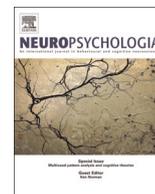




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Neural correlates of active vision: An fMRI comparison of natural reading and scene viewing

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ABSTRACT

Theories of eye movement control during active vision tasks such as reading and scene viewing have primarily been developed and tested using data from eye tracking and computational modeling, and little is currently known about the neurocognition of active vision. The current fMRI study was conducted to examine the nature of the cortical networks that are associated with active vision. Subjects were asked to read passages for meaning and view photographs of scenes for a later memory test. The eye movement control network comprising frontal eye field (FEF), supplementary eye fields (SEF), and intraparietal sulcus (IPS), commonly activated during single-saccade eye movement tasks, were also involved in reading and scene viewing, suggesting that a common control network is engaged when eye movements are executed. However, the activated locus of the FEF varied across the two tasks, with medial FEF more activated in scene viewing relative to passage reading and lateral FEF more activated in reading than scene viewing. The results suggest that eye movements during active vision are associated with both domain-general and domain-specific components of the eye movement control network.

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1. Introduction

Visual perception and visual cognition are active processes in which saccadic eye movements play a central role (Dodge, 1903; Buswell, 1935; Findlay and Gilchrist, 2003; Henderson and Ferreira, 2004; Henderson, 2013; Rayner, 2009; Yarbus, 1967). For example, in both natural scene viewing and reading, the eyes move from location to location to enable the acquisition of information as it is needed in real time. Current theoretical approaches and computational models of reading and scene viewing therefore attempt to account for how attention and particularly eye movements are controlled during these activities (e.g., Reichle et al., 1998; Engbert et al., 2005; Nuthmann et al., 2010; Torralba et al., 2006). An important issue in understanding active vision is the degree to which eye movement control systems are domain-specific (i.e., dedicated to a particular active vision domain such as reading or scene perception) versus domain-general (i.e., dedicated to all active vision tasks in which eye movements are controlled in the service of perception and cognition). Evidence from eyetracking shows strong correlations in basic eye movement measures within individuals across tasks like reading, scene viewing, and search, suggesting common neurocognitive eye

movement control processes across domains (Andrews and Copola, 1999; Castelano and Henderson, 2008; Henderson and Luke, 2014; Rayner et al., 2007). Several computational models of eye movement control that have been developed to account for one domain have been extended to other domains, implicitly endorsing the domain-general hypothesis. For example, the E-Z Reader and SWIFT models of eye movement control in reading have both been extended to non-reading tasks (Reichle, et al., 2012; Trukenbrod and Engbert, 2012), and the CRISP model of eye movement control in scene perception has been extended to reading (Nuthmann et al., 2010; Nuthmann and Henderson, 2012). Yet there has been very little direct investigation of the degree to which the eye movement control system is similar or different across domains. In the present study we examined this issue by investigating the similarities and differences in the cortical eye movement control network during natural reading and scene viewing.

Past studies using single-step eye movement paradigms as in the gap and anti-saccade tasks have provided evidence for a frontal-parietal eye movement control network that includes as core components the frontal eye fields (FEF), supplementary eye fields (SEF), and intraparietal sulcus (IPS). Additional cortical areas often observed in single-step eye movement studies include dorsolateral prefrontal cortex (DLPFC), likely associated with maintaining task goals in these tasks. Recently, Hillen et al. (2013) found blood oxygenation level dependent (BOLD) activation in FEF, SEF,

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and IPS during a target-search task through texts and pseudo-texts that required sequences of saccadic eye movements. These results indicate that the eye-movement network observed for single-saccade tasks is also engaged during sequential scanning. In addition, Choi et al. (2014) compared BOLD activation during natural reading using normal texts and pseudo-reading using nonword control texts. No secondary task was administered when participants read paragraphs of normal texts. Choi et al. also found common brain areas such as FEF, SEF and IPS associated with the control of eye movements in both reading and pseudo-reading.

Whether this eye movement network is also functional in other active vision tasks such as scene viewing is currently unknown. The present study investigated similarities and differences in the eye movement control network in natural reading and scene viewing by comparing the natural reading condition from Choi et al. (2014) to a scene viewing condition. The data for natural reading in the current study is the same as that reported in Choi et al. (2014). The purpose of the present report is to compare the similarities and differences in the neural correlates of eye movements during natural reading from Choi et al. (2014) with the neural correlates of eye movements in scene viewing to investigate the domain-specificity of eye movement control systems.

A secondary issue investigated here was whether differential activation in cortical regions associated with reading and scene viewing can be observed during active viewing. The majority of neuroimaging studies of both reading and scene viewing have used brief presentation (rapid serial visual presentation or RSVP) methods in which saccadic eye movements are not possible or are discouraged¹. In general, reading via RSVP tends to activate a left-lateralized frontal-temporal-parietal network associated with language processing (Friederici, 2011; Martin, 2003; Price, 2012). This activation typically involves an occipital-temporal network including the purported visual word form area (VWFA), middle and superior temporal gyrus/sulcus (MTG, STG/STS), and inferior frontal gyrus (IFG). In comparison, scene viewing tends to activate a right-lateralized frontal-temporal-parietal network associated with visual scene analysis (Epstein, 2005; 2008; Grill-Spector, 2003; Maguire, 2001). This network notably includes temporal-occipital junction (TOJ) associated with visual objects, and areas of

et al., 2008, 2007; Henderson et al., 2011; Park and Chun, 2009; Walther et al., 2009). Here we investigated whether active vision tasks involving extended viewing with eye movements in reading versus scene viewing lead to the type of differential activation that is typically observed in brief presentations of words and scenes. Similar activation in the hypothesized eye movement network in spite of differential activation in domain-specific processing networks associated with reading and scene viewing would provide additional evidence for the domain-generalty of eye movement control.

To investigate these issues, we combined simultaneous high-resolution eyetracking and fMRI data acquisition while subjects read passages and viewed photographs of real-world scenes. Each stimulus was presented for 12 s and was viewed actively. Eyetracking was used to ensure that subjects were engaging naturally with the stimuli. We hypothesized that the eye movement control network identified in single-saccade tasks also supports these active vision tasks, but that reading and scene viewing may also draw on independent eye movement sub-systems given that these tasks use partially independent cognitive operations. We also hypothesized that actively engaging in reading and scene viewing would produce activation similar to that observed previously in brief-presentation RSVP studies of reading and scene perception.

2. Method

2.1. Subjects

Thirty-three subjects (12 male) participated in this study. They were all right-handed, native speakers of English, aged 18–35 years (Mean Age: 21.45). Thirty subjects were students from the University of South Carolina and three were recruited from the Columbia, South Carolina community. All subjects gave informed consent and were screened for MRI safety. They all reported normal or corrected-to-normal vision and were given \$10 per hour for participation in the study. Two did not finish the experiment, one due to technical problem with the scanner, and the other due to falling asleep during the experiment. Therefore, data from 31



Fig. 1. Example stimuli used in the Experiment.

What a marvelous fabric, he said then. I'll certainly tell the
Emperor. The two scoundrels rubbed their hands gleefully. They
had almost made it. More thread was requested to finish the work.
Finally, the Emperor received the announcement that the two
tailors had come to take all the measurements needed to sew his
new suit.

fusiform gyrus and the parahippocampal cortex associated with scene analysis (Bar et al., 2001; Epstein et al., 2000; Henderson

participants were included in the analysis.

2.2. Materials

Twenty-two paragraphs were selected from two sources, *The Emperor's New Clothes*, written by Hans Christian Andersen (11 paragraphs), and a Nelson-Denny Practice Test (11 paragraphs). Each paragraph consisted of 49–66 words. Text was presented in Courier New font with 4.3 characters subtending 1° of visual angle.

¹ Neural substrates for normal reading and scene viewing have previously been examined using naturalistic stimuli (Altmann et al., 2014; Bartels and Zeki, 2004; Malinen et al., 2007). For example, Bartels and Zeki (2004) attempted to functionally segregate neural correlates of language, face, color, and the human body by presenting a short movie clip to participants. However, these studies did not monitor participants' eye movements during the tasks.

Twenty-two indoor and outdoor natural scenes were selected from scenes used in previous eyetracking studies (e.g., [Henderson and Luke, 2014](#)). They were 24 bit images at a resolution of 1024×768 and subtended a visual angle of $17.59^\circ \times 12.91^\circ$. [Fig. 1](#) shows examples of text paragraphs and scenes used in the experiment. Two pseudo-text conditions were also included and were not analyzed for this study (see [Choi et al., 2014](#)).

2.3. Apparatus

Stimuli were presented using an Avotec Silent Vision 6011 projector with its native resolution (1024×768) and a refresh rate of 60 Hz. Eye-movements were monitored via a SR Research Eye-link 1000 long-range MRI eyetracker with a sampling rate of 1000 Hz. Viewing was binocular and eye-movements were recorded from one eye.

2.4. Procedure

Subjects were instructed to read paragraphs silently as if they were reading a novel, and were instructed to view scenes in order to remember specific objects and details about them for a later memory test. Both of these tasks required subjects to move their eyes naturally. In the scanner, a thirteen-point calibration procedure was administered before each functional run to correctly map eye position onto screen coordinates. Eye movements were recorded during entire runs to ensure that appropriate eye-movements were executed during the experiment.

Each functional run consisted of 22 critical trials (11 text paragraphs and 11 scenes) as well as 22 filler trials. Each trial was presented for 12 s following a fixation cross for 6 s. Within each run, paragraphs, scenes, and fillers were presented in a random order for each participant. Participants had two functional runs, resulting in 22 reading trials and 22 scene trials over the two runs. Each functional run lasted about 14 min.

2.5. MRI data acquisition

MR data were collected on a Siemens Medical Systems 3T Trio. A 3D T1-weighted “MPRAGE” RF-spoiled rapid flash scan in the sagittal plane, and a T2/PD-weighted multi-slice axial 2D dual Fast Turbo spin-echo scan in the axial plane was used. The multi-echo whole brain T1 scans had 1 mm isotropic voxel size and sufficient field of view to cover from the top of the head to the neck with the following protocol parameters: TR=2530 ms, TE1=1.74 ms, TE2=3.6 ms, TE3=5.46ms, TE4=7.32 ms, flip angle=7°. All functional runs were acquired using gradient echo, echo-planar images with the following protocol parameters: TR=1850 ms, TE=30 ms, flip angle=75°. Volumes consisted of 34 3 mm slices with transversal orientation. Each volume covered the whole brain with FOV=208 mm and 64×64 matrix, resulting in $3.3 \times 3.3 \times 3$ mm³ voxel size.

2.6. MRI analysis

Image analysis was conducted using AFNI ([Cox, 1996](#)). Within-subject analysis involved slice timing correction, spatial co-registration ([Cox and Jesmanowicz, 1999](#)) and registration of functional images to anatomy ([Saad et al., 2009](#)). Voxel-wise multiple linear regression was performed with the program 3dREMLfit, using reference functions representing each condition convolved with a standard hemodynamic response function. These regressors modeled the responses from the onset of each trial to the end of the trial. Reference functions representing the six motion parameters were included as covariates of no interest. In addition, the signal extracted from CSF and WF was also included as noise

covariates of no interest. General linear tests were conducted to obtain contrasts between conditions of interest.

The individual statistical maps and the anatomical scans were projected into standard stereotaxic space ([Talairach and Tournoux, 1988](#)) and smoothed with a Gaussian filter of 5 mm FWHM. In a random effects analysis, group maps were created by comparing activations against a constant value of 0. The group maps were thresholded at voxelwise $p < 0.01$ and corrected for multiple comparisons by removing clusters smaller than 873 μl to achieve a map-wise corrected $p < 0.05$. Using the 3dClustSim program with 10,000 iterations, the cluster threshold was determined through Monte Carlo simulations that estimate the chance probability of spatially contiguous voxels exceeding the voxelwise p threshold, i.e., of false positive noise clusters. The smoothness of the data was estimated with the AFNI program 3dFWHMx using regression residuals as input. The analysis was restricted to a mask that excluded areas outside the brain, as well as deep white matter areas and the ventricles.

3. Results

3.1. Eye-movement analysis

The eye-movement data were analyzed to obtain fixations and saccades in the reading and scene viewing conditions ([Table 1](#)). All fixations meeting the following criteria were included in this analysis: A fixation could not have a blink immediately before or after, and had to have a duration between 50 and 1500 ms. Data during track losses were also rejected. In total, 13.4% of fixations (11.2% for the reading condition and 16.7% for the scene viewing condition) were excluded. The summary eye movement measures were similar when no data selection criteria were applied. Eye movements in each condition are similar to those reported in analogous studies outside the scanner (e.g., [Henderson and Luke, 2014](#)). These eye movement data demonstrate that participants moved their eyes normally in the reading and scene viewing conditions.

3.2. fMRI analysis

3.2.1. Scene viewing > fixation

The results of a whole-brain analysis for the scene viewing condition against the fixation baseline are displayed in [Table 2](#) and [Fig. 2](#). Several bilateral areas activated more for scene viewing relative to fixation, including occipital cortex (lingual gyrus and occipital pole), retrosplenial cortex (BA30), medial temporal lobe (hippocampus and parahippocampal area), IPS, medial FEF, SEF, precentral sulcus, and IFG. Lateralized areas included right post-central sulcus, left insula, and left paracentral gyrus and sulcus. Subcortical areas included mid-brain regions (superior colliculus,

Table 1

Summary eye movement data. Mean fixation duration and saccade amplitude for passage reading and scene viewing as a function of condition.

		Passage reading	Scene viewing
Fixation duration (ms)	Mean	215	288
	Number of cases	30,214	21,138
	Standard deviation	87	154
Saccade amplitude (deg)	Mean	2.86°	2.74°
	Number of cases	29,785	20,546
	Standard deviation	3.02°	2.21°

Table 2
Activation in the Main Contrasts of Interest. Locations of peak activation are shown for each cluster with significant activity ($p < 0.01$ corrected for multiple comparisons). Multiple peaks required separation by a minimum of 35 mm. Number of voxels, maximum z-score, MNI coordinates, and the anatomical structures for each cluster are shown. L=left hemisphere, R=right hemisphere.

Volume	Max	x	y	z	Anatomical structure
Scene viewing > fixation					
10172	8.684	28	-61	-6	R Lingual Gyrus, R Parahippocampal Gyrus, R Retrosplenial Cortex, R Middle Occipital Gyrus, R Occipital Pole, R Hippocampus, R Cerebellum
	7.919	-26	-95	8	L Middle Occipital Gyrus, L Lingual Gyrus, L Occipital Pole, L Parahippocampal Gyrus, L Retrosplenial Cortex, L Hippocampus, L Cerebellum
	7.872	-19	-28	1	L Superior Colliculus, L Thalamus, L Ventral DC, L Caudate
	6.664	26	-68	54	R Superior Parietal Gyrus, R Intraparietal Sulcus
	6.367	-22	-72	49	L Superior Parietal Gyrus, L Intraparietal Sulcus
	5.437	-20	-39	-41	L Cerebellum
	4.672	15	7	10	R Caudate, R Superior Colliculus, R Thalamus, R Ventral DC
575	5.102	-45	12	31	L Precentral Sulcus, L Superior Frontal Sulcus, L Medial Frontal Eye Field
333	4.828	54	13	32	R Precentral Gyrus/Sulcus, R Middle Frontal Gyrus
	3.511	57	39	3	R Pars Triangularis
264	5.166	3	12	64	R/L Superior Frontal Gyrus, Supplementary Eye Field
123	4.702	29	6	50	R Superior Frontal Sulcus, R Medial Frontal Eye Field
93	4.02	-29	25	-1	L Insula
59	5.228	-46	47	-8	L Pars Orbitalis, L Pars Triangularis
53	4.033	-6	-32	61	L Paracentral Gyrus/Sulcus
47	3.986	42	-30	44	R Postcentral Sulcus
Reading > scene viewing					
2453	7.208	-52	8	-15	L Superior Temp Gyrus/Sulcus, L Middle Temporal Gyrus
	6.988	-55	-32	2	L Superior Temp Gyrus/Sulcus, L Middle Temporal Gyrus, L Inferior Frontal Gyrus
	5.966	-45	3	55	L Precentral Gyrus, L Lateral Frontal Eye Field
	3.76	-41	-62	55	L Inferior Parietal Lobule, L Angular Gyrus
1633	6.835	57	5	-19	R Superior Temporal Gyrus/Sulcus, R Middle Temporal Gyrus
	6.77	61	-28	-1	R Superior Temporal Gyrus/Sulcus, R Middle Temporal Gyrus
	6.189	61	-57	29	R Inferior Parietal Gyrus, R Angular Gyrus
844	6.205	5	66	15	R/L Superior Frontal Gyrus
598	6.854	9	-54	36	R/L Precuneus, R/L Superior Parietal Sulcus
465	6.068	0	-8	12	L/R Thalamus
133	5.704	57	28	-6	R Inferior Frontal Gyrus, R Pars Triangularis
129	4.864	48	20	42	R Middle Frontal Gyrus, R Precentral Gyrus, R Lateral FEF
82	4.804	1	9	64	L/R Superior Frontal Gyrus, Supplementary Eye Field
54	4.687	9	-16	26	L/R Middle-Posterior Cingulate Gyrus/Sulcus
42	4.528	-42	-49	-16	L Fusiform Gyrus
	6.913	-20	-79	-30	L Cerebellum
	6.39	18	-72	-25	R Cerebellum
Scene viewing > reading					
9226	-8.232	28	-61	-6	R Lingual Gyrus, R Parahippocampal Gyrus, R Retrosplenial Cortex, R Middle Occipital Gyrus, R Occipital Pole, R Hippocampus
	-7.541	-35	-88	20	L Middle Occipital Gyrus, L Superior Parietal Lobule, L Intraparietal Sulcus
	-7.47	-26	-48	-3	L Middle Occipital Gyrus, L Lingual Gyrus, L Occipital Pole, L Parahippocampal Gyrus, L Retrosplenial Cortex, L Hippocampus
	-6.892	19	-61	57	R Superior Parietal Lobule, R Intraparietal Sulcus
	-5.059	45	-30	44	R Postcentral Sulcus, R Intraparietal Sulcus
	-4.913	-13	-48	-43	L Cerebellum
458	-5.122	-3	41	-9	L Anterior Cingulate Gyrus/Sulcus
279	-5.11	-36	62	9	L Middle Frontal Gyrus, L Dorsal Lateral Prefrontal Cortex
279	-5.619	25	2	47	R Superior Frontal Sulcus, R Medial Frontal Eye Field
207	-5.569	-22	11	57	L Superior Frontal Sulcus, L Medial Frontal Eye Field
171	-5.33	-35	-34	39	L Postcentral Sulcus, L Intraparietal Sulcus
138	-4.264	-39	-18	4	L Posterior Insula
89	-4.69	44	42	6	R Middle Frontal Sulcus
68	-4.086	-26	37	-11	L Orbitofrontal Sulcus
68	-4.186	51	12	23	R Precentral Sulcus
54	-5.082	3	6	27	R/L Middle Posterior Cingulate Gyrus/Sulcus
42	-4.793	28	37	-15	R Orbitofrontal Sulcus

thalamus, ventral diencephalon, and caudate) and bilateral cerebellum. This overall pattern showed that areas typically associated with scene perception were activated during active scene viewing (Bar et al., 2001; Epstein et al., 2000; Henderson et al., 2007; see Epstein, 2005) and the eye movement network.

3.2.2. Reading > fixation

The results of the whole-brain analysis for the reading condition against the fixation baseline have been reported by Choi, Desai, and Henderson (2014).

3.2.3. Reading versus scene viewing

In addition to similarities across the two tasks, we also observed qualitatively and quantitatively unique patterns of activation for reading and scene viewing. To examine these differences, we conducted separate contrasts for greater activation of reading over scene viewing and for scene viewing over reading. The results of these whole-brain analyses are presented in Table 2 and Fig. 3.

3.2.4. Reading > scene viewing

The areas activated more by reading than scene viewing were bilateral STG, bilateral STS, bilateral MTG, bilateral angular gyrus,

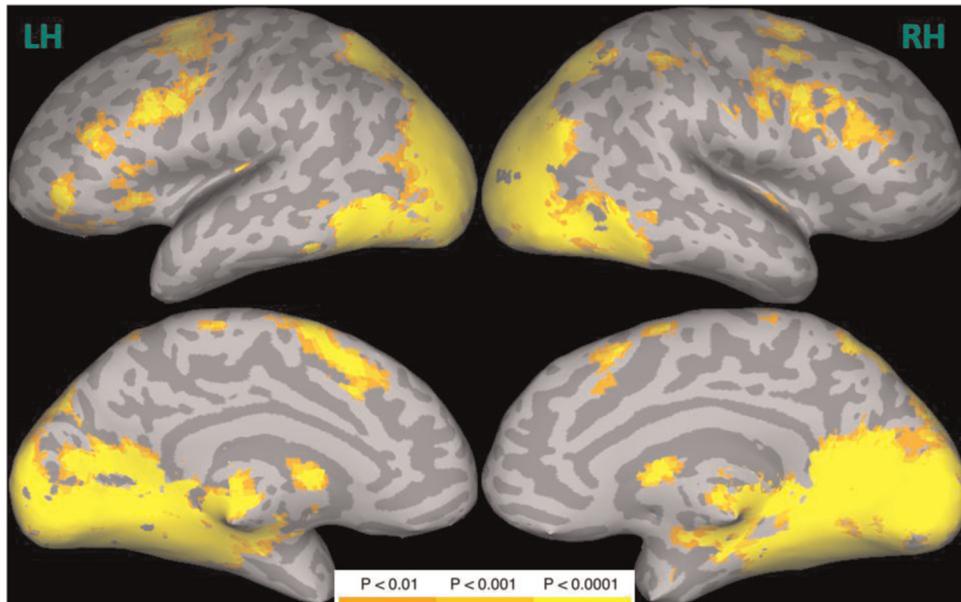


Fig. 2. Areas of significant activation for the scene viewing condition in a whole-brain analysis. The maps are displayed using Caret (Van Essen et al., 2001) on an inflated cortical surface of a representative subject, with gyri shown as light gray and sulci shown as dark gray. LH=Left Hemisphere; RH=Right Hemisphere.

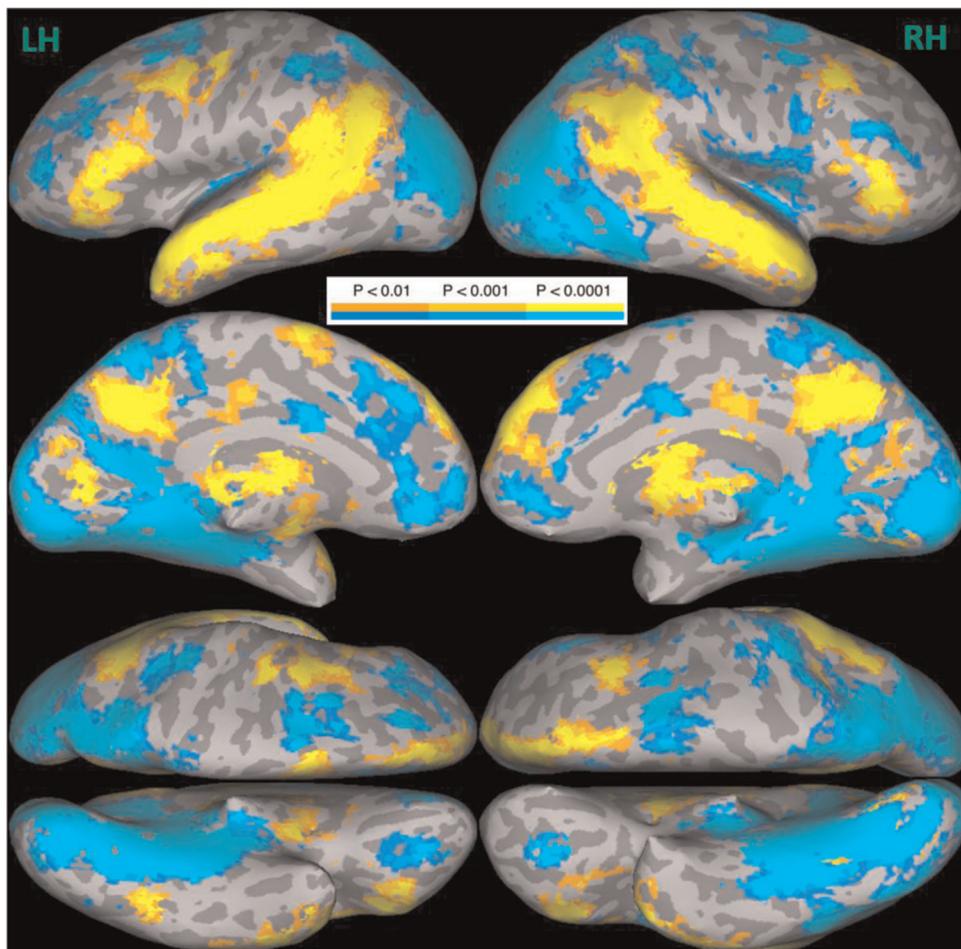


Fig. 3. Areas activated by the direct contrast of the reading versus scene viewing conditions in a whole-brain analysis. The maps are displayed using Caret (Van Essen et al., 2001) on an inflated cortical surface of a representative subject, with gyri shown as light gray and sulci shown as dark gray. Rows show lateral, medial, dorsal, and ventral views respectively. Hot regions represent more activation in reading whereas cool regions reflect more activation in scene viewing. LH=Left Hemisphere; RH=Right Hemisphere.

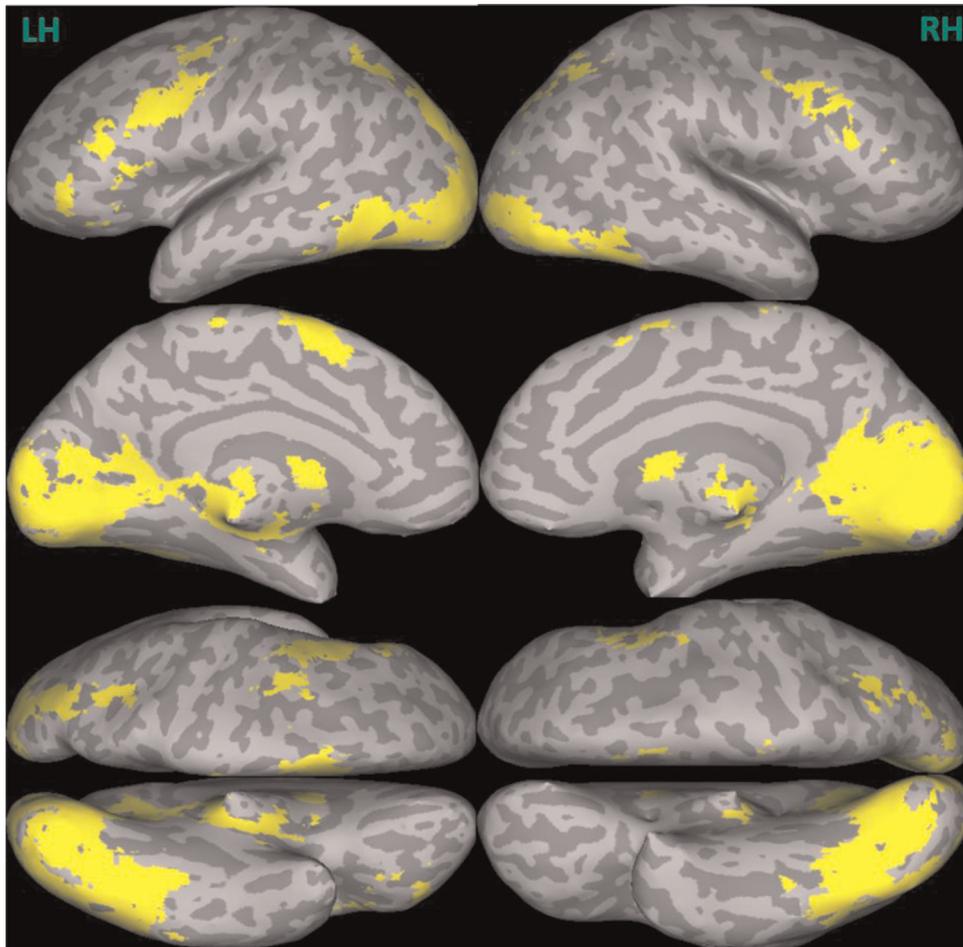


Fig. 4. Conjunction results between the passage reading and scene viewing conditions (paragraph reading – fixation \cap scene viewing – fixation) ($p < .01$, corrected for multiple comparisons). The maps are displayed using Caret (Van Essen et al., 2001) on an inflated cortical surface of a representative subject, with gyri shown as light gray and sulci shown as dark gray. Rows show lateral, medial, dorsal, and ventral views respectively. LH=Left Hemisphere; RH=Right Hemisphere.

bilateral IFG, bilateral superior frontal gyrus (SFG), bilateral lateral FEF and SEF, bilateral precuneus, bilateral posterior cingulate, left fusiform gyrus, bilateral cerebellum, and bilateral thalamus.

3.2.5. Scene viewing > reading

The areas activated more by scene viewing than reading were bilateral lingual gyrus, bilateral retrosplenial cortex (BA 30), bilateral medial temporal gyrus including parahippocampal place area (PPA), bilateral IPS, bilateral postcentral sulcus, bilateral SFG, bilateral middle frontal gyrus, bilateral medial FEF, bilateral orbitofrontal sulcus, bilateral middle-posterior cingulate cortex, left anterior cingulate cortex, left posterior insula, right precentral sulcus, and left anterior cerebellum.

3.2.6. Conjunction of paragraph reading and scene viewing

To directly examine the similarities in activation for the passage reading and scene viewing tasks, we conducted a conjunction analysis of the passage reading and scene viewing activation maps against the fixation baseline (paragraph reading – fixation \cap scene viewing – fixation). The conjunction analysis is conservative because the two activation maps were already thresholded separately ($p < .01$, corrected for multiple comparisons) and shows the common regions that are activated in both maps. As seen in Fig. 4, we observed large common activation areas for the two tasks including bilateral occipital cortex, bilateral inferior temporal cortex, bilateral middle frontal gyrus (pre-motor area), precentral sulcus/gyrus (FEFs), inferior frontal gyrus, SEF, and mid-brain areas.

4. Discussion

An important issue in understanding active vision is the degree to which eye movement control is domain-specific (i.e., dedicated to a particular active vision task such as reading or scene perception) versus domain-general (i.e., dedicated to all active vision tasks in which eye movements are controlled in the service of perception and cognition). The current study was designed to investigate this issue by examining the similarities and differences in brain activity elicited by two active vision tasks, reading and scene viewing, both of which require extended sequences of saccadic eye movements. Previous research using single-step saccade tasks has identified a common eye movement network, but little is known about the role of this network in natural active vision and how its function is similar and different across domains. To investigate these issues, eyetracking and fMRI were recorded simultaneously while subjects read passages of text and viewed photographs of scenes in an MRI scanner, and neural activation was compared for the two tasks.

Individual analyses of reading and scene viewing (Choi et al., 2014, and Fig. 2, respectively), corroborated by the conjunction analysis (Fig. 4), showed that some regions support both tasks. There was extensive overlap in bilateral visual cortex known as a core region for initial visual encoding of stimuli (e.g., Dyckman et al., 2007). More importantly given our theoretical question, several frontal and parietal areas (SEF, FEF, and IPS) were activated in both conditions, as well as mid-brain structures including superior colliculus, thalamus, and caudate. These results are

consistent with previous findings identifying an eye-movement network based on single-saccade eye movement tasks (Jamadar et al., 2013; McDowell et al., 2008) as well as reading and reading-like tasks (Choi et al., 2014; Hillen et al., 2013). Although FEF was activated in both the reading and scene viewing conditions in the present study, the actual location of this region was relatively different in the two conditions, which we return to below. Additional activation in both conditions was observed in bilateral frontal areas including MFG (pre-motor area), IFG, and precentral sulcus/gyrus, which we also return to below.

The common activated areas observed across tasks in the present study were very similar to those reported by Choi et al. (2014) and Hillen et al. (2013). Hillen et al. (2013) examined sentence reading, pseudo-reading, and “Landoldt reading” with a target-search task, and found a common eye movement network that included bilateral FEF, SEF, IPS, and left caudate and left putamen, areas observed in the current study. In addition, Choi et al. (2014) also reported that the frontoparietal eye movement network (FEF, SEF, and IPS) was activated during normal and nonword text reading. The similarity of the areas observed across all of these active viewing conditions supports the hypothesis that these regions are generally associated with active viewing via saccadic eye movements regardless of viewing task.

4.1. Differential role of lateral and medial FEF

It has been suggested that FEF can be divided into a lateral and medial regions, and that these regions have different functions (Ettinger et al., 2008; Grosbras et al., 2001; Jamadar et al., 2013; McDowell et al., 2008; McDowell et al., 2005). In a review article, McDowell et al. (2008) proposed that medial FEF is more involved in volitional saccadic eye movements whereas lateral FEF is more involved in reflexive saccadic eye movements. More recently, Jamadar et al. (2013) performed a meta-analysis of pro- and anti-saccade studies and tentatively concluded that lateral FEF may be involved in both reflexive and volitional eye movements whereas medial FEF may be solely related to reflexive eye movements. These studies suggest that different regions of FEF play differential functional roles in eye movement control. However, the specific nature of the functional roles of medial and lateral FEF has not yet been fully determined, and the role that they play in sequential active vision has not been established.

In our study, the scene viewing condition elicited more activation in bilateral medial FEF, whereas the paragraph reading condition produced more activation in lateral FEF. The nature of eye movements in the two tasks of the current study was different from the single-saccade eye movement tasks used in previous studies. During passage reading, eye movements are relatively automatized motor behaviors for skilled readers. Given that lateral FEF is more associated with reflexive eye movements, the current finding that reading activated lateral FEF more than scene viewing is consistent with the idea that eye movements during reading are relatively automatized, and that automatized eye movements are supported by lateral FEF. In contrast, scene viewing produced more activation in the medial FEF relative to reading. Because the task during scene viewing was to remember details of the scenes, participants may have moved their eyes more carefully to spatially encode specific objects and scene details, leading them to execute eye movements with specific intention. These intentional eye movements would lead to more activation in the medial FEF. Note that the functional dissociation between separate FEF regions is not yet fully understood (Jamadar et al., 2013; McDowell et al., 2008), and additional research will be needed to fully establish the roles of these FEF sub-regions.

4.2. Additional eye-movement networks or domain-general

processes?

As noted, although there were subtle differences, the neural networks for eye movement control observed in the present study were generally similar to those observed in previous studies in which single-step eye-movement tasks were employed: Bilateral FEFs, SEF, and IPS were activated regardless of the characteristics of eye movements engaged in particular tasks. In addition to these areas, the current study found frontal activation in bilateral precentral sulcus/gyrus, bilateral MFG, (premotor area, BA6), and bilateral IFG (pars triangularis and pars orbitalis) for both the reading and scene viewing conditions. These regions are not typically reported in studies using simpler eye movement tasks.

Premotor activation is typically associated with motor-related behaviors. Why was this area activated above and beyond the traditional eye-movement network in the present study? There are at least two speculative explanations for this result. First, it has been suggested that lateral FEF can extend to the premotor area (Tehovnik et al., 2000). This activation might therefore reflect an additional component of the eye-movement control network. In the present study, reading passages and viewing scenes for 12 s in each trial required complex coordination of eye movement sequences with perceptual and cognitive systems, such that additional motor-related brain areas might be needed during these tasks. Alternatively, some studies using pro- and anti-saccade tasks have observed that right IFG and/or MFG are activated during those tasks, suggesting that these regions are associated with inhibition of responses such as reflexive eye movements during the anti-saccade task (Aichert et al., 2012; Brown et al., 2006; for a review, see Jamadar et al., 2013). Note that several computational models of eye-movement control in active vision propose that autonomous oculomotor programming is inhibited by cognitive processing during reading and scene viewing (e.g., Engbert et al., 2005; Nuthmann et al., 2010). The activation in the right IFG and/or MFG may reflect this inhibitory processing by cognitive factors during active vision.

The left IFG (LIFG) activation common to reading and scene viewing could be due to the involvement of domain-general integrative processes (e.g., Fedorenko and Thompson-Schill, 2014; Hagoort, 2005). For example, Hagoort (2005) argued that the LIFG including BA 44, 45, and 47 is associated with unification operations in which a variety of types of information are integrated. In particular, a more ventro-anterior area of LIFG (close to pars orbitalis) appears to be related to semantic integration (Bookheimer, 2002; Hagoort et al., 2004; Sabb et al., 2007). Given that both passage reading and scene viewing require semantic integration of different aspects of information, one possibility is that this LIFG activation is associated with domain-general semantic integration. Alternatively, left premotor cortex and LIFG have been shown to be associated with processes related to inner speech (e.g., Fiez et al., 1996; Paulesu et al., 1993; for a review, see Price (2012)). Vigneau et al. (2006) demonstrated in a meta-analysis that the left posterior frontal lobe including premotor area and IFG is involved in phonological processing. It may be that participants in the current study executed covert articulation during both reading and scene viewing. During reading, subjects may generate inner speech (Perrone-Bertolotti et al., 2014), and in a scene viewing task requiring memorization as used here, subjects might exploit covert verbal rehearsal to remember the details of the scenes. Accordingly, this covert articulation may have activated the areas associated with phonological processing in the frontal lobe. Further research will be needed to evaluate whether the LIFG activation observed during active vision is a sub-component of the eye-movement network or a sub-region of domain-general cognitive processes (e.g., semantic integration, phonological recoding) that is not directly related to the coordination of eye movements.

4.3. Functional areas for natural reading and scene viewing

In addition to the eye movement control network, the present study allowed us to investigate functional activation associated with natural reading and scene viewing in which subjects engaged with the stimuli in an active manner via saccadic eye movements. Based on the contrast analysis between the passage reading and the scene viewing conditions (passage reading > scene viewing vs. scene viewing > passage reading), we found differential activation in each condition. As expected, the passage reading condition elicited more activation in language related areas including bilateral STG/STS, MTG, IFG, precuneus, and angular gyrus compared to the scene viewing condition, which is consistent with the finding reported by Choi et al. (2014) in which these same natural reading data were compared to a nonword pseudo-reading conditions. On the other hand, the scene viewing condition produced more activation in scene perception areas including bilateral retrosplenial cortex and parahippocampal gyrus compared to the paragraph reading condition. In addition, the scene viewing condition also produced more activation in regions related to the processes of memory encoding including bilateral medial temporal lobe (Schacter and Wagner, 1999), IPS (Uncapher and Wagner, 2009), and orbitofrontal sulcus (Frey and Petrides, 2000; 2002). The activation related to memory encoding was likely observed because the task for the scene viewing condition was to remember the details of scenes. Recently, we examined neural substrates associated with each fixation during scene viewing (Henderson and Choi, 2015). In that report, we used a fixation-related analysis of the present data set to investigate how the BOLD signal is modulated by fixation durations during active scene viewing. We found that fixation durations were positively correlated with activation in occipital lobes and in right DLPFC, such that longer fixation durations were associated with more brain activation in these regions. This result suggests that increased fixation durations involve effortful processes in visual encoding and in controlling ongoing processing difficulty. This interpretation is also consistent with the finding that fixation durations during natural reading are related to the anatomical structure of V1 (Henderson et al., 2014). Henderson and Choi (2015) also found negative correlations between fixation durations and activations in the medial temporal lobe, indicating that less efficient scene processing might increase fixation durations.

4.4. Functional role of the VWFA

The role of the so-called visual word form area (VWFA) in the left ventral occipito-temporal cortex is modulated by different types of tasks. The function of VWFA is still under debate. Some researchers have shown that increased brain activity is observed in the VWFA when subjects process words relative to other stimuli such as consonant strings, digits, and objects (Cohen et al., 2002; Cohen and Dehaene, 2004; Dehaene and Cohen, 2011; McCandliss et al., 2003). However, others have found that the VWFA is also activated for picture stimuli (Bar et al., 2001; Ben-Shachar et al., 2007; Kherif et al., 2011; Ploran et al., 2007; Price and Devlin, 2011; 2003; Starrfelt and Gerlach, 2007; Van Doren et al., 2010; Vogel et al., 2012). For example, Van Doren et al. (2010) found the same amount of activity in the VWFA when viewing words and pictures, suggesting that the VWFA is not specialized for word processing. The studies examining the functional specialization of the VWFA have been mostly performed with an isolated RSVP stimulus presentation paradigm in which one word (or object) is displayed at a time in each trial. The present study provided an opportunity to examine whether the VWFA is exclusively and/or preferentially activated for words when more ecologically valid materials and task (e.g., naturally reading a passage instead of

reading a single word) are used during a task period.

In our study, the reading condition produced more activation in a region consistent with the VWFA, located in the ventral occipito-temporal gyrus, compared to the scene viewing condition. Additionally, note that the same VWFA cluster that preferentially activated in reading over scene viewing also elicited more activation in scene viewing compared to the fixation baseline. These results indicate that this region is preferentially (not exclusively) activated by word processing. The current result supports the view that the VWFA preferentially responds to words relative to other complex stimuli (Dehaene and Cohen, 2011), extending these results to natural reading, but that it also responds to other complex stimuli such as scenes.

Based on the current comparison between paragraph reading and scene viewing, it is not possible to specify which level(s) of word processing elicited the reading-related activation of the VWFA cluster. Vinckier et al. (2007) examined the role of the ventral stream of occipito-temporal cortex by manipulating the level of orthographic characteristics from false font strings to real words. They observed that more anterior regions of occipito-temporal cortex were activated as the stimuli became more linguistically meaningful (see also Nosarti et al. (2010)). In an extensive review, Price (2012) concluded that “more anterior areas are involved in lexico-semantic processing of the whole word” (p. 836). Based on the location of the activated cluster in the present study (maximum Z value in $-40, -46, -16$ in Talairach coordinates) and reported locations in previous studies, we tentatively conclude that the preferential activation of VWFA for the passage reading condition was driven by lexico-semantic integration of each word in our natural reading condition.

5. Conclusions

The present block-design fMRI study demonstrated common and differential brain activation in two active vision tasks that required sequences of saccadic eye movements, reading and scene viewing. As expected, language-related cortical areas including IFG, STG, and MTG were more active in the reading condition relative to the scene viewing condition, whereas ventral occipito-medial areas including PPA and RSC produced more activation for the scene viewing condition. In addition, anterior areas of ventral occipito-temporal cortex were preferentially activated for passage reading compared to scene viewing, suggesting that lexico-semantic integration might occur in this region during passage reading. This result provides additional evidence that the ventral occipito-temporal region is a core part of lexical processing even when subjects read more natural linguistic materials like passages. In the future it will be important to study more directly the functional organization of the ventral occipito-temporal stream during natural reading as a supplement to the isolated single-word presentation paradigm that has been used to date.

Most importantly given our primary theoretical concern, the results showed that a common eye-movement network was activated for both passage reading and scene viewing despite clear differences in the cognitive computations (and associated neural systems) needed for each task, supporting the hypothesis that much of eye movement control in active vision draws on domain-general control processes. In addition, differences in the eye-movement network were observed for each condition: Bilateral medial FEF was more activated in the scene viewing condition whereas lateral FEF was more activated for natural reading, consistent with the idea that FEF activation during eye movements is modulated by characteristics of the task (McDowell et al., 2008; Jamadar et al., 2013). These results suggest that eye movements in complex tasks also draw on domain-specific control processes.

Further study will be needed to determine the nature of the task-based functional differentiation of FEF within the eye movement network.

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