

Morphology of Primary Visual Cortex Predicts Individual Differences in Fixation Duration during Text Reading

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Abstract

■ In skilled reading, fixations are brief periods of time in which the eyes settle on words. E-Z Reader, a computational model of dynamic reading, posits that fixation durations are under real-time control of lexical processing. Lexical processing, in turn, requires efficient visual encoding. Here we tested the hypothesis that individual differences in fixation durations are related to individual differences in the efficiency of early visual encoding. To test this hypothesis, we recorded participants' eye movements during reading. We then examined individual differences

in fixation duration distributions as a function of individual differences in the morphology of primary visual cortex measured from MRI scans. The results showed that greater gray matter surface area and volume in visual cortex predicted shorter and less variable fixation durations in reading. These results suggest that individual differences in eye movements during skilled reading are related to initial visual encoding, consistent with models such as E-Z Reader that emphasize lexical control over fixation time. ■

INTRODUCTION

Reading requires systematically moving the eyes through text (Henderson, 2013; Rayner, 1998). Fixations are brief periods of time in which the high-acuity fovea settles on words, and saccades are quick jumps that step the eyes from fixation to fixation (Figure 1). Because eye movements are critical for efficient and effective reading, the nature of the processes that control them has been a focus of intense research (Engbert, Nuthmann, Richter, & Kliegl, 2005; Reichle, Pollatsek, Fisher, & Rayner, 1998).

Skilled readers typically fixate each word once, although some words are fixated more than once and other words are skipped. Fixation durations average 225 msec across readers, with considerable interindividual variability in this average (Henderson & Luke, in press; Rayner, Li, Williams, Cave, & Well, 2007). Individual differences in fixation duration can provide important data informing basic reading theory (Henderson & Luke, in press; Veldre & Andrews, 2014; Staub & Benatar, 2013; Kuperman & Van Dyke, 2011) and can also provide a behavioral index of reading ability and its change over time (Miller & O'Donnell, 2013; Blythe & Joseph, 2011). However, despite the importance of individual differences in fixation durations during reading, little is known about the neurocognitive processes that give rise to them.

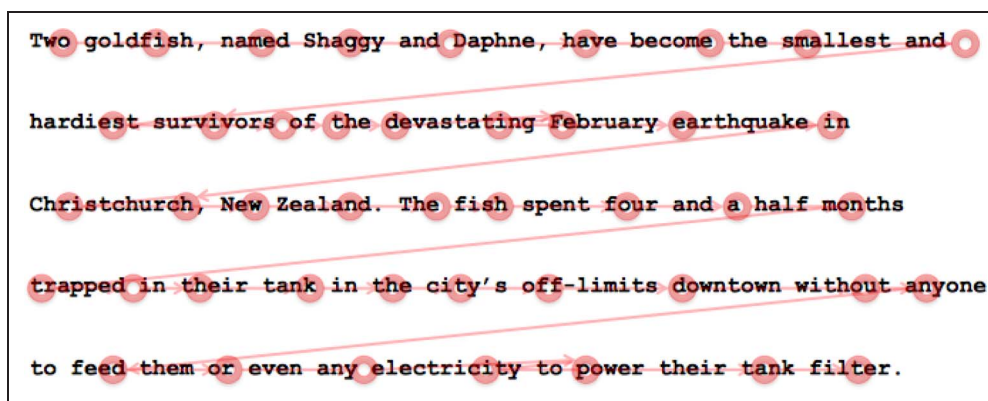
E-Z Reader is a detailed computational model of reading (Reichle, Rayner, & Pollatsek, 2003; Reichle et al., 1998). E-Z Reader posits that the earliest levels of visual word analysis influence eye movement control decisions

(Reichle & Reingold, 2013; Reichle et al., 1998, 2003). In E-Z Reader, the eyes are driven through text primarily by operations tied to lexical analysis via a two-stage process. An initial lexical familiarity check stage (L1) initiates oculomotor programming and is followed by a full word recognition stage (L2) that triggers an attentional shift. Stage L1 processing is assumed to follow preattentive visual analysis that takes place in early visual cortex (Reichle et al., 2013; Reichle, Tokowicz, Liu, & Perfetti, 2011). The model therefore predicts that early visual analysis contributes to the durations of fixations that are produced during reading because faster visual encoding by visual cortex enables more efficient L1 processing downstream. Here we tested this prediction by focusing on individual differences. Specifically, we hypothesized that individual differences in fixation duration during reading are related to ease of visual encoding enabled by individual differences in the morphology of early visual cortex. To test this hypothesis, we recorded the eye movements of participants while they read passages of text. We then examined individual differences in fixation duration distributions during reading as a function of the morphology of primary visual cortex determined from MRI scans.

Any observed individual differences in visual cortex related to fixation duration in reading could be domain-specific to reading or could be associated with visual processes supporting domain-general sequential eye movements of the type used in reading. To tease apart these possibilities, we compared eye movements in text-reading to eye movements in a pseudoreading control condition. In our pseudoreading condition, a meaningless geometric shape replaced each letter of text. This

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Figure 1. Eye movements in reading. Illustration of the reading pattern for a single participant during dynamic reading. Circles represent fixations and lines represent saccades.



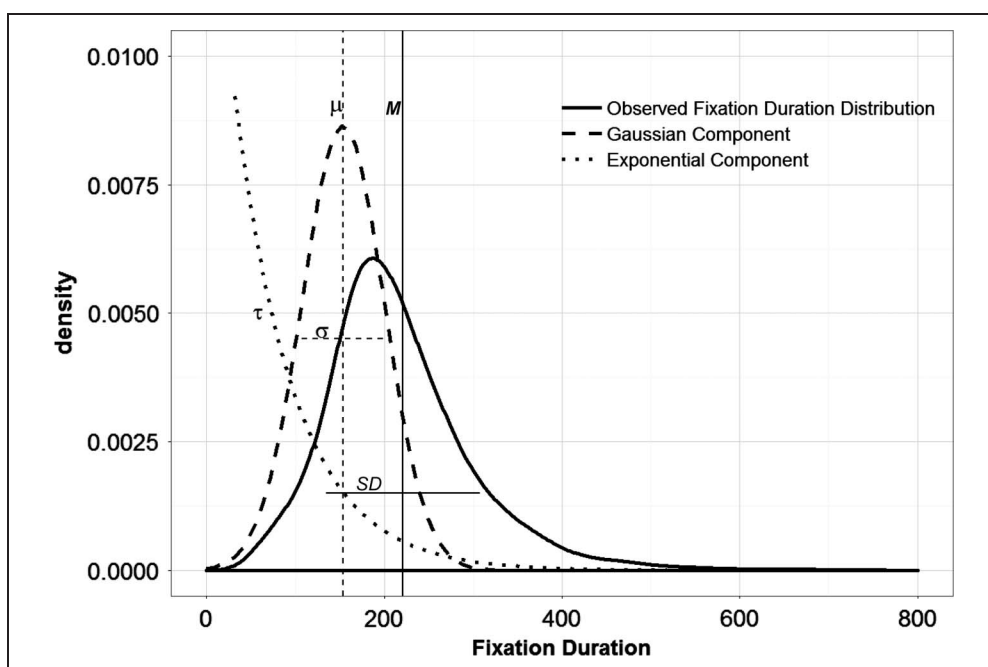
manipulation preserves word length and spacing as well as the spatial structure of text but removes language at all levels of analysis (e.g., orthographic, phonological, syntactic, semantic). Eye movements are globally very similar in text-reading and pseudoreading (Henderson, Luke, Schmidt, & Richards, 2013; Luke & Henderson, 2013; Henderson & Luke, 2012; Nuthmann & Engbert, 2009; Nuthmann, Engbert, & Kliegl, 2007; Rayner & Fischer, 1996; Vitu, O'Regan, Inhoff, & Topolski, 1995), making this comparison useful for testing whether observed effects are related to meaning or to perceptual and oculomotor processes independent of text comprehension.

To characterize the fixation durations of each participant, we generated the ex-Gaussian parameters of their fixation duration distributions (Figure 2; Balota & Yap, 2011). The use of fixation duration distributions to explore eye movement control has become an important tool in reading research (Henderson & Luke, in press; Luke & Henderson, 2013; Staub & Benatar, 2013; Reingold,

Reichle, Glaholt, & Sheridan, 2012; White & Staub, 2012; Staub, White, Drieghe, Hollway, & Rayner, 2010; Rayner et al., 2007; Yang & McConkie, 2001). The ex-Gaussian distribution provides three parameters (Figure 2), mu (μ) capturing central tendency, sigma (σ) capturing variability, and tau (τ) capturing the rightward skew of the distribution.

Participants read 22 text passages and scanned 22 pseudotext passages in the text-reading and pseudoreading conditions. Fixation duration distributions were characterized for each participant in each condition using the three parameters of the ex-Gaussian distribution. Morphology of primary visual cortex was operationalized for each participant as pericalcarine cortex defined by FreeSurfer (Desikan et al., 2006; Figure 3). We have previously observed strong functional activation along the calcarine sulcus in a block-design analysis comparing eye movements to RSVP reading (Henderson, Choi, Luke, & Schmidt, submitted-a).

Figure 2. Representative fixation duration distribution during reading. Solid curve shows an observed fixation duration distribution. Solid vertical line shows distribution mean (M) and solid horizontal line shows distribution standard deviation (SD). The observed distribution can be deconvolved into the components of the ex-Gaussian distribution. The dashed curve represents the normal component, with the vertical dashed line representing ex-Gaussian mu (μ) and the horizontal dashed line representing ex-Gaussian sigma (σ). The dotted curve shows the exponential component of the ex-Gaussian distribution captured by tau (τ).



METHODS

Participants

Twenty-nine right-handed members of the University of South Carolina community gave informed consent in accordance with the University of South Carolina institutional review board. All had normal or corrected-to-normal vision and none reported any reading disability. Data from four participants were removed from analysis because of excessive movement or lack of attention (closed eyes or lack of eye movements) in the scanner. Data from the remaining 25 participants (mean age = 27.5 years) were included in the analysis.

Materials

Text passages were taken from popular online news sources. Each passage contained 40–61 words. Word length averaged 4.96 characters (range = 1–19 characters). Text was displayed in Courier New font with 4.76 characters subtending 1° of visual angle. Each text paragraph was converted into pseudotext using a custom font in which each letter was replaced by a geometric shape that preserved letter and word locations and word shapes but eliminated meaning (Henderson et al., 2013; Luke & Henderson, 2013; Luke, Schmidt, & Henderson, 2013; Henderson & Luke, 2012). Both fonts were monospaced, and all letters, words, and lines of text appeared in the same locations across the text and pseudo fonts.

Apparatus

Stimuli were presented using an Avotec Silent Vision 6011 projector (Stuart, FL) in its native resolution (1024×768) and at a refresh rate of 60 Hz. Eye movements were recorded via an SR Research Eyelink 1000 long-range MRI eyetracker (spatial resolution of 0.01°) sampling at 1000 Hz. Viewing was binocular, and eye movements were recorded from one eye.

Procedure

Each participant saw 22 text passages and 22 pseudopassages in an MRI scanner as part of a larger fMRI study,

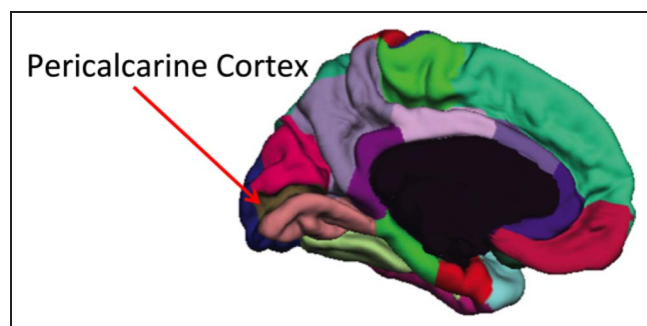


Figure 3. Pericalcarine cortex. Illustration of pericalcarine cortex (Klein & Tourville, 2012).

11 of each type of passage in each of two scanner runs. Within each run, passages and conditions were presented in a random order for each participant. Texts were rotated through conditions across participants. Text appeared in paragraph form on the display and participants were instructed to read text normally for comprehension and to move their eyes through pseudotext “as though they are reading.” Each passage was presented for 12 sec, with an intertrial interval of 6 sec between passages. Texts were rotated through conditions across participants. The text-reading and pseudoreading conditions were interleaved with two other conditions (reading via rapid serial visual presentation) not relevant for this study.

Eye Movement Data Collection

Before each run, a 9-point calibration routine was used to map eye position to screen coordinates. Successful calibration required an average error of less than 0.49° and a maximum error of less than 0.99° . A fixation cross was presented on the screen before each trial, with the first word in the text appearing at that location. Eye movements were recorded continuously throughout each run.

Eye Movement Data Processing

Initial analysis of the raw eye-tracking data was conducted using SR Research Dataviewer software to identify individual fixations and fixation durations. Saccade detection used three thresholds: the eye had to move at least 0.1° , with a velocity equal to or greater than $30^\circ/\text{sec}$ and with an acceleration of at least $8000^\circ/\text{sec}^2$. Fixations were defined as periods of time between saccades that were not part of blinks. Fixations were removed from analysis when they did not fall within a word region, were immediately preceded or followed by a blink, and were less than 50 msec or greater than 1500 msec. Saccades were removed from analysis if they contained a blink or comprised a return sweep from the end of one line to the beginning of the next. We have previously observed test–retest reliabilities of individual differences in mean fixation duration of 0.89 and 0.86 for text-reading and pseudoreading, respectively, and in residual standard deviations (controlling for correlations between mean and standard deviation) of 0.52 and 0.60, respectively (Henderson & Luke, in press), indicating that fixation duration is a relatively stable individual difference measure. An ex-Gaussian distribution was fit to the fixation duration data for each participant using QMPE software (Heathcote, Brown, & Cousineau, 2004). The ex-Gaussian distribution is the convolution of a normal (Gaussian) and an exponential distribution, with two parameters representing the normal component (μ , the mean, and σ , the standard deviation) and a single exponential parameter (τ). Central tendency and variability in the Gaussian component are captured by μ and σ , whereas τ reflects skew (Figure 2).

MRI Data Collection

MRI data were collected on a Siemens Medical Systems 3T Trio (Erlangen, Germany). A 3-D T1-weighted MP-RAGE RF-spoiled rapid flash scan in the sagittal plane was used with a 1-mm³ resolution and a field of view from the top of the head to the neck. For eight participants, sagittal T1-weighted MPRAGE (repetition time = 2250 msec, echo time [TE] = 4.18 msec, flip angle = 9°) anatomical reference images were acquired. For 17 participants, multiecho T1 (repetition time = 2530 msec, TE1 = 1.74 msec, TE2 = 3.6 msec, TE3 = 5.46 msec, TE4 = 7.32 msec, flip angle = 7°) were acquired.

MRI Data Analysis

The FreeSurfer (v. 5.3) software package was used to analyze participants' anatomical scans (Fischl, 2004, 2012; Desikan et al., 2006; Fischl & Dale, 2000; Dale, Fischl, & Sereno, 1999; Fischl, Sereno, & Dale, 1999). FreeSurfer (surfer.nmr.mgh.harvard.edu/) provides an algorithm for automated parcellation of cortical structure and registration with a standard atlas. For the current analysis, we used a nonrigid registration on the inflated brain surface to register individuals with the atlas, resulting in the parcellation of the cerebral cortex (Desikan et al., 2006). For each participant, the shape and position of the pericalcarine cortex (the ROI in this study) generated by FreeSurfer was visually inspected to ensure proper registration and to determine if manual correction was needed. In all cases registration was good, and so no manual correction was used. The gray matter volume and surface area of pericalcarine cortex for each participant as determined by FreeSurfer served as the dependent measures.

RESULTS

Table 1 shows the intercorrelations among the three ex-Gaussian parameters. In this sample, μ and σ were correlated in both the text-reading, $t(23) = 4.754, p < .001$, and pseudoreading, $t(23) = 4.247, p < .001$, conditions, whereas τ was not correlated with either μ or σ ($ts < 1.00$). These results replicate those reported in a large-

Table 1. Ex-Gaussian Correlations

Text-reading		Pseudoreading	
Parameters	Pearson <i>r</i>	Parameters	Pearson <i>r</i>
μ, σ	0.704*	μ, σ	0.663*
μ, τ	-0.208	μ, τ	0.085
σ, τ	-0.075	σ, τ	0.145

Intercorrelations among the ex-Gaussian parameters μ , σ , and τ for fixation durations during text-reading and pseudoreading.

* $p < .001$.

Table 2. Summary Eye Movement Data

Eye Movement Measure	Text-reading	Pseudoreading
μ	155.63	167.65
σ	45.52	52.47
τ	65.94	106.25
All fixation durations (msec)	225	280
First fixation durations (msec)	230	280
Gaze durations (msec)	273	349
Saccade amplitude (degrees)	2.30	2.19
Regression rate (%)	11.2	9.5

Global eye movement data for text-reading and pseudoreading averaged over participants. μ , σ , and τ = ex-Gaussian parameters for fixation duration distributions. All fixation duration = durations of all fixations; First fixation duration = duration of the initial fixation on each word; Gaze duration = sum of all fixations from first entry to first exit on each word; Saccade amplitude = amplitudes of all saccades; Regression rate = percent regressive (backward) interword saccades.

sample study examining ex-Gaussian parameters in fixation duration distributions during reading (Staub & Benatar, 2013). There were no significant correlations for each of the three parameters across text-reading and pseudoreading. Table 2 shows summary eye movement data collapsed over participants for text-reading and pseudoreading. These data are similar to those observed in previous studies comparing the same conditions (Henderson & Luke, in press) and demonstrate that participants were able to read normally in the scanner.

The primary data of interest involved relationships between the morphology of individuals' pericalcarine cortex and the ex-Gaussian parameters of their fixation duration distributions. For text-reading (Table 3 and Figure 4), significant negative correlations were observed between left pericalcarine cortex and μ and σ for both the gray matter volume and surface area measures. A similar negative correlation was observed between right pericalcarine cortex and μ for surface area. For pseudoreading (Table 3 and Figure 5), significant negative correlations were again observed between left pericalcarine cortex and μ and σ for both gray matter volume and surface area similar to those observed with text-reading. In addition, significant negative correlations were found between right pericalcarine cortex and μ and σ for both gray matter volume and surface area, extending the right hemisphere effect seen between μ for surface area in text-reading.

DISCUSSION

The results showed strong negative correlations between the morphology of pericalcarine cortex (gray matter volume and surface area) and individual differences in the

central tendency and variability of fixation duration distributions in both text-reading and pseudoreading. These results are the first to demonstrate a relationship between cortical morphology and individual differences in eye movements during text reading. The results support the general hypothesis that fixation duration in part reflects initial visual encoding, as well as the specific hypoth-

Table 3. Correlations between Intersubject Variability in Pericalcarine Cortex Morphology and Fixation Durations for Both Text-reading and Pseudoreading

Region	Parameter	Pearson r	p	Regression Equation
<i>Text Reading</i>				
Gray matter volume (mm ³)				
LH	μ	-.451	.0155	$Y = -0.01498 * X + 187.2$
LH	σ	-.437	.0447	$Y = -0.01019 * X + 67.02$
Surface area (mm ²)				
LH	μ	-.577	.0025	$Y = -0.02840 * X + 196.5$
LH	σ	-.488	.0132	$Y = -0.01932 * X + 73.33$
RH	μ	-.517	.0082	$Y = -0.02944 * X + 202.7$
<i>Pseudoreading</i>				
Gray matter volume (mm ³)				
LH	μ	-.416	.0385	$Y = -0.02389 * X + 218.1$
LH	σ	-.503	.0103	$Y = -0.01578 * X + 85.76$
RH	μ	-.555	.0040	$Y = -0.03230 * X + 245.8$
RH	σ	-.554	.0041	$Y = -0.01761 * X + 95.05$
Surface area (mm ²)				
LH	μ	-.413	.0400	$Y = -0.03732 * X + 221.3$
LH	σ	-.542	.0051	$Y = -0.02672 * X + 90.91$
RH	μ	-.583	.0022	$Y = -0.06094 * X + 265.0$
RH	σ	-.605	.0013	$Y = -0.03453 * X + 107.6$

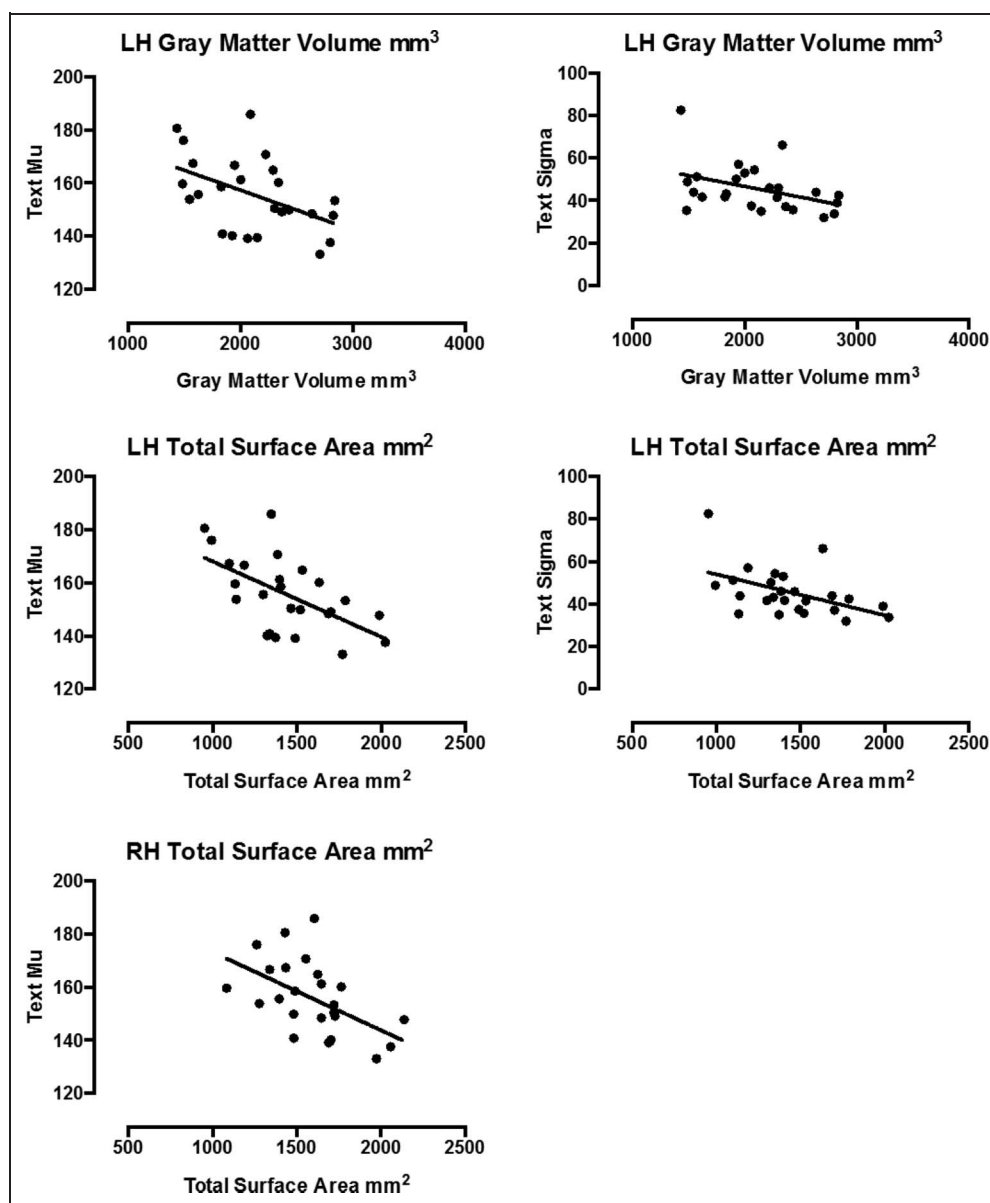
Cortical morphology measures are gray matter volume and surface area. LH = left hemisphere; RH = right hemisphere. Parameters are from ex-Gaussian fixation duration distributions for individuals. The p values (two-tailed) are from the F statistic ($df = 1,23$) for r^2 of the best-fitting linear regression equation (also shown).

esis derived from E-Z Reader that fixation duration in reading is driven by early visual analysis of text. At the same time, the finding that similar relationships were observed for pseudoreading suggests that the intersubject variability in fixation durations that are tied to visual encoding are not text specific. Instead, general encoding operations that are associated with fixation time in reading are also relevant for encoding in other domains. This result is consistent with the finding that individual differences in fixation duration in reading are correlated with individual differences in fixation duration in other tasks including visual search and picture memorization (Henderson & Luke, in press). At the same time, however, the observed associations here tended to be stronger in left hemisphere for text and bilaterally distributed for pseudotext, suggesting the possibility of some reading specialization in left-hemisphere visual cortex based on literacy (Szwed, Qiao, Jobert, Dehaene, & Cohen, 2014). Overall, we conclude that fixation durations are influenced by early visual encoding, consistent with E-Z Reader.

Estimates of the retina-brain lag (time between initial retinal activity and processing in early visual cortex) average on the order of 60 msec (Reichle & Reingold, 2013) with the earliest estimate of about 43 msec (Raij et al., 2010). Given how quickly the eyes move in reading, this leaves little time for text processing to influence saccade programming. At the same time, there is strong evidence that fixation durations are controlled in part by lexical analysis. For example, word frequency and word length account for a great deal of the variance in fixation durations (Rayner, 2009). In order for lexical analysis to be able to exert this rapid control, it is critical that initial visual analysis take place quickly. Therefore, efficient initial visual analysis is necessary for timely eye movements in reading. The present results show that interindividual variation in fixation duration is predicted by the structural properties of early visual cortex, consistent with the important role of initial visual encoding for reading.

All of the observed relationships between pericalcarine cortex and fixation duration in this study involved μ and σ . These results can be contrasted with a recent fMRI study of cortical activation and fixation duration distributions (Henderson, Choi, Luke, & Schmidt, submitted-b). In that study, strong associations were observed between activation in the eye movement control network and τ , a measure of more extreme values in the tail of the fixation duration distribution, with stronger activation leading to a reduction in τ . One interpretation of the differential effects on μ and σ here and τ in the eye movement network is that an individual's fixation duration mean and variability are strongly influenced by visual encoding efficiency, whereas longer durations contributing to the tail of the distribution are influenced by higher-level language processing. This interpretation is consistent with the hypothesis that language processes exert their influence on eye movements in reading via later inhibitory feedback signals (Reichle, Warren, & McConnell, 2009).

Figure 4. Text-reading. Correlations between morphology of pericalcarine cortex and ex-Gaussian distribution parameters for fixation duration during text-reading by participant. Graphs show best-fitting regression lines for significant correlations of cortical morphology (gray matter volume and total surface area) and ex-Gaussian distribution parameters. Left column shows data for μ , and right column shows data for σ .



An interesting trend in our results involved hemispheric differences for the text-reading and pseudoreading conditions. We observed a bias toward stronger left-hemisphere associations between visual cortex and fixation durations in text-reading, with four of five observed effects in the left hemisphere. The associations were more evenly distributed across hemispheres for pseudoreading, with four observed effects in each hemisphere. Another way to look at this is that four of five of the right hemisphere effects involved pseudotext. These differences in hemispheric distribution may simply be because of chance, but they do align with the well-known dominance of the left-hemisphere for language. They also align with recent reports that activation in left-hemisphere visual cortex as measured with fMRI reflects word recognition (Szwed et al., 2011, 2014). It is tempting to speculate that left hemisphere visual encoding during text-reading is particularly important for

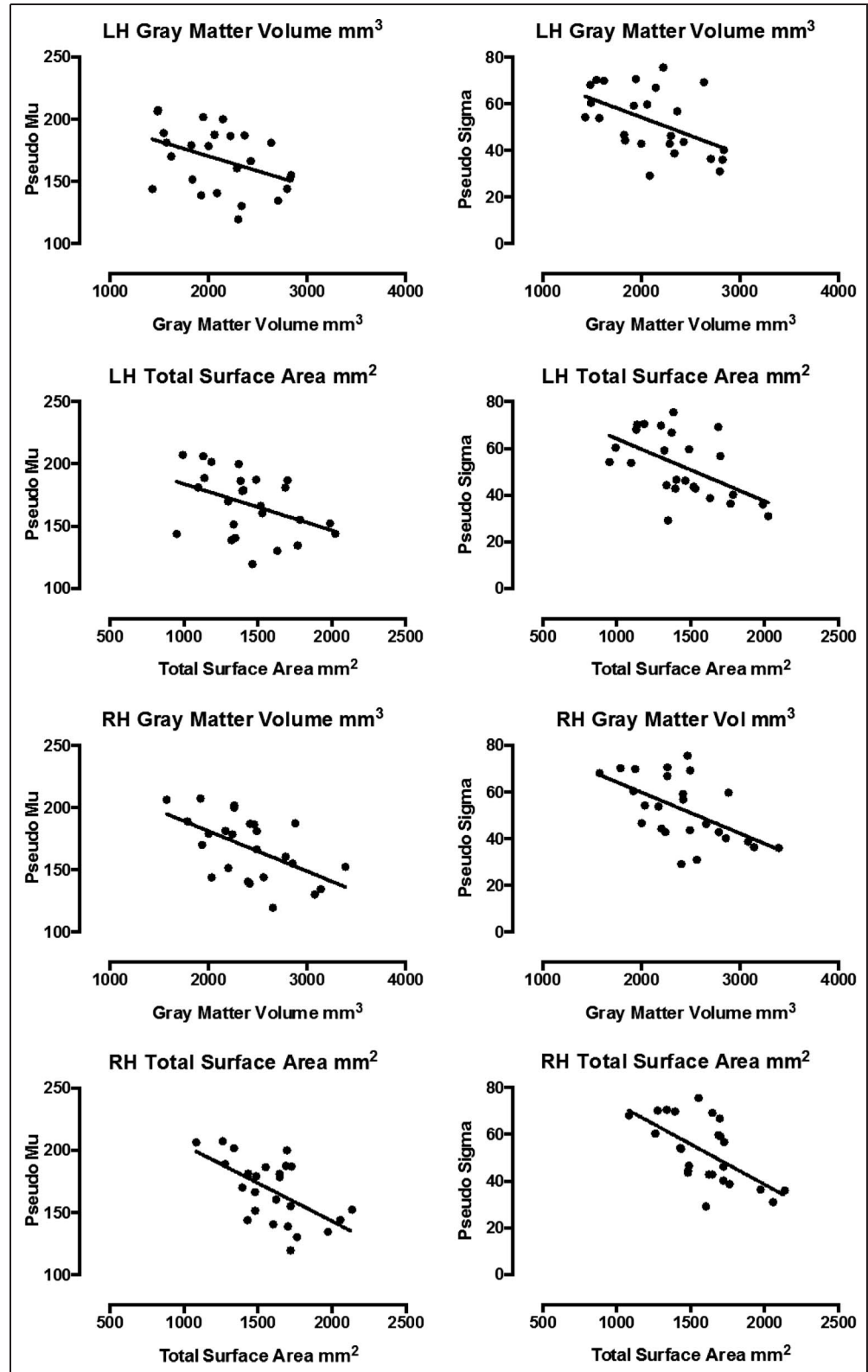
enabling the lexical processes that drive the eyes forward through text as proposed by E-Z Reader. Another possibility is that left-hemisphere visual encoding is particularly important for parafoveal analysis of the upcoming word to the right of the currently fixated word during reading, a phenomenon known as parafoveal preview. Parafoveal preview is thought to play an important role in enabling lexical processing (Reingold et al., 2012; Rayner, 2009). The upcoming word in English appears in the right visual field with initial projection to left primary visual cortex and may therefore especially benefit from efficient left-hemisphere visual analysis.

We note that the cortical structure investigated in this study is not typically thought to be directly tied to lexical analysis (Szwed et al., 2011, 2014). Instead, this study was predicated on the assumption that lexical analysis supporting the L1 and L2 stages of lexical analysis in E-Z Reader

are enabled by initial visual analysis in visual cortex (Reichle et al., 2011), not that those processes take place in primary visual cortex. Presumably early (potentially preattentive) visual analysis produces the primitive features that are then used by systems that support subsequent orthographic

analysis downstream. Consistent with this view, our results suggest that differences in initial visual analysis generated by differences in cortical morphology are predictive of differences in fixation durations. Interestingly, potential hemispheric differences aside, these relationships hold

Figure 5. Pseudoreading. Correlations between morphology of pericalcarine cortex and ex-Gaussian distribution parameters for fixation duration during pseudoreading by participant. Graphs show best-fitting regression lines for significant correlations of cortical morphology (gray matter volume and total surface area) and ex-Gaussian distribution parameters. Left column shows data for μ , and right column shows data for σ .



for both text-reading and pseudoreading. This latter finding is not surprising given that individual differences in fixation durations tend to be correlated across reading and other viewing tasks (Henderson & Luke, in press). Further investigation will be needed to determine whether cortical structures devoted specifically to visual word analysis also predict fixation durations and whether those effects are specific to reading. It will also be important to determine whether the trend toward greater correlation of left-hemisphere visual cortex with fixation duration in text-reading replicates.

Finally, from a methodological perspective, we have shown that eye tracking can be successfully combined with structural MRI to provide new data bearing on contrasting theoretical approaches to eye movement control in reading. This study thus represents proof of concept that combining eye tracking with MRI can provide new insight into reading. Furthermore, we have shown how this type of research can be driven by theoretical models of underlying cognitive processes associated with complex behavior like reading. In the present case, our study was motivated in part by a hypothesis derived from E-Z Reader, an implemented model of the relationship between cognitive processing and eye movement control in dynamic reading.

Conclusion

Eye tracking has proved to be one of the richest and most important behavioral sources of information about the perceptual, cognitive, and linguistic processes that take place during reading (Rayner, 2009). Temporal and spatial sensitivity are critical reasons for the prominence of eye tracking: The durations of individual fixations provide an online measure of lexical processing in the sense that lexical variables associated with the fixated word influence fixation duration on that word. This real-time control of fixation duration by lexical analysis requires that visual information from the fixated word be encoded quickly. Readers vary in their fixation durations during reading, and these differences are stable over time (Henderson & Luke, in press). On the basis of the assumptions of the E-Z Reader model of reading, we hypothesized that differences in the efficiency of visual encoding across individuals might account for individual differences in fixation time. Consistent with this hypothesis, our results show that individual differences in fixation duration are associated with interindividual variability in the structure of primary visual cortex. This study underlines the idea that individual differences can be a powerful method in cognitive neuroscience with which to test specific hypotheses about neurocognitive function (Vogel & Awh, 2008).

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