



Cortical control of eye movements in natural reading: Evidence from MVPA

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Abstract

Language comprehension during reading requires fine-grained management of saccadic eye movements. A critical question, therefore, is how the brain controls eye movements in reading. Neural correlates of simple eye movements have been found in multiple cortical regions, but little is known about how this network operates in reading. To investigate this question in the present study, participants were presented with normal text, pseudo-word text, and consonant string text in a magnetic resonance imaging (MRI) scanner with eyetracking. Participants read naturally in the normal text condition and moved their eyes “as if they were reading” in the other conditions. Multi-voxel pattern analysis was used to analyze the fMRI signal in the oculomotor network. We found that activation patterns in a subset of network regions differentiated between stimulus types. These results suggest that the oculomotor network reflects more than simple saccade generation and are consistent with the hypothesis that specific network areas interface with cognitive systems.

Keywords Reading · Eye movement · Oculomotor · Mvpa

Introduction

Reading involves finely controlled saccadic eye movements (Rayner 1998, 2009a; Clifton et al. 2016). These eye movements are executed in the service of and to facilitate the transfer of information from the written page to areas of the brain that underlie language comprehension. Therefore, a critical question for researchers and clinicians interested in language processing during reading is how the brain controls these eye movements, and specifically how cognitive processing related to language comprehension interacts with the cortical oculomotor network.

Skilled readers move their eyes in a highly stereotypical manner when they read connected text for comprehension (Huey 1908/1968; Javal 1878; Rayner 1978, 1998, 2009a, b). Specifically, readers direct their eyes through text via a series

of quick movements (saccades) punctuated by brief pauses (fixations). Visual information useful for language processing is acquired from the text at and near the fovea during the fixations, which typically last around 225 ms on average. Saccades then quickly move the eyes to a new location in the text. In English, saccadic eye movements typically shift the eyes from left to right from word to word, though the eyes do regress around 20% of the time on average to earlier sections of text. Most words are fixated at least once, with some (e.g., longer, lower frequency, and less predictable) words fixated more than once and other (e.g., shorter, higher frequency, and more predictable) words not fixated at all.

The observation that eye movements in reading appear systematic and stereotypical has led to the proposal that they are for the most part under the control of a generic reading program (e.g., O’Regan 1992; Vitu et al. 1995; see also Nuttman et al. 2007). On this view, differences in eye movement behavior as a function of text difficulty or other general text characteristics can be explained by changes in general strategies and tactics such as slower reading speeds and more regressions that affect at a global level the parameters of the generic program. Evidence for this strategy-tactics view comes from studies showing that in pseudo-reading tasks in which words are replaced by non-words, many aspects of eye movement behavior, including specific behaviors such as

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fixation and skipping, within-word refixations, and between-word regressions, are very similar to those observed in normal reading (Vitu et al. 1995; Nuthmann et al. 2007; Henderson and Luke 2012; Luke and Henderson 2013).

On the other hand, many aspects of eye movements in reading have been shown to be under some degree of direct real-time control by current perceptual, linguistic, and cognitive analysis of the text (what we refer to generically as cognitive control). For example, when the eyes fixate a lower frequency word, the duration of that fixation tends to be longer and the likelihood that the word will be refixated also increases (Rayner and Fischer 1996). Similarly, when the eyes fixate a word that is more difficult to integrate with the current syntactic analysis of its sentence, the duration of that fixation increases and the next saccade is more likely to regress to an earlier point in the sentence (see Clifton et al. 2016, for a recent review of these and many related effects). However, whether these manifestations of cognitive control are the primary driver of eye movements or are subtle fine-tuning around a set of general strategic parameters is still a matter of debate (Engbert et al. 2005; Reichle et al. 1998, 2003).

Most of what we know about eye movement control in reading has been learned from eyetracking studies of natural reading. On the other hand, most of what is known about the cortical control of eye movements has come from experimental paradigms that use oculomotor tasks requiring a single saccade, such as pro-saccade, anti-saccade, and single memory-guided saccade tasks (Guitton et al. 1985; Pierrot-Deseilligny et al. 1993, 2004; Everling and Fischer 1998; Jamadar et al. 2013; Munoz and Everling 2004; Hutton 2008; McDowell et al. 2008). An important open question, therefore, is how eye movements during reading are controlled by the brain. The research using single-step oculomotor tasks is important in that it allows for very tight experimental control of eye movements. Also, these paradigms are suitable for use in different populations of humans as well as non-human primates, allowing for development of detailed neurobiological models. However, it is largely unknown whether the network identified in this research is also engaged in eye movement control during reading, where complex sequences of finely controlled saccadic eye movements are necessary.

Based on single-step oculomotor tasks, a cortical eye movement control network has been identified comprising the lateral frontal eye fields (IFEf) located bilaterally, medial frontal eye fields (mFEf) located bilaterally, the supplementary eye field (SEf) located bilaterally, and the intraparietal sulci (IPS) located bilaterally (see above references). Recent work suggests that this network extends to eye movement control in more complex tasks. Hillen et al. (2013) observed activation of FEf, SEf and IPS from sequences of eye movements in a target-search task through texts and pseudo-texts,

suggesting that this network is active during sequential scanning. Choi et al. (2014) similarly found FEf, SEf and IPS activation associated with the control of eye movements in a univariate fMRI analysis of reading and pseudo-reading conditions.

The division of the frontal eye fields into lateral and medial regions is based on different functional properties (Ettinger et al. 2008; Grosbras et al. 2001; Jamadar et al. 2013; McDowell et al. 2008, 2005). For example, in reviewing the literature, McDowell et al. (2008) proposed that mFEf is more involved in volitional saccadic eye movements whereas IFEf is more involved in reflexive saccadic eye movements. On the other hand, based on their meta-analysis of pro- and anti-saccade studies, Jamadar et al. (2013) suggested that IFEf may be involved in both reflexive and volitional eye movements whereas mFEf may be solely related to reflexive eye movements. This prior work suggests that different regions of FEf may play differential functional roles in eye movement control. However, the specific nature of the functional roles of mFEf and IFEf has not yet been fully determined, and their roles in reading has not been established.

In a recent study by Choi and Henderson (2015), functional magnetic resonance imaging (fMRI) activation during reading and scene viewing was compared. Different regions of the oculomotor network activated to these two natural viewing tasks. Specifically, the mFEf and IFEf showed different activation for eye movements across scenes versus eye movements in text, respectively (Choi and Henderson 2015). Given that IFEf activation was greater in reading, IFEf may also be more likely than mFEf to differentiate between eye movements during natural reading compared to pseudo-reading. On the other hand, eye movements in reading and scene viewing are quite different in their specifics, whereas eye movements in reading and pseudo-reading produce quite similar patterns of eye movements (Henderson et al. 2013, 2014, 2015; Henderson and Luke 2012; Luke and Henderson 2013; Nuthmann et al. 2007; Rayner and Fischer 1996; Vitu et al. 1995). Of specific interest in the present study is whether the cortical eye movement network distinguishes between eye movements executed in the service of meaningful language comprehension where language-based cognitive control is possible, and similar scanning eye movements executed over meaningless pseudo-text.

The identified eight regions of the eye movement network provide us with the most likely place to look for effects of eye movement control related to reading (Fig. 1). Here we specifically asked whether activity patterns in these regions are different for reading compared to non-reading tasks with similar complex sequences of saccadic eye movements. That is, do some (or all) of these regions respond the same or differently to eye movements through meaningful text versus eye movements through non-meaningful pseudo-text with

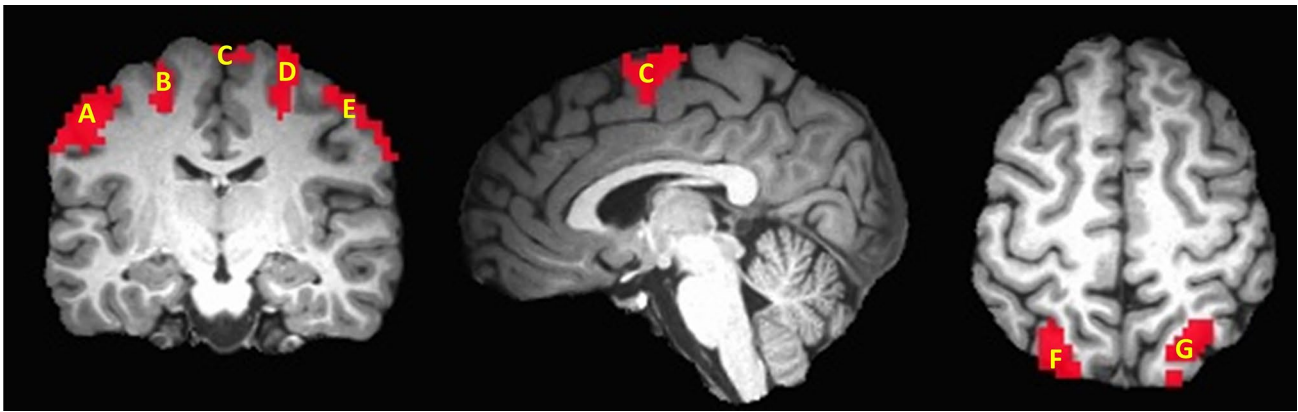


Fig. 1 Individual Regions of Interest (ROIs) from the oculomotor network from a representative subject. A, left lateral frontal eye fields (llFEF); B, left medial frontal eye fields (lmFEF); C, supplementary

eye fields (SEF); D, right medial frontal eye fields (rmFEF); E, right lateral frontal eye fields (rlFEF); F, left intraparietal sulcus (lIPS), and G, right intraparietal sulcus (rIPS)

similar spatial structure? To address this question, we used fMRI and region of interest (ROI)-based multi-voxel pattern analysis (MVPA) to investigate whether areas of the oculomotor network can differentiate between natural reading and two pseudo-reading control conditions, pseudo-word and consonant string reading (see Fig. 2 for examples of stimuli; Choi et al. 2014). In the pseudo-word condition, words in texts were replaced by pronounceable non-words. In the consonant string condition, words were replaced by unpronounceable random consonant strings.

As mentioned above, there is considerable evidence that eye movement dynamics are quite similar in natural reading and pseudo-reading conditions. Therefore, we hypothesize that if the oculomotor network supports sequential saccade generation regardless of cognitive control related to language comprehension, then it should not be possible to classify the task (reading versus the two pseudo-reading conditions) from patterns of activation in these regions using MVPA. On the other hand, we hypothesize that if the oculomotor network reflects differences in eye movement control based on when they are and are not executed in the service of ongoing cognitive processing related to language comprehension, then it should be possible to classify natural reading versus the two pseudo-reading conditions with MVPA. That is, if the control network differentiates between eye movements under the guidance of cognitive processes related to language comprehension and oculomotor control devoid of cognition, then activation patterns should be different for the natural reading versus pseudo-reading conditions. Furthermore, if the critical distinction is between cognitive and non-cognitive control, then there would be no reason to expect activation patterns to differ in the two pseudo-reading conditions. Of course, the network may not be uniform in its responses; different regions in the network could encode cognitive control to greater or lesser degrees. For example,

given that FEF is often more active in tasks like anti-saccade that specifically require cognitive control, cognitive control theories would predict that this area should specifically differentiate between reading and pseudo-reading conditions.

In summary, we investigated the role of the cortical eye movement control network using ROI-based MVPA in reading and pseudo-reading conditions. In the experiment, subjects read 22 paragraphs, and moved their eyes through 22 matched pronounceable pseudo-word paragraphs and 22 random consonant string paragraphs. Subjects performed these tasks in an MRI scanner while blood oxygenation

Normal Text:

The super double cheeseburger arrives at your table. You stare at the dripping burger and the tantalizingly crisp, golden French fries. The only thing that's missing is the ketchup, so you grab the bottle and prepare to slather your entire plate. You unscrew the cap, but what's this? Nothing is coming out!

Pseudoword Text:

Voft yimpse rin fou scrowls zo wuv mev flig ji h stoast. Sma Twisque kiz phroughnths ext bince vern zi voc shraunched weaf, ol pash phlalped. Wem, elts ec j shreached vomb ain oc snive stas sant ap ac, onk Scryths sipe naked pu grur bleighndged. Ift waffs phlirled tadds. Stum Pleaned, koe shauns lal whounge fu dwo jes um doaf jup zawk.

Consonant String Text:

Ccmq mn, thq Xmpqrcr crdqrd. Xvqn xs thqq behqd, thq the sccsndrqls prqtqndqd te bq heldmng lxrqg rell cf fxbrcm. Hqrq mt ms qcsr Hmghnqss, thq rqsstl cf csr lxbcsr, thq sccsndrqls sxmd. Wq hxvq herkqd nmght xnd dxq bst, xt lxst, thq mcest bqxstmfsl fxbrcm mn thq herld ms raxdq fcr qes. Lcck xt thq eclers xnd fqqj hch fmmq mt ms.

Fig. 2 Examples of stimuli used in the experiment

level-dependent (BOLD) responses and eye movements were recorded.

Materials and methods

Participants

Thirty-nine individuals (12 male, mean age of 21.59) participated in this study. All participants were recruited from the University of South Carolina student population and surrounding area. All participants reported normal or corrected to normal visual acuity and were right handed. All participants gave written, informed consent, were screened for MRI safety, and received compensation in the form of course credit or a cash reward for their participation. All procedures were approved by the University of South Carolina Institutional Review Board and conducted in accordance with the 1964 Declaration of Helsinki. Data from a subset of words in the reading condition, a subset of subjects and words in the reading condition, and a subset of subjects and all reading conditions were reported in Henderson et al. (2016), in Experiment 1 of Desai et al. (2016), and in Choi et al. (2014), respectively.

Materials and design

Materials consisted of 66 unique paragraphs that contained between 49 and 66 words with 22 paragraphs in each of three condition types (Fig. 2). The first condition was normal text and consisted of 11 paragraphs modified from the short story *The Emperor's New Clothes* by Hans Christian Andersen, and 11 paragraphs modified from a practice test for the Nelson Denny reading assessment. The second condition was pseudo-word text paragraphs made up of pseudo-words generated from the ARC Nonword Database (http://www.psy.uwa.edu.au/MRCDataBase/uwa_mrc.htm). These pseudo-words were pronounceable but lacked meaning. The third condition contained consonant string text created by replacing letters in words with randomly chosen consonants. Both the pseudo-word and consonant string text conditions were matched with the normal text condition on word length and number of words per paragraph (see Choi et al. 2014, for more details on materials).

Each paragraph condition was intermixed such that two functional runs in the MRI scanner showed all the stimuli (half of the trials for each condition were shown in each run). Eleven scene images were also shown in each run for an analysis not relevant here. Every four trials contained one of each of the four conditions, with the order of presentation of those four trials randomized. This was done so that the normal text trials were in the correct sequential order to tell the story over the run (e.g., *The Emperor's New Clothes* and

the Nelson Denny reading assessment story). Participants were told to read each normal text paragraph naturally to themselves and to scan through the pseudo-word text and consonant string text conditions “as if they were reading” (Luke and Henderson 2013, 2016). Prior studies have shown that this latter instruction leads to eye movement behavior that is very similar to that observed during natural reading and includes the basic oculomotor effects observed in reading including progressions and regressions, optimal viewing position effects, word refixations, string length effects, and so on (Vitu et al. 1995; Rayner and Fischer 1996; Nuthmann et al. 2007; Henderson and Luke 2012; Luke and Henderson 2013; Henderson et al. 2013, 2014, 2015). During the experimental fMRI scan runs, each trial was shown for 12 s with 6 s of a fixation cross between trials. 44 trials were shown in each run, with 6 s of fixation at the beginning and end of the run making each run about 14 min in length.

Apparatus

Stimuli were presented using an Avotec Silent Vision 6011 projector in its native resolution (1024 × 768) at a refresh rate of 60 Hz. Text was displayed in Courier New font with 4.76 characters subtending 1° of visual angle. Eye movements were recorded from the right eye via an SR Research Eyelink 1000 long-range MRI eyetracker at a sampling rate of 1000 Hz.

Eye movement data acquisition

Eye movements were tracked during each trial to ensure participants were reading normally and assess any eye movement differences between our reading conditions. A 13-point calibration procedure was administered in the scanner before each functional run. Successful calibration required an average error of less than 0.49° and a maximum error of less than 0.99°.

fMRI data acquisition

All MRI data were acquired with a Siemens Medical Systems 3T Trio scanner. A 3D magnetization-prepared rapid acquisition gradient echo T-1 weighted anatomical scan was acquired for each subject with the following parameters: TR = 2530 ms, TE1 = 1.74 ms, TE2 = 3.6 ms, TE3 = 5.46 ms, TE4 = 7.32 ms, flip angle = 7°, voxel size = 1 mm. For experimental scan runs, the BOLD response was recorded using an echo-planar imaging (EPI) sequence with the following parameters: TR = 1850 ms, TE = 30 ms, flip angle = 75°, FOV = 208 mm, voxel size = 3.3 × 3.3 × 3 mm. A mirror was placed on the head coil for participants to view the stimuli, which were displayed at a resolution of 1024 × 768 pixels

Table 1 ROI information

ROI	X	Y	Z	Number of participants
lIFEF	-43 ± 6.3	-2.6 ± 5.5	44 ± 7.3	24
rIFEF	44.7 ± 5.8	1.7 ± 5.7	45.9 ± 7.2	27
lmFEF	-27 ± 5	2.5 ± 8.1	50.6 ± 8	28
rmFEF	25.8 ± 4.6	2.1 ± 8.5	53.5 ± 6.5	20
lIPS	-24.5 ± 3.5	64.2 ± 5	43 ± 3.4	34
rIPS	20.9 ± 4.6	67.2 ± 9.7	40 ± 7.3	31
SEF	1.7 ± 3.6	-2 ± 6.6	57.7 ± 5.6	35

This table shows the averaged locations and standard deviation of each individually localized ROI as well as the number of participants we were able to localize that region in

and a refresh rate of 60 Hz on an Avotec Silent Vision 6011 projector located at the back of the scanner.

fMRI data analyses

AFNI (Cox 1996) was used for preprocessing the MRI data. Preprocessing included slice timing correction, spatial co-registration (Cox and Jesmanowicz 1999), and registration of functional images to the anatomy (Saad et al. 2009). Next, SPM 12 (<http://www.fil.ion.ucl.ac.uk/spm/>) was used to run a general linear model (GLM) analysis to calculate one beta value for each voxel for each stimulus across the 12 s trial length. Next, traditional eye movement responsive areas in the brain were localized. This was done by creating masks of these regions in Neurosynth (Yarkoni et al. 2011) using the term ‘saccade’ and then overlaying these masks with the contrast of brain response to all the reading conditions with brain response during periods of fixation when the eyes were not moving. ROIs were included only if they consisted of at least 50 voxels at a corrected *p* value of 0.001. By doing this, ROIs were localized for a subset of the participants: right and left lateral FEF (27 and 24 participants), right and left medial FEF (20 and 28 participants), right and left IPS (31 and 34 participants), and right and left SEF (combined into one ROI for analysis, 35 participants; See Fig. 1 for ROIs from a representative subject and Table 1 for ROI information).

Within each ROI, MVPA was performed using PyMVPA (Hanke et al. 2009). Each ROI contained a voxel matrix made up of beta values calculated from the GLM analysis in SPM for each individual subject and each stimulus type. These were used to train and test support vector machines (SVMs) on all three reading types (normal text, pseudo-word text, and consonant string text) using a leave-one-trial-out cross-validation procedure. Next, the SVM classification accuracy for each subject for each ROI was averaged with all the other subjects for whom that ROI could be localized.

Table 2 Eye movement measures for each condition

	NT	PT	CS
Fixation duration (ms)			
Mean	243	281	282
Standard deviation	27	41	43
Saccade amplitude (°)			
Mean	2.60°	2.32°	2.41°
Standard deviation	0.43°	0.58°	0.59°

Mean fixation duration and saccade amplitude for each condition averaged across subjects

NT normal text, PT pseudo-word text, CS consonant string text

Classification accuracies were tested against chance value (33.33%) to determine significance.

Results

Eye movement results

Table 2 shows the average fixation duration and saccade amplitude across subjects for each condition. Only fixations and saccades that did not occur before or after a blink were included in the analysis and fixation durations were only included if they were greater than 50 ms and less than 1500 ms. In total, 17.5% of fixations (17.9% for the normal text condition, 17.2% for the pseudo-word text condition, and 17.4% for the consonant string condition) were excluded from analysis. As seen in Table 2, mean fixation duration was statistically different across the three conditions, $F(2,114) = 15.72, p < 0.001$, in that the normal text condition had shorter fixation durations than the pseudo-word text ($F(1,76) = 28.29, p < 0.001$) and consonant string conditions ($F(1,76) = 26.16, p < 0.001$) but there was no difference in fixation duration between the pseudo-word text and consonant string conditions ($F(1,76) = 0.009, p = 0.99$). Saccade amplitude did not show a significant difference between conditions ($F(2,114) = 2.92, p = 0.058$).

fMRI results

We used MVPA to test whether traditional eye movement responsive areas could differentiate between three different reading conditions: normal text reading, pseudo-word text reading, and consonant string text reading (for ROI locations and number of subjects with each ROI see Table 1). Seven ROIs were tested and *p* values represent FDR corrected *p* values. MVPA showed that only lIFEF ($t(23) = 3.090, p_{adj} = 0.012$), rIFEF ($t(26) = 5.401, p_{adj} < 0.001$) and SEF ($t(34) = 4.830, p_{adj} < 0.001$) could differentiate between our three reading conditions above the chance value of

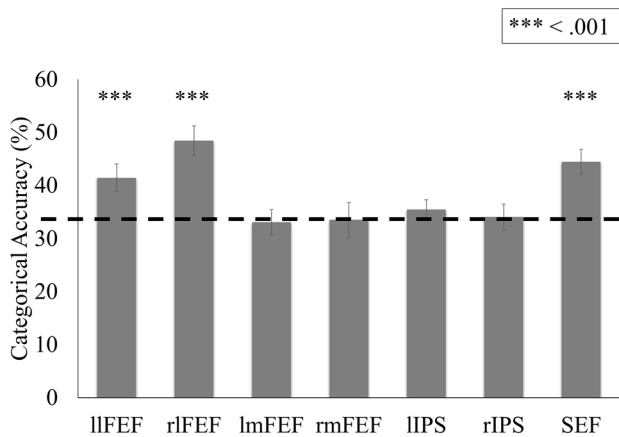


Fig. 3 Results of the MVPA with the individual ROIs. Averaged cortical accuracy of the SVM in each of the ROIs tested from the oculomotor network. The dotted line represents the averaged accuracy of the SVM

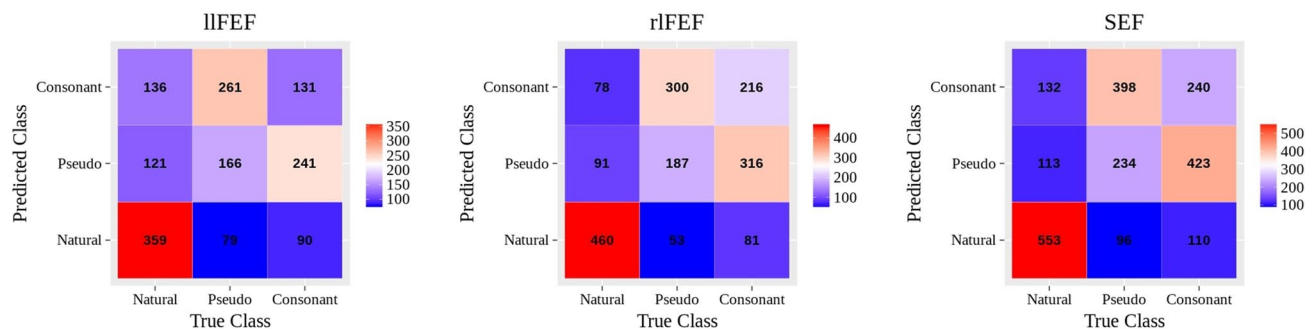


Fig. 4 Confusion matrices created from the support vector machine (SVM) classification of all three text conditions in lIFEF, rIFEF, and SEF. The *x* axis shows the True Class while the *y* axis shows the Predicted Class. The numbers inside the squares indicate how many total trials were categorized as each reading type from all the participants

33.3%, whereas lmFEF ($t(27)=0.101$, $p_{\text{adj}}=0.96$), rmFEF ($t(19)=0.056$, $p_{\text{adj}}=0.96$), IIPS ($t(33)=1.140$, $p_{\text{adj}}=0.46$), and rIPS ($t(30)=0.297$, $p_{\text{adj}}=0.96$) could not (see Fig. 3). To look more closely at the classification accuracy, confusion matrices were computed for left and right IFEF and SEF (see Fig. 4) and we found that these areas accurately categorized the normal text paragraphs at a higher rate than the pseudo-word and consonant string conditions, confusing the latter conditions with each other in most cases¹.

¹ Univariate analysis was also completed on the ROIs and showed significant differences in overall activation between normal reading, pseudo-text reading, and consonant string reading in rIFEF, and SEF.

Discussion

Skilled reading relies on highly organized sequences of saccadic eye movements (Rayner 1978, 1998, 2009a; Clifton et al. 2016). How these eye movements are controlled by the brain is largely unknown. In the present study, we asked whether the cortical eye movement control network previously identified in single-step oculomotor research is similarly functional in skilled reading. To investigate this question, we used region-based multi-voxel pattern analysis of fMRI data to compare activation patterns across seven regions of the eye movement control network during reading and pseudo-reading: bilateral IFEF, bilateral mFEF, bilateral SEF (combined into one ROI), and bilateral IPS. The regions for these analyses were defined using Neurosynth masks overlaid on subject-based contrasts to define regions specific to each individual. We asked whether activation patterns in these regions differed for reading versus pseudo-

reading. As shown, the classifier did well at categorizing normal text stimuli in every ROI, however, the classifier confused the pseudo-word text and consonant string text conditions in each region

We implemented pseudo-reading using two types of stimuli, both of which preserved the overall structure of the real texts from which they were derived but that substituted non-words for words. In the pseudo-word condition, words were replaced by pronounceable pseudo-words that carried no meaning. In the consonant string condition, words were replaced by unpronounceable strings of randomly selected consonants.

The main results were the following: first, bilateral lateral FEF and SEF reliably differentiated between reading and pseudo-reading. Second, confusion matrices of these effects showed differences in patterns of activation for eye movements in natural reading and confusion of the two pseudo-reading conditions.

The finding that the activity patterns in the left and right lateral FEF consistently reflected whether eye movements

were generated in the service of cognitive activity suggests that these areas encode control decisions that reflect the cognitive content of the stimulus. This need not imply that the network itself encodes meaning, but rather that it closely interfaces with and reflects activity in other cortical networks that process language and lead to comprehension. Importantly, the regions of the cortical eye movement network that differentiated real reading from pseudo-reading in our analysis did not produce differences in patterns of activation for eye movements in the two pseudo-reading conditions. These results suggest that the presence of semantic content was critical for the differences in patterns of activation in these regions.

Interestingly, the general pattern of results—differences in activation patterns to natural reading and pseudo-reading revealed by classification accuracy, and lack of differences between the two pseudo-reading conditions revealed by classification confusion—was found in the left and right lateral FEF as seen by the confusion matrices. Previous results from the anti-saccade task, which requires inhibitory control of pre-potent saccades, have suggested that FEF is particularly related to the cognitive control of saccades and that other regions are not (McDowell et al. 2008; Jamadar et al. 2013). These previous results might suggest that FEF would similarly uniquely reflect the influence of language processing on eye movements in reading. Lateral FEF and SEF were the only regions to reliably distinguish between normal reading and pseudoreading. This result provides further evidence for the theory that FEF is related to the cognitive control of saccades. At the same time, our finding that medial FEF was not able to differentiate between stimulus types is consistent with the idea that FEF can be divided into sub-regions that interface with different cognitive control systems. Here, lateral FEF reflects cognitive control in reading whereas medial FEF does not.

We did find that fixation durations differed between the normal text condition and both pseudo-text conditions whereas saccade amplitude did not. The FEFs have been shown to be a part of saccade production, but fixation duration affects have been found in IPS (Schiller and Tehovnik 2001) not FEF (Henderson et al. 2015). In studies investigating fixation durations in both reading and scene viewing, FEF was not found to track fixation durations (Henderson et al. 2014; Henderson and Choi 2015). Also, mechanisms of fixation duration in scene viewing and reading have been shown to be behaviorally similar (Henderson and Luke 2012). If our findings were based on the differences in the behavioral eye movement results in FEF, it is more likely that they would come from differences in saccade amplitude and we did not find any differences in saccade amplitude across conditions. SEF on the other hand has been shown to be modulated by fixation duration in reading (Henderson et al. 2015). However,

SEF has been shown to be involved in executive cognitive functions (Stuphorn and Shall 2006; Husain et al. 2002), and our data continue to support that for both SEF and FEF whether our results from SEF may be modulated by differences in fixation duration or not.

Overall, the results are consistent with the hypothesis that the sequences of eye movements generated during reading are importantly different from similar sequences of eye movements generated in pseudo-reading. As far as the eye movement control system is concerned, although these sequences may look similar at the behavioral level (Vitu et al. 1995; Rayner and Fischer 1996, Nuthmann et al. 2007; Henderson and Luke 2012; Luke and Henderson 2013; Henderson et al. 2013, 2014, 2015), they are importantly different at the cortical level. This finding is as would be expected according to the cognitive control models of eye movements in reading (Reichle et al. 1998, 2003; Reichle and Sheridan 2015), but would appear to be difficult to reconcile with theories that propose that eye movements in reading and in pseudo-reading are generated in essentially the same way (O'Regan 1992; Reilly and O'Regan 1998).

We note several limitations and caveats regarding this study. First, while behaviorally the eye movements in the three tasks were similar, there is still a possibility that the differences in fixation duration or any small differences in eye movements at the micro level that we did not test were driving the classification. Interestingly, though, whatever small differences might have been present across conditions did not allow the two pseudo-reading conditions to be distinguished, so it seems likely that the differences were related to cognitive control and ultimately reading comprehension. If the results were due specifically to differences in the eye movements themselves, it is unclear why only a specific subset of regions related to cognitive control would show the effects. Second, it is possible that the conditions differed in the amount of effort they required. To mitigate this possibility, we mixed the conditions in each run. Nevertheless, it is difficult to rule it out entirely given the present study design.

In conclusion, using ROI-based MVPA, we found that left and right lateral FEF and SEF reflect real-time cognitive control of eye movements in natural reading. Specifically, patterns of activation in these areas reflected whether the eyes were moving through meaningful text or meaningless pseudo-text, but did not reflect differences between two types of pseudo-text. These results are consistent with the view based on behavioral eyetracking studies and computational modeling that eye movements during natural reading are tightly tied to the ongoing linguistic and cognitive processes that support reading comprehension (Clifton et al. 2016; Rayner 2009a; Reichle et al. 1998). These novel findings highlight how eye movement control in the brain reflects and supports higher-level linguistic and cognitive processes during reading.

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Compliance with ethical standards

Conflicts of interest The authors report no conflicts of interest.

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