

# Brain-Behavior Dynamics Between The Left Fusiform and Reading

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## Original Article

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## **Abstract**

The visual word form area (VWFA) plays a significant role in the development of reading skills. However, the developmental course and anatomical properties of the VWFA have only limitedly been investigated. The aim of the current longitudinal MRI study was to investigate dynamic, bidirectional relations between reading and the structure of the left fusiform gyrus at the early-to-advanced reading stage. More specifically, by means of bivariate correlations and a cross-lagged panel model (CLPM), the interrelations between the size of the left fusiform gyrus and reading skills (a composite score of a word and pseudo-word reading task) were studied in a longitudinal cohort of 43 Flemish children (29M, 14F) with variable reading skills in grade 2 (the early stage of reading) and grade 5 (the advanced stage of reading) of primary school. Results revealed that better reading skills at grade 2 lead to a larger size of the left fusiform gyrus at grade 5, whereas there are no directional effects between the size of the left fusiform gyrus at grade 2 and reading skills at grade 5. Hence, according to our results there is behavior-driven brain plasticity and no brain-driven reading change between the early and advanced stage of reading. Together with pre-reading brain studies showing predictive relations to later reading scores, our results suggest that the direction of brain-behavioral influences changes throughout the course of reading development.

## **Keywords**

left fusiform gyrus; longitudinal MRI; reading development; reading skills; visual word form area

## **Declarations**

### **Funding**

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### **Conflicts of Interest**

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

### **Availability of data and material**

The dataset for this manuscript is not publicly available, because the conditions of our ethics approval do not permit public archiving of anonymized study data and consent had only been obtained from participants for participation in the study and not to share data with third parties. Requests to access the data set and/or material should be directed to Pol Ghesquière (pol.ghesquiere@kuleuven.be) explaining the purpose of their request. In accordance with the EU general data protection regulation (GDPR), data will be released to requestors upon the following conditions: consent of the representative of the minor and a formal agreement between parties. Please note that the MRI data cannot be shared under any circumstance as MRI data are person-specific and therefore not anonymous.

### **Code availability**

Not applicable

### **Authors contribution**

- **Caroline Beelen:** conceptualization, methodology, validation, visualization, investigation, software, formal analysis, data curation, writing—original draft, writing—review and editing.
- **Jan Wouters:** methodology, validation, visualization, resources, writing—review and editing, supervision, project administration, and funding acquisition.
- **Maaïke Vandermosten:** conceptualization, methodology, validation, investigation, data curation, writing—review and editing, supervision, project administration, and funding acquisition.
- **Pol Ghesquière:** conceptualization, methodology, validation, resources, writing—review and editing, supervision, project administration, and funding acquisition.

### **Ethics approval**

The study was approved by the local ethical committee of the university hospital (UZ Leuven), and is in accordance with ethical standards described within the declaration of Helsinki.

### **Consent to participate**

Written informed consent to participate in this study was provided by the parents of the participating children.

### **Consent for publication**

All co-authors have approved the manuscript and agreed with its submission to Brain Structure and Function.

## Introduction

Learning to read is a developmental process accompanied by functional and anatomical changes in the brain. According to the traditional reading network (Pugh et al., 2000, 2001), beginning readers mainly rely on phonological representations and grapheme-phoneme conversions and thereby activate dorsal temporal parietal brain regions, whereas more advanced readers mainly rely on orthographic representations and thereby activate ventral occipital temporal brain regions. In particular the visual word form area (VWFA), corresponding to the middle part of the left fusiform gyrus in the ventral occipital temporal cortex, is assumed to play a significant role in reading (Cohen & Dehaene, 2004; Dehaene et al., 2010; Dehaene-Lambertz et al., 2018). The traditional reading network is supported by fMRI (e.g. Glezer et al., 2016) and dMRI studies (e.g. Vandermosten et al., 2012) revealing that in adult readers dorsal temporal parietal regions are sensitive to phonology and ventral occipital temporal regions to orthography. However, developmental aspects of the traditional reading network have been questioned (Richlan, 2012). First, whereas the model assumes that the ventral regions are only involved in later reading stages, in which orthographic whole-word recognition plays an important role, the available studies in pre-to-beginning readers indicate that the VWFA already shows sensitivity for print over symbols after a few weeks of grapheme-phoneme training (Bach et al., 2013; Brem et al., 2010; see Dehaene-Lambertz et al., 2018), or even less than 30 minutes (Pleisch et al., 2019). Second, it is argued that in pre- to beginning readers the left ventral occipital temporal region contributes to phonological processes besides orthographic processes (Beelen et al., 2019; Brem et al., 2010; Conant et al., 2020; see Richlan et al., 2011; Vanderauwera et al., 2018; Vandermosten et al., 2015).

The VWFA is not present from birth, but develops as soon as individuals learn how to read (Dehaene-Lambertz et al., 2018). Saygin et al. (2016) performed a combined functional magnetic resonance imaging (fMRI) and Diffusion Tensor Imaging (DTI) longitudinal study in

5-year-old pre-reading children and observed that connectivity patterns from the ventral visual cortex to distinct language areas predict at which location along the pathway the VWFA develops three years later (see also Dehaene & Dehaene-Lambertz, 2016). The onset of the VWFA was investigated in detail in a longitudinal fMRI study of Dehaene-Lambertz et al. (2018). Children aged 6-7 years were scanned once before reading onset in kindergarten and multiple times at the early stage of reading in the first year of primary school. Results revealed that reading onset leads to functional changes in voxels in the mid-fusiform gyrus that initially are weakly specialized for tools. After reading onset, these voxels remain active for tools, but acquire an additional, stronger response for words, i.e. these voxels form the VWFA. This is also confirmed by EEG studies showing a negative potential (N1) after 188-281 ms occurring over occipital temporal scalp regions in pre-readers and second graders when confronted with print in contrast to symbols or false fonts (Maurer et al. 2006, 2007; Bach et al., 2013; Brem et al. 2013). A few weeks of grapheme-phoneme-coupling training in kindergarten induces the N1-potential already (Brem et al. 2010). In addition, a combined fMRI and EEG study of Pleisch et al. (2019) showed that even very short grapheme-phoneme training (i.e. less than half an hour) in preschoolers induces the N1-potential and leads to altered visual character processing with increased activity for trained false font characters as opposed to untrained ones. Although the onset of the VWFA may occur at a short period of time in early childhood, cross-sectional fMRI studies observed that the VWFA develops over a prolonged trajectory from early childhood into late adolescence (Centanni et al., 2017; Dehaene et al., 2010; Olulade et al., 2013). For instance, Centanni et al. (2017) investigated VWFA sensitivity (print versus non-linguistic faces) and specificity (print versus line drawings of nameable objects) in children aged 7-14 years and adults, and observed that children aged 7-14 years have a similar VWFA sensitivity for print over faces as adults, but that their VWFA specificity for print over object line drawings is not at the level of that of adults yet. Results therefore suggest that in the VWFA

sensitivity for print (relative to non-linguistic stimuli) develops before the age of 7, but specificity for print still develops after the age of 14.

With regard to poor readers and children with dyslexia (i.e., children with severe and persistent reading or spelling deficits), cross-sectional child (f)MRI studies revealed that the VWFA differs between poor and typical to strong readers (Maurer et al., 2007, 2011; Shaywitz et al., 2007; Van der Mark et al., 2009; Beelen et al., 2019). For instance, Beelen et al. (2019) reported in their MRI study a smaller fusiform gyrus in pre-reading children who a few years later were classified as having dyslexia. Additionally, a small number of available longitudinal child (f)MRI studies reported differences in activation in the region that will later form the VWFA between children who develop into poor or strong readers (Bach et al., 2013; Centanni et al., 2019). Centanni et al. (2019) indicated in their fMRI study that pre-reading children with dyslexia at the end of the second grade have accompanying reductions in print responses in the location that will become the VWFA, both for familiar letters and novel letter-like false fonts. Bach et al. (2013) observed in their fMRI study that in pre-readers activation of the region that develops into the VWFA together with behavioral assessment scores predicts their reading performance in the second grade. Because these studies focused on the pre-reading phase in which children have none to very limited reading experience yet, observed differences between children who will become poor or strong readers are presumably not caused by variation in reading experience. Furthermore, a longitudinal fMRI study of Preston et al. (2016) observed that print-speech co-activation in the left hemispheric reading network (amongst which the fusiform gyrus) of beginning to advanced readers (readers between 6 and 10 years old) predicts their reading achievement two years later, suggesting that not only pre-reading, but also during reading development, impairments in the fusiform gyrus will lead to later observed reading difficulties. Particularly, the pre-reading studies suggest that impairments in the fusiform gyrus, and more specifically the VWFA, will lead to later observed reading difficulties in a

unidirectional way. However, reading skills might also impact the development of the left fusiform gyrus, similar to having reciprocal associations between reading and cognitive skills, with good phonological skills being important for learning to read, and reading improving phonological skills in turn. According to the interaction specialization theory, brain structures and functions develop as a result of continuous dynamic interactions between genetics, the brain, the body and the environment (Johnson, 2001, 2011), hence arguing that brain development is not solely the result of a unidirectional genetic-driven maturation process, but is also influenced by daily activities. This view supports the idea of a reciprocal, dynamic relation between reading skills and the structure of the left fusiform. In a similar vein, the neural recycling theory states that brain changes may be behavior-induced, in which a weakly specified cortical region, after acquiring a skill for which it was not genetically programmed, becomes specialized for the new skill (Dehaene, 2005; Dehaene & Cohen, 2007; Dehaene et al., 2010; Olulade et al., 2013; Dehaene-Lambertz et al., 2018). So, learning to master the writing system can be thought of as a new skill, which gradually develops in an originally weakly specified area of the mid-fusiform gyrus as a result of print experience. After reading skills are acquired, the area still responds to other visual inputs, but to a larger extent to print. The area is referred to as the VWFA. Hence, early reading development induces neuronal recycling and shapes the development of the VWFA.

The function of the VWFA has extensively been investigated in adult studies, but its developmental course has only limitedly been investigated (Dehaene-Lambertz et al., 2018; Bach et al., 2013; Centanni et al., 2019, Preston et al., 2016, Saygin et al., 2016). The aim of the current longitudinal MRI study is to investigate the dynamic, bidirectional relations between the left fusiform gyrus (encompassing the VWFA) and reading skills at the early-to-advanced reading stage. More specifically, the interrelations between the size of the left fusiform gyrus

and reading skills (a composite score of a word and pseudo-word reading task) will be studied in a longitudinal cohort of children with variable reading skills in grade 2 (the early stage of reading) and grade 5 (the advanced stage of reading) of primary school. We chose to have our focus on the relation between the size of the left fusiform gyrus and reading skills, since in our former study (Beelen et al., 2019) we observed significant differences in the size of the fusiform gyrus between pre-readers who subsequently develop dyslexia and pre-readers who later on become typical readers. In the current study, children of the same cohort are investigated, but now at the early (grade 2) and advanced (grade 5) reading stage. In the current study, we will use bivariate correlations and a cross-lagged panel model (CLPM) to investigate the relations between the size of the left fusiform gyrus and reading skills. By means of the CLPM we can examine whether (1) the left fusiform structure during the early stage of reading has an impact on reading skills during the advanced stage of reading, or whether (2) reading skills during the early stage of reading have an impact on the left fusiform structure during the advanced stage of reading (see figure 1). The first pattern of results resembles longitudinal (f)MRI studies in pre-readers (Bach et al., 2013; Centanni et al., 2019) and readers (Preston et al., 2016), showing that the structure of left fusiform gyrus predicts later reading skills. The second pattern of results is congruent with the interaction specialization theory and neuronal recycling. In addition, we hypothesize to find autoregressive relations, in the sense that the size of the left fusiform gyrus at grade 2 will predict the size of the left fusiform gyrus at grade 5, and that reading skills at grade 2 will predict reading skills at grade 5.



## Fig 1 Hypothetical cross-lagged panel model

[Insert Fig 1]

**Fig 1** shows our hypothetical cross-lagged panel model (CLPM). Cross-lagged predictive relations between the size of the left fusiform gyrus and reading skills (word and pseudo-word standardized reading tests) are investigated in early stage readers (grade 2) and advanced readers (grade 5) with a wide range of reading skills. Single-headed arrows represent regressions and double-headed arrows covariations between the variables. Covariations were constrained to equality (“).

## Method

### *Participants*

The study contained 43 Flemish children (29M, 14F) with a wide range of reading scores (word reading 2<sup>nd</sup> grade:  $M = 100.83$ ;  $SD = 15.54$ ;  $CI [70, 135]$ , pseudo-word reading 2<sup>nd</sup> grade:  $M = 95.83$ ;  $SD = 14.77$ ;  $CI [70, 135]$ , word reading 5<sup>th</sup> grade:  $M = 85.35$ ;  $SD = 20.25$ ;  $CI [55, 125]$ , pseudo-word reading 5<sup>th</sup> grade:  $M = 92.38$ ;  $SD = 16.64$ ;  $CI [55, 120]$ , of which 16 children with (DR) and 27 children without (TR) a dyslexia classification (see Beelen et al., 2019). The study sample is part of a large longitudinal project (DYSCO) in which participants were followed-up from kindergarten until grade 5 of primary school. In this period participants underwent cognitive-behavioral testing sessions once a year, and EEG and MRI scanning sessions once every two years alternately.

In the current study, MRI data of grade 2 and grade 5 of primary school were included. MRI data acquired in kindergarten were not taken into account due to absence of concurrent reading data. During the MRI session at the end of grade 2 of primary school 65 participants were scanned ( $M = 95.4$  months;  $SD = 3.1$  months). As a result of excessive motion in the scanner, 17 participants were excluded from the study. Images of excluded participants had severe blurring, ringing or ghosting artifacts according to the Blumenthal criteria (Blumenthal et al., 2002; Vân Phan et al., 2018) and were unusable for analyses purposes. Images of remaining participants showed none, mild or moderate ringing, blurring or ghosting artifacts. During the MRI session at the middle of grade 5 of primary school ( $M = 127.6$  months;

SD = 3.3 months) 63 participants were scanned. No participants were excluded from the study due to excessive motion in the scanner; none of the images showed severe blurring, ringing or ghosting artifacts. From all participants with no severe imaging artifacts (48 in grade 2 and 63 in grade 5), 43 participated in both the MRI session of grade 2 and grade 5, and were included in our study. In addition, reading data, i.e. a standardized one-minute word reading test, 'EMT' (Brus & Voeten, 1973), and a two-minute pseudo-word reading test, 'de Klepel' (Van den Bos et al., 1994), obtained from these 43 participants at the beginning of grade 2 ( $M = 86.2$  months;  $SD = 3.3$  months;  $CI [80, 92 \text{ months}]$ ) and at the middle of grade 5 ( $M = 127.8$  months;  $SD = 3.2$  months;  $CI [122, 134 \text{ months}]$ ), were included in the current study. The study was not pre-registered. Approval was given by the ethical research committee of the local university hospital of Leuven (KU/UZ Leuven), Belgium. The study is in accordance with ethical standards described within the declaration of Helsinki. Informed consent had been obtained from the parents.

### *Image Acquisition*

Participants were scanned at the local university hospital of Leuven (KU/UZ Leuven), Belgium. For each MRI session, T1-weighted images were acquired within 6 min. and 22 sec. During both MRI sessions, the same Philips 3T-scanner (Best, The Netherlands) with 3D Turbo field echo and a 32-channel head coil was used. In addition, applying the following parameter settings:  $TR = 9.6 \text{ ms}$ ;  $TE = 4.6 \text{ ms}$ ; flip angle =  $8^\circ$ ;  $FOV = 250 \times 250 \times 218 \text{ mm}^3$ ; voxel size =  $1 \times 1 \times 1.2 \text{ mm}^3$ , per participant 182 contiguous coronal slices were collected at both scanning sessions. The period between the MRI session of grade 2 and grade 5 was about 2.5 years ( $M = 32.4$  months;  $SD = 1.0$  months;  $CI [30, 34 \text{ months}]$ ).

### *Image Processing*

T1-weighted images acquired in the MRI scanning session of grade 2 and grade 5 were automatically processed by the cross-sectional reconstruction processing stream of FreeSurfer, version 5.3, which was installed on a Linux Ubuntu software system, version 14.02. In our former study (Beelen et al., 2020), it has been shown that the automatically Freesurfer processed data does not necessarily has to undergo further manual edits. Therefore, the fully automatically processed data (i.e. without additional manual editing) were included in the current study. The processing steps of the cross-sectional reconstruction processing stream contained skull stripping by a hybrid watershed/surface deformation procedure (Ségonne et al., 2004), motion and b1-bias field correction, white matter segmentation (Fischl et al., 2002, 2004), intensity normalization (Sled et al., 1998), gray/white matter boundary tessellation, automated topological correction (Fischl et al., 2001; Ségonne et al., 2007) and surface deformation (Dale et al., 1999; Dale & Sereno, 1993; Fischl & Dale, 2000). Additionally, the Desikan-Killiany atlas was implemented, automatically subdividing the inflated brain images into 34 gyral regions-of-interest (Desikan et al., 2006; see also Beelen et al., 2019, 2020). For the current study, the left fusiform gyrus was selected from the Desikan-Killiany atlas, since in this region morphological differences have been observed between children with poor and strong reading skills (Beelen et al., 2019) and the current study is based on nearly the same sample.

### *Statistical Analyses*

Statistical analyses were performed in IBM SPSS, version 26.0 (IBM corp. 2019), R version 3.6.3 (RCore Team, 2020) and RStudio version 1.2.5033 (RStudio Team, 2020). First, bivariate correlations between all variables were calculated. Second, a cross-lagged panel model (CLPM) analysis was performed. In the CLPM, the first time point refers to MRI data and behavioral reading data obtained in grade 2 and the second time point refers to MRI data and behavioral reading data obtained in grade 5. Additionally, MRI data correspond to the

surface area of the left fusiform gyrus, and behavioral reading data correspond to an average score of the Dutch standardized one-minute word reading task ‘EMT’ (Brus & Voeten, 1973) and the Dutch standardized two-minutes pseudo-word reading task ‘de Klepel’ (Van den Bos et al., 1994) (see Figure 1). Furthermore, in the CLPM goodness-of-fit indices are chi-square ( $\chi^2$ ), comparative fit index (CFI), Tucker-Lewis index (TLI), root mean square error of approximation (RMSEA) and the standardized root mean square residual (SRMR). Models with chi-square being non-significant (i.e. testing the null hypothesis that the suggested model matches the actual data) indicate a good model fit. In addition, models with TLI and CFI values  $> .95$  indicate a good model fit and  $> .90$  an acceptable model fit, and models with RMSEA and SRMR values  $< .05$  indicate a good model fit and  $< .08$  an acceptable model fit (Hu & Bentler, 1999). The proposed model will be evaluated and results of within-variable predictive relations will be presented, followed by results of cross-lagged predictive relations between the variables. Note that concurrent correlations are expected to remain stable over time and are therefore constrained to equality. The equality constraint helps to reduce the total number of parameters that need to be estimated by the model, making the model more parsimonious (Cole & Maxwell, 2003).

## Results

With regard to bivariate correlations, there is a strong, highly significant correlation between the same variables at both time points: for the size of the left fusiform gyrus:  $r = .72$ ;  $p < .001$ , and for reading skills:  $r = .80$ ;  $p < .001$ . Furthermore, concurrent correlations indicated that at grade 2 there was a non-significant correlation between the size of the left fusiform gyrus and reading skills ( $r = .20$ ;  $p = .202$ ), and at grade 5 there was a significant correlation between the size of the left fusiform gyrus and reading skills ( $r = .38$ ;  $p = .014$ ). Finally, the size of the left fusiform gyrus at grade 2 and reading skills at grade 5 showed a weak, non-significant correlation:  $r = .23$ ;  $p = .164$ , and reading skills at grade 2 and the size

of the left fusiform gyrus at grade 5 showed a moderate, significant correlation:  $r = .44$ ;  $p = .003$  (see figures 2a and 2b). Results of all bivariate correlations are presented in figure 3a.

With regard to the crossed-lagged panel model (CLPM) analyses, the CLPM model that was tested revealed:  $\chi^2(1, N = 43) = 1.34$ ,  $p = 0.248$ ; RMSEA = 0.093, 90% CI (<0.001, 0.45),  $p = 0.270$ ; CFI = .995 ; TLI = .972; SRMR = 0.085. The values of Chi-square, CFI and TLI indicate a good model fit, whereas the values of the RMSEA and the SRMR are slightly below an acceptable model fit. However, RMSEA can incorrectly indicate a poor model fit if the sample size is small ( $N < 100$ ) and the degrees of freedom are low (Kenny et al., 2015). The cross-lagged predictive relations indicate that reading skills at grade 2 predict the size of the left fusiform gyrus at grade 5:  $\beta = 12.6$ ,  $SE = 4.1$ ;  $Z = 3.1$ ;  $p = .002$ . Hence, reading ability in grade 2 influences the size of the left fusiform gyrus in grade 5, with better reading skills scaling up with larger left fusiform size. Contrary, the size of the left fusiform gyrus at grade 2 does not predict reading skills at grade 5:  $\beta = .001$ ,  $SE = .003$ ;  $Z = .5$ ;  $p = .596$ . Results of the CLPM are presented in figure 3b.

#### **Fig 2a Bivariate correlation between the left fusiform (grade 2) and reading (grade 5)**

**[Insert Fig 2a]**

**Fig 2a** shows the bivariate correlation between the sizes of the left fusiform gyrus (grade 2) and the reading composite scores (grade 5).

#### **Fig 2b Bivariate correlation between reading (grade 2) and the left fusiform (grade 5)**

**[Insert Fig 2b]**

**Fig 2b** shows the bivariate correlation between the reading composite scores (grade 2) and the sizes of the left fusiform gyrus (grade 5).

#### **Fig 3a Bivariate correlations between the variables**

**[Insert Fig 3a]**

**Fig 3a** shows the bivariate correlations between the variables. \*  $p < .05$ ; \*\*  $p < .01$ ; \*\*\*  $p < .001$ .

### **Fig 3b Cross-lagged regressions in the CLPM**

[Insert Fig 3b]

**Fig 3b** shows the outcomes of the cross-lagged regressions in the CLPM.  $\beta$ -coefficients and their standard errors (between brackets) are presented. \*  $p < .05$ ; \*\*  $p < .01$ ; \*\*\*  $p < .001$ . A solid line indicates a significant relation and a dashed line a non-significant relation between the variables. Single-headed arrows represent regressions and double-headed arrows covariations between the variables. The concurrent covariations were constrained to equality (“).

## **Discussion**

In the current study, interrelations between the size of the left fusiform gyrus and reading skills (a composite score of a standardized word and pseudo-word reading task) were investigated in a longitudinal cohort of children with a variety of poor to strong skills, assessed in grade 2 (the early stage of reading) and grade 5 (the advanced stage of reading) of primary school. Specifically, it was examined whether we could observe directional effects between the size of the left fusiform gyrus and reading skills at two different time points. Results of bivariate correlations revealed that the size of the left fusiform gyrus and reading skills both show a high association over time, suggesting longitudinal stability. In addition, there is an association between the size of the left fusiform gyrus and reading skills at grade 5, and between reading skills at grade 2 and the size of the left fusiform gyrus at grade 5. With regards to the directional effects, results of the CLPM-analysis revealed that better reading skills at grade 2 lead to a larger size of the left fusiform gyrus at grade 5, whereas directional effects between the size of the left fusiform gyrus at grade 2 and reading skills at grade 5 were not observed. Hence, between grade 2 and grade 5 there is behavior-driven brain plasticity, but we could not observe a brain-driven reading behavior change.

The main outcome of our study is that better reading skills at the early reading stage (e.g. grade 2) lead to a larger size of the left fusiform gyrus at the advanced reading stage (e.g. grade 5). Bivariate correlations showed that there is a significant association between reading skills at grade 2 and the size of the left fusiform gyrus at grade 5, and the CLPM analyses demonstrated the directionality, namely that early reading skills are impacting the size of the fusiform at a later stage. Our prior study (Beelen et al., 2019) revealed that pre-readers with a retrospective classification of dyslexia (as determined from reading measures obtained at the early-to-advanced reading stage) have a smaller left fusiform gyrus in their pre-reading stage. The smaller fusiform gyrus cannot be a consequence of poor reading skills, since pre-readers have no reading experience yet. Therefore, during the pre-reading stage, the size of the left fusiform gyrus influences later reading skills. The current study, consisting of largely the same sample, reveals that the direction of influence switches at the early stage of reading development, since results indicate that reading skills in grade 2 determine the size of the left fusiform in grade 5. At the cognitive level, reading development shows a similar kind of reciprocal relation, in which phonological awareness predicts later reading achievement pre-reading, and reading skills influence the development of phonological awareness after reading onset (Hogan et al., 2005).

A dynamic interplay between reading skills and the structure of the left fusiform gyrus is supported by the interaction specialization theory, which states that cortical functions develop and specialize through continuous dynamic interactions between genetics, the brain, the body and the environment (Johnson, 2001, 2011). The outcome of our MRI study is also congruent with the recent observation that behavioral-induced neuronal recycling of the left fusiform gyrus shapes the development of the VWFA (Dehaene-Lambertz et al., 2018). Neuronal recycling has often been indicated by functional studies, but is now supported by our structural MRI study. Throughout the first two decades of human development, changes in brain volume

are non-linear; cortical and sub-cortical gray matter volume change according to an inverted U-shape, peaking in adolescence (Lenroot & Giedd, 2006; Tanaka et al., 2012). According to a longitudinal fMRI study of Ben-Shachar et al. (2011), there is an increase in grey matter volume in the posterior left occipital temporal sulcus (nearby the anatomical location of the VWFA) from the age of 7 up until the age of 9, which levels off at the age of 10 to 12, followed by a decrease at the age of 13 to 15, in which time period grey matter volume in the left occipital temporal sulcus reaches adulthood level. In similar vein, EEG/ERP studies revealed that the N1-potential has its peak between grade 2 and grade 5 (e.g. between 8-11 years), and decreases thereafter (Brem et al., 2013; Maurer et al., 2006, 2007, 2011). Results of our MRI study and these studies (Ben-Shachar et al., 2011; Brem et al., 2013; Maurer et al., 2006, 2007, 2011) suggest that acquiring reading skills causes an increase in gray matter volume, which decreases again as soon as sufficient reading skills have been obtained.

The outcome of our study contradicts Preston et al. (2016), who reported in their longitudinal fMRI study that print-speech co-activation in the reading network (encompassing the fusiform gyrus) of beginning to advanced (e.g. 6 to 10 years old) readers predicts their reading achievement two years later. However, Preston et al. (2016) performed an fMRI study, whereas our study was an MRI study. According to few studies, functional activation is preceded by structural connectivity (Saygin et al., 2016; Osher et al., 2016; Ekstrand et al., 2020). Hence, functional and structural plasticity processes may not happen simultaneously, and reading skills may predict the function (e.g. activation) of the left fusiform gyrus at a later reading stage than the structure (e.g. size) of the left fusiform gyrus, i.e. at the advanced instead of the early reading stage.

Another observation in our study is that both the size of the left fusiform gyrus and the reading skills show a high association over time, which suggests that they are stable over time. Several studies reported that typical and poor readers show longitudinal stability in reading



across primary and high school (Juel, 1988; Ferrer et al., 2015; Kwiatkowska-White et al., 2015). Poor reading performance, however, can mostly be changed through intervention throughout primary and high school (Scammacca et al., 2016), including in young children at risk for reading difficulties (Simmons et al., 2008; Cavanaugh et al., 2004; O'Connor et al., 2005; Scanlon et al., 2005). Simmons et al. (2008) revealed in their behavioral study on kindergartners, which were followed up from grade 1 until grade 3, that intervention in at-risk children works effectively in the majority of cases. Additionally, a meta-analysis of Wanzek & Vaughn (2007) comparing large intervention studies performed in kindergarten and the first few grades of primary school, revealed that interventions performed in kindergarten or grade 1 have higher effect sizes than interventions performed in grade 2 or grade 3. In that perspective, early (e.g. at the pre-to-early reading stage) intervention might be most effective. In addition, our results might support early intervention, since in our study it is shown that having better reading scores by grade 2 is a determinant for later structural development of the fusiform. Training reading skills at the pre-to-early reading stage could lead to a more regular development of the left fusiform gyrus. Improving the reading level at a later stage of reading than in grade 2, the typical intervention window in clinical practice, might be too late to have a direct effect on brain development in the fusiform gyrus, as suggested by our study, although further investigation will be necessary. Another observation of our study is that concurrent correlations are non-significant at grade 2, and significant at grade 5. The data obtained in grade 5 might be a bit more reliable than the data obtained in grade 2, since participants were more familiar with the testing procedure, both regarding the MRI session and the reading tasks, and showed less head motion in the MRI (although it should be mentioned that participants with excessive head motion had been excluded from the analysis).

A limitation to our study is that the sample size is small ( $N = 43$ ), since not all participants of the original sample underwent an MRI at both time points, which was an

inclusion criteria of our study. Another limitation of our study is that the classical CLPM-analysis is not capable of fully separating between-persons from within-person effects. The classical CLPM-analysis may reflect either one of them, or both, to a certain extent, and it is very difficult to unravel which observed effects reflect within-person changes or between-persons differences (Berry & Willoughby, 2016). Furthermore, it should be noted that we have not gathered data yet on how advanced reading skills influence the size of the fusiform gyrus beyond grade 5 of primary school.

Altogether, results indicate that reading skills at the early stage of reading impact the size of the left fusiform gyrus at the advanced stage of reading, whereas the size of the left fusiform gyrus at the early stage of reading does not influence reading skills at the advanced stage of reading. The outcome is in accordance with behavior-driven brain plasticity at the early-to-advanced reading stage.

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## Figures

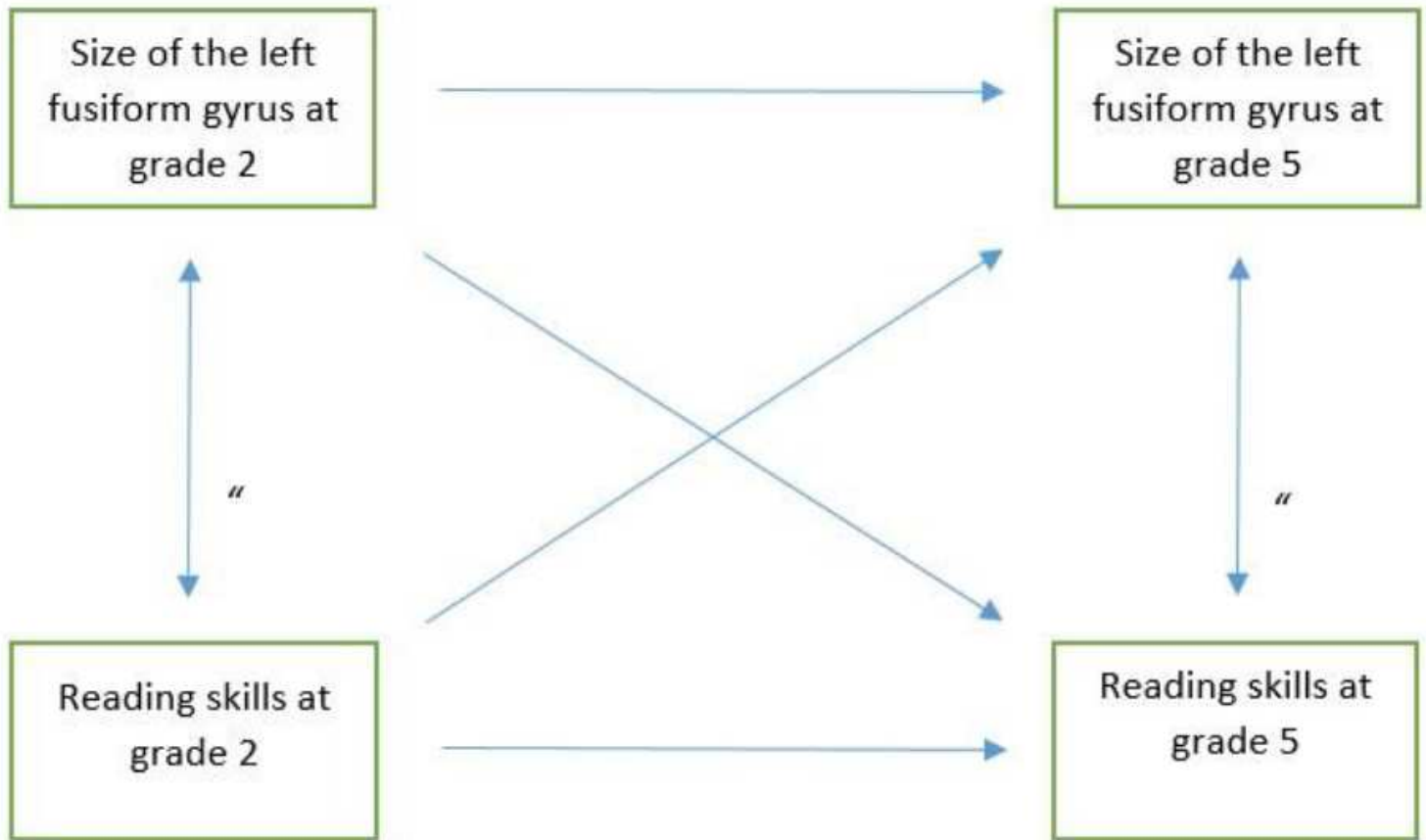


Figure 1

Hypothetical cross-lagged panel model





**Figure 2**

a Bivariate correlation between the left fusiform (grade 2) and reading (grade 5) b Bivariate correlation between reading (grade 2) and the left fusiform (grade 5)

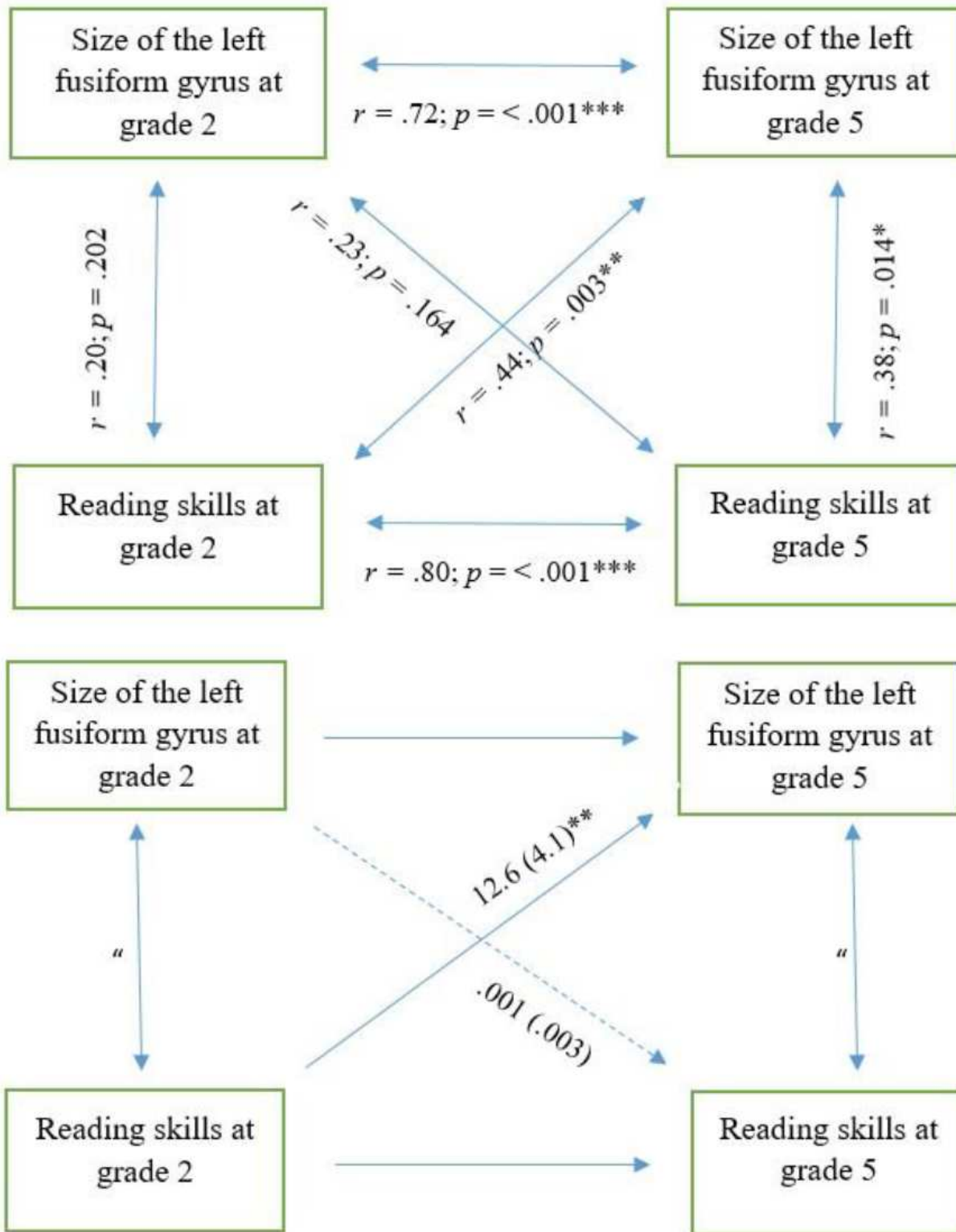


Figure 3

a Bivariate correlations between the variables b Cross-lagged regressions in the CLPM