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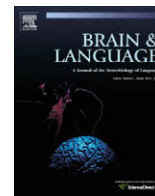
Alternate reading strategies and variable asymmetry of the planum temporale in adult resilient readers

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ABSTRACT

Resilient readers are characterized by impaired phonological processing despite skilled text comprehension. We investigated orthographic and semantic processing in resilient readers to examine mechanisms of compensation for poor phonological decoding. Performance on phonological (phoneme deletion, pseudoword reading), orthographic (orthographic choice, orthographic analogy), and semantic (semantic priming, homograph resolution) tasks was compared between resilient, poor and proficient readers. Asymmetry of the planum temporale was investigated in order to determine whether atypical readers showed unusual morphology in this language-relevant region. Resilient readers showed deficits on phonological tasks similar to those shown by poor readers. We obtained no evidence that resilient readers compensate via superior orthographic processing, as they showed neither exceptional orthographic skill nor increased reliance on orthography to guide pronunciation. Resilient readers benefited more than poor or proficient readers from semantic relationships between words and experienced greater difficulty when such relationships were not present. We suggest, therefore, that resilient readers compensate for poor phonological decoding via greater reliance on word meaning relationships. The reading groups did not differ in mean asymmetry of the planum temporale. However, resilient readers showed greater variability in planar asymmetry than proficient readers. Poor readers also showed a trend towards greater variability in planar asymmetry, with more poor readers than proficient readers showing extreme asymmetry. Such increased variability suggests that university students with less reading skill display less well regulated brain anatomy than proficient readers.

1. Introduction

Traditionally, the development of reading skill is proposed to rely crucially on skilled phonological processing. This perspective holds that individuals who possess ample knowledge of speech sounds will find it easier to match those speech sounds to letters than individuals whose phonological knowledge is incomplete (Wagner & Torgesen, 1987). Consistent with this role of phonological knowledge in reading acquisition, there is an extensive literature linking individual differences in pseudoword reading and phonological awareness to reading ability in children (Duncan & Johnston, 1999; Pratt & Brady, 1988; Rack, Snowling, & Olson, 1992). While such studies demonstrate that phonological skills are typically good predictors of reading success, there are some individuals who nonetheless achieve normal or skilled reading comprehension despite poor phonological processing skills. The existence of such readers challenges the notion that strong phonological knowledge is absolutely necessary for skilled reading and suggests that alternative mechanisms may support reading comprehension in some individuals. In this study, we explore the orthographic skills and use of semantic information in a group of college-age readers with poor phonological skills but skilled reading comprehension (Welcome, Chiarello, Halderman, & Leonard, 2009). We contrast these "resilient" readers to those with high skill in both domains (proficient readers), and to those with low skill in both domains (poor readers). Additionally, we investigated whether the reading groups differed in morphology of the planum temporale. It has been suggested that readers with intact comprehension and impaired phonological processing may show a pattern of extreme leftward asymmetry of the planum (reviewed in Leonard and Eckert (2008)), and we examined that hypothesis here.

Some individuals display a pattern of skilled comprehension and poor phonological skills without an apparent history of childhood reading difficulty. Jackson and Doellinger (2002) identified a group of six university students termed "resilient readers" because they obtained average or above average scores on tests of text comprehension despite poor decoding ability, as measured by standardized pseudoword reading tests. Three additional case

studies of individuals with similar reading profiles support the finding that some adults with impairments in phonological decoding are skilled at comprehending text (Holmes & Standish, 1996; Howard & Best, 1997; Stothard, Snowling, & Hulme, 1996). Another group of individuals who possess strong reading comprehension skills despite poor phonological analysis skills are referred to as compensated or high-functioning dyslexics. Some individuals with reading impairments in childhood go on to become skilled readers as adults (Felton, Naylor, & Wood, 1990). Despite normal reading comprehension, these compensated dyslexics continue to show phonological deficits, as evidenced by poor performance on phonological awareness and pseudoword reading tasks (e.g. Bruck, 1992; Parrila, Georgiou, & Corkett, 2007; Wilson & Lesaux, 2001). These groups of readers demonstrate that skilled comprehension can be achieved in the absence of skilled phonological decoding.

A discrepancy between phonological decoding skills and reading comprehension suggests that other reading skills may compensate for impaired phonological analysis. One possibility is that these readers rely more heavily on orthographic analysis. As explained by dual route theory (Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001), these individuals may achieve skilled word recognition through greater reliance on the direct route (in which visual word forms are associated with word meanings) and less reliance on the indirect route (which requires the grapheme-to-phoneme conversion which is difficult for resilient readers). An additional possibility is that resilient readers rely more heavily on context to guide recognition of individual words. The Interactive-Compensatory Model (Stanovich, 1980) posits that poor readers rely more on contextual information in response to their decoding difficulties. These possibilities are discussed in more detail below.

There is some evidence that individuals with deficits in phonological processing may have preserved or enhanced orthographic processing skills. A resilient reader was shown to excel at an orthographic choice task, selecting the correct spellings of words more quickly than most control subjects (Holmes & Standish, 1996). Another resilient reader responded more quickly to irregular words than to regular words, suggesting decreased reliance on the indirect route, a pattern opposite to that found in control subjects (Howard & Best, 1997). Some studies have found that orthographic processing is less severely or persistently impacted in dyslexics than is phonological processing (Greenberg, Ehri, & Perin, 1997). For example, dyslexic children show better performance than reading-level matched controls on an orthographic awareness task in which they are required to select from two pseudowords the one that is more like a word (Siegel, Share, & Geva, 1995).

The theory that orthographic analysis can be used as mechanism for compensation rests on the assumption that orthographic and phonological skills are at least partially independent. Orthographic processing skills predict word reading over and above phonological skills (Barker, Torgesen, & Wagner, 1992; Cunningham, Perry, & Stanovich, 2001; Juel, Griffith, & Gough, 1986). Studies conducted with twins have demonstrated that there is a genetic influence on orthographic coding partly independent of the genetic influence on phonological decoding (Gayan & Olson, 2003). One possible non-phonological factor contributing to the development of orthographic ability is reading experience, as individuals with more exposure to print have greater orthographic processing skills (Stanovich, West, & Cunningham, 1991). If orthographic skills are partially independent of phonological skills, and develop as a result of exposure to print, orthographic knowledge could serve as a source of compensation in the present sample of college students with poor phonological decoding abilities. Hence, resilient readers would be predicted to show orthographic skills superior to those of poor readers, and possibly even superior to those of proficient readers.

An alternate perspective holds that phonological and orthographic analysis skills are tightly related and that the development of orthographic knowledge depends on phonological decoding skill. Models of reading development, including Share's "self-teaching" hypothesis (Share, 1995), suggest that multiple instances of accurate phonological decoding of new words lead to the development of orthographic knowledge. In this framework, poor phonological decoding skills would interfere with proper word identification and consequently impair the development of orthographic knowledge. Previous studies have demonstrated associations between phonological and orthographic processing skills (reviewed in Burt (2006)). If orthographic processing skill is tightly coupled to phonological analysis skill, orthographic skill is an unlikely mechanism of compensation for poor phonological decoding. Consistent with this view, several studies of compensated dyslexics and resilient readers have found no evidence for superior orthographic skills (Stothard et al., 1996; Kemp, Parrila, & Kirby, 2009; Meyler & Breznitz, 2003). Under this framework, both resilient and poor readers would be predicted to show inferior orthographic skills relative to proficient readers.

The present study allowed us to investigate orthographic compensation in resilient readers in the same university environment as their typical reading peers. Because of this shared environment, it is likely that the groups in the current study have more similar exposure to print than reading-level matched groups in previous studies (Siegel et al., 1995). Additionally, we were able to compare resilient readers to poor readers in order to investigate whether enhanced orthographic processing is related to preserved comprehension or common to both groups of poor phonological decoders.

Contextual information may also serve to support reading in those with poor phonological decoding. The Interactive-Compensatory Model (Stanovich, 1980) suggests that reliance on context can increase when there are deficiencies in lower-level reading processes. This hypothesis is supported by a number of studies showing that younger and poorer readers rely more on context while reading than older, more skilled readers. Younger readers and poorer readers benefit more from the presentation of a word or a pseudohomophone (like BRANE) in the context of a meaningful sentence than older and more skilled readers (Briggs, Austin, & Underwood, 1984; Juel, 1980; Nation & Snowling, 1998). These findings suggest that individuals who are poor readers may rely more heavily upon context than typical readers. It is possible that this increased reliance on context generalizes across poor phonological decoders, extending to those whose comprehension skills are high. While previous studies have examined the use of context in individuals whose reading remains poor, we consider the possibility that resilient readers are individuals for whom the use of context allows for such successful compensation that their comprehension skills are normal.

Additional support for the theory that semantic information can support skilled reading comes from studies indicating that general world knowledge can prevent the development of adult reading problems in some individuals at risk for dyslexia. In children with a family history of dyslexia, it has been suggested that high IQ and good oral language skills serve as protective factors (Snowling, Gallagher, & Frith, 2003). Thus, strong verbal knowledge may help to prevent the development of reading disabilities. Similarly, in adults with a childhood diagnosis of dyslexia, the relationship between phonological skill and reading comprehension is moderated by listening comprehension and vocabulary (Ransby & Swanson, 2003).

Previous studies have suggested that individuals with poor decoding skills may be more sensitive to contextual information. A case study of an individual with phonological impairments showed greater improvement than controls in the ability to read pseudohomophones when they were preceded by semantic associ-

ates (e.g. "TOMATO-SAWCE") (Stothard et al., 1996). University students with a history of reading difficulties were slowed by unrelated context to a greater extent that control readers (Corkett & Parrila, 2008). Another study compared sixth graders who are good readers (as measured by reading comprehension) and poor spellers with good readers/good spellers and poor readers/poor spellers (Bruck & Waters, 1990). The good readers/poor spellers in this study show impaired nonword reading and high vocabulary scores, mirroring the pattern of performance shown by resilient readers. These individuals were more easily able to generate plausible sentence completions than poor readers/spellers and show greater context effects than good readers/spellers, suggesting that they were both competent at using sentence context and reliant on this skill during reading.

The present study was designed to explore potential mechanisms of behavioral compensation in college students who are poor at phonological decoding, and to investigate whether they share altered planar asymmetry with other groups of impaired decoders who are skilled comprehenders. Resilient readers (individuals with skilled Passage Comprehension and impaired Word Attack), poor readers (individuals with impaired performance on both subtests), and proficient readers (individuals with skilled performance on both subtests) were identified from the undergraduate population. Resilient readers' performance on a battery of tests designed to measure skill and reliance on orthographic and semantic processes was compared to the performance of proficient readers and poor readers. To assess each group's phonological processing abilities, an auditory phoneme deletion task was used. Therefore, group differences in this measure would confirm that resilient readers' phonological deficit extends beyond grapheme-to-phoneme conversion.

Speed and accuracy of orthographic processing were measured using an orthographic choice task and an ambiguous pseudoword reading task. It is possible for a reader to infer the pronunciation of a new word or pseudoword from the pronunciations of other words with similar spelling patterns (Goswami, 1986; Treiman, Goswami, & Bruck, 1990; Wood & Farrington-Flint, 2001). In order to investigate the degree to which readers rely on orthographic analogy, we examined the pronunciation of ambiguous pseudowords (e.g., "*dearl*"), in which individual letter-to-sound conversion will yield a different pronunciation than use of knowledge of word body pronunciation. If orthographic processing is not reliant on phonological ability, and instead serves a compensatory role in resilient readers, resilient readers were predicted to show preserved or enhanced skill on the orthographic choice task and greater reliance on orthographic analogy in the ambiguous pseudoword reading task. However, if orthographic knowledge depends heavily on phonological skills, resilient readers were predicted to perform similarly to the poor readers on these orthographic tasks.

Effects of meaningful relationships between words were examined using a semantic priming task and a homograph resolution task. If resilient readers rely more heavily on semantic information to guide word recognition, they were predicted to show greater semantic priming than the other groups. In the homograph resolution task, participants read sentences ending in homographs (e.g. "*The man fished from the river bank*") and were asked to determine whether target words related to the meaning of the sentence. Some of the target words were related to the meaning of the homograph inconsistent with the sentence meaning (e.g., "*CASH*"). With the long separation between the final word of the sentence and the target word used in this experiment, proficient readers were expected to show little interference and should be able to quickly and accurately reject inappropriate associates (Dixon & Twilley, 1999; Gernsbacher, Varner, & Faust, 1990). Previous studies have shown that poor comprehenders are less able to use the sentence context to suppress contextually inappropriate meanings (Gernsbacher &

Faust, 1991). Thus, poor readers were predicted to show less suppression than proficient readers. If resilient readers make efficient use of context, they are predicted to show suppression effects similar to proficient readers and greater than those of poor readers. If resilient readers, like poor readers, fail to make efficient use of context, they are predicted to show less suppression of the inappropriate meanings of homographs than proficient readers.

It is presently unknown whether there are any neuroanatomical features associated with the resilient reading profile. However, one extensively investigated structure thought to relate to reading skill is the planum temporale, the cortical area posterior to primary auditory cortex. Some studies have found alterations of asymmetry of this structure in dyslexics, while others have found no such morphological differences between reading groups (reviewed in Beaton (1997) and Eckert (2004)). A previous case study of brain morphology in a compensated dyslexic showed an extreme leftward asymmetry of the planum temporale (Chiarello, Lombardino, Kacinik, Otto, & Leonard, 2006). Such a pattern of extreme asymmetry of the planum may characterize readers with intact comprehension and impaired phonological processing (reviewed in Leonard and Eckert (2008)). Dyslexic engineering students show more leftward asymmetry of the parietal operculum than controls (Robichon, Levrier, Farnarier, & Habib, 2000). Thus, resilient readers were predicted to show more leftward asymmetry of the planum temporale than proficient readers. Poor readers, in contrast, were predicted to show less leftward asymmetry of the planum temporale. Reduced or reversed asymmetry has been associated with language and reading deficits in some studies (see Morgan & Hynd, 1998), although others have found that dyslexics show no alterations in planar asymmetry (reviewed in Eckert (2004)).

2. Method

2.1. Participants

A total of 55 university students participated in the study. All participants were native speakers of English with normal or corrected-to-normal vision and ranged in age between 18 and 34. Informed consent was obtained from all participants, and the study had the approval of the institutional review board of the University of California, Riverside. Fifty-two of these individuals were recruited through their earlier participation in the Biological Substrates for Language Project (Chiarello, Welcome, et al., 2006). As part of their participation in this project, 200 university students completed the WRMT-R/NU Word Attack and Passage Comprehension subtests (Woodcock, 1998). We considered individuals with scores below the 35th percentile on both subtests to be poor readers. The 35th percentile reflects a scaled score of 95, indicating that their performance was at least half of a standard deviation below the aged-based norm. As the poor readers' scores were in the lowest 10% of a 200-university student sample, they represent the lower extreme of reading ability. Resilient readers scored below the 35th percentile on the Word Attack subtest and above the 45th percentile on the Passage Comprehension subtest, with a discrepancy of at least 20 percentile points between an individual's Word Attack score and Passage Comprehension score. We considered individuals who scored above the 45th percentile on both subtests to be proficient readers. Mean scores and standard deviations on the reading tasks used to classify individuals, as well as other demographic and psychometric measures, are presented in Table 1. Because of the selection criteria, there were significant group difference in Word Attack scores $F(2, 52) = 68.08$, $p < .0001$, $\eta^2 = 0.72$. Pairwise comparisons revealed that proficient readers performed better than both poor ($t(32) = 9.27$, $p < .0001$, $d = 3.28$) and resilient readers ($t(41) = 13.17$, $p < .0001$, $d = 4.11$), and poor

	Proficient readers (N = 22)	Resilient readers (N = 21)	Poor readers (N = 12)
Word attack percentile rank	62.3 (13.5)	20.2 (5.7)	20.8 (10.1)
Pass. comp. percentile rank	69.5 (12.9)	66.0 (15.5)	28.8 (5.1)
Sex	11 Males	13 Males	4 Males
	11 Females	8 Females	8 Females
Age	22.0 (3.8)	20.2 (2.6)	21.1 (3.9)
Language experience	19 Monolinguals	19 Monolinguals	7 Monolinguals
	3 Bilinguals	2 Bilinguals	5 Bilinguals
SES	3.3 (0.8)	3.5 (0.9)	3.0 (1.4)
Handedness quest.	0.8 (0.4)	0.6 (0.6)	0.7 (0.6)
Direction of handedness	20 Right-handed	18 Right-handed	11 Right-handed
	2 Non-RH	3 Non-RH	1 Non-RH
Word ident. percentile rank	60.7 (8.1)	40.1 (12.1)	25.5 (10.1)
Verbal IQ	111.9 (13.3)	109.2 (9.7)	97.5 (6.8)
Performance IQ	109.8 (11.6)	105.9 (11.0)	105.5 (8.3)

and resilient readers did not significantly differ in performance ($t < 0.25$). The groups also significantly differed in Passage Comprehension performance $F(2, 52) = 45.30$, $p < .0001$, $\eta^2 = 0.64$. Pairwise comparisons indicated that the poor readers performed worse than both proficient ($t(32) = 10.43$, $p < .0001$, $d = 3.69$) and resilient readers ($t(41) = 8.01$, $p < .0001$, $d = 2.50$), while proficient and resilient readers did not reliably differ ($t < 0.80$). This classification scheme had the advantage that resilient and proficient readers were matched in comprehension scores, and resilient and poor readers were matched in decoding scores.

2.2. Behavioral stimuli and procedures

In a 2-h preliminary session, participants completed a 5-item hand preference questionnaire (Bryden, 1982), questionnaires regarding language and family background, and standardized measures of reading skill and intelligence. Parental education was assessed on a scale ranging from 1 ("Some high school") to 5 ("Post-graduate or professional degree"). Scores on the hand preference questionnaire range from −1.0, representing extreme left-handedness, to +1.0, representing extreme right-handedness. Individuals with scores less than +0.3 on this index were classified as non-right-handed. The language history questionnaire was used to verify that all participants were native speakers of English and to assess their degree of experience with other languages. While all participants came from environments in which the majority of communication from birth was conducted in English, 18% had substantial early exposure to another language. The Word Identification, Word Attack, and Passage Comprehension subtests of the WRMT-R/NU (Woodcock, 1998) were administered to assess participants' ability to read real words, pseudowords, and to supply contextually appropriate completions to stimuli of increasing complexity. Age norms from the normative update were used to calculate scaled scores and percentile ranks. Verbal and Performance intelligence were assessed using the Wechsler Abbreviated Scale of Intelligence (Wechsler, 1999). After the final task, participants completed the Adult Reading History Questionnaire (ARHQ) (Lefly & Pennington, 2000).

In a second session performed on a different day, participants completed six experimental tasks in a 90-min session. For the computerized tasks (semantic priming, orthographic choice, homograph resolution, ambiguous pseudoword reading, and verbal working memory), all stimuli were presented in uppercase, black

20 point Helvetica font on a white background. Macintosh Power PC computers were used for stimulus presentation. Psyscope programming software (Cohen, MacWhinney, Flatt, & Provost, 1993) was used to control experimental events and record responses. Participants were seated 60 cm in front of the monitor, using a headrest to stabilize head position. For those experiments requiring manual responses (semantic priming, orthographic choice, and homograph resolution), participants used their index fingers on the '.' and 'x' keys to indicate one response and the middle fingers on the '/' and 'z' keys to indicate the other response. This configuration was designed to accommodate both left- and right-handed participants. A Sony ECM-MS907 microphone was used to register vocal responses. Vocal responses in the ambiguous pseudoword task were entered into the data file by an experimenter. Special codes were entered for spurious vocal responses (a cough, for example), or failure to respond, and such trials were not analyzed. Details of each task are presented below:

2.3. Phoneme deletion

A phoneme deletion task was used as a measure of the accuracy of phonological processing. Stimuli were 32 one-syllable pseudowords (e.g., "smab"). Stimuli varied in the position of deletion, with the first phoneme being deleted from the first 16 items and the last phoneme being deleted from the last half of the stimuli. For half of the first-phoneme items and half of the last-phoneme items, the deleted sound was a single consonant and for half the deleted phoneme was part of a blend (a pair of consonants in which the sound of both is retained). Four additional trials, in which the sound to be deleted was a digraph, were included to ensure that participants were using a sound-based strategy rather than deleting the first or last letter from an imagined spelling.

On each trial, the experimenter pronounced a pseudoword. Participants repeated each pseudoword to verify that they had perceived the item correctly. Participants were then asked to pronounce what would be left when the first/last sound was deleted from each pseudoword. Accuracy of response was recorded.

2.4. Orthographic choice

An orthographic choice task was used to assess each participant's speed and accuracy at the recognition of familiar word forms. Items ranged in difficulty with easier items selected from previously published studies with younger participants (Cunningham, Perry, Stanovich, & Share, 2002) and more difficult items designed for the present study. Thirty-two pairs of spellings were presented. Across the items, correct and incorrect spellings had equal bigram frequency and equal length. Stimulus characteristics are presented in Table S1. Participants were asked to determine which of two spellings of a word was correct. The two spellings were simultaneously presented above and below a fixation cross and participants indicated the correct spelling by keypress. Stimuli were presented until a response was made. Accuracy and response time were recorded.

2.5. Ambiguous pseudowords

To determine the relative use of phonology and orthography, the pronunciation of visually presented ambiguous pseudowords was examined. Thirty ambiguous pseudowords were constructed by adding a consonant to a word body that is pronounced irregularly in all English words. For example, the nonword "*dearl*" was constructed to represent the body_earl, which is pronounced irregularly in all the English words in which it occurs, such as earl and pearl. These word bodies were identified as having no body friends (Rastle, Harrington, & Coltheart, 2002). Our pool of participants

gave multiple correct pronunciations for each item, confirming that the pseudowords were ambiguous. Ambiguous pseudowords were interspersed with 30 pseudowords based on stems that are pronounced regularly in some English words and irregularly in others (e.g., "*nost*"). These filler trials were intended to prevent participants from developing a strategy of pronouncing all pseudowords irregularly based on seeing only irregularly pronounced stems. Each pseudoword was presented in the center of a computer screen until a response was given.

Participants pronounced each pseudoword aloud. Responses were classified as correct if the pronunciation of each letter or pair or letters corresponded to a pronunciation present in English words. For example, correct responses to the stimulus "*dearl*" included [dÎùrl], [dirl], [dArl], and [dE«rl]. Correct responses to ambiguous pseudowords were further classified as analogous if the word body was pronounced in accordance with the irregular pronunciation of the stem (e.g., [dÎùrl]) or phonologically decoded if the pronunciation obeyed typical grapheme–phoneme conversion rules (e.g., [dirl]). The percentage of responses classified as analogous was compared across groups.

2.6. Semantic priming

A semantic priming task was used to measure the degree to which semantic information was activated during single word reading. On each trial, a fixation cross flickered prior to stimulus presentation. A prime word was presented for 200 ms. A 3–6 letter target word or pseudoword appeared in the same location as the prime word and remained on the screen until the participant's response was made. Participants decided whether the target stimulus was a word or a pseudoword and indicated their response by keypress. For half of the word trials, the target was a primary or secondary associate of the prime, and primes and targets were also categorically related (e.g., dog–cat, Chiarello, Liu, Shears, Quan, & Kacinik, 2003); in the other half the prime and target words were unrelated. Different words were used in the related and unrelated conditions. A pilot study conducted with 20 participants (none of whom participated in the current study) confirmed that in the absence of primes, words to be used in the related and unrelated conditions were responded to equally quickly ($F(1, 38) < 0.1$). Across conditions, prime and target words were equated for length, familiarity, imageability, and frequency (Wilson, 1988). Stimulus characteristics are presented in Table S2.

Overall performance was assessed as the speed and accuracy of word responses, collapsed over semantic relatedness of the prime word. An RT priming measure was calculated for each subject by subtracting the subject's mean response time on related trials from their mean response time on unrelated trials. Analogously, an accuracy priming measure was calculated for each subject by subtracting percent correct on unrelated trials from percent correct on related trials.

2.7. Homograph resolution

To examine the role of context in reading, participants read a sentence ending in a homograph and then determined if a target word was related to the meaning of the sentence. Five to nine word sentences were constructed to bias one meaning of a homograph. A norming study, in which different participants rated the relatedness of sentences and targets, allowed us to select stimuli judged as highly related or highly unrelated. Of the 96 trials in the homograph resolution experiment, 72 sentences ended in a word with two different meanings (e.g. "*The man fished from the river bank*"); the other 24 were filler trials that ended in a non-ambiguous synonym (synonym trials). Of the 72 trials ending in an ambiguous word, 24 were followed by a target word consistent with the

meaning of the sentence ("*EDGE*") (appropriate trials), 24 were followed by a target word consistent with the other meaning of the homograph but not the sentence ("*CASH*") (inappropriate trials) and 24 were followed by an unrelated word ("*BIRD*") (unrelated trials). Sentence-final words were equated across conditions for length, imageability, and frequency (Wilson, 1988). Target words were equated across conditions for length, imageability, frequency (Wilson, 1988), and strength of association (Nelson, McEvoy, & Schreiber, 1998) to the sentence-final word. Stimulus characteristics are presented in Table S3. All participants received the same trials.

Each trial began with a central fixation cross, followed by the presentation of the sentence. The participant pressed the space key to indicate that they had finished reading the sentence. The time taken to press the space key was recorded as an informal measure of reading speed. After an ISI of 1000 ms, the target word was presented in uppercase. Participants were asked to determine whether the target word was related to the meaning of the sentence and indicate their response with a keypress. Accuracy and response time were recorded.

Inability to suppress the meaning of the homograph that is inconsistent with the sentence context will result in longer RTs and lower accuracies when the target word is inappropriate. Suppression effects for each subject were calculated by subtracting RTs from unrelated trials (in which the target relates to neither meaning of the homograph) from inappropriate trials (in which the target relates to the meaning of the homograph inconsistent with the sentence context). The cost in reaction time to reject the inappropriate associate has been taken as a measure of efficiency of suppression mechanisms (Gernsbacher et al., 1990). Hence, greater costs are associated with less efficient suppression. An analogous measure was calculated for accuracy.

For all tasks, accuracy was represented by percent correct. For reaction time measures, only correct responses were considered. Outliers (responses more than 2.5 standard deviations from the subject's mean RT) were removed. This procedure resulted in dropping 2.7% of the orthographic choice RT data, 2.5% of the semantic priming RT data, and 4.3% of the homograph resolution RT data.

2.7.1. Imaging procedure

In a separate session following behavioral testing, participants received a structural magnetic resonance image (MRI) scan in a GE 1.5T scanner equipped with Horizon echoplanar software at the Computerized Diagnostic Imaging Center in Riverside, California. The field of view was 24 cm and the voxel size was .94 × .94 × 1.2 mm. The images were reviewed for neuropathology by a neuroradiologist and then transferred to compact disks at the Imaging Center and sent to the McKnight Brain Institute at the University of Florida. Preprocessing the images was performed using FSL scripts (http://www.fmrib.ox.ac.uk/) (Smith et al., 2004). Extraction of the brain parenchyma from scalp and skull was performed with BET (Smith, 2002) before registration (FLIRT) (Jenkinson & Smith, 2001) to a 1 mm isovoxel study-specific template image aligned into the Talairach planes. No nonlinear warping was performed on the images. Hence, changes in the images were restricted to the translation and rotation necessary to align the midline and the anterior commissure–posterior commissure axis with the standard Talairach planes. Segmentation into separate gray matter, white matter and cerebrospinal fluid (CSF) volumes was performed using FAST (Zhang, Brady, & Smith, 2001). In these volumes, each voxel is represented as a partial volume estimate of a particular tissue type. The volume of each tissue type was calculated by multiplying the number of voxels times the average partial volume estimate of those voxels as described on the FSL website. Volumes, surface areas, means, standard deviations, and average asymmetries were automatically accumulated in a data

file for statistical analysis. Each structure was measured twice by at least two different investigators who were blind to hemisphere and subject characteristics. When there was more than 15% disagreement between the average values for the two measurements, the experimenters conferred and identified the reason for disagreement and then remeasured until the two measures agreed.

Gray, white and cerebrospinal fluid (CSF) volumes of each hemisphere were estimated by outlining every fifth sagittal image starting at the midline. The brainstem was excluded by transection in the midcollicular plane. The midsection was traced twice and half the slab volume added to each hemisphere. The inter-rater reliability of this measure is >.98 (intraclass correlation). Preliminary studies showed that the accuracy of volumes sampled in this way was equivalent to that in which every section was measured.

Surface area of the planum temporale was calculated between $x = 47$ and 56 (sagittal positions normalized for hemisphere width and chosen to maximize lateral asymmetry as well as reliability, Chiarello, Kacinik, Manowitz, Otto, & Leonard, 2004; Leonard et al., 1996). In individuals with one clearly defined Heschl's gyrus, the anterior border of the planum temporale was defined as the depth of the sulcus that formed the posterior border of Heschl's gyrus (Heschl's sulcus). The posterior boundary was defined as the origin of the posterior ascending ramus or the termination of the Sylvian fissure. Inter-rater reliability for these measurements is .85. These measurements are depicted in Fig. 1. A comparative study of techniques to measure the planum temporale (Best & Demb, 1999) found that asymmetry measures using this index agreed well with those gained using other techniques. An asymmetry coefficient was calculated by subtracting the left measure from the right and dividing by the average, so that leftward asymmetries yielded positive coefficients.

3. Results

3.1. Subject characteristics

Mean scores and standard deviations on demographic and psychometric measures are presented in Table 1. The three reading groups did not significantly differ in the proportion of males, $\chi^2(2, N = 55) = 2.50$, $p > .20$, proportion of fluently bilingual participants, $\chi^2(2, N = 55) = 5.81$, $p > .10$, age, $F(2, 52) = 1.53$, $p > .20$, parental education, $F(2, 52) = 0.81$, $p > .20$, average hand preference indices, $F(2, 52) = 0.86$, $p > .20$, or performance IQ, $F(2, 52) = 0.94$, $p > .20$. The three reading groups did significantly differ on the Word Identification subtest of the WRMT-R $F(2, 52) = 49.88$, $p < .0001$, $\eta^2 = 0.66$. Pairwise comparisons revealed that proficient readers scored significantly higher than both resilient $(t(41) = 6.57$, $p < .0001$, $d = 2.05)$ and poor readers $(t(32) = 11.03$, $p < .0001$, $d = 3.90)$ and resilient readers scored significantly higher
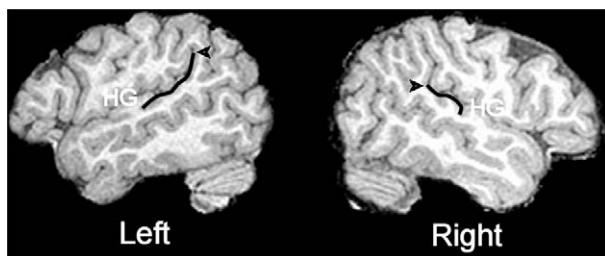

Fig. 1. Sagittal images 50 mm from the midline in an individual with typical leftward asymmetry of the planum temporale. Black lines outline the surface of the planum temporale in the left and right hemisphere. The planum temporale extends from Heschl's gyrus (HG) to the origin of the planum parietale (indicated by arrowhead).

than poor readers $(t(31) = 3.52$, $p < .005$, $d = 1.26)$. The groups also differed in verbal IQ, $F(2, 52) = 7.17$, $p < .005$, $\eta^2 = 0.22$. Pairwise comparisons reveal that poor readers scored significantly lower than proficient $(t(32) = 3.49$, $p < .005$, $d = 1.23)$ and resilient readers $(t(31) = 3.69$, $p < .001$, $d = 1.33)$. Proficient and resilient readers did not differ in verbal IQ $(t < 1)$.

We examined scores on the Adult Reading History Questionnaire (ARHQ) (Lefly & Pennington, 2000) in order to examine group differences in the prevalence (self-reported) of childhood history of reading disability. This questionnaire was designed to classify individuals as positive or negative for a childhood history of reading disability. While a score over 0.40 was considered indicative of a positive history of reading disability by the designers of the ARHQ (Lefly & Pennington, 2000), several items queried frequence of newspaper reading and we used a more stringent cut-off of 0.45 to account for the fact that few of our college student participants routinely read newspapers. Using this cut-score, the proportion of individuals with a positive history differed between groups, χ^2 $(2, N = 55) = 15.84$, $p < .001$. This reflects group differences in the proportion of readers with positive histories of reading disability (4.5% of the proficient readers, 23.8% of the resilient readers, and 66. 7% of the poor readers).

3.2. Phoneme deletion

A $3 \times 2 \times 2$ mixed design analysis of variance (ANOVA) was performed on percent correct with the following variables: reading group (proficient, resilient, or poor), position of deletion (first or last), and blend status (single consonant or blend). Mean accuracies are given in Table 2. There was a main effect of group $F(2, 208) = 7.82$, $p < .0005$, $h = 0.07$. Pairwise comparisons were consistent with our a priori predictions; proficient readers were more accurate than both poor $(t(32) = 2.49$, $p < 0.05$, $d = 0.88)$ and resilient $t(41) = 2.45$, $p < 0.05$, $d = 0.77)$ readers, who did not differ in performance $(t(31) < 1)$. None of the interactions involving group were significant $(Fs < 2)$, suggesting that the reading groups show similar patterns of performance across the different stimulus types.

3.3. Orthographic choice

One-way ANOVAs with three levels compared mean percent correct and mean correct RTs across reading groups. Group means

Table 2
Mean percent correct (standard deviation) on phoneme deletion task by reading group and stimulus type.

	Single consonant		Blend	
	First phoneme consonant	Last phoneme	First phoneme	Last phoneme
Proficient readers	100.0 (0.0)	91.5 (17.8)	41.5 (41.8)	87.5 (22.5)
Resilient readers	94.0 (16.6)	73.8 (25.3)	25.0 (32.4)	73.8 (29.8)
Poor readers	97.9 (4.9)	79.2 (16.3)	13.5 (15.5)	80.2 (18.0)

Table 3
Mean (standard deviation) performance on orthographic choice and ambiguous pseudoword reading tasks.

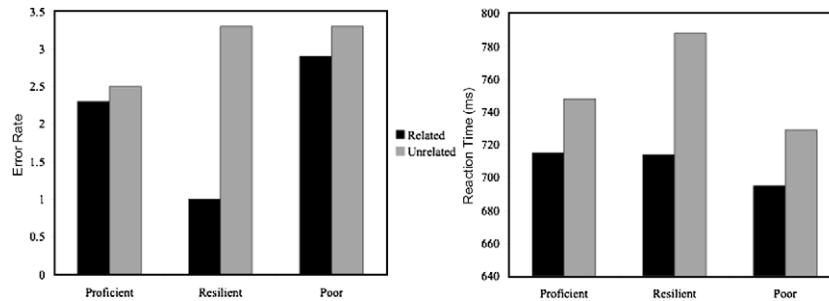|	Orthographic choice		Pseudoword reading
	Accuracy	Reaction time	Percent analogous
Proficient readers	86.5 (7.9)	1456 (308)	41.4 (9.4)
Resilient readers	81.3 (7.6)	1635 (318)	40.1 (7.6)
Poor readers	79.3 (8.4)	1495 (356)	41.5 (17.1)

Fig. 2. Performance on semantic priming task within each reading group.

are given in Table 3. The reading groups significantly differed in orthographic choice accuracy, $F(2, 52) = 5.07$, $p < 0.01$, $\eta^2 = 0.16$. Pairwise comparisons revealed that proficient readers were more accurate than both poor ($t(32) = 2.86$, $p < .01$, $d = 1.01$) and resilient ($t(41) = 2.22$, $p < .05$, $d = 0.69$) readers, who did not differ from each other ($t(31) < 2$). The reading groups did not differ in orthographic choice RT $F(2, 52) < 2$. These findings provide no evidence that resilient readers have superior orthographic skill and instead suggest that resilient readers are less accurate, and perhaps slower, at applying orthographic analysis than proficient readers.

3.4. Ambiguous pseudowords

Although accuracy and mean correct RT were recorded for this task, our main research question was whether the percent of responses based on orthographic analogy differed across reading groups. In order to address this question, a one-way ANOVA was used to compare percent of analogous responses. Group means are given in Table 3. The reading groups did not significantly differ on this measure, $F < 1$, indicating that the groups produced a roughly equivalent percentage of analogous responses.

3.5. Semantic priming

Results from the semantic priming task are presented in Fig. 2. In order to investigate group differences in the extent to which individuals benefit from meaningful relationships between words, priming was calculated for each subject as the difference in RT or error rate between unrelated trials and related trials. Priming was compared between reading groups using a one-way ANOVA. The reading groups significantly differed in the extent of priming for RT $F(2, 52) = 3.53$, $p < .05$, $h = 0.12$. Pairwise comparisons confirmed our *a priori* prediction that resilient readers would show greater priming than both proficient readers ($t(41) = 2.35$, $p < .05$, $d = 0.73$) and poor readers ($t(31) = 2.12$, $p < 0.05$, $d = 0.76$), who did not differ ($t(32) < 1.0$). The reading groups did not show reliable differences in accuracy priming, $F < 2$. However, accuracy priming was numerically higher in the resilient readers, arguing against a speed/accuracy trade-off. These findings suggest that resilient readers experience greater facilitation of word recognition from semantic relatedness than both proficient and poor readers.

3.6. Homograph resolution

Results from the homograph resolution task are displayed in Fig. 3. In order to investigate group differences in the suppression of contextually inappropriate meanings of homographs, an interference measure was calculated separately for accuracy and RT for each individual by subtracting the mean RT/error rate to reject an unrelated item from the mean RT to reject a contextually inappropriate associate following a procedure similar to that used in

previous work (Faust & Gernsbacher, 1996; Gernsbacher et al., 1990). These accuracy and RT interference measures were subjected to one-way ANOVAs. The groups did not reliably differ in interference effects in accuracy, $F < 1.1$, or RT, $F < 1$. However, we obtained some evidence that the groups did differ in their ability to make relatedness judgments. Accuracy and mean correct RT to unrelated items were subjected to one-way ANOVAs. The reading groups significantly differed in accuracy $F(2, 52) = 3.27$, $p < .05$. Pairwise comparisons reveal that proficient readers had higher overall accuracy (95.5%) than resilient (91.4%, $t(41) = 2.43$, $p < .05$) or poor readers (90.8%, $t(32) = 2.17$, $p < .05$). The reading groups did not show reliable differences in RT, $F < 1.5$. Thus, both poor and resilient readers were less skilled at rejecting unrelated targets than proficient readers.

3.6.1. Cerebral volume

Cerebral volume was compared between reading groups using a one-way ANOVA. The reading groups did not significantly differ in total cerebral volume, $F < 1.2$. When volumes of gray matter and white matter were examined separately, no significant group differences emerged, Fs < 1.2. Groups did not significantly differ in total, gray matter, or white matter volume in either the right or left hemisphere, Fs < 1.5. Group means are given in Table 4.

3.6.2. Planum temporale asymmetry

To examine whether the left planum temporale was significantly longer than the right in each reading group, the asymmetry index was compared to zero using a one-sample t-test. Each group showed significant leftward asymmetry (proficient $t(21) = 4.26$, $p < .001$; resilient $t(20) = 2.22$, $p < .05$; poor $t(11) = 2.32$, $p < .05$).

Asymmetry of the planum temporale was compared between reading groups using a one-way ANOVA. Group means and standard deviations are provided in Table 5. The groups did not significantly differ, $F < 1$. One-way ANOVAs confirmed that the groups did not significantly differ in mean length of either the left or right planum temporale, $F < 1.5$. However, Levene's test for equality of variances indicated that resilient ($F = 7.45$, $p < .05$) readers showed greater variability in planar asymmetry than proficient readers, and poor readers showed a trend in the same direction ($F = 3.34$, $p < .10$).[1] These results are depicted in Fig. 4, which indicates a greater range of asymmetry scores for resilient, relative to proficient, readers. In order to quantify the extremity of asymmetry values, we calculated z-scores based on the mean and standard deviation of asymmetry scores among proficient readers. This z-score indicates, in units of proficient-reader-standard deviations, how far an individual's asymmetry scores is from the average for proficient readers. In order to classify individuals with both extreme leftward and extreme rightward asymmetries as atypical, we calculated the

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[1] These differences remained significant when only right-handed participants were considered (proficient versus resilient: $F = 4.77$, $p < .05$; $F = 6.86$, $p < .05$).
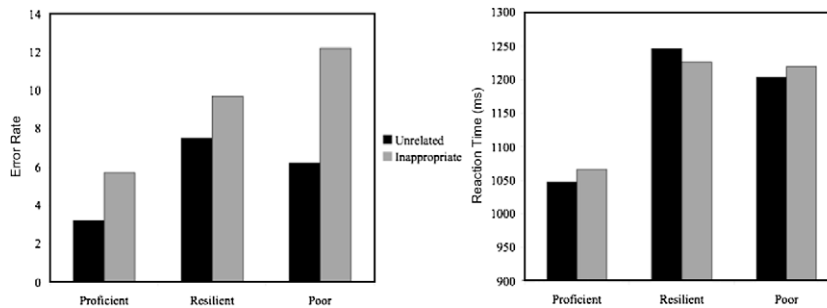
Fig. 3. Performance on homograph resolution task within each reading group.

Table 4
Mean (standard deviation) cerebral volume (cubic centimeters).

	Cerebral volume			Gray matter			White matter		
	Total	Left	Right	Total	Left	Right	Total	Left	Right
Proficient readers	1254 (149)	635 (77)	650 (77)	610 (63)	307 (32)	310 (32)	473 (72)	243 (36)	248 (37)
Resilient readers	1282 (164)	613 (76)	630 (81)	605 (57)	295 (28)	298 (29)	495 (83)	238 (38)	243 (40)
Poor readers	1196 (968)	618 (73)	634 (74)	579 (44)	291 (24)	295 (22)	452 (52)	221 (29)	225 (31)

absolute value of this z-score. Z-scores greater than 2 were considered extreme for this analysis. This classification identified 1 proficient reader, 5 resilient readers, and 4 poor readers with extreme asymmetry. Chi-square tests confirmed that more individuals with planar asymmetries more than two standard deviations from the mean were present among resilient readers ($\chi^2(1, N = 43) = 5.78$, $p < .05$) and poor readers ($\chi^2(1, N = 34) = 3.87$, $p < .05$) relative to proficient readers. Further analyses indicated that resilient showed greater variability than proficient readers in the length of the right planum ($F = 4.73$, $p < .05$), but not left planum ($F = 1.30$, $p > .10$). Poor readers showed a trend towards greater variability in the length of right planum temporale ($F = 2.80$, $p < .10$), but no significant difference in variability in left planum length ($F = 0.78$, $p > .10$).

While the handedness distribution does not significantly differ between the groups, non-right-handers are numerically overrepresented among resilient and poor readers. In order to address this possible confound, we compared planar asymmetries between right-handers (RH) and non-right-handers (NRH). A t-test showed that the difference in planar asymmetry between RH and NRH was not significant, $t(54) = -.51$, $p > .20$. However, Levene's test for equality of variances indicated that RH showed greater variability than NRH ($F = 4.05$, $p < .05$; standard deviation of RH = 0.96, NRH = 0.26). Consistent with this finding, RH show greater absolute values of planum temporale z-scores than NRH ($t = -2.11$, $p < .05$). None of the individuals with z-scores greater than 2, classified as those with extreme asymmetry, were NRH. Thus, it appears that the reading group differences are not explained by underlying group differences in handedness distribution.

3.6.3. Brain/behavior relationships

In order to investigate relationships between planum temporale asymmetry and reading performance, correlations between planar

Table 5
Mean (standard deviation) length and asymmetry of the planum temporale.

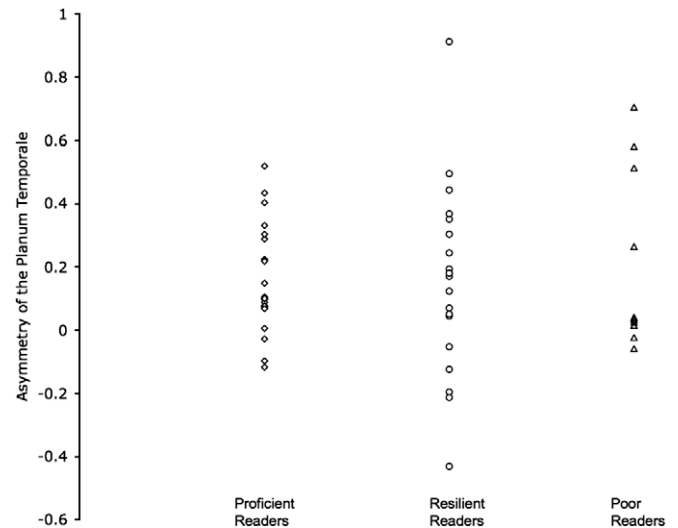|	Left planum temporale length	Right planum temporale length	Asymmetry index
Proficient readers	3.43 (1.10)	2.50 (0.81)	.152 (.169)
Resilient readers	3.16 (1.04)	2.46 (1.14)	.143 (.307)
Poor readers	3.20 (1.06)	2.37 (1.02)	.210 (.286)

Fig. 4. Asymmetry of the planum temporale within each reading group.

asymmetry and scaled scores on the reading subtests were performed on the full sample. Neither Word Attack ($R = -0.06$, $p > .20$) nor Passage Comprehension scores ($R = -0.13$, $p > .20$) scores were significantly correlated with planar asymmetry. However, the absolute value of z-scored asymmetry, representing extremity of asymmetry, was significantly correlated with Word Attack ($R = -0.30$, $p < .05$) but not Passage Comprehension performance ($R = -0.01$, $p > .20$). Those individuals whose planar asymmetries were the most extreme were those whose Word Attack scores were lowest.

4. Discussion

Resilient readers were identified on the basis of having poor phonological decoding skills and skilled reading comprehension. It was predicted that these readers would show greater reliance on word meanings than other reading groups and might show enhanced orthographic processing skills. Resilient readers and poor readers showed roughly equivalent deficits in phonological decoding and phoneme deletion. We obtained no evidence that resilient

readers showed preserved or enhanced orthographic processing skills. Instead, resilient readers differed from both proficient and poor readers in tasks that involved word meaning. They derived an increased benefit from the presence of meaningful relationships between words in the semantic priming task and showed a decreased ability to reject unrelated targets in the homograph resolution task. Resilient readers showed no differences from poor or proficient readers in cerebral volume. However, resilient readers showed greater variability in asymmetry of the planum temporale than proficient readers, driven by increased variability in the length of the right planum.

Before discussing our results, we first consider the limitations of our study. The sample of poor readers was small, and therefore the study may have lacked the power to uncover subtle behavioral differences between poor readers and the other groups. Our sample included some non-right-handers and some individuals with early exposure to both English and another language. These individuals were included to give the largest possible samples of resilient and poor readers and our groups show the range of handedness and language exposure present in a university population. However, it is possible that these factors, in addition to reading ability, might contribute to individual differences in the anatomical and behavioral characteristics we investigated. Additionally, even the poor readers in this study were attending college and had higher scores on the reading subtests than typical dyslexic subjects. While it may be seen as an advantage in that the poor readers were in a similar educational setting as the other reading groups, this sample is likely not representative of the population of reading disabled participants as a whole. Future studies should include reading disabled individuals from outside a university setting in order to include the full range of reading disabled individuals. As the participants in this study were all adults, some aspects of their educational background, including their method of reading instruction and objective childhood reading abilities, were not known. Longitudinal studies identifying and tracking resilient and poor readers from early in development might provide additional insight into the development of compensatory strategies.

Despite the limitations of the current study, we were able to gain information about possible alternative reading mechanisms employed by resilient readers. The existence of resilient readers represents a challenge for reading models that emphasize the role of phonological processes in reading (Frost, 1998). As resilient readers made up a non-trivial portion of our unselected sample of college students (20%), it is important that reading models be able to account for their reading performance. Additionally, the presence of resilient readers in the university population indicates that skilled text comprehension may be achieved through reliance on different mechanisms in different individuals. Understanding the variability in the mechanisms that support skilled reading is important for future studies exploring the behavioral and neural underpinnings of reading.

Resilient readers' accuracy on the pseudoword reading and phoneme deletion tasks was worse than that of proficient readers and similar to that of poor readers. In this way, resilient readers appear to resemble compensated dyslexics, who show lingering phonological deficits (Bruck, 1992; Wilson & Lesaux, 2001). Resilient readers did not outperform poor readers on the phonologically challenging task. This argues against the possibility that resilient readers are better at comprehending text because their phonological processing skills, while worse than those of proficient readers, are better than those of poor readers. Resilient readers' dissociation between phonological processing skill and comprehension instead suggests that they may rely on alternate mechanisms to support skilled reading.

We found no evidence for superior orthographic processing skill or increased reliance on orthographic analysis in resilient readers.

Resilient readers were less accurate than proficient readers at the orthographic choice task, with similar accuracy to poor readers. Resilient readers were no more likely than proficient or poor readers to produce analogous responses in the ambiguous pseudoword reading task. Prior studies of individuals with profiles similar to resilient readers have been inconsistent; two case studies demonstrated enhanced orthographic skills (Holmes & Standish, 1996; Howard & Best, 1997) and a third showed no evidence for increased reliance on orthographic analogy (Stothard et al., 1996).

It is possible that the tasks used in the present study failed to uncover superior orthographic processing in resilient readers or that some resilient readers rely heavily on orthographic information, as case studies have suggested (Holmes & Standish, 1996; Howard & Best, 1997). Both spelling and pseudoword reading are tasks with which compensated dyslexics typically have difficulty (Bruck, 1993). It is possible that resilient readers as a group would show better performance on a more implicit orthographic choice task, such as deciding which of two pseudoword strings is more wordlike or demonstrate enhanced ability to read irregular, but real words. Nonetheless, orthographic compensation does not appear to generalize across resilient readers or tasks designed to put demands on orthographic analysis.

Our finding that resilient readers show deficits in orthographic, as well as phonological processing supports the perspective that phonological and orthographic analysis are linked. The present pattern of results can be explained by theories such as Share's "self-teaching" hypothesis (Share, 1995) that hold that orthographic knowledge is gained by successful experience decoding new words. Under this framework, resilient readers' deficit in phonological decoding has led to difficulty gaining orthographic knowledge, resulting in less accurate orthographic knowledge.

Resilient readers showed greater benefit from meaningful relationships between words than poor and proficient readers. Resilient readers showed greater facilitation of lexical decision performance when a word was primed by a related word. This result is in agreement with a case study showing that a resilient reader's accuracy in reading pseudohomophones was improved by preceding the pseudohomophone with a related word (Stothard et al., 1996). In both cases, it appears that resilient readers activate semantic information during processing of the prime, and use this information to guide recognition of subsequent stimuli to a greater extent than proficient readers.

We investigated whether resilient readers differed in their ability to reject inappropriate associates in the homograph resolution task. Previous studies have shown that poor comprehenders have difficulty suppressing contextually inappropriate meanings (Gernsbacher & Faust, 1991), while proficient readers show little interference (Dixon & Twilley, 1999; Gernsbacher et al., 1990). In our study, the groups did not differ in interference effects. The poor readers in our sample were able to suppress contextually inappropriate meanings as quickly and accurately as readers in the other groups, a result that conflicts with a prior study of poor college readers (Gernsbacher & Faust, 1991). However, both poor and resilient readers were less accurate in rejecting unrelated words than proficient readers. This may indicate that these groups of readers attempt to find meaningful relationships even where they do not exist. This might result from a reading mechanism that relies on the use of semantic context and anticipates semantic associations between words.

Mean values of planum temporale asymmetry did not significantly differ between the reading groups, indicating that simple relationships between asymmetry of this structure and reading skill were not present in our sample. However, resilient readers showed a wider range of asymmetries of the planum temporale than proficient readers and were more likely than proficient readers to show asymmetry indices more than two standard deviations

from the mean. This difference between the groups did not appear to reflect differences in handedness distribution as planar asymmetries were less extreme in non-right-handers. Extremity of planar asymmetry was significantly correlated with phonological decoding scores such that more skilled decoders showed more typical asymmetry of the planum temporale. Previous studies have suggested that exaggerated leftward asymmetry of this region characterizes poor phonological decoders who are good comprehenders (Leonard & Eckert, 2008; Robichon et al., 2000), while reduced asymmetry may characterize individuals with both decoding and comprehension difficulties (reviewed in Leonard and Eckert (2008)). In our sample, however, resilient readers seem to show both extreme leftward asymmetry and exaggerated rightward asymmetry. This might indicate that multiple neurobiological pathways might support alternate reading strategies in university students with poor phonological skills. Greater variability in planar asymmetry among resilient readers might indicate that this atypical reading population is less subject to genetic constraints on neurodevelopment.

In summary, resilient readers show deficits in phonological and orthographic processing and increased benefit from meaningful relationships between words during single word reading. These results suggest that resilient readers benefit more than the other groups from semantic relationships between words and experience difficulty when such relationships are absent. Resilient readers, then, may achieve skilled text comprehension through a reading process that relies heavily on word meanings. Relative to proficient readers, resilient readers show increased variability in the asymmetry of the planum temporale. Such variability suggests that individuals who rely on alternate reading strategies show a greater range of brain morphology than those with more typical reading profiles. The underlying biological pathways that allow readers to achieve skilled comprehension through alternate reading mechanisms need further study.

Acknowledgments

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.bandl.2010.01.003.

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