Saccades and Handedness Interact to Affect Scene Memory

Timothy M. Ellmore[1,2*], Bridget Mackin[1], and Kenneth Ng[1]

[1]Department of Psychology, The City College of New York, New York, NY USA

[2]Program in Behavioral and Cognitive Neuroscience, The Graduate Center, The City University of New York, NY USA

[*]Corresponding author

Timothy M. Ellmore, Ph.D.
Associate Professor
The City College of New York
Department of Psychology, NAC 7/120
160 Convent Ave
New York, NY 10031
E-mail: tellmore@ccny.cuny.edu
Phone: (212) 650-5714; Fax: (212) 650-5659

Abstract

Repetitive bilateral saccades are reported to benefit memory when they are made before retrieval. Effects are greatest for episodic memory in consistent-handers who are presumed to have lower baseline levels of interhemispheric interaction. Many questions remain, however, including what effects saccades have on scene memory, especially since visual memories for the context in which previous events occurred constitute episodic memory. The present study was designed to test how repetitive saccades affect working and recognition memory for novel scenes. Laterality quotients (LQ) were computed from an 8-question handedness inventory completed by 111 adults. Each then performed either 30 seconds of repetitive horizontal saccades or fixation before or after tasks of scene working memory and scene recognition. Regression analyses revealed that when subjects made saccades before scene working memory, better working memory accuracy was obtained as a function of increased right-handedness (significant non-zero slope y=0.1028*LQ+77.79%, p=0.0251). Subjects who made saccades before scene working memory also performed worse during a subsequent test of recognition memory, while subjects who fixated or made saccades after the working memory task performed better. Saccades made before recognition resulted in recognition accuracy that was higher (Cohen's d=0.3729) but not significantly different from accuracy obtained when subjects fixated before recognition. The results demonstrate that saccades and handedness interact to affect scene memory with larger effects on encoding than recognition. Saccade execution before scene encoding in working memory is detrimental to both short- and long-term scene memory, especially for those who are not consistently right-handed. Moreover, saccade execution before scene recognition does not appear to benefit recognition accuracy appreciably. This could be because optimal scene processing is lateralized and therefore scene memory does not benefit from increased interhemispheric interaction.

Keywords: Eye Movements, Working Memory, Encoding, Recognition, Laterality, Regression Analyses

Introduction

As few as thirty seconds of horizontal bilateral saccadic eye movements before testing selectively enhances episodic memory retrieval for laboratory and everyday events. (Christman et al. 2003). Beneficial effects are selective and are not found for implicit memory or after smooth pursuit or vertical eye movements. It has been suggested that horizontal eye movements enhance interhemispheric interaction, which is associated with superior episodic memory (Christman & Propper 2001). Increased interhemispheric interaction is related to decreased false memories in a semantic associates paradigm (Christman et al. 2004). Strong right-handedness, which is associated with decreased interhemispheric interaction, was associated with higher rates of false memories while bilateral saccades were associated with fewer false memories. Other evidence suggests that mixed-handers display better episodic memory in comparison with strong right-handers on assessments of word recall, word fragment completion, and recall of real world events (Propper et al. 2005). Mixed-handedness and bilateral saccadic eye movements have also both been associated with an earlier offset of childhood amnesia and support the idea that interhemispheric interaction exerts effects on retrieval but not encoding of episodic memories. Mixed-handed subjects also demonstrate greater autobiographical recollection on components of seeing hearing and emotion compared to right-handed individuals, and 30 sec of bilateral eye movements induce greater levels of autobiographical recollection across a range of components (Parker & Dagnall 2010).

Bilateral eye movements also appear to enhance some types of recognition memory. Subjects who made bilateral eye movements were more likely to correctly recognize previously presented words, but less likely to falsely recognize critical non-studied associates (Parker & Dagnall 2007). A study of both recall and recognition with strongly right-handed (SR) and non-

strongly right handed (nSR) subjects found that eye movements made little difference or could even be detrimental in nSR subjects. This finding supports the hemispheric interaction hypothesis but with the caveat that eye movements could be harmful for nSR individuals (Lyle et al. 2008a). Better memory without eye movements is thought to exist in nSR individuals because nSR handedness is thought to be a behavioral marker for greater interhemispheric interaction. Consistent with this idea, middle-age nSR subjects perform better on tasks like paired associate recall and source memory, which likely depend on hemispheric interaction, compared to tasks like face recognition and forward digit span which depend less on hemispheric interaction (Lyle et al. 2008b). For example one study (Lyle & Orsborn 2011) required subjects to classify faces as famous or novel with face presentation occurring in the left and right visual fields simultaneously (bilaterally) or in one field only (unilaterally). Famous faces were classified more quickly and accurately during bilateral presentation, reflecting that interhemispheric interaction facilitates famous face recognition, but neither inconsistent handedness nor saccades increased the size of bilateral gain.

Other research shows that bilateral eye movements 1) enhance item recognition by increasing the hit rate and decreasing the false alarm rate, with analysis of remember-know responses showing that eye movements increase remember responses, 2) enhance associative recognition by increasing correct responses to intact pairs and decreasing false alarms to rearranged pairs, and 3) increase correct recall for intrinsic color and extrinsic spatial location context (Parker et al. 2008). More recently, the horizontal saccade-induced retrieval enhancement effect has been extended beyond the visual domain in a study that showed retrieval enhancement in the somatosensory system after alternating left-right tactile stimulation (Nieuwenhuis et al. 2013). In what appears to be the only study of the effects of horizontal

saccadic eye movements on the retrieval of landmark shape and location information, increased recognition sensitivity and decreased response times were reported in a spatial memory test with effects only seen when eye movements preceded episodic memory retrieval but not when they preceded encoding (Brunye et al. 2009). Furthermore, these same authors found that the eye movements were only beneficial with recognition tests demanding a high degree of right and left hemisphere activity and were greatest for strongly right-handed subjects.

Another experiment tested whether saccades enhance retrieval by increasing interaction among brain hemispheres. Subjects were shown arrays of lateralized letters and were asked whether target letters matched either of two probe letters (Lyle & Martin 2010). Matching targets and probes were presented to either the same hemisphere or to separate hemispheres. Interhemispheric interaction was required on the across-hemisphere trials and intrahemispheric processing was required on the same hemisphere trials. Increased match detection accuracy was found on the within-hemisphere trials suggesting saccades enhance intrahemispheric processing but not interhemispheric interaction. The nSR subjects showed higher across-hemisphere accuracy suggesting that an absence of strong right-handedness may reflect greater interhemispheric interaction. A recent comparison of consistent and inconsistent left- and right-handers on associative memory tests after saccade or no-saccade conditions showed that saccades enhanced retrieval for consistent-handers only, but impaired retrieval for inconsistent-handers (Lyle et al. 2012). This important study established that handedness consistency, regardless of left or right direction, is an important factor to consider when studying memory.

Despite the significant clinical and applied implications for the effects of bilateral saccades (Lyle & Jacobs 2010; Propper & Christman 2008; Stickgold 2002), it is surprising that there are so few studies employing neuroscientific methods to measure brain-based correlates of

bilateral saccades. A recent EEG study found scant evidence that eye movements altered interhemispheric coherence or that improvements in recall were correlated with changes in coherence (Samara et al. 2011). Moving beyond the interhemispheric interaction interpretation of bilateral saccade effects is the more recent idea that saccade execution enhances cognition by altering attentional control. Performance on the well-established revised attentional network test (Fan et al. 2009) was assessed after either repetitive bilateral saccades or central fixation (Edlin & Lyle 2013). Saccade execution increased the executive function network, which encompasses attentional control, by decreasing response times to target stimuli in presence of response-incongruent flankers. In this study, the saccade-induced enhancement of attentional control occurred independently of handedness consistency. This raises the possibility that there could be a larger role for top-down attention when memories are more difficult to access, and recent results support that saccade execution has a greater facilitative effect on retrieval when recall and recognition are more difficult (Lyle & Edlin 2015).

There remain several questions about the behavioral effects of repetitive saccades that have not yet been explored. The first is how do repetitive saccades affect memory for complex novel visual stimuli? The second involves how saccades affect stages of memory processing other than retrieval. Most previous investigations have had subjects perform bilateral saccades after encoding but before retrieval. It is not well understood how bilateral saccades affect the encoding of complex novel visual stimuli, nor is it understood how these effects are modulated by handedness. To address these questions, we conducted an exploratory study of the effects of repetitive bilateral saccades and handedness on scene memory. We utilized a variant of the well-known Sternberg working memory paradigm (Sternberg 1966) in which pre-experimentally novel scenes were presented at a fixed load of 5 and held online during a short 6 sec delay

period. After a 10-minute period of awake rest, we tested subjects' long-term recognition memory for scenes previously maintained in short-term working memory. We have shown previously that subjects perform this type of working memory task with scenes as stimuli and can recognize far above chance dozens of scenes shown during the working memory task after a long-term retention interval (Ellmore et al. 2015). Recent source analysis of scalp EEG acquired with this task has implicated a right hemisphere parieto-occipital region that is active when maintaining scenes in working memory, with temporal-spectral delay activity that correlates with subsequent probe memory retrieval (Ellmore et al. 2017).

The specific objective of the present study was to test alternative hypotheses that making repetitive saccades before or after encoding novel scenes in working memory would have either beneficial or detrimental effects on subsequent memory as a function of handedness. A between-subjects design was employed that allowed us to test 1) whether making repetitive saccades *before* working memory encoding modulates subsequent working and long-term memory retrieval as a function of handedness and 2) whether making repetitive saccades *after* working memory encoding and before recognition modulates subsequent long-term recognition as a function of handedness.

Materials and Methods

Subjects

A total of 111 subjects (*M*=20.74, *SD*=3.91, range 18 to 40; 68 females, 43 males) were recruited through the Sona Systems online experimental scheduling system of the City College of New York Psychology Department. Each provided written informed consent, completed a revised Edinburgh Handedness Inventory (EHI) (Williams 2010), and completed study procedures according to a protocol approved by the Institutional Review Board of the City College of New

York Human Research Protection Program. At the end of the study, each subject received extra course credit for a total of one hour of participation.

Experimental Design

All subjects completed a working memory task, followed by a 10-minute period of quiet awake rest, followed lastly by a test of recognition memory. The study utilized a between-subjects design to manipulate eye movements by performance of two different eye tasks (saccade or fixation) executed either before performance of the working memory task (encoding group) or after the working memory task but before a test of recognition memory (recognition group). There was a total of 65 subjects (*M*=20.86, *SD*=3.63, range 18 to 38; 41 females, 24 males) in the encoding group and a total of 46 subjects (*M*=20.56, *SD*=4.30, range 18 to 40; 27 females, 19 males) in the recognition group. Within these groups subjects were assigned to perform either the saccade or fixation task using a pre-determined randomization schedule to minimize experimenter bias.

Apparatus

All subjects completed tasks inside a closed room to minimize auditory and visual distractions. Tasks were programmed in SuperLab 5 (Cedrus Corporation). Tasks were displayed on a 28-inch LED monitor with a refresh rate of 60 Hertz and a screen resolution of 1920 by 1080 pixels. Participants sat 96 cm from the monitor. The experimenter remained in the room for the duration of the experiment but was seated outside of subjects' view. An infrared light emitter and a 220 Hz eye-tracking camera (*ViewPoint EyeTracker®* by Arrington Research, Inc, www.ArringtonResearch.com) were placed in between the monitor and the subject to track the pupil of one eye. Subjects sat on an adjustable stool in the dark and positioned their head in an

Ultra Precision Head Positioner™ (Arrington Research, Inc), a combined chin and forehead rest, to help minimize head movements during the performance of the tasks. The experimenter monitored eye position in real-time during task performance to ensure subjects complied with instructions when required to make saccades or fixation. A black curtain was draped between the monitor and head positioner to minimize visual distractions for the subjects and allow them to focus on the task. Subject responses were collected using a Cedrus RB-740 response pad placed on the table in front of them.

Tasks

Working Memory

Subjects completed 40 trials of a variant of a Sternberg working memory task (Sternberg 1966) used in previous experiments (Ellmore et al. 2015; Ellmore et al. 2017). Each trial consisted of a fixed load of 5 scene stimuli. A total of 220 pre-experimentally novel scenes were shown across the 40 trials of the working memory task. Each was a 24-bit color image of an outdoor scene sampled from the SUN database (Xiao et al. 2010). Scene stimuli were 800 by 600 pixels and were presented at the center of the monitor subtending a visual angle of 16 by 12 degrees. On each trial, five scenes appeared sequentially for 2 sec each, followed by a 6 sec delay period consisting of a white screen with a foveal crosshair, during which subjects were required to keep these scenes in mind, and then a probe scene was displayed for 2 sec (Fig. 1a). Each trial was separated by 5 sec of black screen. Half (20) of the trials contained a positive probe, which was one of the five scenes presented before the delay period. The other 20 trials contained a negative probe, a new scene not previously shown in the set of scenes presented before the delay period. Positive and negative probe trials were randomly distributed across the set of 40 working memory trials. Upon the presentation of the probe in each working memory trial, subjects were

instructed to press a green button on the response pad if the probe scene matched one of the scenes presented in the set of 5 scenes shown before the 6 sec delay period; subjects were instructed to press a red button if the probe scene did not match one of the scenes presented in the set of 5 scenes shown before the delay. Before performing the working memory task, subjects were given a 5-minute demonstration task with different stimuli (animals) to ensure that they understood task instructions before the actual working memory task began.

Recognition Memory

After completing the working memory task, subjects were allowed to disengage from the head restraint and rest quietly in the experiment room for ten minutes. At the end of this ten-minute retention interval, subjects completed a task of recognition memory (Fig. 1b) that included a total of 200 scenes. One hundred of these scenes were randomly sampled from the sets of scenes presented before the delay in each of the 40 previous working memory trials. The other 100 scenes were completely new scenes sampled randomly from the SUN database. The 100 old and 100 new scenes were presented one at a time for 2 sec each in random order as individual trials. A 2 sec black screen separated each trial. For each trial, subjects were instructed to press the green button on the response pad to indicate that they recognized having previously viewed the scene; subjects were instructed to press the red button to indicate that they did not recognize the scene.

[insert Figure 1 here]

Eye Tasks

The main experimental manipulation required subjects to perform one of two eye tasks (saccade or fixation) either before the working memory task or before the recognition memory task. The saccade task required subjects to make deliberate repetitive horizontal saccades for 30 sec. Each horizontal saccade was cued by the appearance of a white disc on a black background. Each dot appeared for 500 ms and alternated its position between the right and left sides of the screen for a total of 30 sec (Fig. 2a). The fixation task required that subjects fixate a single disc (same size as the white dot in the saccade task) that was stationary at the center of the screen. The disc appeared on a black background for 30 sec and cycled through 6 colors (red, blue, yellow, green, pink, and purple), with each color presented individually for 500 ms (Fig. 2b). To keep subjects' attention on the different eye tasks, subjects were instructed to count covertly the number of times the disc alternated positions between the left and right screen positions; during the fixation task, subjects were instructed to count covertly the number of times the disc changed colors. The number of disc alternations and color changes was equal.

[insert Figure 2 here]

Analysis

The analysis began with the computation of a laterality quotient (LQ) from the responses to the eight questions of the EHI-R (Williams 2010). This inventory asked the subject to indicate which hand they use to complete various everyday activities (e.g., striking a match, using a computer mouse). Participants indicated their handedness preference for each item by checking off one of the following response options (with corresponding point values): "always right" (50) "usually right" (25), "no preference" (0), "usually left" (-25), and "always left (-50). The LQ was then calculated by tallying the point values for all eight items and dividing the total score by four,

resulting in LQ scores that ranged from +100 (right handed) to -100 (left handed). The next step in the analysis was to compute for each subject performance accuracy as percentage correct for the 40 trials of the working memory task and separately for the 200 trials of the recognition memory task. Regression and statistical analyses relating subjects' working memory and recognition memory task performance accuracy to LQ for eye tasks performed before each of the memory tasks were executed with GraphPad Prism version 7.0, GraphPad Software, La Jolla California USA, www.graphpad.com. Statistical analysis of the regression slopes was done to quantify differences in performance as a function of laterality and eye task timing; statistical analysis of regression intercepts (elevations) was done to quantify differences in overall performance as a function of eye task timing. The raw data input to these analyses is provided in the Supplemental File.

Results

Working Memory Performance

Analysis of Regression Slopes

Linear regression was used to quantify the relationship between working memory performance and laterality as a function of the eye task. The statistical test assessed whether the slope of the regression equation differed significantly from zero.

When fixation occurred before the working memory task, working memory percent correct accuracy increased non-significantly as a function of laterality (slope=0.03098 ± 0.03765 SE, $F_{(1,31)}$= 0.6774, p=0.4168, Fig 3 blue line and blue circles).

When saccades occurred before the working memory task, working memory percent correct accuracy increased significantly as a function of laterality (slope=0.1029 ± 0.04365 SE, $F_{(1,30)}$= 5.56, p=0.0251, Fig 3 red line and red triangles).

The subjects who performed fixation and saccades after the working memory task serve as a control group, as one would expect no influence of these eye tasks on working memory performance if they occur after the working memory task.

Consistent with this prediction, when fixation occurred after the working memory task, working memory percent correct accuracy increased non-significantly as a function of laterality (slope= 0.02973 ± 0.02872 SE, $F_{(1,21)}$=1.072, p=0.3123, Fig 3 grey line and grey boxes).

When saccades occurred after the working memory task, working memory percent correct accuracy increased non-significantly as a function of laterality (slope= 0.005429 ± 0.02251 SE, $F_{(1,21)}$=0.05818, p=0.8117, Fig 3 cyan line and cyan stars).

Analysis of Regression Intercepts

While analysis of regression slopes indicates change in performance as a function of laterality and eye task timing, evaluation of the regression intercepts (i.e., elevations) indicates whether the overall levels of performance differ. The four intercepts of Fig 3 were significantly non-zero ($F_{(3,106)}$=6.164, p=0.0007) with best working memory performance when saccades were made after the working memory task (93.28% ± 1.844 SE, 95% C.I.: 89.45 to 97.12) and worst working memory performance when saccades were made before the working memory task (77.79% ± 3.84, 95% C.I.: 69.95 to 85.64%).

[insert Figure 3 here]

Recognition Performance

Analysis of Regression Slopes

Linear regression was also used to quantify the relationship between recognition memory performance and laterality as a function of the eye task. The statistical test assessed whether the slope of the regression equation differed significantly from zero.

When fixation occurred before the working memory task, later recognition percent correct accuracy increased non-significantly as a function of laterality (slope=0.03746 ± 0.04449 SE, $F_{(1,31)}$=0.7091, p=0.4062, Fig 4 blue line and blue circles)

When saccades occurred before the working memory task, later recognition percent correct accuracy increased non-significantly as a function of laterality (slope=0.06502 ± 0.04615 SE, $F_{(1,30)}$=1.985, p=0.1691, Fig 4 red line and red triangles).

When fixation occurred after the working memory task and before the recognition memory task, recognition percent correct accuracy increased significantly as a function of laterality (slope=0.08738 ± 0.03277 SE, $F_{(1,21)}$=7.111, p=0.0144, Fig 4 grey line and grey boxes).

When saccades occurred after the working memory task and before the recognition memory task, recognition percent correct accuracy increased non-significantly as a function of laterality (slope=0.03398 ± 0.03797 SE, $F_{(1,21)}$=0.8009, p=0.3810, Fig 4 cyan line and cyan stars).

Analysis of Regression Intercepts

Analysis of regression intercepts was conducted to determine whether the overall level of recognition performance differed as a function of the eye task timing. The four intercepts of Fig 4 were significantly non-zero ($F_{(3,106)}$=4.721, p=0.0039) with best recognition memory performance in the condition of fixation occurring before the working memory task (70.08% ±

3.899 SE, 95% C.I.: 62.12 to 78.03%, Fig 4 blue line and blue circles) and the lowest recognition memory performance in the condition of saccades occurring before the working memory task (60.67% ± 4.06, 95% C.I.: 52.38 to 68.96%, Fig 4 red line and red triangles). Recognition performance during the condition when saccades were made before the recognition memory task (70.06% ± 3.111, 95% C.I.: 63.59 to 76.53, Fig 4 cyan line and cyan stars) was greater than performance during the condition of fixation before the recognition memory task (64.75% ± 2.819, 95% C.I.: 58.38 to 70.62%, Fig 4 grey line and grey boxes), but the difference was not significantly different (two-tailed $t_{(44)}$=1.2648, p=0.2126, Cohen's d=0.3729). The level of recognition performance in the condition when saccades were made before the recognition task was nearly identical to performance after the condition of fixation before the working memory task (70.08% ± 3.899, 95% C.I.: 62.12 to 78.03%, Fig 4 blue line and blue circles). These virtually identical levels of performance make the blue and cyan lines of Fig 4 appear to overlap.

[insert Figure 4 here]

Discussion

Humans have a remarkable ability to remember a large number of scenes and other complex visual stimuli even when given only a short period of time to encode them (Brown & Scott 1971; Shepard 1967; Standing 1973; Standing et al. 1970). Scene memory is also an important component of episodic autobiographical memory. Normal as well as disordered reminiscence often includes vivid mental recollection of scenes where past events took place (Brewin 2014; Burgess et al. 2002). In addition, recognition of a previously encountered scene in, for example an old photograph, is often quick, highly accurate, and can trigger episodic memory retrieval. Therefore, it is important to understand how scene memory is influenced by multifactorial traits

like handedness and by simple behavioral manipulations (e.g., bilateral saccades) shown previously to influence episodic memory retrieval.

The present study was conducted to understand how both short- and long-term scene memory is modulated by handedness and by bilateral horizontal saccades made before scene encoding and recognition. Previous studies have shown that strongly right-handed and consistently-handed benefit most from bilateral saccades (Chu et al. 2012; Lyle et al. 2012; Lyle & Orsborn 2011; Prichard & Christman 2017; Propper et al. 2017), but these studies focused on mostly verbal aspects of memory retrieval and had subjects make the saccades after encoding and before retrieval. The two novel aspects of the present study include, first, the focus on visual scene memory and, second, having different groups of subjects make saccades before encoding as well as before recognition.

There are two main findings of the present study. First, when saccades were made *before* encoding scenes in working memory, performance covaried significantly as a function of handedness, with right-handers (+LQ) performing better than left-handers (-LQ). Performance did not correlate significantly as a function of handedness when either the saccade or fixation condition came *after* the scene working memory task. The second result is that there was no apparent benefit as a function of handedness to making saccades before scene recognition. If anything, fixation before recognition was more beneficial to the right-handed subjects. Recognition performance in the group of subjects who made saccades before recognition increased non-significantly as a function of laterality, while recognition performance in the group of subjects who fixated before recognition did increase significantly as a function of laterality, with better performance as laterality quotient increased. Additionally, the subjects who

made saccades before the working memory task performed the poorest during a subsequent test of recognition memory.

Why would making saccades before encoding scenes in working memory result in better performance for strongly right-handed (+LQ) individuals? There is some neuroimaging evidence suggesting that scene encoding may be right lateralized in the brain (Brewer et al. 1998), but that the lateralization of encoding processes is affected by the verbalizability of the visual stimuli (Golby et al. 2001). Our recent source analysis of working memory delay period EEG implicates right parieto-occipital focus of activity that covaries positively as a function of performance. Due to limited sample size in that study, it's not possible to draw conclusions about whether mixed- or left-handers have a more symmetrical pattern of activity that correlates with worse performance, but a tentative explanation that strongly right-handed individuals have an advantage over mixed- and left-handers during short-term scene encoding processes is worth future investigation.

A growing number of studies have demonstrated saccade induced benefits specifically on recognition (Brunye et al. 2009; Lyle & Orsborn 2011; Parker & Dagnall 2007; Parker et al. 2008). In the present study, when bilateral saccades were made before scene recognition but not before scene working memory, we found a small but not statistically significant increase in performance relative to simple fixation. Performance was best for consistent right-handers, which includes those who have an LQ near +100 in Fig 3 and Fig 4 because they indicate they perform all tasks "always" with their right hand. A finding reported recently is that beneficial effects of pre-task saccades occur in consistent-handed individuals (Lyle et al. 2012), those who perform most actions consistently with either their right or their left hand. If this pattern was present in our data, we might see an inverted U-shaped distribution of data points in Fig 4 with

lower baseline performance for both -LQ (consistent left-handers) and +LQ (consistent right-handers) relative to mixed-handers. The ends of the inverted U-shaped might then be shifted up and/or flattened relative to fixation following saccades. Benefits are not seen in Fig 4 for both left and right consistent-handed individuals. The simplest parsimonious explanation for this lack of benefit of pre-task bilateral saccades is that scene memory is not modulated by increased interhemispheric interaction or attentional control in consistent handers. Rather, it appears that only consistent right-handers are better able to deal with the detrimental effects of bilateral saccades made before scene working memory (as indicated by the significant slope of the red line in Fig 3). Consistent right-handers also have better recognition memory in general because when they fixate before the recognition test they perform better (as indicated by the significant slope of the grey line in Fig 4).

The result of the present study represents a novel amendment to the important findings of previous studies showing better overall memory in inconsistent handers and beneficial effects of saccades in consistent-handers. Those findings have replicated in more recent studies (Chu et al. 2012; Parker et al. 2017; Prichard & Christman 2017; Propper et al. 2017). Many of the tasks used to assess episodic and/or autobiographical memories operate in the verbal domain. In the present study, subjects might default to a familiarity-based and highly-visual implicit “know” strategy rather than rely on a verbal episodic-like type of remembering. Many recognition tasks shown to benefit from bilateral saccades rely on word lists for memoranda (Parker & Dagnall 2007; Propper et al. 2017; Samara et al. 2011), content that is much different from the novel scene stimuli used in the present study. However, it is also worth noting that the beneficial effects of saccades do not manifest in implicit memory tasks even when those tasks involve words. Christman et al. (Christman et al. 2003) had participants study a short word list and then

tested them on a word-stem completion task, consisting of an equal mix of new and previously seen words. The findings showed that neither the eye movement nor fixation conditions elicited significant improvement, which indicates that saccades do not enhance implicit forms of memory that are likely reflective of intra-hemispheric activity (Christman et al. 2003).

One recent study of saccade related enhancement is notable for its use of visual-spatial stimuli and an exploration of whether effects could be obtained when eye movements were made before encoding. Brunye et al. (Brunye et al. 2009) used an encoding task that lasted a total of only 120 seconds and comprised a small number of just four stimuli, all aerial maps that were acquired from satellite pictures. On the basis of the HERA model (Nyberg et al. 1996), Brunye et al. theorized that eye movements would not benefit encoding due to unilateral activity, and but instead, saccades should only assist retrieval due to processes that involve bilateral activations.

The present study has some limitations. The working memory task utilized a relatively high load of 5 and required a large number of scenes to be memorized and later discriminated in the recognition test. This increased the overall difficulty of the memory tasks with performance during the working memory task nowhere near ceiling. Prior studies involving saccade manipulation have used relatively smaller numbers of items for encoding and have frequently required participants to view stimuli passively during learning, rather than engage them in working memory. Both the limited number of items and the nature of the encoding tasks used in previous research require a lower degree of cognitive processing compared to the high-load working memory and recognition tasks used here. Both tasks far exceeded the numbers of stimuli used in prior studies and could have potentially decreased overall encoding and consolidation into long-term memory given the short 10-minute interval separating working memory and recognition testing. While our sample included 111 participants, the study design

relied on between-subjects manipulation of conditions, which has a tendency to increase variance and decrease statistical power relative to a within-subject design.

Conclusion

We found that the performance of repetitive horizontal saccades before tasks of scene working memory and recognition interacts with handedness to modulate memory performance. Making saccades before encoding scenes in working memory has detrimental effects on both short- and long-term scene memory, most notably for those who are not strongly right-handed. Moreover, saccade execution before scene recognition does not appear to benefit recognition accuracy appreciably. The lack of robust enhancement could be because optimal scene processing is lateralized and does not benefit from increased interhemispheric interaction.

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Competing interests

The authors declare that no competing interests exist.

Figure Legends

Figure 1. Example Scene Working and Recognition Memory Trials. Each working memory trial (a) consisted of an encoding phase of five scene stimuli, each presented for 2 sec, followed by a 6 sec delay period of crosshair fixation and a 2 sec presentation of either a positive probe (scene from the encoding set) or a negative probe (new scene). On each trial, there was a 50% chance of a positive probe appearing. Each recognition memory trial (b) consisted of alternating presentation of a scene stimuli for 2 sec followed by a black screen for 2 sec. Old and new scenes were randomly intermixed. Subjects were instructed to press a green button if they had seen a stimulus in any of the previous working memory trials and a red button if they had never seen the stimulus before.

Figure 2. The Saccade and Fixation Eye Tasks. The saccade task (top left) required subjects to alternate for 30 seconds looking toward the left and right as a white disc moved back and forth across the screen. Example eye traces (top right) show saccadic movements with large periodic deviations in the x position (horizontal) trace with a stable y position (vertical) trace. The fixation task (bottom left) required subjects to maintain fixation on a center disc as it changed color. Example eye-tracking traces (bottom right) show fixation, with minimal deviations in the x (horizontal) and y position (vertical) traces.

Figure 3. Scene Working Memory Performance as a Function of Laterality and Eye Task Timing. There was a significant relationship in working memory performance as a function of laterality when saccades were made before the working memory task (non-zero slope of 0.1029 ± 0.04365 SE, $F_{(1,30)}$= 5.56, p=0.0251, red line and red triangles). Overall mean performance

among conditions differed (non-zero intercepts, $F_{(3,106)}$=6.164, p=0.0007) with lowest working memory performance obtained when saccades were made before the working memory task (77.79% ± 3.84, 95% C.I.: 69.95 to 85.64%) and best performance when saccades were made after the working memory task (93.28% ± 1.844 SE, 95% C.I.: 89.45 to 97.12).

Figure 4. Scene Recognition Memory Performance as a Function of Laterality and Eye Task Timing. There was a significant relationship in recognition performance as a function of laterality during the condition of fixation before the recognition memory task (non-zero slope=0.08738 ± 0.03277 SE, $F_{(1,21)}$=7.111, p=0.0144, grey line and grey boxes). Overall mean performance among the conditions differed ($F_{(3,106)}$=4.721, p=0.0039) with best recognition memory performance during the condition of fixation before the working memory task (70.08% ± 3.899 SE, 95% C.I.: 62.12 to 78.03, blue line and blue circles) and lowest recognition memory performance during the condition when saccades were made before the working memory task (60.67% ± 4.06, 95% C.I.: 52.38 to 68.96, red line and red triangles).

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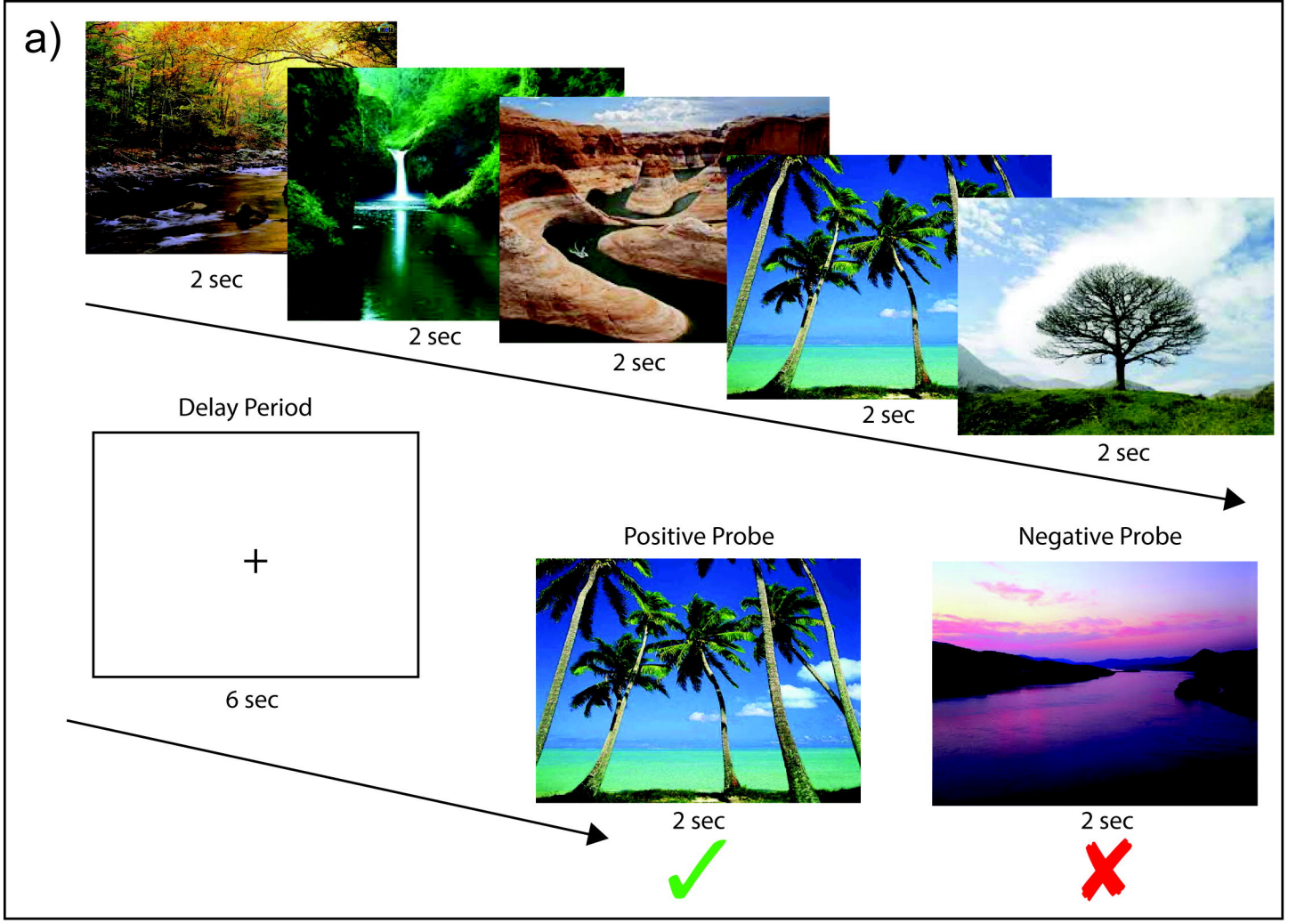
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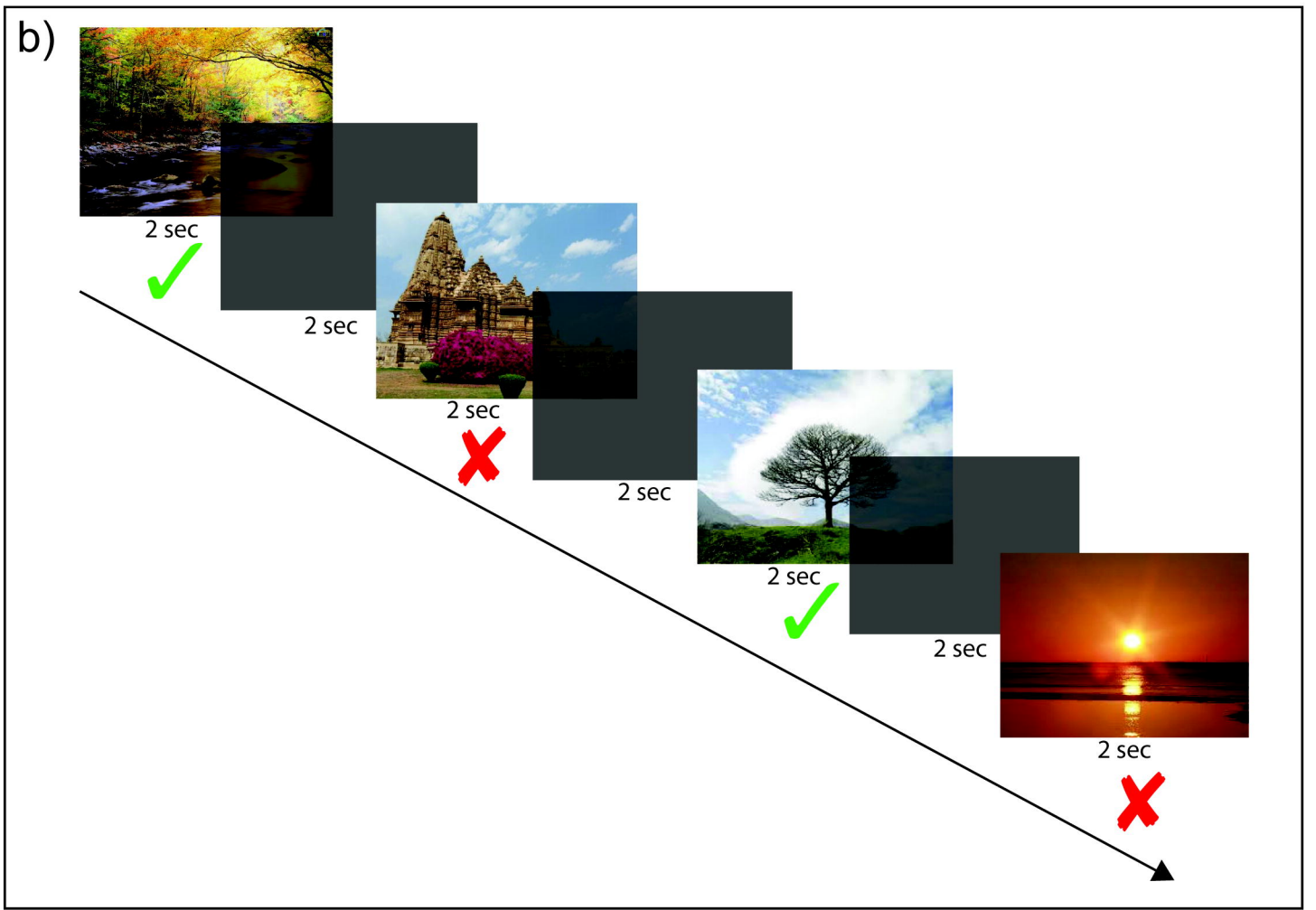
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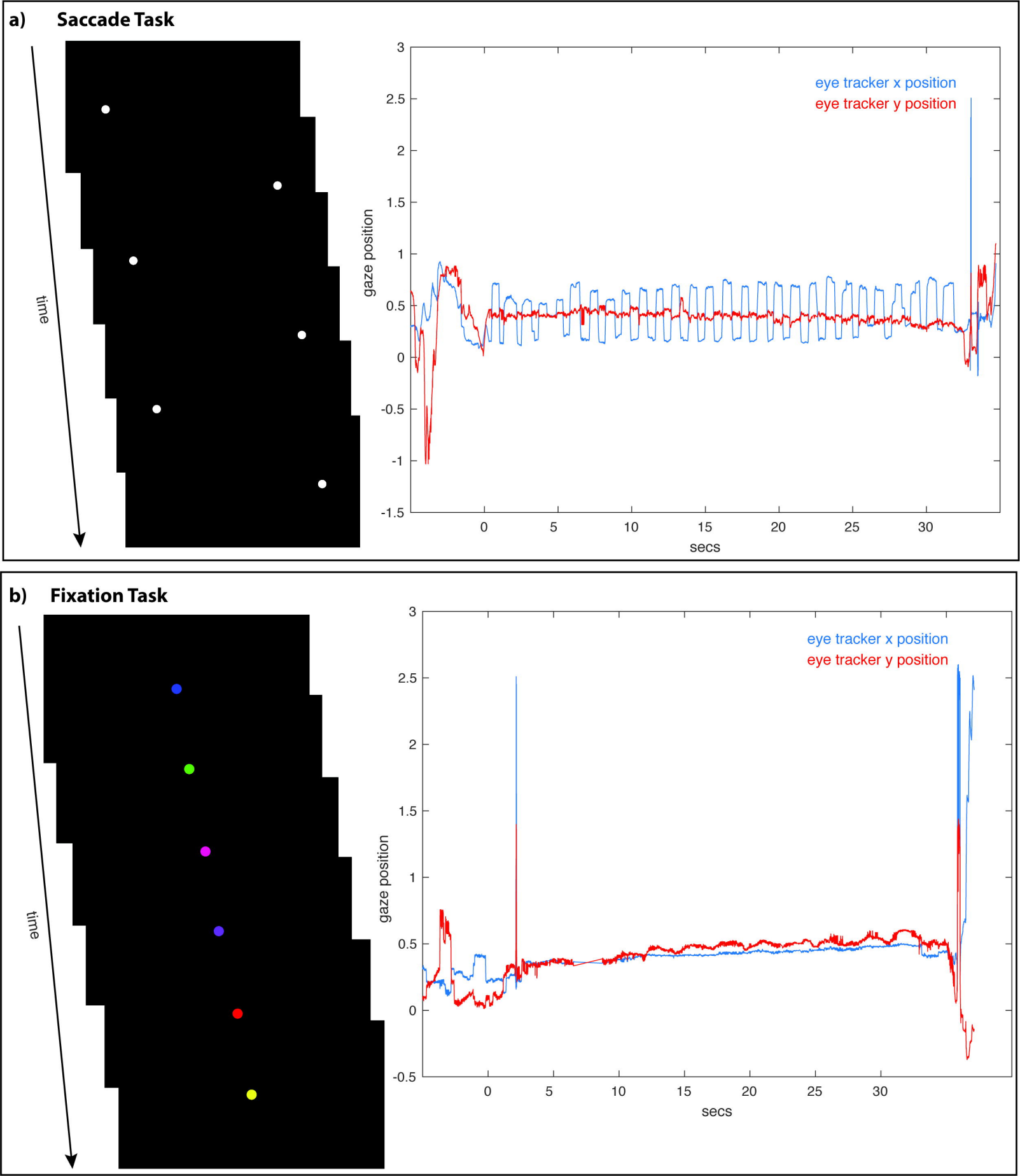
a)
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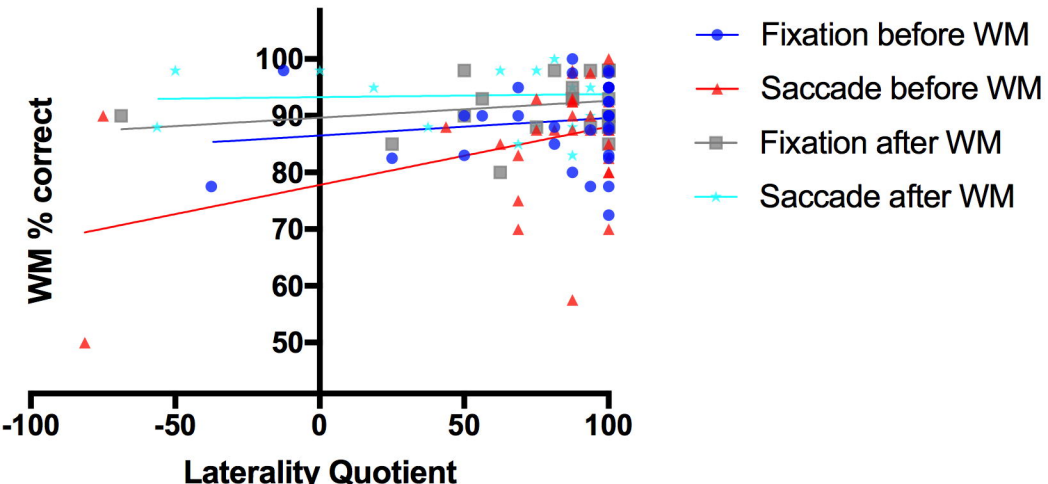
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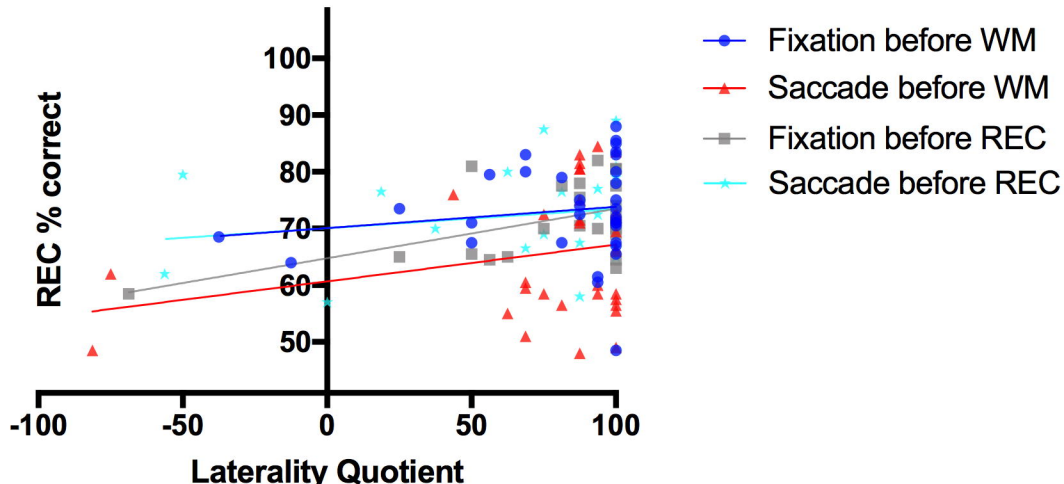
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