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; seven boys) with dysfluent readers with normal IQ (n = 18; six boys) and with low IQ (n = 18; ten 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; seven boys) vs. higher-SES (n = 14; seven 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

Introduction

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; Krafknic 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 (Torjesen 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. Gucluk 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 frontal fasciculi and that the microstructure of the inferior longitudinal fasciculi in kindergarteners 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 gyrus, 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 2019).
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.

**Methods**

**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 $> 0.48$), two were left-handed (LI $= − 0.80$ and LI $= − 0.40$) 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 s (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 ($n = 820$, grades 1–4; 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 min 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 min, 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

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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 and 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 1.5 T 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, 8° flip angle; 160 contiguous sagittal slices, 250 × 250 mm² 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/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 samples 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 (ps < 0.003), which did not differ from each other (ps > 0.30). Accuracy scores were similar across groups (ps > 0.08). As in Tanaka et al. (2011), dysfluent readers with normal IQ had higher IQ than reading fluency scores, t(17) = 11.83, p < 0.001, whereas the low IQ dysfluent group did not, t(17) = 1.62, p = 0.12. The three groups were similar in age, F(2, 51) = 2.55, p = 0.09; sex, $\chi^2(2) = 1.97, p = 0.37$; SES, $\chi^2(2) = 0.15, p = 0.93$; handedness, $FET, p = 0.23$; and TIV, F(2, 51) = 1.65, p = 0.20.

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.

### 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                             | $\chi^2(2) = 1.97$ |
| SES (lower/higher)       | 9/9                    | 10/8                                 | 10/8                             | $\chi^2(2) = 0.15$ |
| Handedness* (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 (cm³)                | 1440.78 ± 127.74       | 1353.52 ± 121.29                     | 1418.46 ± 190.02                 | F(2, 51) = 1.65 |
| Full-scale IQb           | 100.39 ± 6.94          | 99.83 ± 6.21                         | 78.39 ± 6.34                     | F(2, 51) = 6.70*** |
| Verbal IQ                | 101.17 ± 9.15          | 100.33 ± 7.13                        | 81.72 ± 9.34                     | F(2, 51) = 29.41*** |
| Performance IQ           | 101.56 ± 9.67          | 100.28 ± 7.10                        | 83.56 ± 8.12                     | F(2, 51) = 22.64*** |
| WCPM index               | 99.56 ± 3.57           |                                      |                                  |                  |
| 3DM reading testsc       |                        |                                      |                                  |                  |
| High-frequency words     | 104.22 ± 8.84          | 89.61 ± 7.11                         | 84.78 ± 9.89                     | F(2, 51) = 24.45*** |
| Low-frequency words      | 104.50 ± 7.05          | 91.00 ± 7.84                         | 86.72 ± 8.66                     | F(2, 51) = 25.00*** |
| Pseudowords              | 100.44 ± 7.02          | 87.72 ± 10.31                        | 85.11 ± 9.02                     | F(2, 51) = 15.35*** |
| Reading age test         | 101.83 ± 11.12         | 87.00 ± 13.06                        | 81.67 ± 12.93                    | F(2, 51) = 12.78*** |
| WCPM index               | 99.56 ± 3.57           | 77.28 ± 6.82                         | 73.72 ± 13.62                    | F(2, 51) = 43.25*** |
| Discrepancy (IQ–WCPM score) | .83 ± 6.56           | 22.56 ± 8.09                         | 4.67 ± 12.23                     | F(2, 51) = 28.13*** |

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

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

*Edinburgh Handedness Inventory. ‡Wechsler Intelligence Scale for Children, WISC-III. ‡Differential Diagnosis Dyslexia Maastricht Battery

### 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 for-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 non-parametric 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.

**Table 2** Sociodemographic and neuropsychological characteristics of lower- and higher-SES dysfluent readers in the matched subgroups (see text)

| Test | Lower-SES \((n = 14)\) | Higher-SES \((n = 14)\) | Test |
|------|-----------------|-----------------|------|
| Sex (girl/boy) | 7/7 | 7/7 | \(\chi^2 (1) = 0.00\) |
| Handedness* (R/L/A) | 12/1/1 | 13/1/0 | FET = 1.22 |
| Age (years) | 8.20 ± 0.39 | 8.19 ± 0.30 | \(t(26) = 0.09\) |
| 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 | \(t(26) = 0.09\) |
| Full-scale IQ* | 92.14 ± 15.14 | 88.71 ± 10.57 | \(t(26) = 0.70\) |
| Verbal IQ | 91.29 ± 14.58 | 92.71 ± 11.87 | \(t(26) = -0.28\) |
| Performance IQ | 96.64 ± 15.69 | 88.21 ± 9.62 | \(t(26) = 1.71\) |
| 3DM reading tests | | | |
| 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) | \(t(26) = -0.52 (t(26) = -.21)\) |
| Discrepancy (IQ–WCPM score) | 16.21 ± 16.46 | 10.93 ± 11.51 | \(t(26) = -0.99\) |

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

*p < .05

*Edinburgh Handedness Inventory. bWechsler Intelligence Scale for Children, WISC-III. cDifferential Diagnosis Dyslexia Maastricht Battery
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 (Fig. 1a; Table 3), where fluent readers had a larger volume than both groups of dysfluent readers ($p_s < 0.001$), 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

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

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temporale, including the Heschl’s sulcus, and the left middle temporal gyrus extending to superior temporal sulcus (Fig. 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 = 45,260.70, *p* < 0.001 cFWE, *k* = 129; Fig. 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* = 0.40, 95% CI [0.04, 0.68], *p* = 0.03), reading age (*r* = 0.42, 95% CI [0.06, 0.69], *p* = 0.03), and high-frequency word reading (*r* = 0.48, 95% CI [0.13, 0.72], *p* = 0.01), three measures tapping into lexical and semantic processing. No correlations were found with low-frequency word reading (*r* = 0.37, 95% CI [−0.00, 0.65], *p* = 0.05) and pseudoword reading (*r* = 0.33, 95% CI [−0.05, 0.63], *p* = 0.09) or additional accuracy measures (*p*s > 0.13; Supplementary Fig. 1a). Analogous correlations computed separately for higher- and lower-SES dysfluent readers only reached significance in the higher-SES group (Supplementary Fig. 1b, 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

**Table 3** Significant clusters of gray matter volume differences in the VBM analysis (*p* < 0.05, 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        |
|---------------------------------------------|-------------------------------|--------------------|----------|-------------|
| **Main effect of group**                    |                               |                    |          |             |
| Superior temporal gyrus                     | R                             | 66                 | 0        | −6          | 265          | .01          | 10,081.02   |
| 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      |

MNI Montreal Neurological Institute; TFCE Threshold-free Cluster Enhancement

**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
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, \( r = 0.52, 95\% \text{ CI } [0.18, 0.75], p < 0.01; \) (Fig. 3a), and in the higher-SES group, \( r = 0.69, 95\% \text{ CI } [0.25, 0.89], p < 0.01 \) (Fig. 3b), but not in the lower-SES group, \( r = -0.16, 95\% \text{ CI } [-0.64, 0.40], p = 0.58 \) (Fig. 3b). 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, \( R^2 = 0.50, F(4, 23) = 5.80, p < 0.01, \) adjusted \( R^2 = 0.42 \) (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, \( R^2 = 0.78, F(4, 9) = 7.84, p < 0.01, \) adjusted \( R^2 = 0.68 \) (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

![Fig. 3](image-url) 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)
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 gyrus when processing phonemes (Blau et al. 2010). Regions in the superior temporal gyrus 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; Hoef et al. 2011; Romeo et al. 2018). Hoef 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 (Hoef 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 socioeconomic 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. \( M = 12.5 \), \( t(13) = -1.46, p = 0.17 \)). 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-year 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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**Availability of data and material** The data that support the findings from this study are available from the corresponding author upon reasonable request.

**Code availability** Not applicable.

**Declarations**

**Conflict of interest** The authors declare they have no conflicts of interest.

**Ethics approval** All experimental procedures were approved by the ethics committee of the Faculty of Psychology and Education Sciences, University of Porto (reference number FPCEUP 2015.1.23) and conducted in accordance with the Declaration of Helsinki.

**Consent to participate** Written informed consent was obtained from all parents and from local school authorities, and children gave their verbal assent at the start of data collection.

**Consent for publication** Not applicable.

**References**

Ashburner J (2007) A fast diffeomorphic image registration algorithm. Neuroimage 38:95–113. [https://doi.org/10.1016/j.neuroimage.2007.07.007](https://doi.org/10.1016/j.neuroimage.2007.07.007)

Barquero LA, Davis N, Cutting LE (2014) Neuroimaging of reading intervention: a systematic review and activation likelihood estimate meta-analysis. PLoS One 9:e83668. [https://doi.org/10.1371/journal.pone.0083668](https://doi.org/10.1371/journal.pone.0083668)

Benjamin CF, Gaab N (2012) What’s the story? The tale of reading fluency told at speed. Hum Brain Mapp 33:2572–2585. [https://doi.org/10.1002/hbm.21384](https://doi.org/10.1002/hbm.21384)

Binder JR, Medler DA, Desai R, Conant LL, Liebenthal E (2005) Some neurophysiological constraints on models of word naming. Neuroimage 27:677–693. [https://doi.org/10.1016/j.neuroimage.2005.04.029](https://doi.org/10.1016/j.neuroimage.2005.04.029)

Black JM, Tanaka H, Stanley L, Nagamine M, Zakerani N, Thurstont A, Kesler S et al (2012) Maternal history of reading difficulty is associated with reduced language-related gray matter in beginning readers. Neuroimage 59:3021–3032. [https://doi.org/10.1016/j.neuroimage.2011.10.024](https://doi.org/10.1016/j.neuroimage.2011.10.024)

Blau V, Van Atteveldt N, Ekkebus M, Goebel R, Blomert L (2009) Reduced neural integration of letters and speech sounds links phonological and reading deficits in adult dyslexia. Curr Biol 19:503–508. [https://doi.org/10.1016/j.cub.2009.01.065](https://doi.org/10.1016/j.cub.2009.01.065)

Blau V, Reithler J, Van Atteveldt N, Seitz J, Gerretsen P, Goebel R, Blomert L (2010) Deviant processing of letters and speech sounds as proximate cause of reading failure: a functional magnetic resonance imaging study of dyslexic children. Brain 133:868–879. [https://doi.org/10.1093/brain/awp308](https://doi.org/10.1093/brain/awp308)

Blomert L (2011) The neural signature of orthographic–phonological binding in successful and failing reading development. Neuroimage 57:695–703. [https://doi.org/10.1016/j.neuroimage.2010.11.003](https://doi.org/10.1016/j.neuroimage.2010.11.003)

Blomert L, Vaessen A (2009) 3DM differential diagnostics for dyslexia, cognitive analysis of reading and spelling. Boom Test Publishers, Amsterdam

Bradley RH, Corwyn RF (2002) Socioeconomic status and child development. Annu Rev Psychol 53:371–399. [https://doi.org/10.1146/annurev.psych.53.100901.135233](https://doi.org/10.1146/annurev.psych.53.100901.135233)

Breznitz Z (2006) Fluency in reading: synchronization of processes. Lawrence Erlbaum Associates Publishers, New Jersey

Breznitz Z, Shaul S, Horowitz-Kraus T, Sela I, Nevat M, Karni A (2013) Enhanced reading by training with imposed time-constraint in typical and dyslexic adults. Nat Commun 4:1486. [https://doi.org/10.1038/ncomms2488](https://doi.org/10.1038/ncomms2488)

Brito NH, Piccolo LR, Noble KG (2017) Associations between cortical thickness and neurocognitive skills during childhood vary by family socioeconomic factors. Brain Cogn 116:54–62. [https://doi.org/10.1016/j.bandc.2017.03.007](https://doi.org/10.1016/j.bandc.2017.03.007)

Chambers CD, Payne JM, Stokes MG, Mattingley JB (2004) Fast and slow parietal pathways mediate spatial attention. Nat Neurosci 7:217–218. [https://doi.org/10.1038/nn1203](https://doi.org/10.1038/nn1203)

Christodoulou LA, Del Tufo SN, Lymberis J, Saxler PK, Ghosh SS, Triantafyllou C, Whitfield-Gabrieli S et al (2014) Brain bases of reading fluency in typical reading and impaired fluency in dyslexia. PLoS One 9:e100552. [https://doi.org/10.1371/journal.pone.00100552](https://doi.org/10.1371/journal.pone.00100552)

Cohen MS (2008) Handedness questionnaire. [http://www.brainmapping.org/shared/Edinburgh.php](http://www.brainmapping.org/shared/Edinburgh.php). Accessed 19 Nov 2015

Correia AI, Branco P, Martins M, Reis AM, Martins N, Castro SL, Lima CF (2019) Resting-state connectivity reveals a role for sensorimotor systems in vocal emotional processing in children. Neuroimage 201:116052. [https://doi.org/10.1016/j.neuroimage.2019.116052](https://doi.org/10.1016/j.neuroimage.2019.116052)

Daniels PT, Share DL (2017) Writing system variation and its consequences for reading and dyslexia. Sci Stud Read 22:101–116. [https://doi.org/10.1080/10888438.2017.1379082](https://doi.org/10.1080/10888438.2017.1379082)

Duke NK (2000) For the rich it’s richer: Print experiences and environments offered to children in very low-and very...
high-socioeconomic status first-grade classrooms. Am Educ Res J 37:441–478. https://doi.org/10.3102/0028312037002441

Duncan GJ, Magnuson K (2012) Socioeconomic status and cognitive functioning: moving from correlation to causation. Wiley Interdiscip Rev Cogn Sci 3:377–386. https://doi.org/10.1002/wics.1176

Eckert MA, Leonard CM, Wilke M, Eckert M, Richards T, Richards A, Berninger V (2005) Anatomical signatures of dyslexia in children: unique information from manual and voxel based morphometry brain measures. Cortex 41:304–315. https://doi.org/10.1016/j.cortex.2005.07.026

Eckert MA, Berninger VW, Vaden KL, Gebregziabher M, Tsu L (2016) Gray matter features of reading disability: a combined meta-analytic and direct analysis approach. eNeuro 3:1–15. https://doi.org/10.1523/EJNRO.0103-2015.2015

Fernandes S, Querido L, Verhaeghe A, Marques C, Araújo L (2017) Reading development in European Portuguese: relationships between oral reading fluency, vocabulary and reading comprehension. Read Writ 30:1987–2007. https://doi.org/10.1007/s11145-017-9763-z

Ferrer E, Shaywitz BA, Holahan JM, Marchione K, Shaywitz SE (2010) Uncoupling of reading and IQ over time: empirical evidence for a definition of dyslexia. Psychol Sci 21:93–101. https://doi.org/10.1177/0956797609354084

Fletcher JM, Shaywitz SE, Shankweiler DP, Katz L, Liberman IY, Stuebing KK, Francis DJ et al (1994) Cognitive profiles of reading disability: comparisons of discrepancy and low achievement definitions. J Educ Psychol 86:6–23. https://doi.org/10.1037/0022-0663.86.1.6

Florit E, Cain K (2011) The simple view of reading: Is it valid for different types of alphabetic orthographies? Educ Psychol Rev 23:553–576. https://doi.org/10.1007/s11145-011-9175-6

Fuchs LS, Fuchs D, Hosp MK, Jenkins JR (2001) Oral reading fluency as an indicator of reading competence: a theoretical, empirical, and historical analysis. Sci Stud Read 5:239–256. https://doi.org/10.1207/S1532799XSR0503_3

Graves WW, Binder JR, Desai RH, Conant LL, Seidenberg MS (2010a) Neural correlates of implicit and explicit combinatorial semantic processing. Neuroimage 53:638–646. https://doi.org/10.1016/j.neuroimage.2010.06.035

Graves WW, Desai R, Humphries C, Seidenberg MS, Binder JR (2010b) Neural systems for reading aloud: a multiparametric approach. Cereb Cortex 20:1799–1815. https://doi.org/10.1093/cercor/bhp245

Gullick MM, Demir-Lira OE, Booth JR (2016) Reading skill–frequency anisotropy relationships in visuospatial tracts diverge depending on socioeconomic status. Dev Sci 19:673–685. https://doi.org/10.1111/desc.12428

Hasbrouck J, Tindal G (2017) An update to compiled ORF norms (Technical Report No. 1702). Eugene, OR, Behavioral Research and Teaching. University of Oregon

Hoefn F, Meyler A, Hernandez A, Juel C, Taylor-Hill H, Martindale Hasbrouck J, Tindal G (2016) An update to compiled ORF norms. Brain Res 1582:34–44. https://doi.org/10.1016/j.brainres.2014.05.034

Horowitz-Kraus T, Grainger M, DiFrancesco M, Vannest J, Holland SK, CMIND Authorship Consortium (2015) Right is not always wrong: DTI and fMRI evidence for the reliance of reading comprehension on language comprehension networks in the right hemisphere. Brain Imaging Behav 9:19–31. https://doi.org/10.1007/s11682-014-9341-9

Hasbrouck J, Tindal G (2000) Cognitive processing of low achievers and children with reading disabilities: a selective meta-analytic review of the published literature. Sch Psychol Rev 29:102–119. https://doi.org/10.1080/02796015.2000.12086000

Inness SG (2005) Stability of IQ measures in teenagers and young adults with developmental dyslexia. Dyslexia 12:81–95. https://doi.org/10.1002/dys.306

Jarosz A, Wiley J (2014) What are the odds? A practical guide to computing and reporting Bayes factors. J Probl Solving 7:2–9. https://doi.org/10.1077/jpros.1973-6246.1167

Jeffreys H (1961) Theory of probability, 3rd edn. Oxford University Press, Oxford

Jenkins JR, Fuchs LS, Van Den Broek P, Espin C, Deno SL (2003) Sources of individual differences in reading comprehension and reading fluency. J Educ Psychol 95:719–729. https://doi.org/10.1037/022-0663.95.4.719

Karpilidis I, Pleisch G, Brandeis D, Roth A, Rühlisberger M, Schneeberger M, Wälti Z et al (2018) Simulating reading acquisition: the link between reading outcome and multimodal brain signatures of letter-speech sound learning in prereaders. Sci Rep 8:7121. https://doi.org/10.1038/s41598-018-24099-8

Katzir T, Shaul S, Breznitz Z, Wolf M (2004) The universal and the unique in dyslexia: a cross-linguistic investigation of reading and reading fluency in Hebrew-and English-speaking children with reading disorders. Read Writ 17:739–768. https://doi.org/10.1007/s11145-004-2655-z

Kim Y-S, Wagner RK (2015) Text (oral) reading fluency as a construct in reading development: an investigation of its mediating role for children from grades 1 to 4. Sci Stud Read 19:224–242. https://doi.org/10.1080/10888438.2015.1007375

Kim Y-S, Wagner RK, Lopez D (2012) Developmental relations between reading fluency and reading comprehension: a longitudinal study from grade 1 to grade 2. J Exp Child Psychol 113:93–111. https://doi.org/10.1016/j.jecp.2012.03.002

Kim Y-S, Park C, Wagner RK (2014) Is oral/text reading fluency a “bridge” to reading comprehension? Read Writ 27:79–99. https://doi.org/10.1007/s11145-013-9434-7

Klauda SL, Guthrie JT (2008) Relationships of three components of reading fluency to reading comprehension. J Educ Psychol 100:310–321. https://doi.org/10.1037/0022-0663.100.2.310

Krafcnik AJ, Flowers DL, Luetje MM, Napolieo EM, Eden GF (2014) An investigation into the origin of anatomical differences in dyslexia. J Neurosci 34:901–908. https://doi.org/10.1523/JNEURSCI.2092-13.2013

Kronbichler M, Wimmer H, Staffen W, Hutzler F, Mair A, Ladurner G (2008) Developmental dyslexia: gray matter abnormalities in the occipitotemporal cortex. Hum Brain Mapp 29:613–625. https://doi.org/10.1002/hbm.20425

Kroschnabel J, Brem S, Maurer U, Brandeis D (2014) The level of audiovisual print–speech integration deficits in dyslexia. Neuropsychologia 62:245–261. https://doi.org/10.1016/j.neuropsychologia.2014.07.024

Landerl K, Wunner H (2008) Development of word reading fluency and spelling in a consistent orthography: An 8-year follow-up. J Educ Psychol 100:150–161. https://doi.org/10.1037/0022-0663.100.1.150
Landerl K, Ramus F, Moll K, Lyytinen H, Leppänen PH, Lohvansuu K, O’Donovan M et al (2013) Predictors of developmental dyslexia in European orthographies with varying complexity. J Child Psychol Psychiatry 54:686–694. https://doi.org/10.1111/jcpp.12029

Langer N, Benjamin C, Minas J, Gaab N (2015) The neural correlates of reading fluency deficits in children. Cereb Cortex 25:1441–1453. https://doi.org/10.1093/cercor/bht330

Lawson GM, Hook CJ, Farah MJ (2018) A meta-analysis of the relationship between socioeconomic status and executive function performance among children. Dev Sci 21:e12529. https://doi.org/10.1111/12579

Lebel C, Benischek A, Geeraert B, Holahan J, Shaywitz S, Bakhshi K, Shaywitz B (2019) Developmental trajectories of white matter structure in children with and without reading impairments. Dev Cogn Neuro 36:100633. https://doi.org/10.1016/j.dcn.2019.100633

Leinonen S, Müller K, Leppänen PH, Aro M, Ahonen T, Lyytinen H (2001) Heterogeneity in adult dyslexic readers: relating processing skills to the speed and accuracy of oral text reading. Read Writ 14:265–296. https://doi.org/10.1023/A:1011176208915

Linkersdörfer J, Lonnemann J, Lindberg S, Hasselhorn M, Fiebach CJ (2012) Grey matter alterations co-localize with functional abnormalities in developmental dyslexia: an ALE meta-analysis. PLoS One 7:e43122. https://doi.org/10.1371/journal.pone.0043122

Lotze M, Domin M, Schmidt CO, Hosten N, Grabe HJ, Neumann N (2020) Income is associated with hippocampal/amygdala and education with cingulate cortex grey matter volume. Sci Rep 10:1–8. https://doi.org/10.1038/s41598-020-75809-9

Magalhães A (2010) O senhor do seu nariz e outras histórias. Edições Sílabo

Martin A, Schurz M, Kronbichler M, Richlan F (2015) Reading in the brain of children and adults: a meta-analysis of 40 functional magnetic resonance imaging studies. Hum Brain Mapp 36:1963–1981. https://doi.org/10.1002/hbm.22749

Martins M, Neves L, Rodrigues P, Vasconcelos O, Castro SL (2018) Orff-based music training enhances children’s manual dexterity and bimanual coordination. Front Psychol 9:2616. https://doi.org/10.3389/fpsyg.2018.02616

Mol SE, Bus AG (2011) To read or not to read: A meta-analysis of print exposure from infancy to early adulthood. Psychol Bull 137:267–296. https://doi.org/10.1037/a0021890

Moll K, Gangl M, Banfi C, Schulte-Körne G, Landerl K (2019) Stability of deficits in reading fluency and/or spelling. Sci Stud Read 24:241–251. https://doi.org/10.1080/10888438.2019.1659277

Moura O, Simões MR, Pereira M (2014) WISC-III cognitive profiles in children with developmental dyslexia: Specific cognitive disability and diagnostic utility. Dyslexia 20:19–37. https://doi.org/10.1002/dys.1468

Moura O, Moreno J, Pereira M, Simões MR (2015) Developmental dyslexia and phonological processing in European Portuguese orthography. Dyslexia 21:60–79. https://doi.org/10.1002/dys.1489

Neuman SB, Celano D (2001) Access to print in low-income and middle-income communities: an ecological study of four neighborhoods. Read Res Q 36:8–26. https://doi.org/10.1598/RRQ.36.1.1

Noble KG, Wolmetz ME, Ochs LG, Farah MJ, McCandliss BD (2006) Brain–behavior relationships in reading acquisition are modulated by socioeconomic factors. Dev Sci 9:642–654. https://doi.org/10.1111/j.1467-7678.2006.00542.x

Noble KG, Houston SM, Kan E, Sowell ER (2012) Neural correlates of socioeconomic status in the developing human brain. Dev Sci 15:516–527. https://doi.org/10.1111/j.1467-7687.2012.01147.x

Noble KG, Houston SM, Brito NH, Bartsch H, Kan E, Kuperman JM, Akshoomoff N et al (2015) Family income, parental education and brain structure in children and adolescents. Nat Neurosci 18:773. https://doi.org/10.1038/nn.3983

Noble KG, McCandliss BD (2005) Reading development and impairment: behavioral, social, and neurobiological factors. J Dev Behav Pediatr 26:370–378. https://doi.org/10.1097/00004703-200510000-00006

O’Donnell PS, Miller DN (2011) Identifying students with specific learning disabilities: school psychologists’ acceptability of the discrepancy model versus response to intervention. J Disabil Policy Stud 22:83–94. https://doi.org/10.1111/j.1467-739X.2010.00974.x

OECD (2016) PISA 2015 results (volume I): excellence and equity in education. OECD Publishing, Paris. https://doi.org/10.1787/9789264266490-en

Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9:97–113. https://doi.org/10.1016/0028-3932(71)90067-4

Olson RK, Keenan JM, Byrne B, Samuelsson S (2014) Why do children differ in their development of reading and related skills? Child Stud Rev 18:38–54. https://doi.org/10.1080/10888438.2013.800521

Ozernov-Palchik O, Gaab N (2016) Tackling the ‘dyslexia paradox’: reading brain and behavior for early markers of developmental dyslexia. Wiley Interdiscip Rev Cogn Sci 7:156–176. https://doi.org/10.1002/wics.1383

Ozernov-Palchik O, Norton ES, Wang Y, Beach SD, Zuk J, Wolf M, Gabrieli JD et al (2019) The relationship between socioeconomic status and white matter microstructure in pre-reading children: a longitudinal investigation. Hum Brain Mapp 40:741–754. https://doi.org/10.1002/hbm.24407

Pace A, Luo R, Hirsh-Pasek K, Golinkoff RM (2017) Identifying pathways between socioeconomic status and language development. Annu Rev Linguist 3:285–308. https://doi.org/10.1146/annurev-linguistics-011516-034226

Price AR, Bonner MF, Peelle JE, Grossman M (2015) Converging evidence for the neuroanatomic basis of combinatorial semantics in the angular gyrus. J Neurosci 35:3276–3284. https://doi.org/10.1523/JNEUROSCI.3446-14.2015

Pugh KR, Mencl WE, Jenner AR, Katz L, Frost SJ, Lee JR, Shaywitz SE et al (2000) Functional neuroimaging studies of reading and reading disability (developmental dyslexia). Ment Retard Dev Disabil Res 6:207–213. https://doi.org/10.1002/1098-7799(20006)6:3<207::AID-MRDD8>3.0.CO;2-P

Raschke NM, Chang M, Gaab N (2011) Structural brain alterations associated with dyslexia predate reading onset. NeuroImage 57:742–749. https://doi.org/10.1016/j.neuroimage.2010.09.055

Reis A, Castro SL, Inácio F, Pacheco A, Ararijo S, Santos M, et al (2020) Versão Portuguesa da Bateria 3DM para avaliação da leitura e da escrita [3DM Portuguese version to assess reading and spelling skills]. Manuscrito em preparação.

Richlan F (2019) The functional neuroanatomy of letter-speech sound integration and its relation to brain abnormalities in developmental dyslexia. Front Hum Neurosci 13:21. https://doi.org/10.3389/fnhum.2019.00021

Richlan F, Kronbichler M, Wimmer H (2009) Functional abnormalities in the dyslexic brain: a quantitative meta-analysis of neuroimaging studies. Hum Brain Mapp 30:3299–3308. https://doi.org/10.1002/hbm.20752

Richlan F, Kronbichler M, Wimmer H (2011) Meta-analyzing brain dysfunctions in dyslexic children and adults. NeuroImage 56:1735–1742. https://doi.org/10.1016/j.neuroimage.2011.02.040

Richlan F, Kronbichler M, Wimmer H (2013) Structural abnormalities in the dyslexic brain: a meta-analysis of voxel-based morphometry studies. Hum Brain Mapp 34:3055–3065. https://doi.org/10.1002/hbm.22127
Schwab JF, Lew-Williams C (2016) Language learning, socioeconomic status, and child-directed speech. Wiley Interdiscip Rev Cogn Sci 7:264–275. https://doi.org/10.1002/wcs.1393

Shaywitz SE, Morris R, Shaywitz BA (2008) The education of dyslexic children from childhood to young adulthood. Annu Rev Psychol 59:451–475. https://doi.org/10.1146/annurev.psych.59.103006.093630

Simons PG, Fletcher JM, Rezaie R, Papanicolaou AC (2014) Does IQ affect the functional brain network involved in pseudoword reading in students with reading disability? A Magnetoencephalography Study. Front Hum Neurosci 7:932. https://doi.org/10.3389/fnhum.2013.00932

Smith SM, Nichols TE (2009) Threshold-free cluster enhancement: addressing problems of smoothing, threshold dependence and localisation in cluster inference. Neuroimage 44:83–98. https://doi.org/10.1016/j.neuroimage.2008.03.061

Stuebing KK, Fletcher JM, LeDoux JM, Lyon GR, Shaywitz SE, Shaywitz BA (2002) Validity of IQ-discrepancy classifications of reading disabilities: a meta-analysis. Am Educ Res J 39:469–518. https://doi.org/10.3102/0018163X039002469

Stuebing KK, Barth AE, Molfeje PJ, Weiss B, Fletcher JM (2009) IQ is not strongly related to response to reading instruction: a meta-analytic interpretation. Except Child 76:31–51. https://doi.org/10.1177/014424020907600102

Sucena A, Castro SL (2010) Aprender a ler e avaliar a leitura. O TIL: Teste de Idade de Leitura [Learning how to read and the assessment of reading]. Almedina, Coimbra. ISBN: 978-972-40-3919-0

Swanson HL (2012) Adults with reading disabilities: Converting a meta-analysis to practice. J Learn Disabil 45:17–30. https://doi.org/10.1177/0022219411426856

Tal S, Arnon I (2018) SES effects on the use of variation sets in child-directed speech. J Child Lang 45:1423–1438. https://doi.org/10.1111/jcll.12228

Tanaka H, Black JM, Hulme C, Stanley LM, Kesler SR, Whitfield-Gabrieli S, Reiss AL et al (2011) The brain basis of the phonological deficit in dyslexia is independent of IQ. Psychol Sci 22:1442–1451. https://doi.org/10.1177/0956797611419521

Taylor PC, Muggleton NG, Kalla R, Walsh V, Eimer M (2011) TMS of the right angular gyrus modulates priming of pop-out in visual search: combined TMS-ERP evidence. J Neurophysiol 106:3001–3009. https://doi.org/10.1152/jn.00121.2011

Tijms J, Fraça-González G, Karipidis II, Brem S (2020) The role of letter-speech sound integration in normal and abnormal reading development. Front Psychol 11:1441. https://doi.org/10.3389/fpsyg.2020.01441

Torgesen JK, Hudson RF (2006) Reading fluency: critical issues for struggling readers. In: Samuels SJ, Farstrup AE (eds) What research has to say about fluency instruction. International Reading Association, Newark, pp 130–158

Torppa M, Lyytinen P, Erskine J, Eklund K, Lyytinen H (2010) Language development, literacy skills, and predictive connections to reading in Finnish children with and without familial risk for dyslexia. J Learn Disabil 43:308–321. https://doi.org/10.1177/0222191410369006

Turkeltaub PE, Gareau L, Flowers DL, Zeffiro TA, Eden GF (2003) Development of neural mechanisms for reading. Nat Neurosci 6:767–773. https://doi.org/10.1038/nn1065

Tzourio-Mazoyer N, Landeau B, Papathanassiou D, Crivello F, Etard O, Delcroix N, Mazoyer B et al (2002) Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. Neuroimage 15:273–289. https://doi.org/10.1016/S1053-8119(01)00079-5

Van Atteveldt N, Ansardi D (2014) How symbols transform brain function: a review in memory of Leo Blomert. Trends Neurosci Educ 3:44–49. https://doi.org/10.1016/j.tine.2014.04.001

Van Atteveldt N, Formisano E, Goebel R, Blomert L (2004) Integration of letters and speech sounds in the human brain. Neuron 43:271–282. https://doi.org/10.1016/j.neuron.2004.06.025

Wadsworth SJ, Olson RK, DeFries JC (2010) Differential genetic etiology of reading difficulties as a function of IQ: an update. Behav Genet 40:751–758. https://doi.org/10.1007/s10519-010-9349-x

Waldie KE, Mosley JL (2000) Developmental trends in right hemispheric participation in reading. Neuropsychologia 38:462–474. https://doi.org/10.1016/S0028-3932(99)00091-3

Wechsler D (2003) Escala de Inteligência de Wechsler para Crianças - terceira edição (WISC-III) [Portuguese adaptation by MR Simões, AM Rocha, C Ferreira]. Cegoc-Tea, Lisboa.

Wexler J, Vaughn S, Edmonds M, Reuthebuch CK (2008) A synthesis of fluency interventions for secondary struggling readers. Read Writ 21:317–347. https://doi.org/10.1007/s11145-007-9085-7

Wilke M, Holland SK, Altaye M, Gaser C (2008) Template-O-Matic: a toolbox for creating customized pediatric templates. Neuroimage 41:903–913. https://doi.org/10.1016/j.neuroimage.2008.02.056

Wimmer H, Schurz M, Sturm D, Richlan F, Klackl J, Kronbichler M, Ladurner G (2010) A dual-route perspective on poor reading in a regular orthography: an fMRI study. Cortex 46:1284–1298. https://doi.org/10.1016/j.cortex.2010.06.004

Winkler AM, Ridgway GR, Webster MA, Smith SM, Nichols TE (2014) Permutation inference for the general linear model. Neuroimage 92:381–397. https://doi.org/10.1016/j.neuroimage.2014.01.060
Wolf M, Katzir-Cohen T (2001) Reading fluency and its intervention. Sci Stud Read 5:211–239. https://doi.org/10.1207/S1532799XS SR0503_2

Yaple ZA, Yu R (2020) Functional and structural brain correlates of socioeconomic status. Cereb Cortex 30:181–196. https://doi.org/10.1093/cercor/bhz080

Ziegler JC, Bertrand D, Tóth D, Csépe V, Reis A, Faísca L, Saine N et al (2010) Orthographic depth and its impact on universal predictors of reading: a cross-language investigation. Psychol Sci 21:551–559. https://doi.org/10.1177/0956797610363406

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