

Reading Skill is Related to Individual Differences in Brain Structure in College Students

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Abstract: We compared cortical anatomy, using 3D brain MRI scans, between three groups of university students: proficient readers (skilled at phonological decoding and text comprehension), poor readers (impaired at phonological decoding and text comprehension), and resilient readers (impaired at phonological decoding but skilled in text comprehension). This latter group provides a unique opportunity to investigate associations between cortical morphology and phonological decoding deficits in individuals without attendant reading comprehension deficits. We predicted widespread reductions in gray matter thickness and brain size in temporal and frontal regions in poor readers, and more focal differences in brain morphology in resilient readers. Typical asymmetry of gray matter thickness in the temporo-parietal region was reduced in both poor and resilient readers. Poor readers also exhibited smaller brain sizes in the right inferior frontal region than both proficient and resilient readers. Altered asymmetry in the temporo-parietal region may therefore be associated with poor phonological decoding and impaired text comprehension may be associated with altered frontal morphology. Resilient readers show relatively focal behavioral differences from typical readers, so it is interesting that they show reliable differences in brain morphology. *Hum Brain Mapp* 32:1194–1205, 2011. © 2011 Wiley-Liss, Inc.

Key words: MRI; temporal lobe; frontal lobe; dyslexia; cerebral cortex

INTRODUCTION

Relationships between neuroanatomy and reading skill have long been sought. Although there is a wide range of reading abilities among nondyslexic readers, most prior studies have compared individuals with dyslexia to those with typical reading abilities. In the current study, we investigate brain morphology in a sample of university students with different reading profiles, including a group that showed a dissociation between phonological decoding and text comprehension abilities. The existence of such individuals challenges the widely held belief that strong phonological skills are necessary for skilled reading comprehension and allows us to investigate differences in cortical anatomy between individuals with specific deficits in phonological processing. Such an approach allows us to investigate morphological differences between groups of

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readers with more focal behavioral differences than prior studies have considered. A demonstration that cortical morphology differs between individuals with relatively minor and focal reading deficits may suggest that relationships exist between reading ability and brain anatomy even among those with highly skilled reading comprehension. To gain insight into potential neuroanatomical characteristics of this novel group, prior studies of developmental changes in brain morphology and function that may relate to typical reading development and studies comparing reading impaired individuals to typical readers should be considered.

Studies investigating associations between neurodevelopmental changes and changes in reading skill have suggested that frontal and temporal lobe maturation may relate to reading acquisition. In typically developing children, gray matter thickening in the inferior frontal cortex was associated with improving phonological abilities [Lu et al., 2007]. Reading ability also correlated with fractional anisotropy, a measure of white matter integrity derived from diffusion-weighted imaging, in the left temporal lobe in individuals between the age of 8 and 18 [Nagy et al., 2004]. Between the ages of 6 and 22, individuals with better reading skills showed more activity in left inferior frontal and middle temporal cortex, and less activity in right infero-temporal regions [Turkeltaub et al., 2003].

These developmental studies largely agree with studies comparing cortical anatomy between impaired and normal readers. Across studies, perhaps the most consistent finding is altered morphology in the left temporal lobe. Decreased tissue volume throughout the left temporal lobe was observed in dyslexic men [Brown et al., 2001; Eliez et al., 2000]. In other samples, more focal group differences in temporal lobe anatomy have been reported in the left supramarginal gyrus [Eckert et al., 2005], the posterior superior temporal gyrus and temporo-parieto-occipital junction [Brown et al., 2001], and in the left superior temporal gyrus [Brambati et al., 2004]. Some have found that dyslexics have altered morphology in more ventral cortical regions [Brambati et al., 2004; Eckert et al., 2005; Kronbichler et al., 2008; Vinckenbosch et al., 2005]. These reductions in gray matter are frequently more extensive in the left hemisphere, resulting in a reduction of the typical leftward asymmetry.

Reduced asymmetry of temporal regions has long been proposed to be associated with dyslexia [Galaburda, 1989; Galaburda et al., 1985]. Such reductions in asymmetry in language relevant regions have also been observed in functional imaging studies [Shaywitz et al., 2002], suggesting that the left-lateralized regions that support normal reading have not developed properly in dyslexic individuals. Some more recent studies have found reductions in temporal asymmetry in dyslexics, while others have found no reading group differences [reviewed in Beaton, 1997; Eckert, 2004]. Others have suggested that reading disability may be associated with increased leftward asymmetry. It has been proposed that extreme asymmetry of the pla-

num may characterize readers with intact comprehension and impaired phonological processing [reviewed in Leonard and Eckert, 2008]. In a case study, a compensated dyslexic adult showed extreme leftward asymmetry of the planum temporale [Chiarello et al., 2006a]. Dyslexic engineering students show more leftward asymmetry of the parietal operculum than controls [Robichon et al., 2000].

Inferior frontal morphology also may differ between reading groups, given its role in language processing. Dyslexic men showed reduced gray matter volume in the left orbital and frontal pole and bilaterally in the inferior and superior frontal gyri [Brown et al., 2001]. Relatives of dyslexics who themselves showed either clinically evident or compensated dyslexia had reduced gray matter volume in left superior and inferior frontal gyri [Brambati et al., 2004]. It has also been reported that dyslexic children had smaller pars triangularis volumes bilaterally [Eckert et al., 2003].

These previous studies of brain morphology in reading disabled individuals have been somewhat inconsistent in the extent and localization of morphological differences. These inconsistencies may result from different subject selection criteria, as readers varied greatly in age and severity of reading disability across studies. In the present sample, we had the opportunity to investigate whether different neural substrates relate to phonological decoding and reading comprehension. Such a finding might explain apparent inconsistencies between prior studies in which reading skills were not considered independently. Additionally, prior studies have employed a variety of image processing techniques. The present study used sophisticated cortical matching algorithms to investigate differences in brain morphology. Compared to voxel-based morphometry (VBM), cortical pattern matching controls for variation in gyral anatomy across subjects, increasing our ability to identify group difference in some anatomical regions. We examined gray matter thickness, radial expansion (a measure of local brain size), and left-right asymmetries of gray matter thickness across the entire cortical surface of the brain at thousands of anatomical points matched across subjects. We identified proficient readers (skilled in both phonological decoding and reading comprehension), poor readers (impaired at both phonological decoding and reading comprehension), and resilient readers (impaired at phonological decoding, but skilled at reading comprehension) from a large sample of college students. Resilient readers have phonological and orthographic skills similar to those of poor readers, and show greater semantic priming than both poor and proficient readers [Welcome et al., submitted for publication]. Additional behavioral characteristics of resilient readers have been described previously [Jackson and Doellinger, 2002; Welcome et al., 2009]. Because resilient and poor readers were identified by shared deficits in phonological decoding, morphological alterations common to these two groups might shed light onto the neural substrates of phonological decoding. Poor readers were distinguished from

resilient readers by reading comprehension; therefore, morphological differences between these groups may reflect, at least in part, neural substrates of reading comprehension level.

Functional imaging studies using tasks that place differing demands on various reading processes have identified brain regions that are active during reading, and we used these findings to inform our predictions regarding brain morphology. A bilateral ventral frontal region, including the inferior frontal gyrus, has been implicated in semantic processing [reviewed in Fiez, 1997]. The left inferior frontal region has also been shown to be active during phonological processing [reviewed in Pugh et al., 1996]. A left lateral temporal region, centered on the middle temporal gyrus, has shown activation during semantic processing tasks [Vandenberghe et al., 1996; Hoenig and Scheef, 2005]. A left ventral region, including ventral extrastriate cortex and the fusiform gyrus, has been proposed to support pre-lexical orthographic analysis [Cohen et al., 2000]. A left temporo-parietal region, including the posterior superior temporal, supramarginal and angular gyri, showed activation during the conversion of orthography to phonology [Booth et al., 2002; Joubert et al., 2004].

In our sample, relative to proficient readers, poor readers showed deficits in both phonological decoding and reading comprehension. Therefore, poor readers were predicted to show structural brain abnormalities throughout the frontal and temporal regions thought to support phonological processing and meaning access. Specifically, we hypothesized that poor readers would show (1) bilateral reductions in gray matter thickness and radial expansion in the lateral ventral frontal region relative to proficient readers; (2) less leftward asymmetry of the temporo-parietal region than proficient readers; and (3) reduced size and gray matter thickness in the left temporal lobe compared to both proficient and resilient readers. Resilient readers show a more focal behavioral deficit, with primary impairments in phonological processing. Therefore, they were predicted to show alterations in brain structure confined to regions thought to support phonological processing. Resilient readers were predicted to show (1) reduced radial expansion and gray matter thickness in the posterior inferior frontal region relative to proficient readers; and (2) alterations in leftward asymmetry of the temporo-parietal region relative to proficient readers.

METHODS

Participants

A total of 55 university students participated in the study. Fifty-two of these individuals were selected on the basis of their reading profile from a pool of 200 university students who participated in the Biological Substrates for Language Project [Chiarello et al., 2006b]. To increase the number of poor readers in the study, an additional three participants were recruited from the Riverside community

through ads targeting individuals with a history of reading disability. All participants were native speakers of English with normal or corrected-to-normal vision and ranged in age between 18 and 34 years of age (mean age = 21.1, SD = 3.4 years). Participants with a history of brain injury or disease or conditions incompatible with MRI were excluded. A neuroradiologist confirmed the absence of visible neuropathology.

This sample included 22 proficient readers, 21 resilient readers, and 12 poor readers identified on the basis of their performance on the Word Attack and Passage Comprehension subtests of the Woodcock Reading Mastery Test Revised/Normative Update (WRMT-R/NU) [Woodcock, 1998]. All proficient readers had scaled scores above 98 on both subtests, indicating that their reading performance was at least typical for their age. All poor readers had scaled scores below 95 on both subtests, indicating that their performance was at least a third of a standard deviation below the age-based norm. As the poor readers' scores were in the lowest 10% of 200 university students, they represent the lower extreme of reading ability in our sample. Resilient readers had scaled scores below 95 on the Word Attack subtest and above 98 on the Passage Comprehension subtest, with a discrepancy of at least 10 scaled score units between an individual's Word Attack score and Passage Comprehension score. Mean reading scores are presented in Table I. Overall, the sample consisted of 51% males, 89% right-handers, and had a mean age of 21.1 years. Groups did not significantly differ in proportion of males, age, handedness, or level of parental education [Welcome et al., 2009; Welcome et al., submitted for publication].

Procedures

In a 2-h preliminary session, participants completed measures of handedness, questionnaires regarding language and family background, and standardized measures of reading skill and intelligence. The Word Attack and Passage Comprehension subtests of the WRMT-R/NU [Woodcock, 1998] were administered to assess participants' ability to read pseudowords and to supply contextually appropriate completions to increasingly complex stimuli. Age norms were used to calculate scaled scores and percentile ranks. Performance of the reading groups on other standardized measures and experimental tasks is

TABLE I. Mean scaled scores (standard deviations) on the WRMT-R/NU

	Proficient readers (N = 22)	Resilient readers (N = 21)	Poor readers (N = 12)
Word attack	104.9 (5.8)	87.2 (3.2)	86.4 (8.0)
Passage comprehension	108.5 (6.8)	107.0 (7.2)	91.7 (2.3)

described in a previous manuscript [Welcome et al., 2009; Welcome et al., submitted for publication].

Imaging Acquisition

Each participant received a volumetric MRI scan (3-D SPGR, 1.2-mm thick slices) in a GE Signa 1.5 Tesla Scanner at the Computerized Diagnostic Imaging Center in Riverside. The imaging parameters used were as follows: TR 11 ms; TE 2.2 ms; flip angle 25°; field of view 24 cm; acquisition matrix 256 × 256; acquisition time, 4.36 min.

Image Processing

The image analysis procedures have been described in detail previously [Sowell et al., 2001, 2004]. Briefly, MRI scans from each individual were processed through a series of manual and automated procedures including: (1) nonbrain tissue (i.e., scalp, orbits) was removed from a brain mask [Dogdas et al., 2005]; (2) the hemispheres were separated and the cerebellum was removed; (3) magnet inhomogeneity was corrected using a Bias Field Correcting algorithm; (4) a tissue classification algorithm categorized each voxel in the image as white matter, gray matter, or CSF [Shattuck et al., 2001]; (5) the processed image was temporarily converted to a standard space using a completely automated 12-parameter transformation which employs scaling [Woods et al., 1993]; (6) signal intensity midway between the average value for gray matter and the average value for CSF was used to guide an automatic extraction of the cortical surface [MacDonald et al., 1994]. This step results in a spherical mesh of 131,072 triangulated elements spanning 65,536 surface points that follows the contour of the brain surface; (7) 17 sulci in each hemisphere were manually traced on the lateral surface (Sylvian fissure, central sulcus, precentral sulcus, postcentral sulcus, superior temporal sulcus (STS) main body, STS ascending branch, STS posterior branch, primary intermediate sulcus, secondary intermediate sulcus, inferior temporal sulcus, superior frontal sulcus, inferior frontal sulcus, intraparietal sulcus, transverse occipital sulcus, olfactory sulcus, occipito-temporal sulcus, and collateral sulcus). An additional set of 12 sulci was outlined on the medial surface of each hemisphere (callosal sulcus, inferior callosal outline, superior rostral sulcus, inferior rostral sulcus, paracentral sulcus, anterior, and posterior segments of the cingulate sulcus, outer segment double parallel cingulate sulcus, parieto-occipital sulcus, anterior and posterior segments of the calcarine sulcus, and the subparietal sulcus). A set of six curves was outlined to establish gyral limits at midline. Protocols, including criteria for start and stop points, have been developed and reliability has been previously reported [Sowell et al., 2002, 2004]; (8) the 12-parameter transformation that was used to scale each participant's brain was inverted and the surface, lines, and images were transformed back into reoriented space; (9)

the first and last points of each sulcal line were used to compute a rigid-body transformation that put subjects into a common orientation while retaining the native size and shape of the brain; (10) averaged sulcal landmarks were used as anchors to drive the cortical surface mesh models from each subject into correspondence [Thompson et al., 2004]. In this way, points were matched across individuals relative to specific sulci so that comparisons of gray matter and surface location were based on homologous surface points, as far as possible.

The measure of radial expansion has been developed primarily to quantify group differences in local brain shape. Radial expansion was calculated by measuring the distance, in mm, from the center of mass of the hemisphere to each of the 65,536 brain surface points [Sowell et al., 2001]. This measure presumably reflects expansion of the cortical surface due to both underlying gray and white matter. Gray matter thickness was calculated using the Eikonal Fire Equation [Sapiro, 2001; Thompson et al., 2004]. The 3D Eikonal equation was applied only to voxels that segmented as gray matter. The image data were supersampled to create voxel dimensions of 0.33 mm³. Cortical thickness (in millimeters) was averaged within a 15-mm sphere centered on each surface point. This approach allowed us to calculate cortical thickness with an effective resolution finer than the original voxel size given that the error associated with localizing anatomy on the inner and outer cortical surfaces was averaged with the unbiased error of all other voxels within the smoothing kernel (i.e., ~42,000 0.33-mm³ voxels). This approach has been shown to be both valid and reliable [Sowell et al., 2004].

To investigate group differences in asymmetry of gray matter thickness, asymmetry maps for each measure were created for each individual. Each subject's right hemisphere was reflected in the midsagittal plane, to have the appearance of a left hemisphere, and sulcal matching was performed on the full set of left and "flipped" right hemispheres. In this way, sulcal anatomy was matched not only across individuals but also between hemispheres. We then used these flipped sulcally matched brain surface representations to assess ratios of gray matter thickness at analogous surface points. Gray matter thickness asymmetry was calculated as the ratio of gray matter thickness on the left to gray matter thickness on the right. This ratio is greater than 1 if gray matter is thicker on the left and less than 1 if gray matter is thicker in the right hemisphere.

Statistical Analyses

To visualize group differences in local brain size and gray matter thickness, uncorrected statistical maps were created comparing groups of proficient, resilient, and poor readers. In these maps, the correlation (Pearson's r) between group membership and thickness or brain size was calculated. Proficient readers were compared with



Figure 1.

ROIs used in permutation analyses. Regions are coded as follows: Lateral dorsal frontal, green; lateral ventral frontal, red; lateral parietal, pink; temporo-parietal, yellow; lateral occipital, dark blue; temporal, purple; medial frontal, blue; medial posterior, teal.

both poor and resilient readers separately, and resilient and poor readers were compared. A surface-point significance threshold of $P = 0.05$ (uncorrected) was considered significant.

These maps allow for easy visualization of the spatial patterns of relationships between brain morphology and performance or group membership. To confirm localization of effects and to correct for multiple comparisons, permutation methods [Bullmore et al., 1999] were used. To localize effects at a lobar level, eight coarse regions of interest (ROIs) were modified from a probabilistic atlas [Evans et al., 1994]. On the lateral surface, parietal, temporal, and occipital ROIs were used. The lateral frontal lobe was separated into ventral and dorsal regions by dividing it in half along the dorsal/ventral axis. A temporo-parietal ROI was created by centering a sphere 20 mm in diameter at the posterior extent of the Sylvian fissure on an average brain image. Medial ROIs encompassed the 11 slices closest to midline. The medial surface was divided in frontal and posterior portions. The ROIs in standard space were transformed into each individual's native space, and then averaged across individuals to create regional masks. An example showing these ROIs displayed over a representative brain surface is displayed in Figure 1. The area encompassing the corpus callosum, ventricular wall, and brain stem was not analyzed, as no gray matter is present in those regions.

In the permutation analyses, group membership was randomly reassigned 10,000 times and new correlation analyses were conducted for each reassignment. This resulted in a null distribution of results that occurred by chance that was compared to the results from the real assignment. For each permutation, the number of points that reached significance within each ROI are counted and compared to the number of points that reach significance with the actual subject assignments. A statistical threshold of 0.01 was used to identify voxels in which significant group differences were observed. If fewer than 5% of the random reassignments resulted in more points below the 0.01 threshold than the real assignment, the effect within an ROI was considered significant.

RESULTS

Poor Readers Compared With Proficient Readers

Comparisons between poor ($N = 12$) and proficient ($N = 22$) readers were performed to explore differences in brain anatomy between individuals who decode and comprehend text well and those who do not. Group differences in radial expansion, gray matter thickness, and gray matter thickness asymmetry are shown in Figure 2 and statistical values are presented in Table II. Compared with proficient readers, poor readers show significantly less radial expansion in the right lateral inferior frontal, right lateral superior frontal, and right lateral parietal regions (Fig. 2A). The magnitude of difference in radial expansion between poor and proficient readers is illustrated in Figure 2B. In regions of maximal difference, brain surface extent is reduced up to 5 mm in poor readers. Proficient and poor readers show no reliable differences in gray matter thickness (Fig. 2C,D). Compared with proficient readers, poor readers show a decrease in leftward asymmetry in the temporo-parietal region (Fig. 2E). The magnitude of this alteration in asymmetry is shown in Figure 2F. In the temporo-parietal region, gray matter asymmetry is reduced by a maximum of 20% in poor readers. Proficient readers show a leftward asymmetry in this region (with ~10% more gray matter in the left hemisphere in areas of maximal asymmetry), but poor readers show a rightward asymmetry (with ~10% less gray matter in the left hemisphere in areas of maximal asymmetry).

Resilient Readers Versus Proficient Readers

Comparisons of resilient ($N = 21$) and proficient ($N = 22$) readers were performed to investigate differences in brain anatomy between individuals who are impaired at phonological decoding and those who are not in samples matched for reading comprehension scores. Group differences in radial expansion, gray matter thickness, and gray matter thickness asymmetry are shown in Figure 3 and Table II. Resilient and proficient readers did not reliably differ in radial expansion (Fig. 3A) and maximal differences in radial expansion did not exceed 3 mm (Fig. 3B). Resilient and proficient readers did not significantly differ in gray matter thickness (Fig. 3C,D). Resilient readers show significantly less leftward asymmetry in the temporo-parietal region (Fig. 3E). The magnitude of differences of asymmetry between resilient and proficient readers (Fig. 3F) was similar to the magnitude of difference between poor and proficient readers (Fig. 2F).

Poor Readers Versus Resilient Readers

Comparisons of resilient ($N = 21$) versus poor readers ($N = 12$) were performed to investigate differences in brain anatomy between individuals who are skilled at Passage Comprehension and those who are not in samples

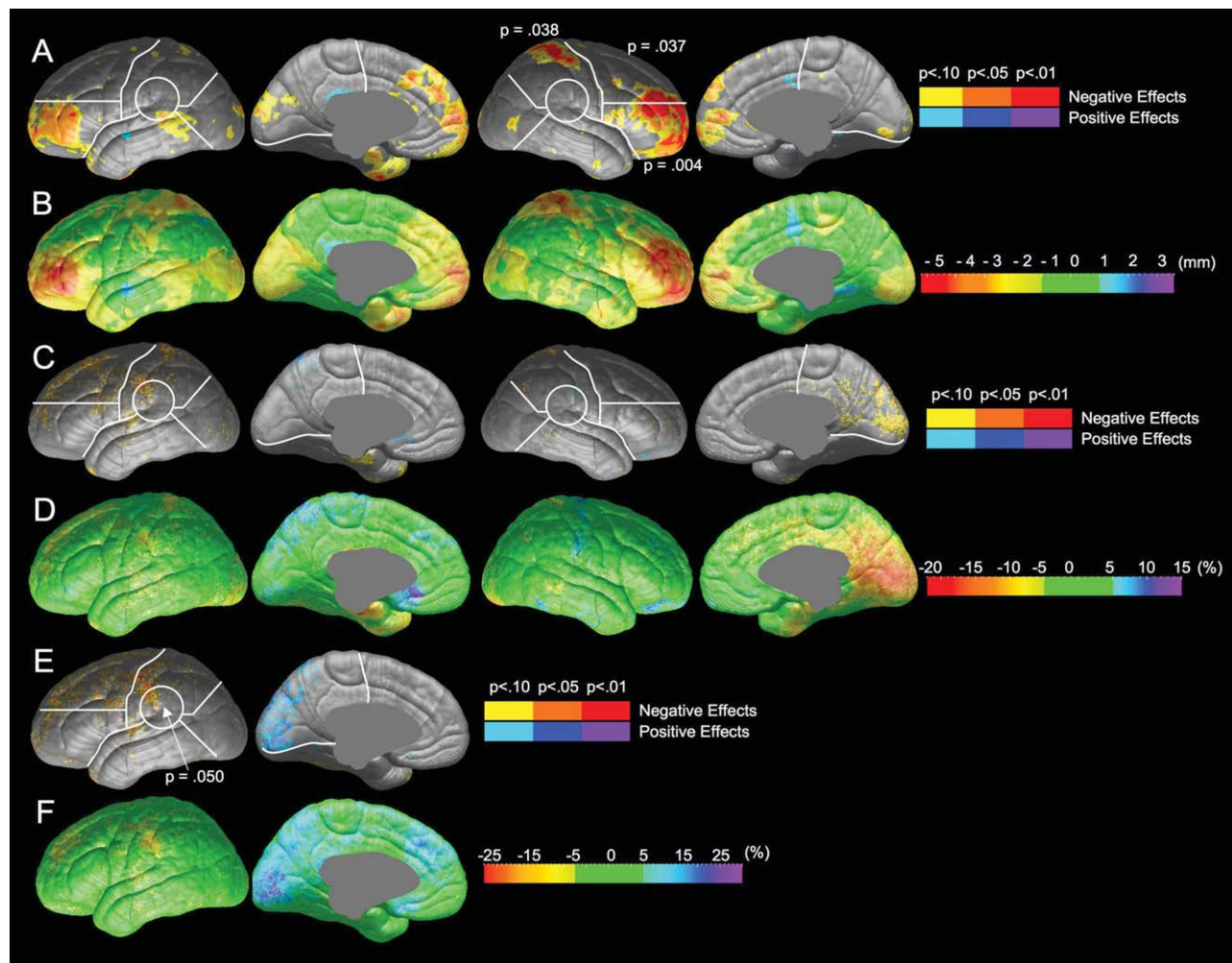


Figure 2.

Comparison of brain morphology between proficient and poor readers. Probability values, represented by color, are mapped onto an average cortical surface model. Regions shown in hot colors (yellow, orange, and red) are areas in which poor readers have less radial expansion, thickness, or leftward thickness asymmetry than proficient readers; regions in cool colors (blue and purple) are areas in which poor readers have greater radial expansion, thickness, or leftward thickness asymmetry than proficient readers. Significance values from permutation tests are shown for each ROI in which group differences were significant

by permutation. **(A)** Statistical comparison of radial expansion between proficient and poor readers. **(B)** Magnitude of differences in radial expansion between proficient and poor readers. **(C)** Statistical comparison of gray matter thickness between proficient and poor readers. **(D)** Magnitude of differences in gray matter thickness between proficient and poor readers. **(E)** Statistical comparison of gray matter thickness asymmetry between proficient and poor readers. **(F)** Magnitude of differences in gray matter thickness asymmetry.

equally impaired in phonological decoding. Group differences in radial expansion, gray matter thickness, and gray matter thickness asymmetry are shown in Figure 4 and Table II. Compared to poor readers, resilient readers show a significant increase in radial expansion in the right lateral inferior frontal and right lateral parietal regions (Fig. 4A). The magnitude of the reduction in radial expansion in poor readers (shown in Fig. 4B) is similar to the reduction shown in poor readers relative to proficient readers (Fig.

2B). Resilient and poor readers do not show reliable differences in gray matter thickness (Fig. 4C,D). Resilient and poor readers did not reliably differ in the asymmetry of gray matter thickness (Fig. 4E,F).

DISCUSSION

Several studies have examined neural correlates of reading ability, but this study was the first to examine brain

TABLE II. Significance of permutation values from each ROI at a threshold of 0.01

Region	Poor versus proficient readers			Proficient versus resilient readers			Resilient versus poor readers		
	Radial exp.	Thickness	Asymmetry	Radial exp.	Thickness	Asymmetry	Radial exp.	Thickness	Asymmetry
Left inf. frontal lat.	0.08	NS	NS	NS	NS	NS	NS	NS	NS
Left sup. frontal lat.	NS	NS	NS	NS	NS	NS	NS	NS	NS
Left parietal lat.	NS	NS	NS	NS	NS	NS	NS	NS	NS
Left occipital lat.	NS	NS	NS	NS	NS	NS	NS	NS	NS
Left temporal	NS	NS	NS	NS	NS	NS	NS	NS	NS
Left temporo-parietal	NS	0.10	0.05	NS	0.08	0.04	NS	NS	NS
Left frontal med.	NS	NS	NS	NS	NS	NS	0.06	NS	NS
Left posterior med.	NS	NS	NS	NS	NS	NS	NS	0.05	NS
Right inf. frontal lat.	0.00	NS	NS	NS	NS	NS	0.01	NS	NS
Right sup. frontal lat.	0.04	NS	NS	NS	NS	NS	0.07	NS	NS
Right parietal lat.	0.04	NS	NS	NS	NS	NS	0.04	NS	NS
Right occipital lat.	NS	NS	NS	NS	NS	NS	NS	NS	NS
Right temporal	NS	NS	NS	NS	0.10	NS	NS	NS	NS
Right temporo-parietal	NS	NS	NS	NS	NS	NS	NS	NS	NS
Right frontal med.	NS	NS	NS	NS	NS	NS	NS	NS	NS
Right posterior med.	NS	NS	NS	NS	NS	NS	NS	NS	NS

morphology in adults with impaired phonological processing and intact reading comprehension. Such individuals are of theoretical interest because they suggest that skilled reading comprehension can develop in individuals with relatively poor phonological skills. Because we classified readers according to performance on subtests that represent two different dimensions of reading ability, we were able to detect differences in brain structure between groups that differ in specific reading subskills. This may allow us to observe more precise anatomical-functional associations than generalized comparisons between normal and dyslexic readers. Proficient readers were compared with resilient readers (poor phonological decoders with good passage comprehension) and poor readers (poor phonological decoding and passage comprehension). We predicted that resilient readers would show altered morphology in the posterior inferior frontal and temporo-parietal regions thought to support skilled phonological decoding. These predictions were partially supported by the finding that resilient readers, compared to proficient readers, showed less leftward asymmetry of gray matter thickness in the temporo-parietal region. We predicted that poor readers would share this reduced asymmetry with resilient readers, and show additional anatomical differences in the lateral ventral frontal region, and inferior temporal lobe. These predictions were partially supported, as we found that poor readers showed less leftward asymmetry of the temporo-parietal region and an additional reduction in radial expansion in the frontal lobes that was not seen in resilient readers.

Our finding of less leftward asymmetry in the temporo-parietal region of both poor and resilient readers agrees with prior findings that reading disabled participants show reduced gray matter in the left supramarginal gyrus [Eckert et al., 2005] and the posterior superior temporal

gyrus and temporo-parieto-occipital junction [Brambati et al., 2004; Brown et al., 2001]. This observed reduction in asymmetry in both groups with poor phonological skills is consistent with the findings of Galaburda et al. [1985]. Our findings extend these prior findings to suggest that less leftward gray matter asymmetry in this region may characterize individuals with poor phonological skills, regardless of reading comprehension abilities. Using cortical matching techniques, we found no evidence for exaggerated asymmetry in the temporo-parietal region in resilient readers similar to that observed in a compensated dyslexic [Chiarello et al., 2006b] and dyslexic engineering students [Robichon et al., 2000]. It should be noted that the temporo-parietal asymmetry measured in this study differs considerably from the sulcal length measures employed by these prior studies. As poor and resilient readers show similarly decreased performance on pseudoword reading tasks and an auditory phoneme deletion task [Welcome et al., 2009; Welcome et al., submitted for publication], it is suggestive that the two groups show a similar pattern of reduced asymmetry in this region. Functional imaging studies suggest that the left temporo-parietal region is active during the conversion of orthography to phonology [Booth et al., 2002] and tasks that require assembled phonology [Chen et al., 2002].

Alternately, it is possible that altered morphology in the temporo-parietal region relates to text comprehension. Reading disabled children show overactivation in the left superior temporal region in response to sentence comprehension tasks [Rimrodt et al., 2008]. Poor readers exposed to remedial instruction show increases in activation in the left angular gyrus and left superior parietal lobule during sentence comprehension [Meyler et al., 2008]. Our behavioral findings with these participants suggest that resilient readers rely more on semantic relationships between

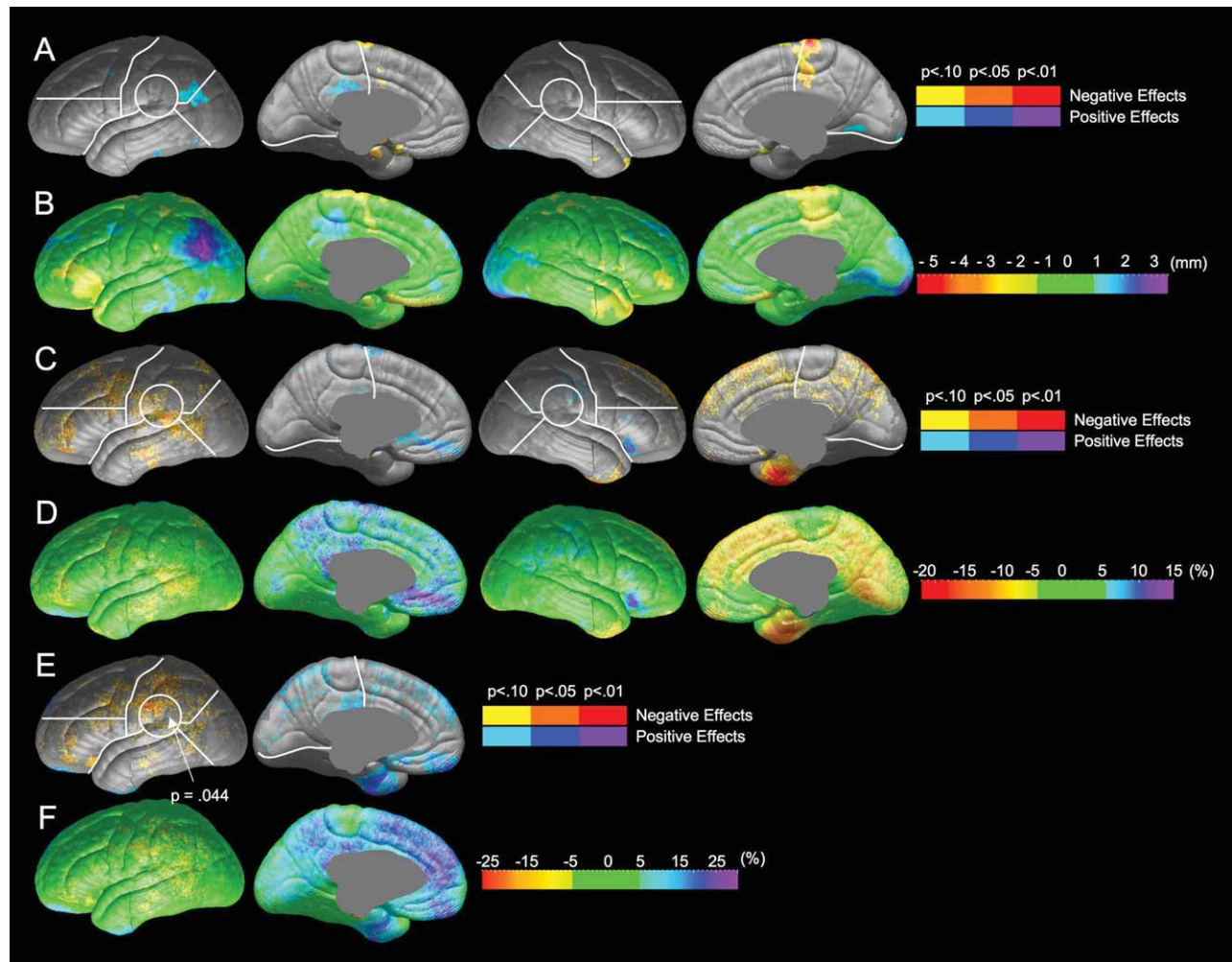


Figure 3.

Comparison of brain morphology between proficient and resilient readers. Negative effects (Proficient > Resilient) are shown in hot colors, and positive effects (Resilient > Proficient) are shown in cool colors. Significance values from permutation tests are shown for each ROI in which group differences were significant by permutation. (A) Statistical comparison of radial expansion between proficient and resilient readers. (B) Magnitude of

differences in radial expansion between proficient and resilient readers. (C) Statistical comparison of gray matter thickness between proficient and resilient readers. (D) Magnitude of differences in gray matter thickness between proficient and resilient readers. (E) Statistical comparison of gray matter thickness asymmetry between proficient and resilient readers. (F) Magnitude of differences in gray matter thickness asymmetry.

words than either of the other groups [Welcome et al., 2009; Welcome et al., submitted for publication]. Given functional studies that suggest a role for this region in text comprehension, it is possible that morphological differences in this region relate to group differences in semantic processing.

The reduced radial expansion in right frontal regions shown by poor, but not resilient, readers is partially consistent with prior findings that dyslexics show altered morphology in bilateral frontal regions [Brown et al., 2001; Eckert et al., 2003]. Our findings suggest that this morphological feature characterizes individuals with less skill at

reading comprehension. This interpretation is supported by functional imaging studies that suggest a role for a bilateral ventral frontal region in semantic processing [reviewed in Fiez, 1997]. Poor readers show reduced radial expansion of the ventral frontal region that is reliable in the right hemisphere, but not the left. These findings suggest that right ventral frontal morphology, as well as left, may relate to text comprehension ability. Consistent with this finding, bilateral activation in the inferior frontal region was seen during concrete/abstract decisions [Chee et al., 1999], semantic category generation [Shaywitz et al., 1994], comprehension of complex sentences [Just et al.,

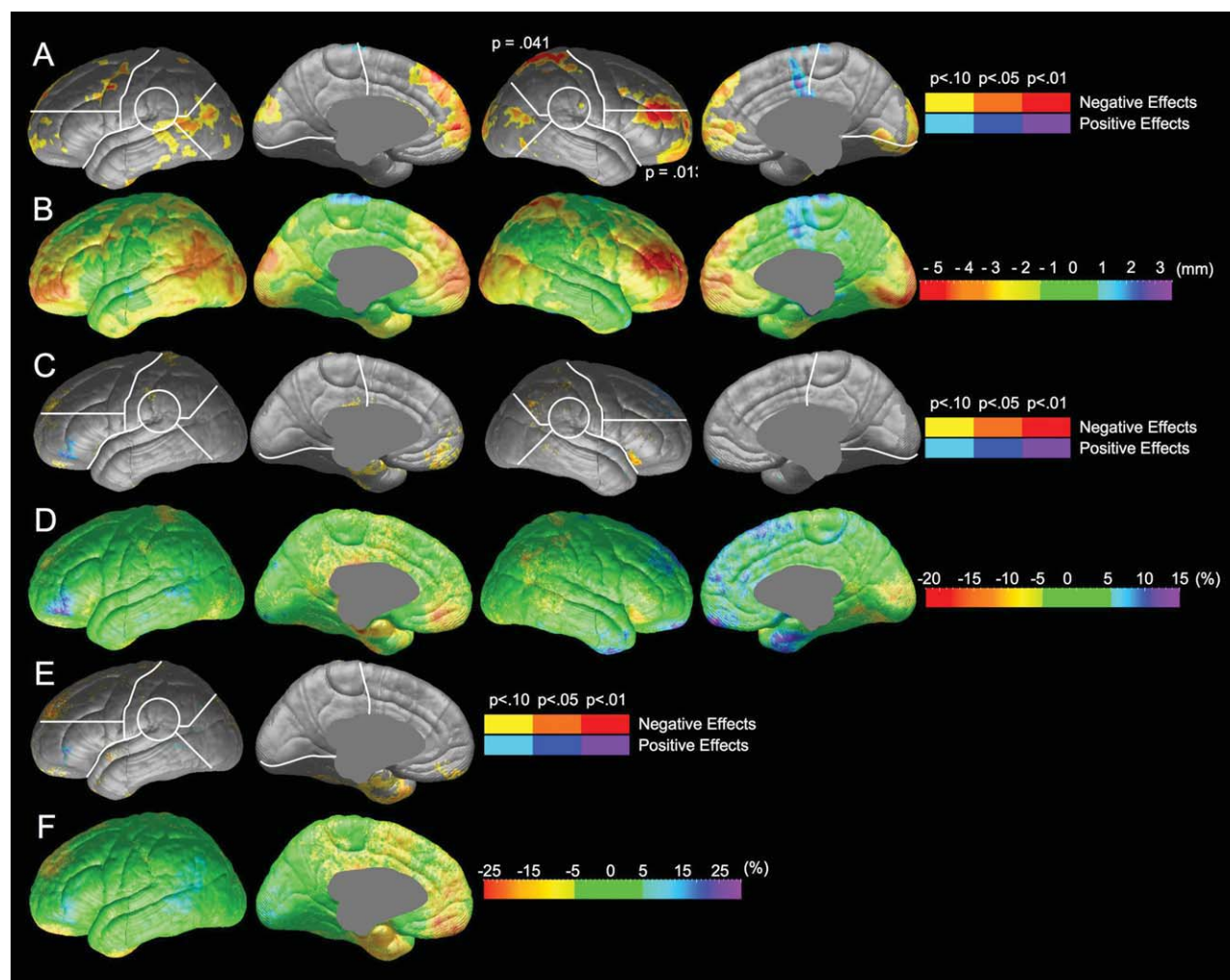


Figure 4.

Comparison of brain morphology between resilient and poor readers. Negative effects (Resilient > Poor) are shown in hot colors, and positive effects (Poor > Resilient) are shown in cool colors. Significance values from permutation tests are shown for each ROI in which group differences were significant by permutation. **(A)** Statistical comparison of radial expansion between resilient and poor readers. **(B)** Magnitude of differences in radial

expansion between resilient and poor readers. **(C)** Statistical comparison of gray matter thickness between resilient and poor readers. **(D)** Magnitude of differences in gray matter thickness between resilient and poor readers. **(E)** Statistical comparison of gray matter thickness asymmetry between resilient and poor readers. **(F)** Magnitude of differences in gray matter thickness asymmetry.

1996], and discourse processing [St. George et al., 1999] suggesting that both left and right inferior frontal regions may be involved in tasks that involve meaning access.

Neither poor nor resilient readers in our sample showed the predicted reductions in gray matter thickness and brain size in the left posterior inferior frontal region, although this region is typically active during phonological processing [reviewed in Pugh et al., 1996]. There were also no reductions in the inferior temporal regions that are active during orthographic processing [Cohen et al., 2000]. It is possible that we simply lacked the power to uncover morphological differences in these regions. Alternately, it

is possible that reading impaired groups that have shown these alterations in morphology [e.g., Eckert et al., 2005; Kronbichler et al., 2008] have more extensive reading impairments or more atypical developmental trajectories than the college students in the current study. While both resilient and poor readers showed decreased performance on an orthographic choice task [Welcome et al., 2009; Welcome et al., submitted for publication], the presence of these individuals in a university setting suggests that their reading skills may not be as poor as typical dyslexics, and perhaps that their exposure to print is more similar to that of typical readers. Another possibility is that the sulcal

pattern matching employed in the current study yielded different results from VBM methods used in previous work. Prior work has demonstrated that manual measures and VBM have identified differences between dyslexics and controls in different portions of the reading network [Eckert et al., 2005], suggesting that such differences are sensitive to measurement technique. The cortical pattern matching technique employed in the present study control for variability in sulcal patterns across individuals in a way that current VBM techniques cannot, and it is possible that this methodological difference underlies differences between our findings and those of some prior studies.

In the temporo-parietal region, both poor and resilient readers show less leftward asymmetry of gray matter thickness. This leftward asymmetry appeared to result from a slight, nonreliable, reduction of gray matter thickness in the right temporo-parietal cortex relative to proficient readers. The cellular correlates of gray matter thickness observed with MRI are not fully understood, but this measure may reflect soma size [Wellman and Sengelaub, 1991], neuron number [Wegner et al., 2006], and arborization of dendritic processes [O'Kusky et al., 1996]. Alternately, thinner gray matter may reflect greater myelination of fibers, as unmyelinated axons may be classified as gray matter on the basis of their signal value on MRI [see Sowell et al., 2004], although the absence of a parallel increase in radial expansion argues against this interpretation.

Poor readers show reduced radial expansion in the ventral frontal regions without reduced gray matter thickness in the same region. The cellular determinants of reduced radial expansion without reduced gray matter thickness are again unknown, but this morphological alteration may have implications for processing differences between dyslexics and controls. Similar to our findings, a previous study found that total cerebral volume was reduced in dyslexics, while cortical thickness was not [Casanova et al., 2004]. These alterations were related to reduced gyrification, which the authors suggest could result in more cortical integration and slower processing [Casanova et al., 2004]. Alternately, the reduced radial expansion in our study may indicate reductions in underlying white matter in this region. Reduced connectivity from the inferior frontal region in dyslexics has been demonstrated with diffusion tensor imaging [Richards et al., 2008] and functional connectivity studies [Quaglino et al., 2008]. Thus, reduced radial expansion in the poor readers in the present sample may reflect alterations in underlying white matter, perhaps indicating differences in the connections made between the inferior frontal cortex and other brain regions.

It is interesting to speculate as to whether these anatomical differences are the cause or consequence of the behavioral differences between groups. It is possible that morphology is altered in such a way that sufficiently accurate phonological representations cannot be supported, leading to reading deficits. However, recent studies suggest that brain anatomy can be altered by learning experi-

ences [Draganski et al., 2006] and activation profiles normalize following successful reading remediation [Temple et al., 2003], indicating that brain anatomy may be sensitive to environmental factors. Without detailed knowledge of the educational experiences of our participants, it is not possible to know whether differences in reading instruction might contribute to differences in brain morphology between our reading groups.

Our study had some limitations. Our sample sizes were small, especially for the group of poor readers, and therefore the study may have lacked the power to uncover subtle anatomical differences. Prior studies using this methodology have used similar sample sizes to produce findings that have replicated across independent samples [Sowell et al., 2002]. As the participants in this study were all adults, some aspects of their educational background, including objective measures of their childhood reading abilities, were not available. Longitudinal studies identifying and tracking resilient and poor readers from early in development might provide additional insight into the relationships between brain anatomy and reading ability. An additional limitation of the present study was that multiple comparisons were necessary to examine group differences in brain morphology. Within a statistical map, permutation analyses were used to correct for the number of comparisons for each region of interest evaluated. However, the relatively large number of statistical maps, and ROIs examined within each map, means that many comparisons were made. Nonetheless, the approach of investigating relationships between morphology and specific components of reading was novel and provided unique information about relationships between cortical anatomy and reading abilities, and we feel confident interpreting those results that are consistent with our a priori predictions.

Additionally, it should be noted that even the poor readers in this study were attending college and had higher scores than reading impaired participants of previous studies. The inclusion of less reading impaired individuals may have minimized anatomical differences between groups, and we run the risk of underestimating the extent of anatomical differences related to reading ability. However, the finding that groups with relatively minor reading impairments show reliable differences in brain morphology extends these prior findings and suggests that relationships between reading ability and brain anatomy exist across the entire spectrum of reading skill. Further, the use of resilient readers allowed us to demonstrate that some of these anatomical differences likely relate to phonological decoding impairments, while others may index other reading skills.

Together, our findings suggest that brain morphology differs between college students with different reading profiles. Resilient readers were shown to represent a separate population of readers, distinguishable from poor and proficient readers in neuroanatomy. Resilient readers show relatively subtle behavioral differences from typical

readers, so it is intriguing that they show consistent differences in brain morphology. These differences were focal, and restricted to the temporo-parietal region as predicted. In those students with more extensive reading difficulties, morphological differences were more extensive, present in inferior frontal and temporo-parietal areas thought to support both print-to-sound conversion and meaning access. Future studies may build on these results to provide a more comprehensive picture of the relationships between brain anatomy, brain function, and reading behavior.

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