn, 2011; Shobe et al., 2009) or significantly harmed them (i.e., saccade-induced impairment; Lyle, Hanaver-Torrez, Häcklander, & Edlin, 2012; Lyle et al., 2008).

If attentional control mediates the effect of saccade execution on cognition, then saccades should obviously enhance attentional control (as measured by the executive function network) in consistent-handers, who have routinely shown positive effects of saccades on cognition. The same might occur for inconsistent-handers, who have shown positive saccade effects on some, but not all, measures. However, given that saccades have not significantly affected inconsistent-handers on some measures, and have harmed them on others, one could also predict that saccades either would not affect these individuals' attentional control or would reduce it.

2. Methods

2.1. Subjects

Subjects were undergraduates aged 18–30 who received credit in psychology courses for participating. Using a modified version of Oldfield's (1971) Edinburgh Handedness Inventory (see below), and following our method in Lyle et al. (2012), subjects were classified as consistently-handed if the absolute value of their inventory score was 80 or greater ($n = 95$) or as inconsistently-handed if the absolute value of their inventory score was less than 80 ($n = 67$). Among consistently-handed subjects, 48 (M absolute score = 92.1; 16 males, 1 unknown) were randomly assigned to the saccades activity and 47 (M absolute score = 92.0; 10 males) to the fixation activity. Among inconsistently-handed subjects, corresponding numbers were 32 (M absolute score = 55.5; 7 males) and 35 (M absolute score = 58.7; 8 males).

2.2. Materials

The handedness inventory was a modified version of Oldfield's (1971) Edinburgh Handedness Inventory that we have used in numerous other studies (e.g., Lyle & Martin, 2010; Lyle et al., 2008; Lyle et al., 2012). The inventory queries direction and consistency of hand use for ten activities (writing, drawing, using a

spoon, opening jars, using a toothbrush, throwing, combing hair, using scissors, using a knife without a fork, and striking a match). For each activity, the response options (and corresponding point values for the purpose of scoring) are Always Right (+10), Usually Right (+5), No Preference (0), Usually Left (−5), and Always Left (−10). Scores range from −100 (exclusive left-hand usage) to +100 (exclusive right-hand usage) in 5-point increments.

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

Each trial of the ANT-R involved presentation of a target arrow (see Fig. 1 for an example trial). Two flanker arrows appeared on either side of the target. The flankers' direction was either congruent or incongruent with the target. The target and flanker arrows appeared either left or right of a central fixation cross for 500 ms. Neither, one (either valid or invalid), or both possible stimulus locations were cued by a 100 ms flash. Cues appeared 0 ms, 400 ms, or 800 ms before stimulus onset. Single cues were valid on 75% of trials and invalid on 25%.

2.3. Procedure

Subjects first completed the handedness inventory. Next subjects received instructions for the ANT-R, and performed 24 practice trials. In the original ANT-R, subjects practiced until they achieved 90% accuracy (Fan et al., 2009), but in this study all subjects performed 24 practice trials to ensure constant practice times. Subjects were then randomly assigned to perform either the saccades or fixation activity for 30 s. For the saccades activity, subjects moved their eyes to follow a circle that alternated between the left and right sides of the screen. For the fixation activity, subjects fixated a stationary circle that flashed on and off in the center of the screen without moving their eyes. The experimenter monitored compliance with instructions. Immediately after performance of the activity, subjects began the first of four blocks of ANT-R trials. Each block lasted 7 min. Subjects repeated the initial activity before each block. On each trial of the ANT-R, subjects indicated the direction of the target arrow via key press. Subjects were instructed to respond as quickly and accurately as possible. They were informed that both reaction time and accuracy would be recorded.

3. Results

To ensure sufficient correct trials for analysis, subjects with less than 90% accuracy were excluded. The measure of each attentional network was analyzed via a separate 2 (handedness: inconsistent vs. consistent) × 2 (activity: fixation vs. saccades) between-subjects ANOVA. The alerting and orienting networks are measured as RT difference scores between trials with different cue types, regardless of flanker congruency or incongruency. Specifically, the alerting network is the RT difference between no cue and double cue trials and the orienting network is the RT difference between double cue and valid cue trials. Activity did not affect these networks, largest $F(1, 158) = 1.17, p = .281$. Executive function is measured as the RT difference between trials with incongruent and congruent flankers, regardless of cue type, and, for this measure, there was a significant main effect of activity, $F(1, 158) = 4.88, p = .029, \eta^2 = .03$. Fig. 2a shows that the RT cost of incongruent flankers was smaller following saccades ($M = 152.19$ ms) than fixation ($M = 175.04$ ms). Fig. 2b shows that this effect occurred because saccades significantly reduced RT on incongruent trials ($M = 797.96$ ms) compared to fixation

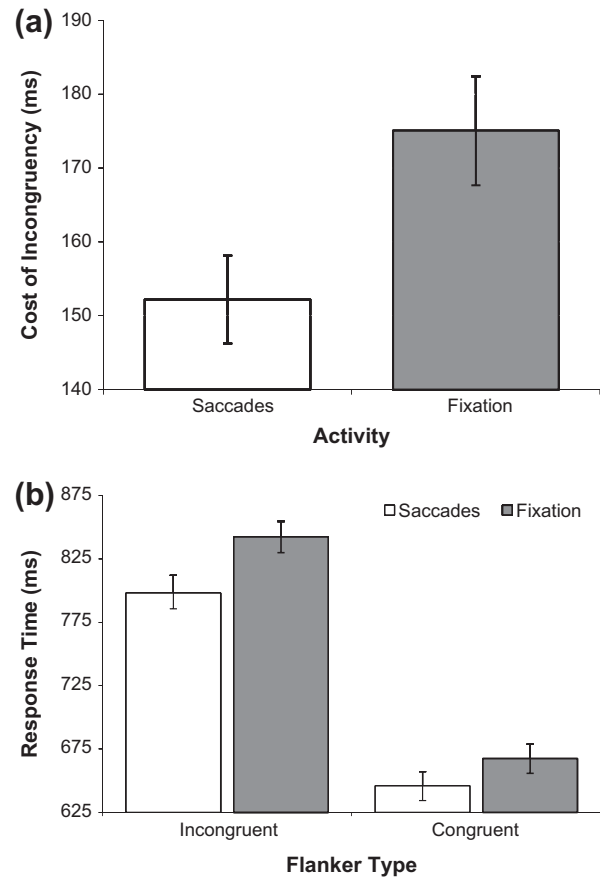


Fig. 2. Mean cost of incongruity (a) as measured by the RT difference between congruent and incongruent trials, and mean RT on incongruent and congruent trials (b) as a function of activity. Error bars indicate ± 1 SEM.

($M = 842.31$ ms), $t(160) = -2.36, p = .019$. Saccades did not significantly reduce RT on congruent trials ($M = 645.77$) compared to fixation ($M = 667.28$), $t(160) = -1.33, p = .184$. Parallel analyses of accuracy found no significant effects, largest $F(1, 158) = 1.92, p = .168$, indicating that the RT result was not a product of a speed-accuracy tradeoff. Despite responding faster, subjects were not less accurate on incongruent trials following saccades ($M = .93$) than they were following fixation ($M = .92$), $t(160) = -.295, p = .768$.

The executive function measure is calculated irrespective of cue type. To further examine the effect of saccades on RT in the presence of incongruent vs. congruent flankers, we submitted mean RTs to a 2 (handedness: inconsistent vs. consistent) × 2 (activity: fixation vs. saccades) × 2 (flanker type: congruent vs. incongruent) × 4 (cue type: double vs. invalid vs. valid vs. none) ANOVA. The three-way interaction between activity, flanker type, and cue type was significant, $F(3, 156) = 2.83, p = .038, \eta^2 = .018$. To examine how saccades affected performance given each cue type, we conducted a separate 2 (activity: fixation vs. saccades) × 2 (flanker type: congruent vs. incongruent) ANOVA for each cue type. There were significant activity × flanker type interactions for valid cue, $F(1, 160) = 3.895, p = .05, \eta^2 = .024$, and no cue trials, $F(1, 160) = 11.93, p = .001, \eta^2 = .069$. Fig. 3 shows that these interactions arose because saccades primarily reduced RT given incongruent flankers rather than congruent flankers. The effect of activity on RT in the valid cue and no cue conditions was significant given incongruent flankers, smallest $t(160) = -2.19, p = .03$, but not congruent flankers, largest $t(160) = -1.41, p = .16$. In contrast to these effects, there was no activity × flanker type interaction for invalid

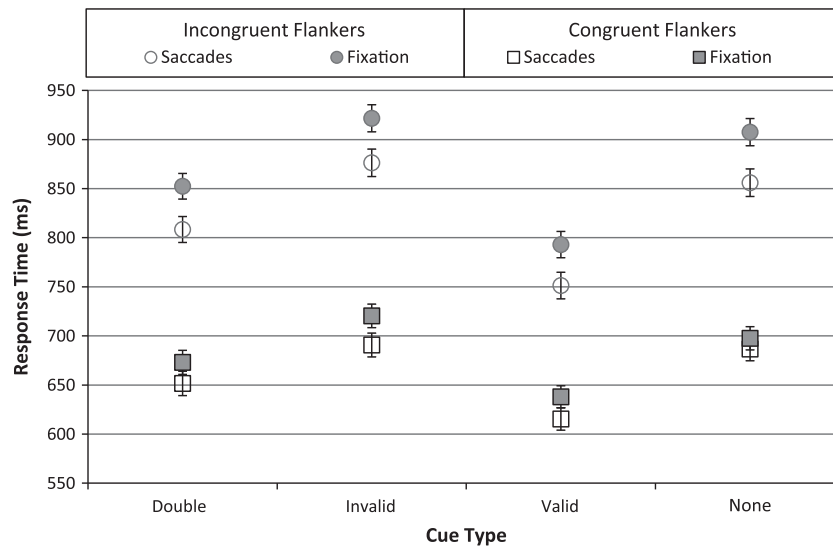


Fig. 3. Mean RT as a function of cue type, flanker type, and activity. Error bars indicate ± 1 SEM.

cue trials, $F(1, 160) = 2.067, p = .152, \eta^2 = .013$, but rather a main effect of activity, $F(1, 160) = 4.54, p = .035, \eta^2 = .028$. In this cue condition only, Fig. 3 shows that saccades reduced RT for congruent or incongruent flankers alike. Finally, the analysis of double cue trials was inconclusive. No effect was significant at the .05 level, but the main effect of activity approached significance, $F(1, 160) = 3.738, p = .055, \eta^2 = .023$.

There were no significant main effects or interactions involving handedness, largest $F(1, 158) = 1.19, p = .278$.

4. Discussion

The primary goal of this study was to test Lyle and Martin's (2010) hypothesis that saccade execution enhances subsequent attentional control. The hypothesis was supported by the finding that saccades increased the operation of the executive function network, which encompasses attentional control, on the ANT-R. The primary importance of this finding is that it establishes increased attentional control as a potential mechanism for other, previously documented instances of SICE. Saccades have been shown to enhance episodic memory retrieval, divergent thinking, and the detection of matching letters from briefly flashed arrays, and all three have been associated with attentional control (e.g., Banich, 1998; Groborz & Necka, 2003; Levy & Anderson, 2002). Of course, the possibility exists that the increase in attentional control is epiphenomenal and not the cause of the other effects. Additional research will be needed to explore causal links between saccade-induced increases in attentional control and saccade-induced increases in other abilities.

One way the saccade-induced increase in attentional control manifested was in faster responding to the target in the presence of response-incongruent flankers—an effect that occurred regardless of how the target was cued (Fig. 3). However, there was evidence of increased attentional control in the presence of congruent flankers, too: in the invalid cue condition, saccades decreased RT to targets given congruent and incongruent flankers alike. One way to summarize these effects is that saccades reduced RT whenever there was incongruent input that required attentional control to overcome. The incongruent input was incongruent flankers and/or an invalid spatial cue. It remains to be determined how saccade execution produced these effects, but it may have increased the neural representation of the target or decreased the neural representation of the incongruent input. These possibilities follow from the fact that

posterior parietal regions including the intraparietal sulcus and superior parietal lobe are activated by goal-driven saccades (Corbetta & Shulman, 2002) and are hypothesized to modulate the activation of neural representations (Yantis, 2008). The superior parietal lobe has been implicated in the operation of the executive function network. Konrad et al. (2005) found that the left superior parietal lobe in adults subjects was more active on incongruent than congruent trials in a modified version of the ANT. Furthermore, the intraparietal sulcus has been implicated when ignoring distracters (Kim & Hopfinger, 2010) and during periods of conflict-related target processing (Luks, Simpson, Dale, & Hough, 2007).

Another region of the frontoparietal network activated by saccade execution is the frontal eye fields (Corbetta, 1998), which also may have contributed to increased performance on incongruent trials. Transcranial magnetic stimulation (TMS) facilitation of the frontal eye fields increases target detection ability (Grosbras & Paus, 2002) and TMS knockout of this region decreases inhibitory control (Muggleton, Chen, Tzeng, Hung, & Juan, 2010). Performing saccades prior to the ANT-R trials may have increased activation of the frontal eye fields (similar to using TMS facilitation), thereby increasing target detection and inhibitory control and enhancing the executive function network.

How might these proposed enhancements of attentional processes improve retrieval of episodic memories? Episodic memory retrieval is the type of cognition for which saccade-induced enhancement has most often been shown, at least for consistently-handed individuals. Numerous studies have indicated that attentional processes mediated by regions in the frontoparietal network can be directed to mnemonic representations in much the same way they are directed to sensory stimuli (e.g., Majerus et al., 2006; Nee & Jonides, 2009; Roth, Johnson, Raye, & Constable, 2009; Trapp & Lepsien, 2012). Episodic memory retrieval could be enhanced by facilitating attentional control processes that increase the activation of targeted mnemonic representations, decrease the activation of nontargeted representations, or inhibit competing memories. These processes are not necessarily central to all retrieval tasks, but they are likely to contribute to performance in the sorts of tasks that have shown SIRE, such as free recall (Christman, Propper, & Dion, 2004; Lyle et al., Experiment 1, 2008), discriminating targets from related, similar, or recombined lures (Lyle et al., 2012; Lyle et al., Experiment 2, 2008; Parker & Dagnall, 2007; Parker & Dagnall, 2012; Parker, Relph, & Dagnall, Experiment 1, 2008), source recollection (Parker et al., Experiment 2, 2008),

and discriminating studied information from misinformation (Lyle & Jacobs, 2010; Parker, Buckley, & Dagnall, 2009).

The alerting and orienting networks are associated with frontoparietal activity (Fan et al., 2005), but these networks were not enhanced by saccades. The absence of an effect on orienting is especially interesting, given that making saccades is itself an orienting task that subjects practiced immediately before the ANT-R. These results suggest that neither performing a task that activates the frontoparietal attention network, nor practicing an attentional task, guarantees that performance of a subsequent cognitive task will be enhanced. In this study, enhancement occurred quite specifically when the task required a high level of attentional control (i.e., when there was incongruent input) but not when the requirement was low (i.e., responding following an alert or orienting to a validly cued location). This mirrors the picture emerging from research on saccades and memory retrieval. Retrieval tasks that do not require a high degree of attentional control have not shown saccade-induced enhancement (Brunyé et al., 2009; Christman et al., 2003, Experiment 1). Additional behavioral studies that vary attentional control demands, and additional neuroimaging studies that can evaluate the potential involvement of specific brain regions, are needed to further test Lyle and Martin's (2010) hypothesis that saccades improve cognition by enhancing attentional control via the frontoparietal network.

These data also speak to the question, raised in the Introduction, of whether exercising attentional control can lead to its improvement. This question has been answered affirmatively in traditional attention and working memory training studies, in which indices of attentional control are improved following repetitive performance over multiple sessions of tasks that not only require control, but often place increasing demands on control (Klingberg, 2010; Morrison & Chein, 2011; Rueda et al., 2005). Here, we examined the effect of a more minimalistic exertion of control. The saccade execution task merely required subjects to shift attention between two constant locations twice a second for 30 s. Nonetheless, improvement followed, similar to traditional training studies. One theoretical framework for understanding training effects is that the repeated operation of attentional processes produces enduring changes in the efficiency of those processes (Posner & Raichle, 1994). In other words, the efficiency of attentional processes is plastic and responsive to the processes' accumulated operational history. The present findings may suggest that there are also moment-to-moment changes in efficiency, with efficiency being greater immediately following the operation of a process.

Finally, the present study advances our understanding of the relationship between handedness consistency and saccade-induced cognitive enhancement. Inconsistently-handed individuals have sometimes failed to exhibit enhancement following saccades (Brunyé et al., 2009; Lyle & Orsborn, 2011; Shobe et al., 2009) and sometimes exhibited impairment (Lyle et al., 2008; Lyle et al., 2012) in situations where only enhancement has occurred for consistently-handed individuals. This suggests that saccades had no effect, or even disrupted mechanisms that supported performance. However, those possibilities would be difficult to reconcile with the fact that inconsistent-handers have exhibited saccade-induced enhancement in other cases, and they are not favored by the present findings. Saccades enhanced executive control, a potential mechanism for cognitive enhancement, for consistent- and inconsistent-handers alike. This suggests that previously documented group differences in cognitive enhancement may be due to as-yet unidentified group differences in how attentional control is allocated during cognitive tasks.

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