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Gray matter correlates of reading fluency deficits: SES matters, IQ does not

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Abstract

Brain correlates of reading ability have been intensely investigated. Most studies have focused on single-word reading and phonological processing, but the brain basis of reading fluency remains poorly explored to date. Here, in a voxel-based morphometry study with 8-year-old children, we compared fluent readers (*n* = 18; 7 boys) with dysfluent readers with normal IQ (*n* = 18; 6 boys) and with low IQ (*n* = 18; 10 boys). Relative to dysfluent readers, fluent readers had larger gray matter volume in the right superior temporal gyrus and the two subgroups of dysfluent readers did not differ from each other, as shown in frequentist and Bayesian analyses. Pairwise comparisons showed that dysfluent readers of normal and low IQ did not differ in core reading regions and that both subgroups had less gray matter volume than fluent readers in occipito-temporal, parieto-temporal and fusiform areas. We also examined gray matter volume in matched subgroups of dysfluent readers differing only in socioeconomic status (SES): lower-SES (*n* = 14; 7 boys) vs. higher-SES (*n* = 14; 7 boys). Higher-SES dysfluent readers had larger gray matter volume in the right angular gyrus than their lower-SES peers, and the volume of this cluster correlated positively with lexico-semantic fluency. Age, sex, IQ, and gray matter volume of the right angular cluster explained 68% of the variance in the reading fluency of higher-SES dysfluent readers. In sum, this study shows that gray matter correlates of dysfluent reading are independent of IQ and suggests that SES modulates areas sub-serving lexico-semantic processes in dysfluent readers — two findings that may be useful to inform language/reading remediation programs.

Keywords: reading fluency deficits, gray matter, IQ, SES, children

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Learning to read is a major goal of early education, and yet about 20% of children from OECD (Organization for Economic Co-operation and Development) countries do not attain the baseline level of reading proficiency (OECD 2016). One reason for this outcome is that reading is a complex ability that requires various neurocognitive systems working together to combine high-level language functions with low-level perceptual and motor processes, and a full understanding of this complex orchestration has not yet been achieved. The brain basis of impaired reading has been intensely studied using functional and structural imaging methods, and functional abnormalities were found mainly, but not exclusively, in the left hemisphere (Richlan et al. 2009, 2011; Martin et al. 2015). Impaired readers tend to show underactivations in dorsal and ventral regions of posterior reading circuits — dorsally, in parieto-temporal areas including the superior temporal gyrus and the inferior parietal lobule, and ventrally, in occipito-temporal areas such as the fusiform gyrus (e.g., Blau et al. 2009, 2010; Hoeft et al. 2007; Wimmer et al. 2010). The dorsal circuit was shown to subtend phonological recoding (audiovisual integration and mapping graphemes to phonemes, a crucial process for novice readers) and the ventral circuit to be involved in word recognition by skilled readers (Pugh et al. 2000). Structural MRI studies added to this picture (e.g., Eckert et al. 2005; Hoeft et al. 2007; Krafnick et al. 2014; Kronbichler et al. 2008), and recent meta-analyses converged in identifying gray matter reductions in dorsal and ventral regions of the reading network; specifically, to the left, in the orbitofrontal cortex (Eckert et al. 2016), superior temporal sulcus (Eckert et al. 2016; Richlan et al. 2013) and occipito-temporal areas including a cluster in the fusiform gyrus (Linkersdörfer et al. 2012); bilaterally, in the supramarginal gyrus and cerebellum (Linkersdörfer et al. 2012); and to the right, in the superior temporal gyrus (Linkersdörfer et al. 2012; Richlan et al. 2013) and cerebellar hemisphere (Eckert et al. 2016).

Most studies on the neural correlates of typical and impaired reading have examined phonological processing and single-word reading. On more ecologically valid measures of reading, such as reading fluency, there is presently limited evidence. Fluent reading is the ability to read accurately and smoothly with proper phrasing and comprehension (Breznitz 2006; Wolf and Katzir-Cohen 2001). It requires not only phonological decoding and word recognition but also automatization of these processes and integration with comprehension and prosody. This is perhaps the reason why it is so difficult, in research, to study reading fluency and, in education, to help learners improve it (Torgesen and Hudson 2006; Wexler et al. 2008; but see Breznitz et al. 2013; Horowitz-Kraus et al. 2014a). Reading fluency deficits are stable over time (e.g., Leinonen et al. 2001; Moll et al. 2019) and conspicuous in different types of orthographies: in consistent or shallow ones where the print-to-speech mapping is regular (e.g., Landerl and Wimmer 2008), and in inconsistent or deep ones where the mapping is complex and not entirely rule-based (Katzir et al. 2004). Dysfluent reading is the most persistent impairment in dyslexia (Shaywitz et al. 2008), and its lead symptom in readers of consistent orthographies (Landerl et al. 2013; Seymour et al. 2003; Torppa et al. 2010; Ziegler et al. 2010). Conversely, reading fluency is vital for reading comprehension (e.g., Fuchs et al. 2001; Jenkins et al. 2003; Kim et al. 2012; Roehrig et al. 2008). For example, text-reading fluency explains variance in reading comprehension over and above word reading fluency and/or listening comprehension (Fernandes et al. 2017; Kim et al. 2012; 2014; Kim and Wagner 2015; Klauda and Guthrie 2008). In their meta-analysis of the simple view of reading (written reading comprehension is the product of word decoding and listening comprehension), Florit and Cain (2011) showed that the impact of reading fluency on reading comprehension depends on orthography and instruction. A case in point is that for young readers of consistent orthographies reading comprehension is better predicted by reading fluency than reading accuracy (most likely because grapheme-phoneme mappings are easier to predict, and thus reading accuracy is mastered early on during reading instruction).

To date, very few studies investigated the neural correlates of reading fluency. Benjamin and Gaab (2012) examined brain activations in core reading areas of 13 adults (all typical readers) using an fMRI task requiring participants to read sentences and letters at different reading rates: normal, slowed down (constrained) and accelerated. Langer and colleagues (2015) used a similar approach with 15 typical and 15 reading disabled children. Both studies unveiled a specific involvement of the fusiform gyrus in fluent reading, namely at accelerated rates. In the adult study, Benjamin and Gaab observed that increasing reading speed was associated with stronger activation of the fusiform gyrus, and in the children's study Langer et al. showed that when reading disabled children were required to read faster than their comfortable reading speed (accelerated rate), the activation in their fusiform gyrus was less than that of typical-reading children. In other words, in reading disability the fusiform gyrus was less responsive to reading speed. A different approach was taken by Christodoulou and colleagues (2014). They compared brain activations in 12 typical and 12 dyslexic adults on an fMRI task requiring to judge whether sentences presented at different rates made sense (semantically) and found a large bilateral network subtending fluent reading in both groups. However, as sentence presentation rate increased, typical readers showed significantly larger activation than dyslexic ones in several brain regions, including areas in the left prefrontal and superior temporal gyri associated with semantic and phonological processes. These three studies did not converge on which regions were singled out as important for fluent reading — probably because of the different tasks used, one based on reading rate proper, and the other emphasizing understanding. However, they highlighted aspects of the brain basis of reading that go beyond the word level and tap fluent reading of connected text. Another aspect highlighted as important for reading fluency is grapheme-phoneme integration (Blomert 2011). Grapheme-phoneme integration has been associated with several brain areas, such as bilateral temporal, occipito-temporal, inferior parietal and frontal regions (Blau et al. 2010; Karipidis et al., 2018; Kronschnabel et al. 2014; Van Atteveldt et al. 2004), but the superior temporal gyri emerged consistently across studies as the most prominent region (Richlan 2019). It is appealing to view the brain basis of grapheme-phoneme integration in the context of a neural circuit for reading as proposed by Ozernov-Palchik and Gaab (2016), of which an important part is attributed to the integration of audiovisual information (Richlan 2019; Tijms et al. 2020; Van Atteveldt and Ansari 2014).

In addition to brain correlates, and in relation to them, two important variables have been invoked in trying to understand reading disability: IQ and socioeconomic status (SES). Let us first consider IQ. For a long time, the etiology of reading disability was assumed to differ as a function of IQ, and the diagnosis of specific reading disability or dyslexia was based on the discrepancy between reading performance and cognitive abilities — the IQ-achievement discrepancy criterion, whereby a diagnosis of specific reading disability required an IQ within normal limits (e.g., O’Donnell and Miller 2011). Behavioral studies found long-term associations between IQ and persistent reading disability (Ingesson 2005; Swanson 2012) and behavioral-genetic studies identified IQ-related differences in the heritability of reading ability in poor readers (Wadsworth et al. 2010). Both types of findings converge with the view that neural systems implicated in reading might differ in struggling readers as a function of IQ. However, several other studies called this view into question. Two meta-analyses (Hoskyn and Swanson, 2000; Stuebing et al. 2002) established that impaired readers differing in IQ performed similarly in phonological awareness, rapid naming and vocabulary tasks, all tapping abilities closely related to reading (they differed, however, in syntax- and lexico-semantic abilities). More recently, Ferrer and colleagues (2010) showed in a longitudinal study that impaired readers' reading abilities developed independently from IQ, and Stuebing and colleagues (2009) showed that response to intervention of impaired readers was also independent of IQ. Additional behavioral (e.g., Fletcher et al. 1994) and neuroimaging evidence (Simos et al. 2014; Tanaka et al. 2011) has also indicated that impaired readers have similar deficits regardless of IQ. For instance, Tanaka and colleagues showed that struggling readers with normal IQ or low IQ have similar patterns of reduced brain activation in regions involved in phonological decoding, namely left parieto-temporal and left occipito-temporal areas. Overall, then, current evidence suggests that functional brain correlates of reading failure are similar in all children with poor reading irrespective of intellectual ability. However, this evidence pertains almost exclusively to phonological decoding in children learning English, an orthography known for its extreme inconsistency (Share 2008). It is presently unknown whether similar conclusions would be drawn if other orthographies or other aspects of reading ability had been considered. It is also unknown whether the reading ability - IQ independence is observable at other levels, such as brain structure and connectivity, and using different imaging methods, such as diffusion-tensor or volumetric techniques.

SES, commonly indexed by family income, parental education, and occupational status (Bradley and Corwyn 2002), is a well-known environmental predictor of reading proficiency (e.g., Olson et al. 2014). It has been consistently related to variation in reading performance, where high SES individuals outperform low SES ones (Noble and McCandliss 2005). SES-related differences are not restricted to behavior. They extend to brain structure and function (for a recent review, see Yaple and Yu 2020). However, studies examining the link between SES, reading ability and brain characteristics in children are rare. Gullick and colleagues (2016) found that word reading (a composite measure of word naming and fluency) correlated positively with the fractional anisotropy of several white-matter tracts, mainly left-sided clusters in high SES children and right visuospatial tracts in low SES children. In another study, Noble and colleagues (2006) found a stronger link between phonological abilities and reading-related activations in the left fusiform gyrus and left perisylvian regions in low SES children than in high SES ones. Recently, Ozernov-Palchik et al. (2019) reported that, compared to their high SES peers, low SES kindergartners had weaker structural connectivity in the left and right inferior longitudinal fasciculi and that the microstructure of the inferior longitudinal fasciculi in kindergarten was positively associated with reading performance in the second grade — in low SES children, but not in high SES ones. The three studies suggest that SES modulates the brain-behavior relationship in reading and evince an interplay between social, cognitive, and neurobiological factors in reading development. Perhaps not surprisingly, this interplay also shows up in intervention. In a recent study with reading disabled children, Romeo and colleagues (2018) showed that SES was positively correlated with vocabulary scores and the cortical thickness of bilateral perisylvian and supramarginal regions before intervention. They also showed that low SES children responded better to intervention than high SES ones, not only behaviorally but also at the neural level: they had greater gains than their peers in reading ability and in cortical thickening of bilateral occipito-temporal and parieto-temporal regions.

In the present study, we focus on gray matter correlates of children's reading fluency deficits and examine whether they are independent of IQ and SES using a voxel-based morphometry (VBM) approach. We compare European Portuguese fluent readers with dysfluent readers with normal IQ or with low IQ and inspect whether SES modulates the brain-behavior relationship in dysfluent readers matched in reading fluency and IQ. Gray matter volume differences are examined within a mask comprising several cortical regions bilaterally: inferior frontal gyrus, superior/middle temporal gyri, inferior parietal lobule and fusiform gyrus. These regions have been consistently associated with reading disability (Linkersdörfer et al. 2012; Martin et al. 2015; Ozernov-Palchik and Gaab 2016; Richlan et al. 2013) and proved to be especially relevant to reading fluency (Benjamin and Gaab 2012; Langer et al. 2015) and grapheme-phoneme integration (Blomert 2011; Richlan 2019). Based on evidence that reading ability and IQ are decoupled in impaired readers (Ferrer et al. 2010) and that functional brain correlates of the phonological deficit are independent of IQ (Tanaka et al. 2011), we expect dysfluent readers (normal- and low-IQ) to show similar characteristics in the core reading network, but to diverge from fluent readers in regions subtending reading ability, including occipito- or parieto-temporal regions. Assuming that grapheme-phoneme integration is especially involved in reading fluency (Blomert 2011; Richlan 2019), we also expect dysfluent readers to differ from their fluent peers in regions subtending the integration of audiovisual information, namely superior temporal areas. Additionally, and extrapolating from Romeo et al.'s (2018) results, we expect dysfluent readers from higher-SES backgrounds to present more gray matter volume than their lower-SES peers in regions subtending comprehension and vocabulary knowledge and known to be modulated by SES, namely inferior frontal and posterior parieto-temporal regions.

Method

Participants

Fifty-four third graders participated in this study (31 girls; age: *M* = 8.24 years, *SD* = 0.31, range = 7.83 - 9.25). All were native speakers of European Portuguese with no known history of neurological or psychiatric disorders, specific language impairment/language learning disability, and not taking any medication at the time of the study. Almost all (n = 49) were right-handed (Laterality Index, LI, > .48), two were left-handed (LI = -80 and LI = -40) and three were ambidextrous (LI = 10, and two LI = 40), according to the criteria defined by Cohen (2008; http://www.brainmapping.org/shared/Edinburgh.php) in a revised version of the Edinburgh Handedness Inventory (Oldfield 1971).

This sample was drawn from a larger group of children (*n* = 71; 42 girls; age: *M* = 8.26 years, *SD* = 0.32, range = 7.75 - 9.25) who were enrolled in a project looking at music training, auditory processing, and brain plasticity in children from public schools in middle- and low-income communities in Northern Portugal (Correia et al. 2019; Martins et al. 2018). Most children attending these schools (55%) receive free or reduced-price meals, a condition that we used as a proxy for lower-SES (higher-SES were children not receiving this social support), and more than 70% of parents or legal guardians have less than secondary education (only 7% have higher education). The study was approved by the ethics committee of the Faculty of Psychology and Education Sciences at University of Porto (reference FPCEUP 2015.1.23) and conducted in accordance with the Declaration of Helsinki. Written informed consent was obtained from parents and local school authorities, and children gave their verbal assent at the start of data collection. Parents also completed a safety form to ensure that the children could be safely scanned. All children completed behavioral and MRI assessments as described below.

Behavioral assessment

The behavioral assessment protocol included measures of handedness, IQ, and reading ability. Handedness was assessed with M. S. Cohen's revised version of the Edinburgh Handedness Inventory (Oldfield 1971; http://www.brainmapping.org/shared/Edinburgh.php), and IQ with the Wechsler Intelligence Scale for Children-3rd Edition (WISC-III; Wechsler 2003, Portuguese version). Reading ability was measured with three different tests: from the Differential Diagnosis of Dyslexia Maastricht battery (3DM; Blomert and Vaessen 2009; Portuguese version by Reis et al. 2020), the word and pseudoword subtests; a reading age test (TIL; Sucena and Castro 2010), and a Words Correct per Minute (WCPM) test (Fuchs et al. 2001). The subtests from 3DM provide measures of high- and low-frequency word reading and a proxy of phonological decoding (pseudoword reading). Stimuli are presented in columns and the child is required to read aloud as many as possible within 30 seconds (the maximum is 75 per subtest); the number of correctly read stimuli is the raw score (rate of words per 30 s), that is transformed into rate per minute. These scores were converted into standard scores ($M = 100$, $SD = 15$) by reference to a large-scale study with Portuguese children ($n = 820$, grade 1 to 4; Reis et al. 2020). An additional measure of accuracy was also computed as the percentage of correctly read stimuli relative to the sum of correctly and incorrectly read ones. The TIL reading age test consists of 36 sentences where the last word is missing; the child has to select the missing word from a set of five alternatives, and the number of correctly completed sentences within 5 minutes is the raw score. Raw scores were converted into standard scores ($M = 100$, $SD = 15$) based on Sucena and Castro's age norms (2010). The WCPM test consisted of a text from a children's tale ("O Senhor do Seu Nariz", *"Master of One's Own Nose",* Magalhães, 2010) that children had to read as quickly and accurately as possible with attention to expression and comprehension; the time limit was 1 minute, and the number of words correctly read per minute was scored. As no standardized age norms for reading fluency in European Portuguese were available, we converted raw scores into standardized scores (*M* = 100, *SD* = 15) based on results from the typical readers of the larger group of children (*n* = 71). Following Shaywitz et al (2002) and others (Ferrer et al. 2010; Lebel et al. 2019), we set the cut-off criterion at 90 (25% percentile) and defined typical readers as those with standard scores equal or above 90 in at least three of the other four reading measures (high- and low-frequency word reading, pseudoword reading, and reading age). This was the case for 44 of the 71 children, who read on average 78.75 words/min (range: 49 - 138, *SD* = 18.41). Interestingly, this reading rate falls within the normative range of the Hasbrouck-Tindal reading fluency norms for fall third graders (Hasbrouck & Tindal 2017; 50th percentile = 83, 25th - 75th percentiles = 59 - 104). WCPM standard scores were computed, and children were classified as fluent readers if they had a standard score equal or above 90 and as dysfluent if their score was below 90. As a result, 35 children were classified as fluent readers (*M* = 84.69, *SD* = 15.88, range = 70 - 138) and 36 as dysfluent readers (*M* = 48.22, *SD* = 13.75, range = 3 - 64). As for the 3DM tests, we calculated an additional measure of accuracy as the percentage of correctly read words over total words read.

MRI acquisition

T1-weighted images were acquired on a 1.5T Siemens Magnetom Sonata Maestro Class (Siemens Medical Systems, Erlangen, Germany) using a 3D magnetization prepared rapid gradient echo sequence with the following parameters: 1680 ms repetition time, 4.12 ms echo time, 8º flip angle; 160 contiguous sagittal slices, 250x250 mm^2 field-of-view. A 1 mm isotropic voxel was used to accomplish a good differentiation between tissue types. Children wore a foam headrest and a forehead strap to minimize head motion during scanning.

Procedure

Behavioral assessments were conducted in two individual sessions in a quiet room of the children’s schools. The WISC-III battery subtests were completed in the first session and the reading tasks in the second one. MRI scans were then acquired in a third session at the neuroimaging center. Before the start of data collection, children’s parents completed a sociodemographic questionnaire. Information regarding socioeconomic support from the public education authorities was derived from school records, i.e., whether children were provided with free or reduced-price meals or had no such reduction, and this was taken as a proxy for lower-SES and higher-SES, respectively.

Image processing

Preprocessing of T1-weighted images was carried out using the SPM12 package (http://www.fil.ion.ucl.ac.uk/spm) and the CAT12.6 r1450 toolbox (http://dbm.neuro.uni-jena.de/cat), running under MATLAB R2015a (Mathworks, Sherborn, MA). Raw data were manually inspected for individual and scanner-based artifacts (e.g., motion). The origin was manually set on the anterior commissure according to the Montreal Neurological Institute (MNI) spatial coordinate system. Tissue probability maps were generated using the Template-O-Matic toolbox (http://dbm.neuro.uni-jena.de/software/tom/) with age ($M = 8.2$ years) and sex as defining variables (Wilke et al. 2008). A study-specific template was created using the Diffeomorphic Anatomical Registration Through Exponentiated Lie Algebra, DARTEL (Ashburner 2007). After preprocessing, images were inspected for poor quality and incorrect preprocessing using the check sample homogeneity function of CAT12. None of the images presented quality problems. Finally, modulated gray matter volumes were smoothed with a Gaussian kernel of 8 mm full width at half maximum. Using the estimation module in CAT12, total intracranial volume (TIV) was extracted as the sum of gray matter, white matter, and cerebrospinal fluid volumes.

Group assignment

Dysfluent readers were divided into two groups based on full-scale IQ, low if below 90, normal otherwise. The IQ cut-off at 90 was chosen because it has been used in numerous studies (e.g., Eckert et al. 2005; Tanaka et al. 2011), including in studies of Portuguese children with reading disabilities (Moura et al. 2014, 2015). This resulted in 18 dysfluent readers with low IQ and 18 with normal IQ. A control group of fluent readers with normal full-scale IQ ($n = 18$) was then drawn from the sample of fluent readers ($n = 35$; see Behavioral assessment) enrolled in the larger project. The control group was composed of children whose IQ matched the IQ of the dysfluent readers with normal IQ and whose age, sex and SES matched as closely as possible those of the dysfluent children. The characteristics of the three groups are presented in Table 1. Fluent readers had significantly higher reading fluency scores than the two groups of dysfluent readers (*p*s < .003), which did not differ from each other (*p*s > .30). Accuracy scores were similar across groups (*p*s > .08). As in Tanaka et al. (2011), dysfluent readers with normal IQ had higher IQ than reading fluency scores, $t(17) = 11.83$, $p < .001$, whereas the low IQ dysfluent group did not, $t(17) = 1.62$, $p = .12$. The three groups were similar in age, $F(2, 51) = 2.55$, $p = .09$; sex, $\chi 2$ (2) = 1.97, $p = .37$; SES, $\chi 2$ (2) = .149, $p = .93$; handedness, *FET,* $p = .23$; and TIV, $F(2, 51) = 1.65$, $p = .20$.

To examine SES-related brain-behavior modulations, we split the dysfluent readers into subgroups of higher- or lower-SES based on, respectively, not receiving or receiving social assistance and compared gray matter volume in these subgroups. Of the 36 dysfluent readers, 16 fell in the higher-SES subgroup, and 20 in the lower-SES subgroup. As children in these subgroups differed on some of the reading fluency scores (see Supplementary Table 1) and our goal was to draw reliable comparisons based on SES alone, we matched children from the two subgroups on age, sex, full-scale IQ, total intracranial volume, and reading fluency. This procedure allowed to identify 28 individually matched children, 14 in each subgroup, whose main characteristics are presented in Table 2. They will be referred hereafter as higher- vs. lower-SES dysfluent readers.

Statistical analyses

Gray matter volume differences between groups were examined with a one-way ANOVA as implemented in SPM12. We tested the main effect of group and planned pairwise comparisons between fluent vs. dysfluent readers and between normal vs. low IQ dysfluent readers. Differences in gray matter volume between dysfluent readers of lower- and higher-SES were tested with a two-sample t-test. We explored the association between reading and SES-related effects using correlation and regression analyses and a principal component analysis (PCA) to aggregate correlated reading measures. TIV was included in all design matrices as a variable of no interest, and an absolute threshold masking was applied to exclude voxels with intensities below 10%.

In addition to the frequentist analyses described above, Bayesian statistics were also calculated. Estimated Bayes factors (BF_{10}) provide a quantification of the degree to which data support the alternative or null hypothesis, and this latter aspect is crucial to ascertain our hypothesis of no difference between dysfluent readers with normal vs. low IQ. These analyses were conducted on JASP Version 0.11.1 (JASP Team 2019) using default priors according to Rouder et al. (2012). The magnitude of BF_{10} was interpreted as put forward in Jeffreys' guidelines (Jarosz and Wiley 2014; Jeffreys 1961): values below 1 correspond to evidence in favor of the null hypothesis, anecdotal if between 1 and 0.33, substantial if between 0.33 and 0.10, strong if between 0.10 and 0.03, very strong if between 0.03 and 0.01, and decisive if below 0.01; and values above 1 correspond to evidence in favor of the alternative hypothesis, analogously graded (1 - 3, anecdotal evidence; 3 - 10, substantial evidence; 10 - 30, strong evidence; 30 - 100, very strong evidence; above 100, decisive evidence).

Ten regions of interest were combined to form a mask comprising the core reading regions as identified in previous neuroimaging studies of reading (dis)ability (Eckert et al. 2005; Hoeft et al. 2007; Kronbichler et al. 2008; Rueckl et al. 2015; reviews: Linkersdörfer et al. 2012; Martin et al. 2015; Richlan et al. 2013), reading fluency (Benjamin and Gaab 2012; Langer et al. 2015) and letter-speech sound integration (Blau et al. 2010; Karipidis et al. 2018; Van Atteveldt et al. 2004; reviews: Blomert 2011; Richlan 2019). The regions are the bilateral inferior frontal gyrus (pars triangularis and pars opercularis), superior and middle temporal gyri, inferior parietal lobule (supramarginal and angular gyri) and fusiform gyri. All of these regions have been associated with processes that are critical for skilled reading (Ozernov-Palchik and Gaab 2016): parieto-temporal areas with the integration of orthographic and phonological information, ventral occipito-temporal areas with rapid written word identification, and the inferior frontal region (with a more diverse profile) with phonological processing, lexical access, semantics, speech planning, and several other cognitive processes. Some of these regions, namely the superior temporal cortex, have also been linked to lower- (sensory) and higher-level processes of grapheme-phoneme integration (Blomert 2011). The mask was created using the Automated Anatomical Labeling atlas (AAL; Tzourio-Mazoyer et al. 2002) in the WFU PickAtlas toolbox (http://fmri.wfubmc.edu/software/PickAtlas). A threshold-free cluster enhancement (TFCE; Smith and Nichols 2009) was applied using the TFCE toolbox (http://dbm.neuro.uni-jena.de/tfce/) for a combined analysis of the height and size of effects. Statistical inference was established via family-wise error correction (FWE, $p < 0.05$; $k > 20$) for multiple comparisons using nonparametric permutation testing (5000 permutations, according to the toolbox default settings). Permutation testing was calculated using the Freedman-Lane method

(Winkler et al. 2014). For completeness, whole brain analyses were also computed; they are presented as supplementary information in a whole brain analysis section.

The REX toolbox (http://web.mit.edu/swg/software.htm) was used to extract individual gray matter volumes from regions showing differences in the comparisons between the three main groups of readers (fluent, normal IQ dysfluent, low IQ dysfluent), and between higher- vs. lower-SES dysfluent subgroups. Extracted gray matter volumes were used to plot group differences in specific regions and compute correlations and regression analyses on the matched subgroups' SES-related effects.

Results

Reading-related differences

The analysis of the main effect of group on gray matter volume revealed a single cluster in the right superior temporal gyrus (Figure 1a; Table 3), where fluent readers had a larger volume than both groups of dysfluent readers (*p*s < .001), which did not differ from each other ($p = 1.00$). This result suggests that gray matter correlates of reading dysfluency are similar across readers irrespective of IQ. To ascertain the magnitude of these effects, we conducted a Bayesian ANOVA on individual gray matter volumes of the right superior temporal cluster. This analysis resulted in decisive evidence for the main effect of group ($BF_{10} = 837.11$), and post-hoc tests indicated decisive evidence for the difference between fluent and normal IQ dysfluent readers ($BF_{10} = 271.40$, posterior odds = 159.42) and very strong evidence for the difference between fluent and low IQ dysfluent readers ($BF_{10} = 63.81$, posterior odds = 37.48). Importantly, post-hoc tests also indicated substantial evidence ($BF_{10} = 0.32$, posterior odds = 0.19) for no differences between normal IQ and low IQ dysfluent readers.

Going back to the main analysis, planned pairwise comparisons showed that fluent readers had significantly larger gray matter volume than their dysfluent peers in reading-related brain regions, specifically in the right superior and middle temporal gyri, right fusiform gyrus, left planum temporale, including the Heschl’s sulcus, and the left middle temporal gyrus extending to superior temporal sulcus (Figure 1b; Table 3). Dysfluent readers did not show regions of significantly larger gray matter volume when compared to fluent readers. Pairwise comparisons between normal IQ and low IQ dysfluent readers did not show any significant clusters.

SES-related differences in dysfluent readers

A two-sample t-test showed that higher-SES dysfluent readers had larger gray matter volume than their lower-SES peers in a cluster in the right angular gyrus ($x = 45$, $y = -52$, $z = 33$, TFCE = 45260.70, $p < .001$ cFWE, $k = 129$; Figure 2).

An exploratory analysis of the association between reading performance and SES-related effects revealed that gray matter volume in the right angular cluster correlated with three of the five reading fluency measures: the WCPM index ($r = .40$, 95% CI = [.04, .68], $p = .03$), reading age ($r = .42$, 95% CI = [.06, .69], $p = .03$), and high-frequency word reading ($r = .48$, 95% CI = [.13, .72], $p = .01$), three measures tapping into lexical and semantic processing. No correlations were found with low-frequency word reading ($r = .37$, 95% CI = [-.00, .65], $p = .05$) and pseudoword reading ($r = .33$, 95% CI = [-.05, .63], $p = .09$) or additional accuracy measures (ps > .13; Supplementary Figure 1 - a). Analogous correlations computed separately for higher- and lower-SES dysfluent readers only reached significance in the higher-SES group (Supplementary Figure 1 – b, c). As the right angular cluster correlated with three reading fluency measures, we sought to reduce collinearity and measure-specific error variance by computing an aggregate variable using PCA (varimax rotation). This analysis extracted a single component explaining 76%, 75% and 58% of the variance of WCPM, reading age, and high-frequency word reading, respectively. Because this component ties together reading fluency abilities with strong involvement of lexical and semantic processes, we will refer to it as lexico-semantic fluency. Lexico-semantic fluency was positively correlated with gray matter volume of the right angular cluster in the matched dysfluent readers, $r = .52$, 95% CI = [.18, .75], $p < .01$; (Figure 3 - a), and in the higher-SES group, $r = .69$, 95% CI = [.25, .89], $p < .01$ (Figure 3 - b), but not in the lower-SES group, $r = -.16$, 95% CI [-.64, .40], $p = .58$ (Figure 3 - b). Thus, the aggregate variable captured the same brain-behavior link as the individual reading measures, a link that seems to be driven by the higher-SES children. To further test this idea, we calculated a hierarchical linear regression with data from all matched dysfluent readers (collapsed across SES subgroups) controlling for age, sex and IQ. After controlling for these variables, the right angular cluster explained 20% of the variance in lexico-semantic fluency, $R^2 = .50$, $F(4, 23) = 5.80$, $p < .01$, adjusted $R^2 = .42$ (cf. Supplementary Table 3). The same analysis computed with data from the higher-SES dysfluent readers yielded a similar result, with the right angular cluster accounting for 14% of the variance after controlling for age, sex and IQ, $R^2 = .78$, $F(4, 9) = 7.84$, $p < .01$, adjusted $R^2 = .68$ (cf. Supplementary Table 4).

Discussion

The present study revealed three novel findings on the role of IQ and SES in relation to gray matter correlates of reading fluency deficits in children. First, gray matter volume in the right superior temporal gyrus was larger in fluent readers than in dysfluent readers with normal IQ or low IQ, but the two dysfluent groups did not differ in gray matter volume, a negative result confirmed with Bayesian analysis. Pairwise comparisons showed that the larger gray matter volume of fluent readers was located mainly in the dorsal reading pathway and confirmed that the dysfluent groups did not differ in gray matter volume of core reading cortical regions. Second, the comparison of dysfluent readers differing in SES showed that higher-SES children had larger gray matter volume than their lower-SES peers in a cluster in the right angular gyrus. Third, gray matter volume of this right angular cluster correlated positively with text-reading fluency, reading age and high-frequency word reading in the higher-SES subgroup and all matched dysfluent readers, but not in the lower-SES subgroup taken separately. Noticeably, after controlling for age, sex and IQ, this cluster's volume accounted for a significant part of the variance of an index of lexico-semantic fluency resulting from the aggregation of three reading fluency measures, 14% in the higher-SES subgroup and 20% in all matched dysfluent readers.

Finding reduced gray matter volume in the right superior temporal gyrus of dysfluent readers agrees well with Linkersdörfer et al.'s (2012) and Richlan et al.'s (2013) meta-analyses that also identified smaller gray matter volumes in regions of the right superior temporal cortex in impaired readers. However, in our study the region associated with dysfluent reading is slightly more anterior than those identified in the meta-analyses. A possible reason for this discrepancy is that we examined third-grade children, whereas most studies included in the meta-analyses were conducted with adolescents or adults, and only one included school-age children (Eckert et al. 2005). Interestingly, the region we found is very similar to the one reported by Blau and colleagues (2010) for 9-year-old dyslexic children in a functional study on grapheme-phoneme integration, a foundational process for achieving fluent reading (Blomert 2011). In their study, in comparison to controls, dyslexic children displayed weaker activity in the anterior part of the superior temporal gyri when processing phonemes (Blau et al. 2010). Regions in the superior temporal gyri have consistently been associated with phoneme processing and grapheme-phoneme integration (Blomert 2011; Richlan 2019), with a division of labor between the posterior part for the integration of visual with auditory information and the anterior/middle part for phoneme processing (e.g., Blau et al. 2009, 2010; Van Atteveldt et al. 2004). Here, atypical volume in the anterior/middle part of the right superior temporal gyrus was a signature of dysfluent reading, a finding that fits well with the heuristic idea that an impairment or less efficiency in processing speech contributes to poor reading fluency.

The bilateral volume differences we found in pairwise comparisons of fluent and dysfluent readers were in occipito-temporal and parieto-temporal regions that partially overlap those Blau and colleagues (2010) ascribed to letter and phoneme processing. Lesser volume in the right fusiform gyrus and the left middle temporal gyrus also overlap with areas identified in functional studies of reading fluency deficits in English-speaking children (Langer et al. 2015). Overall, then, our structural findings are commensurate with functional findings and with the dorsal/ventral neurodevelopmental model of visual word recognition (Pugh et al. 2000). According to this model, the dorsal pathway is implicated in phonological decoding, and skilled reading — that our dysfluent children had not achieved — relies increasingly on the ventral occipito-temporal pathway for visuo-orthographic recognition. The atypical gray matter volume we observed in dysfluent children suggests an insufficiently developed or impaired dorsal pathway. In addition, our results also indicate an involvement of the right hemisphere in fluent reading of young readers. A possibility is that the right hemisphere is more strongly recruited during the early stages of learning how to read, and its role decreases with reading experience (Shaywitz et al. 2007; Turkeltaub et al. 2003; Waldie and Mosley 2000). But it might also be that reduced gray matter in the right hemisphere, namely in the superior temporal gyrus, is already present at birth or arises in early childhood before reading onset (Raschle et al. 2011; Black et al. 2012). The present study does not allow to disentangle these two possibilities, but longitudinal studies with preliterate children and early readers might elucidate this issue.

Dysfluent readers with normal IQ and low IQ did not differ on gray matter volume in any core reading regions. This was not unexpected based on available functional and behavioral evidence. Tanaka et al. (2011) and Simos et al. (2014) have already shown that the functional brain correlates of the phonological deficit are independent of IQ, and Ferrer et al. (2010), Hoskyn and Swanson (2000), and Stuebing et al. (2002) that reading abilities and IQ are not necessarily coupled. Our findings extend this evidence to gray matter correlates of reading fluency deficits, and to an ecologically valid measure of reading, reading fluency. Moreover, because our results come from the Portuguese language, they expand current knowledge about the neural correlates of the IQ-reading relationship to a consistent orthography. Previous evidence (Tanaka et al. and Simos et al.) was entirely based on findings from the English language, which is well-known for its highly inconsistent orthography. Generalizability of findings to diverse languages is especially welcome in reading research (Daniels and Share 2017), and thus our results are valuable to document that reading disability and IQ are orthogonal to each other, across languages.

Higher-SES dysfluent readers presented larger gray matter volume in a cluster of the right angular gyrus compared to lower-SES peers. It is revealing that it was a dorsal region in the right hemisphere to differentiate higher- and lower-SES dysfluent readers. Right-lateralized dorsal circuits appear to be modulated by SES (e.g., Gullick et al. 2016) and involved in poor readers' response to intervention (e.g., Barquero et al. 2014; Hoeft et al. 2011; Romeo et al. 2018). Hoeft et al. (2011) showed that greater activation in right prefrontal regions significantly predicted longitudinal reading improvement in dyslexic children, and the meta-analysis by Barquero et al. (2014) showed that reading intervention induced changes in the activation of the right inferior frontal gyrus. Additionally, fractional anisotropy of the right superior longitudinal fasciculus predicted longitudinal reading gains in dyslexic children (Hoeft et al. 2011). High SES has also been related to greater cortical thickness in bilateral perisylvian and supramarginal regions in poor readers (Romeo et al. 2018). Our results converge these by showing that the right angular gyrus of dysfluent readers reflects SES-related plasticity under stringent conditions of comparison: IQ and reading-level matched subgroups differing only in SES background. From a behavioral point of view, SES-related variation of gray matter volume in the right angular gyrus might reflect home literacy environments differing in exposure to print (Duke 2000; Neuman and Celano 2001) or in quantity and quality of linguistic and cognitive stimulation (Schwab and Lew-Williams 2016; Tal and Arnon 2018), as both exposure to print and stimulation impact language and literacy development (Bradley and Corwyn 2002; Mol and Bus 2011; Noble and McCandliss 2005; Pace et al. 2017). Another possibility is that less gray matter volume in the right angular gyrus relates to deficits in attentional processes, as this region also subtends attention and spatial cognition (Chambers et al. 2004; Shulman et al. 2003; Taylor et al. 2011). Indeed, a meta-analysis (Lawson et al. 2018) showed that children from socioeconomically disadvantaged milieus tend to have poorer attention abilities and executive control than their peers from more favorable contexts.

Gray matter volume of the right angular cluster correlated positively with reading measures involving word knowledge and comprehension. This correlation showed up in all matched dysfluent readers and the higher-SES subgroup, but not in the lower-SES children, suggesting that children from higher-SES backgrounds drive the SES-related modulation. After controlling for age, sex, and IQ, gray matter volume of the right angular cluster survived as a significant predictor of lexico-semantic fluency (a reading index derived from the aggregation of three reading measures) in all matched dysfluent readers and in the higher-SES subgroup taken separately. Interestingly, these correlates of lexico-semantic fluency occur in the right angular gyrus. This is certainly consistent with a growing body of evidence pinpointing the involvement of the right angular gyrus in language and reading comprehension processes, including narrative comprehension (Horowitz-Kraus et al. 2014b, 2015), combinatorial semantics (Graves et al. 2010a; Price et al. 2015), and response to word frequency and imageability (Binder et al. 2005; Graves et al. 2010b). For instance, Graves and colleagues (2010) showed that right parieto-temporal regions (the supramarginal and angular gyri) were associated with combinatorial semantic processing and suggested a hemispheric dissociation between lexical and combinatorial processing. Following this thread, Price and colleagues (2015) proposed that combinatorial semantics implicates the angular gyrus, bilaterally, but with a stronger right-lateralized structure-function link (the right angular gyrus was more sensitive to individual differences than the left one). They suggested that even though lexico-semantic processing should rely more on the left angular gyrus because of left-hemisphere dominance for language, recruitment of the right angular gyrus might confer an advantage to some individuals. In our study, we found a brain structure - behavior correlation consistent with the involvement of the angular gyrus in lexico-semantic processing in reading and consistent with its right-lateralized sensitivity to individual differences driven by SES.

An important aspect related to SES is parental education. A clear understanding of how parental education and SES affect reading development is clouded by differences between studies in the definition of SES and parental education levels, which may, in turn, depend on the socio-economic characteristics of the societies where studies are conducted. A case in point is our study. The parents of *higher*-SES children had similar education level to parents of *low* SES children in Gullick et al.'s study (2016; $M = 11.18$ vs. $M = 12.5$, $t(13) = -1.46$, $p = .17$). Similarly, only 36% of the fathers and 64% of the mothers of our higher-SES subgroup had 12 or more years of schooling, whereas in Ozernov-Palchik et al.'s (2019) study, almost all fathers (95%) and mothers (100%) of the low SES group had 12 years schooling. Therefore, the higher-SES level in the present study may be more comparable to the lower SES level from other studies. Interestingly, Ozernov-Palchik and colleagues (2019) remarked that their low SES group was not representative of the lower SES segment of the United States population. Mutatis mutandis, the same applies to our higher-SES group: it is not representative of the higher SES segment of the Portuguese population. Nevertheless, discrepancies such as these in characteristics of SES comparison groups are misleading. They may be the reason why we found SES-related modulation of the brain correlates of reading in higher-SES children whereas other studies tend to find them in low SES children (Brito et al. 2017; Gullick et al. 2016; Noble et al. 2006; Ozernov-Palchik et al. 2019; Romeo et al. 2018).

The present study has some limitations. One concerns the operationalization of fluency: it would have been helpful to include additional measures of fluency, such as processing or articulation speed, to ascertain whether the dysfluency observed is specific to reading or extends to other domains. Another concerns socioeconomic variables. SES is defined based on different factors, such as income or education, and these have a differential impact on neural (Lotze et al. 2020; Noble et al. 2012; 2015) and behavioral outcomes (Duncan and Magnuson 2012). We classified children as lower- vs. higher-SES based on a criterion derived from parents' income, free or reduced-price meals at school opposed to no such social assistance. However, higher-SES children also had more educated parents than their lower-SES peers, and so it was impossible to dissociate the effects of parental education from those of income. Finally, our higher-SES group is not representative of the prototypical high-level SES; the two subgroups do represent distinct points in a hypothetical SES continuum, but they are not at the extremes of such a continuum. This should be born in mind when comparing our findings with findings from studies in which the SES levels were differently defined.

In sum, we conducted a VBM study on the role of IQ and SES in reading fluency deficits. Differently from previous studies (Simos et al. 2014; Tanaka et al. 2011), which focused on phonological decoding using functional methods, we examined a measure tapping fluent reading of connected text and showed for the first time that gray matter correlates of dysfluent reading — reduced volume in the right superior temporal cortex — do not depend on IQ, they are common to children with normal IQ as well as to those with low IQ. Our results concur with the hypothesis that impaired processing of speech sounds in the superior temporal cortex is the proximal cause of dysfluent reading in beginning readers regardless of IQ. Our study is also the first to show SES-related differences in dysfluent readers matched for (low) reading level and IQ: higher-SES children had larger gray matter volume in the right angular gyrus than in their lower-SES peers, and the volume of this region correlated with reading fluency in dysfluent children from higher-SES backgrounds, but not in those from lower-SES. These two findings — the SES-related gray matter difference and the correlation with reading fluency — add to current evidence of the modulatory effect of SES on the brain-behavior relationship and contribute to an in-depth knowledge of the neurocognitive profile of dysfluent readers.

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Table 1

Sociodemographic and neuropsychological characteristics of fluent readers, normal and low IQ dysfluent readers

	Fluent readers (n = 18)	Normal IQ dysfluent readers (n = 18)	Low IQ dysfluent readers (n = 18)	Test	Post hoc
Sex (girl / boy)	11 / 7	12 / 6	8 / 10	$\chi2$ (2) = 1.97	
SES (lower / higher)	9 / 9	10 / 8	10 / 8	$\chi2$ (2) = .15	
Handedness [a] (R / L / A)	16 / 0 / 2	15 / 2 / 1	18 / 0 / 0	*FET* = 4.71	
Age (years)	8.27 ± 0.29	8.11 ± 0.25	8.33 ± 0.35	F(2, 51) = 2.55	
TIV (cm^3)	1440.78 ± 127.74	1353.52 ± 121.29	1418.46 ± 190.02	F(2, 51) = 1.65	
Full-scale IQ [b]	100.39 ± 6.94	99.83 ± 6.21	78.39 ± 6.34	F(2, 51) = 67.03***	1 vs. 3***, 2 vs. 3***
Verbal IQ	101.17 ± 9.15	100.33 ± 7.13	81.72 ± 9.34	F(2, 51) = 29.41***	1 vs. 3***, 2 vs. 3***
Performance IQ	101.56 ± 9.67	100.28 ± 10.47	83.56 ± 8.12	F(2,51) = 22.64***	1 vs. 3***, 2 vs. 3***
3DM reading tests [c]					
High-frequency words	104.22 ± 8.84	89.61 ± 7.11	84.78 ± 9.89	F(2, 51) = 24.45***	1 vs. 2***, 1 vs. 3***
	(99.84 ± 0.67)	(96.30 ± 4.24)	(95.30 ± 9.98)	(F(2, 51) = 2.61)	
Low-frequency words	104.50 ± 7.05	91.00 ± 7.84	86.72 ± 8.66	F(2, 51) = 25.00***	1 vs. 2***, 1 vs. 3***
	(95.61 ± 4.44)	(95.16 ± 5.09)	(92.74 ± 8.95)	(F(2, 51) = 1.02)	
Pseudowords	100.44 ± 7.02	87.72 ± 10.31	85.11 ± 9.02	F(2, 51) = 15.35***	1 vs. 2***, 1 vs. 3***
	(90.22 ± 10.69)	(84.53 ± 11.15)	(87.05 ± 13.15)	(F(2, 51) = 1.06)	
Reading age test	101.83 ± 11.12	87.00 ± 13.06	81.67 ± 12.93	F(2, 51) = 12.78***	1 vs. 2**, 1 vs. 3***
WCPM index	99.56 ± 3.57	77.28 ± 6.82	73.72 ± 13.62	F(2, 51) = 43.25***	1 vs. 2***, 1 vs. 3***
	(97.74 ± 1.23)	(96.10 ± 2.81)	(91.11 ± 15.05)	(F(2, 51) = 2.73)	
Discrepancy (IQ - WCPM score)	.83 ± 6.56	22.56 ± 8.09	4.67 ± 12.23	F(2, 51) = 28.13***	1 vs. 2***, 2 vs. 3***

Note. Means and standard deviations are presented for all variables except sex, SES and handedness. Test results are given in standard scores (M = 100, SD = 15), except an additional measure of accuracy for 3DM and WCPM tests given in parenthesis and showing the percentage of correctly read stimuli over total read.

SES = socioeconomic status. R = right-handed; L = left-handed; A = ambidextrous. TIV = total intracranial volume. 1 = fluent readers; 2 = normal IQ dysfluent readers; 3 = low IQ dysfluent readers. WCPM = words correct per minute.

[a] Edinburgh Handedness Inventory. [b] Wechsler Intelligence Scale for Children, WISC-III. [c] Differential Diagnosis Dyslexia Maastricht Battery.

*p < .05; **p < .01; ***p < .001 (Bonferroni corrected).

Table 2

Sociodemographic and neuropsychological characteristics of lower- and higher-SES dysfluent readers in the matched subgroups (see text)

	Lower-SES (n = 14)	Higher-SES (n = 14)	Test
Sex (girl / boy)	7 / 7	7 / 7	$\chi2$ (1) = 0.00
Handedness [a] (R / L / A)	12 / 1 / 1	13 / 1 / 0	*FET* = 1.22
Age (years)	8.20 ± 0.39	8.19 ± 0.30	*t*(26) = .09
Parental education (years)	8.11 ± 2.46	11.18 ± 3.38	*t*(26) = -2.75*
TIV (cm^3)	1381.56 ± 144.64	1375.96 ± 200.31	*t*(26) = .09
Full-scale IQ [b]	92.14 ± 15.14	88.71 ± 10.57	*t*(26) = .70
Verbal IQ	91.29 ± 14.58	92.71 ± 11.87	*t*(26) = -.28
Performance IQ	96.64 ± 15.69	88.21 ± 9.62	*t*(26) = 1.71
3DM reading tests [c]			
High-frequency words	86.71 ± 6.63 (96.76 ± 5.15)	91.07 ± 9.22 (96.49 ± 5.34)	*t*(26) = -1.44 (t(26) = .14)
Low-frequency words	87.86 ± 7.55 (92.88 ± 8.77)	92.36 ± 7.41 (94.79 ± 5.83)	*t*(26) = -1.59 (t(26) = -.68)
Pseudowords	85.86 ± 7.81 (82.62 ± 12.07)	90.79 ± 8.08 (89.29 ± 11.51)	*t*(26) = -1.64 (t(26) = -1.50)
Reading age test	83.29 ± 9.97	88.57 ± 12.48	*t*(26) = -1.24
WCPM index	75.93 ± 8.93 (94.96 ± 4.43)	77.79 ± 10.00 (95.31 ± 4.38)	*t*(26) = -.52 (t(26) = -.21)
Discrepancy (IQ - WCPM score)	16.21 ± 16.46	10.93 ± 11.51	*t*(26) = .99

Note. Means and standard deviations are presented for all variables except sex and handedness. Test results are given in standardized scores (*M* = 100, *SD* = 15), except an additional measure of accuracy for 3DM and WCPM tests given in parenthesis and showing the percentage of correctly read stimuli over total read.

R - right-handed; L - left-handed; A - ambidextrous. TIV - Total Intracranial Volume. WCPM - Words correct per minute.

[a] Edinburgh Handedness Inventory. [b] Wechsler Intelligence Scale for Children, WISC-III. [c] Differential Diagnosis Dyslexia Maastricht Battery.

*$p < .05$.

Table 3

Significant clusters of gray matter volume differences in the VBM analysis (*p* < .05, FWE; *k* > 20) for the main effect of group and for planned pairwise comparisons between fluent and dysfluent readers

Region		MNI coordinates of peak voxel			Cluster size (*k*)	*p*	TFCE
		x	*y*	*z*			
Main effect of group							
Superior temporal gyrus	R	66	0	-6	265	.01	10081.02
Fluent > Dysfluent readers							
Superior temporal gyrus	R	66	0	-6	5147	< .001	1067.72
Middle temporal gyrus	L	-48	-3	-22	461	< .01	421.73
Fusiform gyrus	R	42	-38	-15	519	< .01	386.53
Middle temporal gyrus/Inferior occipital gyrus	R	56	-64	0	983	< .01	331.63
Planum temporale/Parietal operculum	L	-52	-30	12	555	.01	263.90
Cerebellum exterior/Fusiform gyrus/Lingual gyrus	R	26	-52	-15	56	.04	223.51
Middle temporal gyrus	L	-57	-21	-15	58	.04	218.23

Note. MNI - Montreal Neurological Institute; TFCE - Threshold-free Cluster Enhancement.

Figure Captions

Fig. 1 a - Group differences in gray matter volume in a cluster in the Superior Temporal Gyrus (STG). b - Regions with increased gray matter volume in fluent readers when compared to dysfluent readers. Error bars indicate standard deviations

Fig. 2 Increased gray matter volume in a cluster of the right angular gyrus of higher-SES dysfluent readers compared to matched lower-SES dysfluent readers

Fig. 3 Scatterplots of the correlations between lexico-semantic fluency and gray matter volume in the right angular cluster (AnC) for matched dysfluent readers (a), and separately for the higher- and lower-SES subgroups (b)