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ORIGINAL ARTICLE

How interindividual differences in brain anatomy shape reading accuracy

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Abstract The capacity to read develops throughout intensive academic learning and training. Several studies have investigated the impact of reading on the brain, and particularly how the anatomy of the brain changes with reading acquisition. In the present study, we investigated the converse issue, namely whether and how reading acquisition is constrained by the anatomy of the brain. Using multimodal MRI, we found that (a) the pattern (continuous or interrupted sulcus) of the posterior part of the left lateral occipito-temporal sulcus (OTS) hosting the visual word form area (VWFA) predicts reading skills in adults; that (b) this effect is modulated by the age of reading acquisition; and that (c) the length of the OTS sulcal interruption is associated with reading skills. Because the sulcal pattern is determined in utero, our findings suggest that individual difference in reading skills can be traced back to early stages of brain development in addition to the well-established socioeconomic and educational factors.

Keywords Reading · VWFA · MRI · Neurodevelopment · SES

Arnaud Cachia and Margot Roell have equally contributed to this study.

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Introduction

The capacity to read, contrary to spoken language, develops throughout intensive academic learning and training. Investigating how the brain is modified by the acquisition of literacy is crucial to clarify the factors that contribute to this cultural acquisition and its individual differences patterns (Dehaene et al. 2015). In expert literate adults of all cultures, reading relies on a left-lateralized network of brain areas that includes the inferior frontal/precentral gyri, the dorsal temporoparietal circuit, and the ventral occipito-temporal pathway (Houde et al. 2010; Martin et al. 2015). Particularly, a region in the left lateral occipito-temporal sulcus (OTS), termed the "visual word form area" (VWFA) (Cohen and Dehaene 2004), is consistently and specifically more activated in response to visually presented words in the learned script than to other categories of stimuli (Dehaene and Cohen 2011).

Reading acquisition affects how visual and phonological information is coded and processed, and induces functional and structural changes in the brain (Dehaene et al. 2015). For instance, a combined electro-encephalogram (EEG)/functional magnetic resonance imaging (fMRI) longitudinal study in 6-year-old children revealed that training with grapheme–phoneme correspondences leads to the rapid emergence of a selective activation of the VWFA (Brem et al. 2010). Reading acquisition also induces structural changes in the brain: a voxel-based morphometry (VBM) study on children aged 9–10 revealed that reading skills were related to gray matter volume in the VWFA, the anterior part of the left inferior occipital gyrus and the left thalamus (Simon et al. 2013). In addition, a longitudinal MRI study (Myers et al. 2014) showed that an increase in white-matter volume in the left temporoparietal region between kindergarten and Grade 3 predicts reading ability at Grade 3, over and above other measures (i.e., family history, socioeconomic status, and pre-reading cognitive skills). Finally, a diffusion MRI (dMRI) study on children aged 7–12 demonstrated that the microstructure of white-matter fibers connectivity between the VWFA and the anterior and medial temporal lobe increases with reading proficiency and age (Yeatman et al. 2012).

Importantly, the age of reading acquisition may modulate the impact of reading acquisition on the brain. Comparisons of ex-illiterate adults, who learned to read during adulthood, with literate adults, who learned to read during their childhood, suggest that reading relies on the same brain network in both populations (Dehaene et al. 2010, 2015; Pegado et al. 2014), but that structural changes in the brain induced by reading acquisition are generally smaller when reading acquisition occurs during adulthood than during childhood (Carreiras et al. 2009; Thiebaut de Schotten et al. 2014). The acquisition of literacy in adulthood has been associated with (a) an increase of gray matter in the bilateral angular, dorsal occipital, middle temporal, left supramarginal, and posterior superior temporal gyri, (b) a thickening of the splenium or the isthmus of the corpus callosum (Carreiras et al. 2009; Castro-Caldas et al. 2009), and (c) an increase in fractional anisotropy and a decrease in perpendicular diffusivity in the temporoparietal portion of the left arcuate fasciculus (Thiebaut de Schotten et al. 2014).

While most studies focused on brain changes induced by reading acquisition, a few studies investigated whether individual difference in pre-readers' brain structure affects their reading skills later in life. Using diffusion MRI, a longitudinal study on 14 children revealed that the white-matter connectivity of the VWFA at age 5, before children learned to read, predicts the location of VWFA peak activation in fMRI at age 8, after children learned to read (Saygin et al. 2016). This study fits with the observation that the major fiber tracts of the human brain are present since infancy (Dubois et al. 2006, 2008, 2014, 2016), and suggests that their presence biases the subsequent emergence of functional specialization in the cortex. Another study provided preliminary evidence that the oral reading skills in sixteen 8-year-old children (Borst et al. 2016) are correlated with the sulcal pattern (continuous or interrupted sulcus) of the left lateral OTS, the sulcus in which the VWFA appears during the course of learning to read. Importantly, interindividual variations in sulcal patterns presumably reflect the early brain differences that predate the acquisition of a cognitive skills, since the sulcal pattern is determined in utero (Mangin et al. 2010) and their major features remain unaffected by neuroplastic processes occurring during brain maturation after birth (Cachia et al. 2016).

In the present study, we aimed to investigate whether the sulcal pattern of the left lateral OTS is predictive of reading skills in a large sample of adults of variable socioeconomic status (SES) and age of reading acquisition. In addition, we examined whether the position of the sulcal interruption was of consequence. Given that the VWFA is consistently located in the posterior part of the left lateral OTS (Dehaene and Cohen 2011; Vinckier et al. 2007), we reasoned that an interruption in the posterior part of left lateral OTS (referred hereafter as 'posterior interruption') should have a greater effect on reading fluency than an interruption in the anterior part of the left lateral OTS (referred hereafter as 'anterior interruption'). In addition, we evaluated whether the effect of the sulcal pattern of the OTS on reading fluency varies with the age of acquisition of reading (i.e., childhood vs adulthood). To this aim, we compared whether the effect of the interruption of left lateral OTS on reading fluency was similar for literate adults who learned to read during childhood, and for ex-illiterate adults who learned to read during adulthood. Finally, we directly tested our hypothesis that the OTS sulcal pattern is a robust feature that is not affected by reading acquisition. To this aim, we compared the distribution of interrupted and continuous left lateral OTS in literate, ex-illiterate, and illiterate adults. If the macroscopic sulcal pattern of the brain truly reflects the early cerebral constraints on cognitive development, then it should not be affected by reading acquisition, as suggested by a recent study indicating stability during development (Cachia et al. 2016).

Method

Participants

Sixty-two Portuguese and Brazilian participants were recruited for this study and divided into three groups according to their literacy profile. The sample included 10 illiterate, 20 ex-illiterate, and 32 literate adults. All subjects were right-handed as estimated using the Edinburgh handedness test (Oldfield 1971). Full demographic information is reported in Table 1.

The illiterate participants were from rural areas or urban centers in the Brasilia vicinity. Participants were illiterates for social reasons, with no history of special difficulty other than the lack of access to schools. The illiterate participants did not attend school at all as children. The families of all these participants were originally from rural areas, and their parents had been illiterate rural workers. The ex-illiterates group includes Brazilian and Portuguese participants who had backgrounds similar to those of the illiterates (illiterate parents from rural areas). Like the illiterates, ex-illiterates had not attended school during childhood, but they differed in having attended adult literacy courses. Finally, the literate group comprised some participants from the same social community as the illiterate group, but with 2–7 years of early education, as well as other participants with higher socioeconomic status and education [for details, see Supplementary Materials in our previous study (Dehaene et al. 2010)].

SES was dichotomized into two levels (‘low’ and ‘high’) based on participant’s occupation: for instance, ‘street vendor’ and ‘rural worker’ were classified as ‘low’ SES, while ‘system analyst’ and ‘geologist’ were classified as ‘high’ SES.

All participants gave their written informed consent (the consent form was read aloud and explained to illiterates).

Reading test

Prior to the MRI session, all participants underwent a battery of neuropsychological tests to assess their reading skills. As a measure of reading performance, the number of words read per minute was calculated. The word reading task comprised 36 words (12 simple, 12 complex, and 12 irregular) to be read aloud. For illiterates, who failed to identify even some single letters, the measure was set to 0.

Anatomical MRI acquisition and analysis

Structural MRIs were acquired with a 3 T Siemens MAGNETOM Trio MR scanner. A sagittal high-resolution structural MRI was obtained for all participants (magnetization prepared rapid gradient echo, 160 slice T1-weighted image, TR 2300 ms, TE 2.98 ms; flip angle 9°, TA 7.46 min, resolution 1 × 1 × 1.1 mm). These MRIs were adapted for sulcus segmentation required for the three-dimensional reconstruction of the fine individual cortical folds.

Analysis of anatomical data was performed with the Morphologist toolbox using BrainVISA 4.2 software with standard parameters (http://brainvisa.info/). We used an automated pre-processing step to skull-strip the T1 MRIs and to segment the brain tissues. The automatic segmentation of the cortical folds throughout the cortex was based on the skeleton of the gray matter/cerebrospinal fluid mask (Mangin et al. 2004). This procedure yields a stable and robust sulcal surface definition that is not affected by variations in the cortical thickness or the gray-matter/white-matter contrast. At each processing step and for each MRI, images were visually checked and we observed no motion artefact and no segmentation error.

Classification of OTS sulcal pattern

We first classified the lateral OTS sulcal pattern in each participant based on Ono’s classification (Borst et al. 2016; Ono et al. 1990). Briefly, a three-dimensional mesh-based reconstruction of the cortical folds was visually inspected to classify the sulcal pattern of the lateral OTS. All MRI data were anonymized, and manual labelling of OTS in left and right hemispheres was carried out blind to the participant’s demographic characteristics (literacy group, gender, SES, etc). The sulcal patterns of the left and right OTS were independently classified by two of the co-authors (MR & AC) using a dichotomous variable code for the continuity or interruption of the sulcus. Reliability was

Table 1 Demographical data and reading performance

	Illiterate ($N = 10$)	Ex-illiterate ($N = 20$)	Literate ($N = 32$)
Age (years)	53.40 (2.83)	49.75 (2.00)	48.75 (1.58)
Gender (F/M)	05/05	13/7	16/16
SES level (high/low)	0/10	0/20	17/15
Early education (years)	0.21 (0.39)	0.24 (0.69)	8.65 (3.46)
Late education (years)	0.61 (1.05)	2.08 (1.22)	2.37 (1.95)
Reading fluency (words per minute)	0 (–)	21.25 (5.90)	96.43 (4.66)

Early (resp. late) education corresponds to the years of education received by the participant before (resp. after) the age of 18. Quantitative data are represented as mean (SD)

100% ($\kappa = 1$) among the two raters for the left and the right hemispheres.

The sulcal pattern of the lateral OTS was characterized as 'interrupted' when the lateral OTS had interruptions and 'continuous' otherwise. In addition, to investigate the possible effect of the position of the left OTS interruption, we identified whether OTS interruption was located in the posterior part of the sulcus hosting the VWFA (Dehaene and Cohen 2011; Vinckier et al. 2007) ('posterior' interruption), or in the anterior part of the sulcus ('anterior' interruption) (see Fig. 1). We used an anatomical criterion, namely the *Y*-coordinate of the posterior extremity of the brainstem (PEB), as a limit to define the anterior and posterior interruptions of the left and right OTS. We considered this anatomical criterion and not the position of the VWFA, because such functional criterion could only be used for the left OTS and in readers (literates and ex-illiterates) but not for the right OTS or the non-readers. The functional validity of this anatomical criterion was a posteriori confirmed for the left OTS (see Fig. 2; Supplementary materials).

Finally, we measured the length of the OTS interruption based on the coordinates of the extremities of the anterior and posterior OTS interruptions. OTS interruption length was calculated after normalization to MNI space, thus controlling for global brain size differences due, for instance, to differences in age or gender. The T1 MRI was spatially normalized to MNI space using only linear transformations, thus avoiding potential biases resulting from the shape deformations that may occur during a non-linear warping process. The length of the sulcal interruption was decomposed in two components: an antero-posterior gap and a left–right gap (see Fig. 3).

Statistical analysis

Continuous variables (e.g., number of words or pseudowords read per minute, OTS interruption length, etc) were analyzed using linear models. When a significant main effect was detected, analysis was continued by post hoc paired comparisons using Tukey's HSD test with Bonferroni correction. Categorical variables (e.g., 'continuous' or 'interrupted' OTS) were analyzed using binomial and multinomial generalized linear models.

We included SES and gender as confounding covariates, because SES was previously shown to have an effect on reading skills and brain anatomy (Farah et al. 2006; Noble and McCandliss 2005; Fluss et al. 2009; Noble et al. 2007; Jednorog et al. 2012) and gender on sulcal anatomy (Duchesnay et al. 2007). Estimates of the mean values of continuous variables were, therefore, linearly adjusted on SES and gender.

Main effects and interactions were probed with *F* tests in the linear models, Chi-squared tests in the generalized linear models, and with *t* tests in the paired post hoc

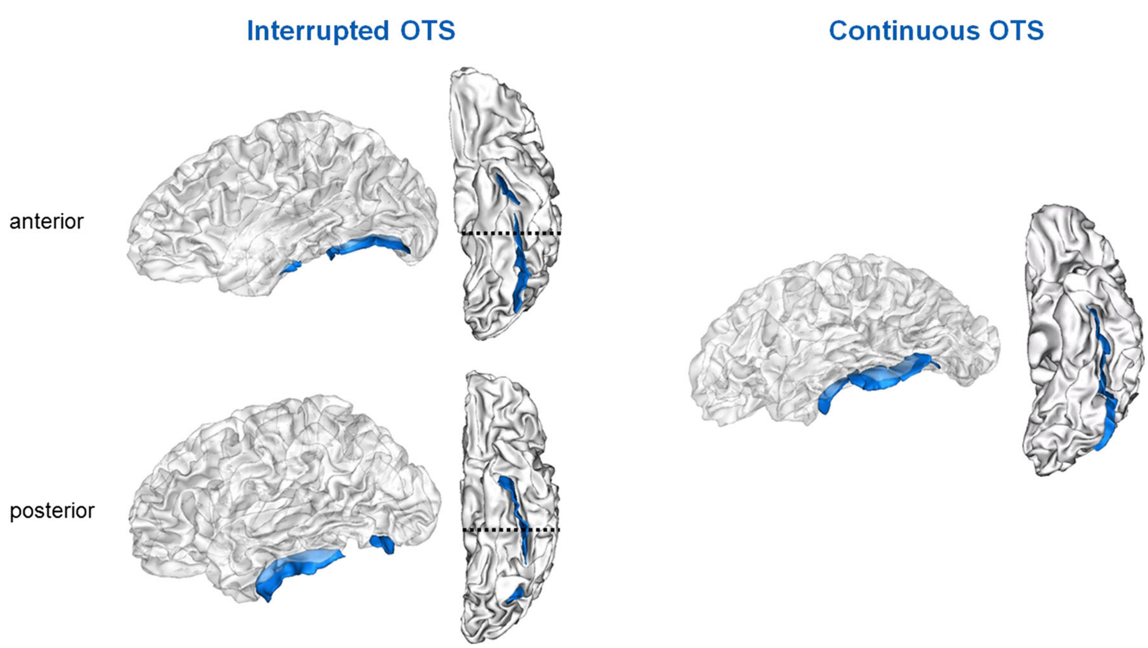

Fig. 1 Sulcal interruptions of the occipito-temporal sulcus (OTS). Examples of a posterior interruption (on the left) and an anterior interruption (on the right) of the left lateral OTS (sulci are depicted in blue). The posterior extremity of the brainstem (dashed line) was used as a limit to define the anterior and posterior interruptions of the OTS

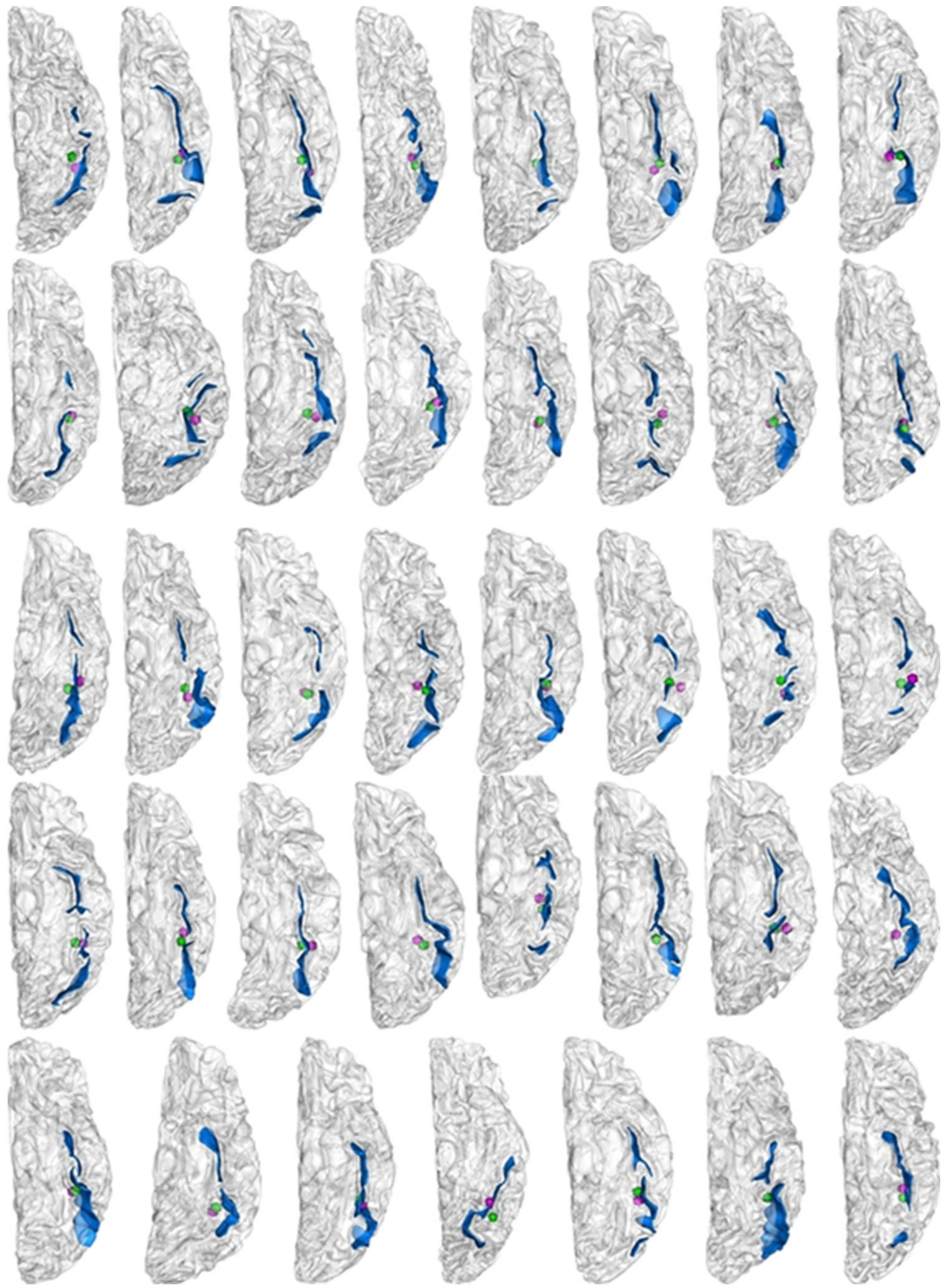

Fig. 2 Sulcal pattern of the left occipito-temporal sulcus (OTS) and position of the Visual Word Form Area (VWFA). 3-D mesh-based reconstructions of the white-matter surface (in semi-transparent white) with left OTS (in blue). Individual VWFA peak activation is represented with a purple sphere. The mean position of the VWFA in MNI space (−44; −50; −14) based on coordinates provided in the literature (Dehaene et al. 2010) is represented with a green sphere

analyses. A two-tailed p value of less than 0.05 was considered statistically significant. The relative importance of each factor in the linear models was estimated using the 'lmg' metric, also known as "hierarchical partitioning", which provides a decomposition of the total variance (adjusted R^2) and has the advantage to robustly adjust for other factors in the model (Grömping 2015).

All the statistical analyses were carried out with R 2.9 software (http://www.r-project.org/) and 'car', 'effects', 'nnet', 'multcomp', and 'relaimpo' libraries.

Results

Effect of OTS sulcal pattern on reading

Literates

We first analyzed across the group of literate subjects whether the sulcal pattern of the lateral OTS was associated with reading fluency as measured by the number of words correctly read per minute. To this aim, we entered fluency in a linear model with five categorical factors: the sulcal

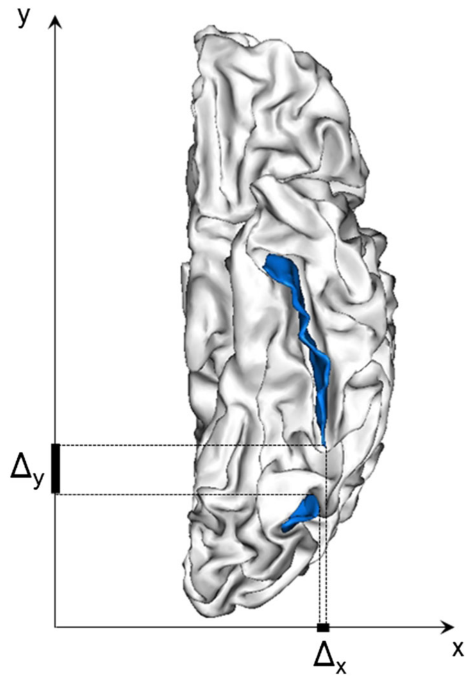

Fig. 3 Sulcal interruption of the left posterior OTS. The length of the sulcal interruption was decomposed in two components: an antero-posterior gap (Δy) and a left–right gap (Δx)

pattern of the lateral posterior OTS in the left hemisphere (‘continuous’ vs ‘interrupted’), the sulcal pattern of the lateral anterior OTS in the left hemisphere (‘continuous’ vs ‘interrupted’), the lateral posterior OTS in the right hemisphere (‘continuous’ vs ‘interrupted’), the lateral anterior OTS in the right hemisphere (‘continuous’ vs ‘interrupted’), and SES (‘low’ vs ‘high’). This analysis revealed that the number of words correctly read was associated with the sulcal pattern of the left posterior lateral OTS ($p < 0.025$) and SES ($p < 0.0001$), but not with the left anterior lateral OTS ($p = 0.49$), right posterior lateral OTS ($p = 0.63$), nor with right posterior lateral OTS ($p = 0.64$). Post Hoc Tukey’s tests showed that participants with a posterior interruption in the OTS had significantly better reading fluency scores (mean ± SD 113.01 ± 7.67 words per minute) than participants that had a continuous OTS (89.94 ± 4.60) ($t = 2.53$; $p = 0.02$) (see Fig. 4). Importantly, no other variables regarding OTS sulcal pattern (i.e., anterior interruption of OTS in left hemisphere, anterior and posterior interruption of OTS in right hemisphere) had any significant effect on reading fluency. These results replicate and extend a previous study in children (Borst et al. 2016) by showing that the interruption of the OTS affects oral reading skills not only in children but also in adults, and additionally that the effect of the OTS interruption on oral reading skills is restricted to interruption of the posterior part of the left lateral OTS, hosting the VWFA.

To check whether SES level had a differential effect depending on OTS sulcal pattern, analyses were ran again including four additional interaction terms between SES level and the OTS anterior and posterior interruptions in both right and left hemisphere. No interaction effect was found between any factor ($p > 0.4$).

To estimate the relative importance of the sulcal pattern of the left posterior lateral OTS and SES on reading fluency, we reran a linear model with only these two factors. The new linear model revealed that the two predictors accounted for 64.5% of the variance in the number of words correctly read, $F(2, 29) = 26.43$, $p < 0.0001$, adjusted $R^2 = 0.645$, with the sulcal pattern of the left posterior lateral OTS explaining 4.25% and SES 60.25% of the variance.

Differences between literates and ex-illiterates

We then investigated whether the effect of the left posterior OTS sulcal pattern on reading fluency differed between literates and ex-illiterates. We, therefore, ran the regression model on the data from literate and ex-illiterate subjects (excluding illiterates), and included a categorical group factor (‘literate’ vs ‘ex-illiterate’) and its interactions. Analyses revealed a significant main effect of group, $F(1,41) = 58.47$, $p < 0.00001$, as well as a main effect of SES, $F(1,41) = 54.83$, $p < 0.00001$, on reading fluency. Importantly a significant interaction between group and left OTS posterior interruption was detected, $F(1,41) = 8.81$, $p < 0.005$, indicating that the effect of left OTS sulcal pattern on reading fluency was different in literate and ex-illiterate groups. Post hoc Tukey revealed that reading fluency was found to be significantly greater ($T = 2.67$, $p = 0.01$) in participants in the literate group with a posterior interruption in the left OTS (102.90 ± 6.74 words read per minute) compared to literate participant with a continuous posterior left OTS (79.21 ± 4.62 words read per minute), while no significant difference was found ($T = 0.49$, $p = 0.9$) between participants with (37.02 ± 6.52 words read per minutes) or without (41.50 ± 7.04 words read per minutes) interruption in the posterior part of the left OTS in the ex-illiterate group (see Fig. 5).

Again, these findings were specific to the sulcal pattern of the left anterior OTS, as complementary analyses involving the left posterior, right anterior, or right posterior OTS pattern did not reveal any significant interaction with the group factor on reading fluency, all ps > 0.2).

Effect of OTS interruption length on reading

We further investigated the effect of left posterior OTS anatomy on reading skills by analyzing the effect of the

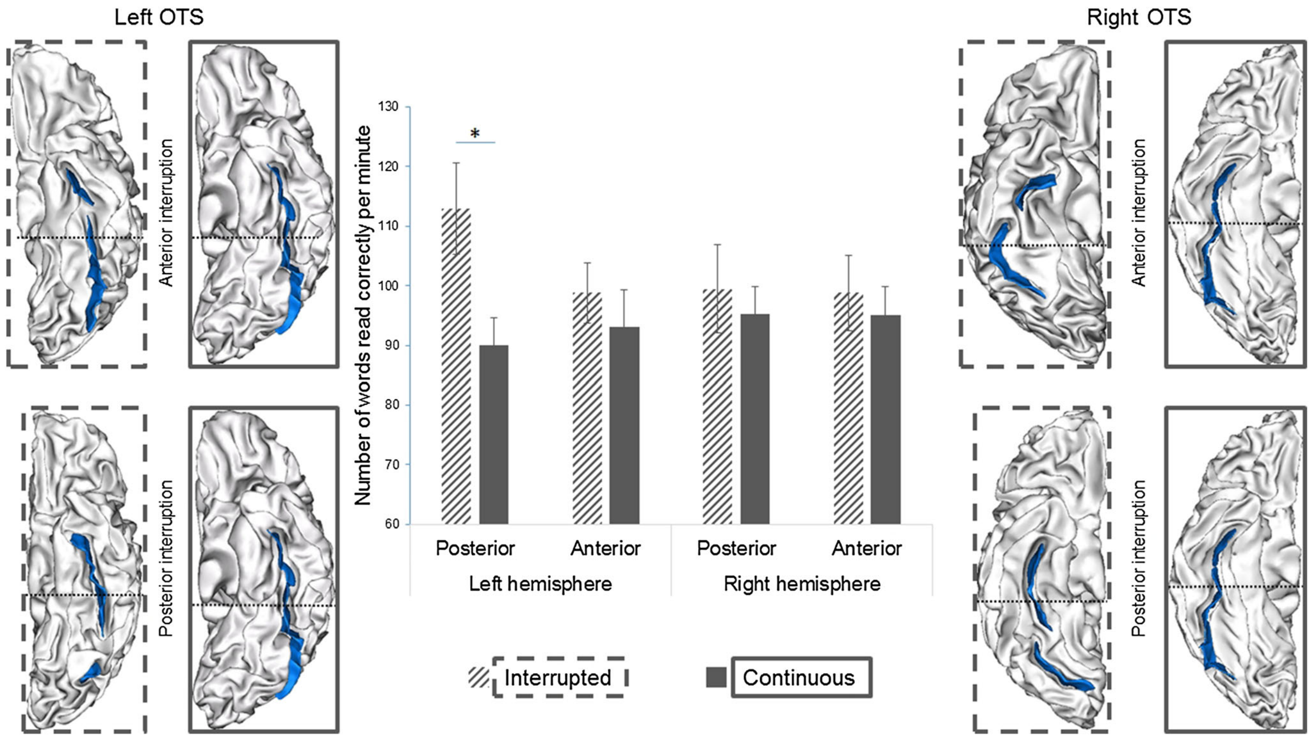

Fig. 4 Effect of OTS sulcal interruption on reading ability. The number of words reads correctly on average in literate adults with continuous (in plain gray) or interrupted (in hatched gray) OTS in left and right hemispheres. The sulcal interruption can be located posteriorly ('below' the back dashed line) or anteriorly ('above' the black dashed line). Error bars depict one standard error of the mean, $^*p < 0.05$. Data were linearly adjusted on gender and SES levels

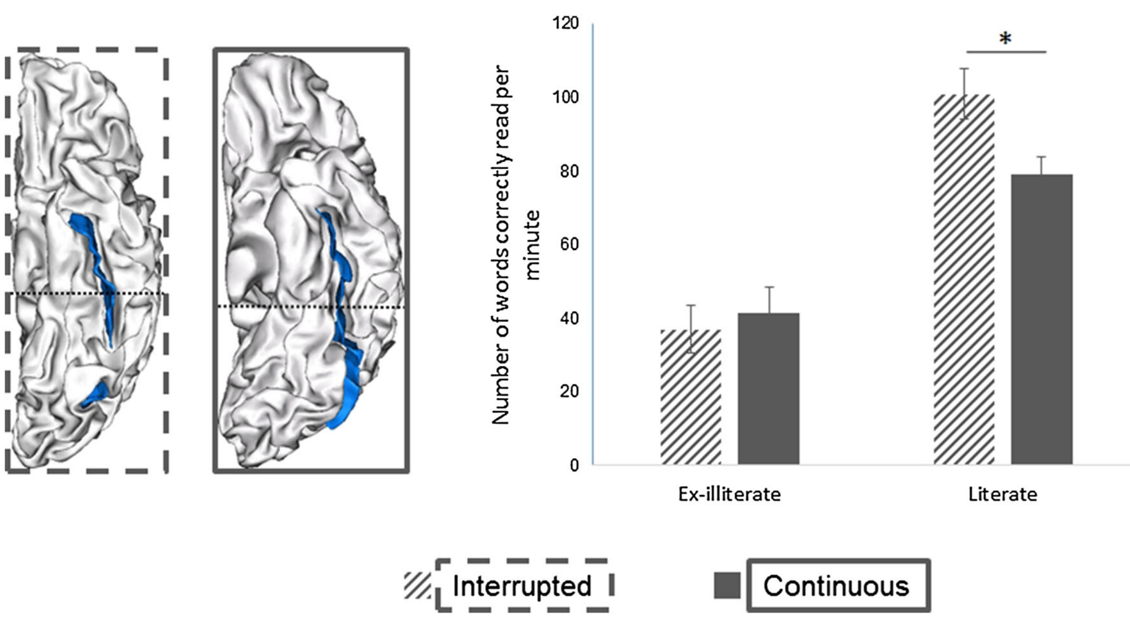

Fig. 5 Differential effect of posterior sulcal interruption of OTS on reading ability in literates and ex-illiterates. The number of words reads correctly on average in literate and ex-illiterate adults with continuous (in gray) or interrupted (in white) OTS in left hemisphere (inside VWFA). Error bars depict one standard error of the mean, $^*p < 0.05$. Data were linearly adjusted on gender and SES levels

length of the sulcal interruption on reading fluency of readers (i.e., literates and ex-illiterates). The analysis focused on readers (i.e., literates and ex-illiterates) with a posterior interruption in the left lateral OTS ($N = 20$).

We ran a linear model with the number of words read correctly as the outcome variable and the antero-posterior gap and the left–right gap as continuous variables. Note that SES was not entered as variable in the model, since all subjects but three literates were 'low' SES. The number of words correctly read was associated with the antero-posterior gap ($F(1,17) = 4.02$, $p = 0.007$) but not with the left–right gap ($F(1,17) = 0.00$, $p = 0.99$). As shown in Fig. 6, the greater the antero-posterior gap, the greater the number of words correctly read ($R^2 = 0.36$).

Effects of reading on OTS sulcal pattern

Finally, to determine whether learning to read modifies the sulcal pattern of the lateral OTS, we evaluated the literacy effect on the distribution of interrupted and continuous posterior left lateral OTS (see Table 2). Multinomial and binomial regression analyses with SES and gender as confounding covariates revealed that the distribution of the sulcal interruption of the left posterior OTS ('continuous' vs 'interrupted') was similar in literates, ex-illiterates, and illiterates ($\chi = 3.95$, $df = 2$, $p = 0.14$), and did not differ ($\chi = 2.83$, $df = 1$, $p = 0.09$) between readers (literates and ex-illiterates) and non-readers (illiterates). For these two analyses, main effects of SES and gender were non-significant ($ps > 0.17$).

Discussion

Several studies have investigated the impact of reading on the brain, and particularly how the anatomy of the brain changes with reading acquisition (Dehaene et al. 2015). The aim of the present study was to investigate the converse issue, namely whether and how reading acquisition is constrained by the anatomy of the brain. We found that the sulcal pattern of the left OTS, a marker of early neurodevelopmental constraints, predicted reading skills in adults. These results replicate and extend in a larger, older, and more variable sample our preliminary findings found in a small sample of sixteen 8-year-old children (Borst et al. 2016). Specifically, adults who had an interrupted left OTS, in particular in its posterior portion hosting the visual word form area (VWFA), had better reading fluency than adults who had a continuous left OTS. Furthermore, we found a linear association between the length of the posterior interruption of the left OTS and reading skills, namely the greater the interruption, the greater the number of words correctly read per minute. Our results also suggest that the position of the sulcal interruption of the OTS is critical: only OTS interruption located in the posterior part of the sulcus, hosting the VWFA, but not its anterior part, affected reading fluency.

In addition, comparison of adults who learned to read during childhood (literates) and adults who learned to read during adulthood (ex-illiterates) revealed that age of reading acquisition modulates the effect of OTS sulcal pattern on reading skills: interruption of the posterior left

Fig. 6 Left posterior OTS sulcal interruption length and reading skills. Linear association between the length of the sulcal interruption of the posterior OTS (antero-posterior gap in mm) and the number of words read per minute. Only subjects with a sulcal interruption on the left posterior OTS were represented (i.e., antero-posterior gap >0)

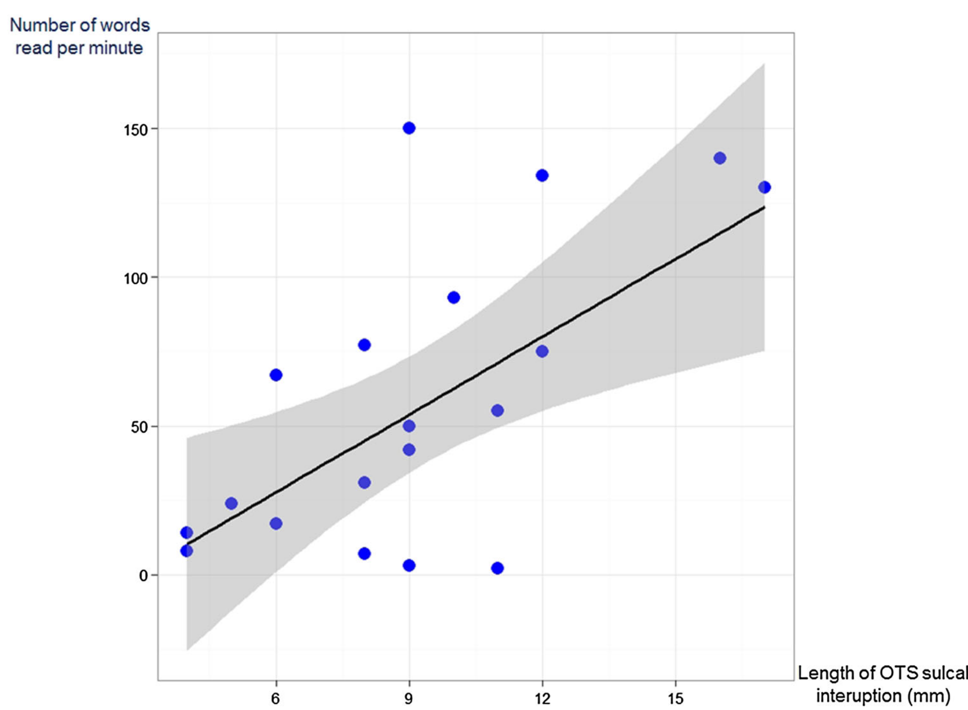

Table 2 Distribution of the posterior and anterior sulcal interruptions of the lateral occipito-temporal sulcus (OTS) in the left and right hemispheres in non-readers (illiterate) and readers (ex-illiterates and literates)

	Non-readers ($N = 10$)	Readers ($N = 52$)		Group difference*	Non-readers vs readers*
	Illiterates ($N = 10$)	Ex-illiterates ($N = 20$)	Literates ($N = 32$)		
Left hemisphere					
Posterior					
Interrupted	2	11	9	$\chi = 3.95$; $p = 0.14$	$\chi = 2.83$; $p = 0.09$
Continuous	8	9	23		
Anterior					
Interrupted	5	12	19	$\chi = 0.17$; $p = 0.91$	$\chi = 0.14$; $p = 0.71$
Continuous	5	8	13		
Right hemisphere					
Posterior					
Interrupted	5	9	9	$\chi = 1.50$; $p = 0.47$	$\chi = 0.08$; $p = 0.77$
Continuous	5	11	23		
Anterior					
Interrupted	7	12	12	$\chi = 5.46$; $p = 0.07$	$\chi = 0.76$; $p = 0.38$
Continuous	3	8	20		

*Distribution difference between groups (illiterates vs ex-illiterates vs literates), or between non-readers and readers, was evaluated using multinomial, or binomial, generalized linear models with gender and SES as confounding covariates

lateral OTS affected reading skills in literates but not in ex-illiterates. This finding probably reflects the fact that the level of reading competence in our sample of ex-illiterates was highly variable, from good fluency to near-illiteracy, and that the primary determinant of this variability is probably the highly variable duration, intensity, and quality of the reading education that those adults received (Dehaene et al. 2010). Thus, this negative finding does not exclude that an effect of the anatomical OTS sulcal pattern would eventually be observed on the asymptotic performance of ex-illiterates adults, once they received extensive education—just like the effect of genetic variability on school-based achievements increases with age, once developmental and educational variability recedes (Plomin and Deary 2015).

Finally, the similar distribution of the left OTS sulcal interruption found in readers and non-readers provides preliminary evidence that the qualitative sulcal pattern is robust to neuroplastic processes underlying brain development and education, in line with our previous study reporting a stability during the development of the qualitative sulcal pattern of the anterior cingulate cortex (ACC) (Cachia et al. 2016). We, therefore, propose that differences in reading skills in individuals with interrupted or continuous left OTS are likely to arise from the early stages of brain development, when the major sulcal patterns appear. We suspect that the relation between the sulcal pattern of the left OTS and reading accuracy might be a consequence of the association between sulcal pattern and white-matter connectivity, whereby the thickness of white-matter bundles and the tension they exert constrain cortical folding (Hilgetag and Barbas 2006; Van Essen 1997; Dehay et al. 1996). More specifically, the sulcal pattern of the left OTS could be associated with oral reading accuracy via the connectivity between the VWFA and the anterior and medial temporal lobe (Yeatman et al. 2012; Bouhali et al. 2014). This interpretation is consistent with a recent study that showed that the white-matter connectivity of the VWFA at age 5, before children learned to read, is predictive of VWFA location at age 8, after they learned to read (Saygin et al. 2016). A larger interruption of the left OTS might confer an advantage in reading by reflecting an underlying difference in the size of white-matter bundles, indicating a higher number, greater fiber diameter, and/or greater myelination in the bundles connecting the VWFA (Bouhali et al. 2014). This interpretation is supported by the previous studies showing that the connectivity between the VWFA and the anterior and medial temporal lobe in 7–12-year-old children increases with reading efficiency and age (Yeatman et al. 2012), and that the anisotropy of the posterior part of the arcuate fasciculus varies with literacy (Thiebaut de Schotten et al. 2014). Another not necessarily incompatible hypothesis is a putative increase in VWFA surface area. OTS sulcal interruption might, therefore, be an indirect marker of an increase in the amount of cortical tissue and connections available for neuroplastic processes underlying reading acquisition. Finally, cytoarchitectonic differences may also contribute to the observed functional differences in reading skills in participants with continuous or interrupted left OTS.

Indeed, several studies suggest not only a relationship between cortical folding and cerebral function, but also with the underlying cytoarchitecture (Fischl et al. 2007; Zilles et al. 2013). In particular, one study showed that the sulcal interruption of left posterior OTS is located within the cytoarchitectonic area 4 of the lateral fusiform gyrus (FG4) which overlaps the VWFA (Weiner et al. 2017), supporting, therefore, a correspondence between cytoarchitectony (FG4), functional segregation (VWFA), and sulcal folding pattern (OTS interruption). In the future, it will be important to examine whether this model also applies to other cognitive domains. There are suggestions that the plasticity in FG2, where face and word responses emerge during development, is greater than in other regions such as the area FG3, which responds to places (Weiner et al. 2017; Gomez et al. 2017). It thus seems possible that the neurodevelopmental mechanisms that constrain VWFA function differ from other cortical regions whose selectivity may be less dependent on experience (Saygin et al. 2016).

Several issues of the present study call for caution when interpreting the results. First, we only studied a single macroscopic variable, sulcal interruption, but other more subtle sulcal patterns may not be so strictly immutable. Indeed, although the major patterns are in place at birth, changes may still be observed in the tertiary gyration during infancy (Leroy et al. 2011). Thus, it remains to be seen whether quantitative (e.g., surface, depth, length, etc) and smaller scale measures of sulcal anatomy than the one studied here might be impacted by education to literacy, numeracy, or other domains such as music (Mongelli et al. 2017). Second, although our findings are suggestive of a causal role of sulcation in determining later reading skills, a direct causal link has yet to be evidenced. To provide such evidence, a longitudinal study would be needed to demonstrate that pre-reading sulcation constrains future reading skill in the same individuals—similar to the longitudinal demonstration that infero-temporal connectivity constrains VWFA location (Saygin et al. 2016). Third, it is also worth remembering that the impact of the OTS sulcal pattern accounted for only $\sim$4% of the variability in reading fluency, as compared to $\sim$65% for SES. The latter variable is likely to summarize several other relevant variables such as presence of books in the family, quality, and duration of schooling, etc. The previous studies have established a strong correlation between SES and language skills, including vocabulary, literacy, phonological awareness, and syntax (Farah et al. 2006; Noble and McCandliss 2005; Fluss et al. 2009; Noble et al. 2007; Jednorog et al. 2012). For instance, socioeconomically disadvantaged children are at risk for reading difficulties (Whitehurst and Lonigan 1998; Lee and Burkam 2002; Evans 2004). SES family environment also impacts reading skills through different home literacy factors such as number of books available in the household and parental involvement in the school (Aikens and Barbarin 2008). SES-related differences in reading tend to be stark at the initial kindergarten assessment and continue to grow through school (Aikens and Barbarin 2008). This would be due to the compounding effect of low-SES environments: low-SES children grow up in home environments poor in literacy and enter schools that have higher proportion of poor children, both factors being associated with poorer reading outcomes (Xue and Meisels 2004). Parental SES can also affect an individual from very early development in utero (Hackman et al. 2010; Tomalski and Johnson 2010). Indeed, stress, nutrition, parental care, and cognitive stimulation mediate the impact of SES on both brain structures and cognitive functions across development (Raizada and Kishiyama 2010; Hackman and Farah 2009; Jednorog et al. 2012). Fourth, a clear limit is that we did not quantify the percentage of the VWFA cluster located within or outside of the OTS sulcal interruption or the selectivity of the voxels within vs. outside the interruption. Indeed, this information would have provided a more direct test of the possible effect of the left OTS interruption on the functional activation of the VWFA. In our study, we identified the VWFA-related cluster of each participant using a coarse-to-fine approach (see Glezer and Riesenhuber 2013 for a similar rationale) in which we determined the nearest local maxima in regards to the mean position of the VWFA in MNI space (−44; −50; −14, Dehaene et al. 2010) from a whole-brain analysis of the individual contrast ‘written strings’ vs ‘checkers’. Because this contrast elicited activations with very variable peak intensities from one participant to the other—likely due to the high variability of participants’ reading fluency, early and late education as well as SES (see Table 1)—we used a participant-specific statistical threshold to detect the VWFA-related cluster (see Supplementary Materials), thus preventing us from comparing the spatial extent of this cluster between participants. Note that analyses based on the cluster peak position, as the one run in the present study, were used in the previous studies investigating the relation between fMRI activations and individual sulcal morphology, e.g., in visual areas (Dumoulin et al. 2000), orbitofrontal cortex (Li et al. 2015), or anterior cingulate cortex (Amiez and Petrides 2014).

In conclusion, we provided evidence that the sulcal pattern of the posterior part of the left lateral OTS, hosting the VWFA which is consistently activated in good readers during the visual presentation of written words, affects reading fluency in adults. In particular, adults with an interruption in the left posterior lateral OTS had better reading fluency than adults with continuous left lateral OTS. This effect was modulated by the age of reading acquisition with a stronger effect of the sulcal pattern of the left posterior lateral OTS on reading fluency for literate than ex-illiterate adults. In addition, the length of the interruption of the left posterior lateral OTS was associated with reading fluency, with a longer interruption leading to better reading fluency. While sulcation—an aspect of brain anatomy which is primarily affected by early neurodevelopmental factors—predicts subsequent cognitive development, it is worth remembering that socioeconomic and educational factors have a much greater, indeed, dominant effect, on ultimate reading fluency, and are also the ones on which we may intervene by modifying our educational policies.

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