Laterality for Reading and Face Recognition in the Fusiform Gyrus covaries with Language Dominance

Authors: Robin Gerrits[1,2*], Lise van der Haegen[1], Marc Brysbaert[1,2], Guy Vingerhoets[1,2]

Affiliations:

1. Department of Experimental Psychology, Ghent University, Belgium

2. Ghent Institute for functional and Metabolic Imaging (GIfMI), Ghent University, Belgium

*Corresponding author: Robin Gerrits, Department of Experimental Psychology, Henri Dunantlaan 2, B-9000, Ghent, Belgium, e-mail: robin.gerrits@ugent.be

Abstract

Recognizing words and faces engages highly specialized sites within the middle fusiform gyrus, known as the visual word form area (VWFA) and fusiform face area (FFA) respectively. The VWFA and FFA have clear but opposite population-level asymmetries, with the VWFA typically being lateralized to the left and the FFA to the right hemisphere. The present study investigates how language dominance may relate to these asymmetries. We hypothesize that individuals with left hemisphere dominance for word production (i.e. left language dominance, LLD) will have typical lateralization for reading and faces in the fusiform gyrus, whereas participants with right language dominance (RLD) will demonstrate 'atypical' rightward laterality for words and leftward dominance for faces. To test this hypothesis, we recruited twenty-seven left-handers who had previously been identified as being LLD or RLD based on a visual half field task. Using fMRI, hemisphere dominance was determined for language (Broca's region) as well as for reading and face recognition in the middle fusiform gyrus for each participant. The direction of asymmetry correlated significantly between language and reading ($\rho = 0.648$, $p < 0.001$) as well as between language and face recognition ($\rho = -0.620$, $p = 0.001$). Moreover, most LLD-participants were typically lateralized for faces and word recognition, while both functions tended to be reversed in individuals with RLD. Segregation between language and face recognition was less clear in participants with RLD, as many of them lacked an obvious asymmetry for faces. Although our results thus suggest there is no one-on-one relationship between asymmetries for language, reading and face recognition, they also argue against a complete independence of their lateralization. Colateralization between language and reading might follow from an effort to optimize connectivity between reading-specific and general language regions, while segregation between face recognition and language might result from pressure to establish an optimal functional segregation pattern and/or from competition for neural resources between written words and faces. The high rates of unclear FFA asymmetry in RLD might indicate resistance against hemisphere reversal for face recognition - working against a potential pressure to maintain functional segregation - or reflect differences in strategies to process faces between individuals with LLD and RLD.

Keywords:

Lateralization - brain asymmetry - language dominance – reading - face recognition

Abbreviations

FFA	Fusiform face area
LI	Laterality index
LHD	Left hemisphere dominant

LLD	Left language dominant
MFG	Middle fusiform gyrus
RHD	Right hemisphere dominant
RLD	Right language dominant
VWFA	Visual word form area

1. Introduction

At first glance, reading and recognizing faces seem to have little in common. Not only are written words and faces characterized by different perceptual features, these abilities also differ in their ontogenetic and phylogenetic developmental trajectories (Plaut & Behrmann, 2011). While face recognition relies on innate predispositions already present in newborns and is spontaneously shaped further by experience later in life (Simion & Di Giorgio, 2015), reading is acquired at a later age and requires explicit instruction and effortful learning to master. Moreover, whereas written language emerged only about 5000 years ago and the transition to widespread literacy happened only recently, face recognition arose much earlier in human evolution (Parr, 2011). Despite these differences, the neural implementation of recognizing symbols (reading) and recognizing faces is remarkably similar, as both engage a broad bilateral but relatively lateralized network with critical nodes located within the middle fusiform gyrus (MFG) (Davies-Thompson, Johnston, Tashakkor, Pancarogly, & Barton, 2016). Recognizing visual words recruits a part of the MFG known as the Visual Word Form Area (VWFA), which is characterized by a strong degree of functional specificity, preferentially processing orthographic strings compared to any other category of visual information (Dehaene & Cohen, 2011). Face recognition on the other hand involves another sub-region of the MFG nearby the VWFA dubbed the Fusiform Face Area (FFA). Like the VWFA, the FFA is highly specialized as it responds more strongly to faces relative to other types of visual stimuli (Kanwisher & Yovel, 2006).

Another striking similarity between recognizing written words and faces is that they have a clear, but opposite, hemisphere asymmetry, with written words typically lateralizing to the left and faces to the right hemisphere (Davies-Thompson, et al., 2016). Neuropsychological observations provide the most compelling evidence for such an asymmetry. Whereas isolated left hemisphere damage suffices to cause specific reading impairment (i.e. alexia) (Starrfelt & Shallice, 2014), specific face recognition deficits (i.e. prosopagnosia) occur following bilateral or right hemisphere damage (Barton, Press, Keenan, & O'Conner, 2002; Sorger, Goebel, Schiltz, & Rossion, 2007). A recent review concluded that there exists a dissociation between reading and face recognition impairments, although the evidence is more convincing of preserved reading in acquired and developmental prosopagnosia than of intact face recognition in acquired or developmental alexia (Robotham & Starrfelt, 2017). In line with the lesion data, neuroimaging and electrophysiological studies typically find that reading tasks elicit stronger activity within left hemisphere regions, including the VWFA (Cohen, et al., 2000; Rossion, Joyce, Cottrell, & Tarr, 2003; Mercure & Cohen Kadosh, 2011; Szwed, et al., 2011), while faces usually evoke stronger activation in the right hemisphere, including in the right FFA (Rossion, Joyce, Cottrell, & Tarr, 2003; Kanwisher & Yovel, 2006).

Given its late emergence in human evolution and reliance on explicit instruction to acquire, it seems unlikely that the brain has evolved a specific neural system dedicated to reading (Ventura, 2014). Instead, the neuronal recycling hypothesis proposes that, owning to its reliance on finely detailed visual analyses, reading acquisition may recruit neurons within the MFG previously devoted to other tasks, giving rise to the VWFA (Dehaene, 2005; Dehaene & Cohen, 2007). As asymmetry of the VWFA similarly cannot be taken as the outcome of an innate lateralizing bias, it may rather follow from pressure to optimize connectivity with the oral language network (Plaut & Behrmann, 2011), whose establishment and lateralization predates that of reading phylogenetically and ontogenetically (Dubois, et al., 2009; Vannasing, Florea, González-Frankenberger, Tremblay, & Paquette, 2016). Some of the most crucial evidence for this account of reading laterality is provided by studies on rare individuals with right hemisphere language dominance (RLD) (Cai, Paulignan, Brysbaert, Ibarrola, & Nazir, 2010; Van der Haegen, Cai, & Brysbaert, 2012). These studies revealed a consistent colateralization between verbal fluency measured in Broca's region and reading measured in the MFG, showing that individuals with RLD also had a strong tendency towards right hemisphere dominance for reading.

If reading is dominant in the right MFG, e.g. as a consequence of RLD, one may wonder what happens to asymmetry for face recognition given that word and face representations occupy quasi- homologues regions within the MFG. While this has hitherto not been directly tested, several studies in left-handers, who are more likely to be RLD than right-handers, indicate that dominance within the FFA might covary with language dominance. Compared to dextrals, left-handers tend to activate the FFA more bilaterally during face processing, which might reflect higher rates of left hemisphere FFA dominance, particularly in left-handers with RLD (Willems, Peelen, & Hagoort, 2007; Badzakova-Trajkov, Haberling, Roberts, & Corballis, 2010; Dundas, Plaut, & Behrmann, 2015; Frässle, Krach, Paulus, & Jansen, 2016). To further investigate the relationship between the asymmetries for language, reading and face recognition in a more direct way, the present study adopts a methodology similar to Van der Haegen, et al. (2012), by determining laterality for both reading and face recognition within the MFG of individuals with left language dominance (LLD) or RLD. We specifically hypothesize that participants with LLD have a leftward dominance for written words and a rightward dominance for faces. Based on previous studies in individuals with RLD which showed that they tended to be atypically lateralized for other functions as well (Cai, Van der Haegen, & Brysbaert, 2013; Vingerhoets, et al., 2013), we expect that participants with RLD will be right hemisphere dominant for reading and left hemisphere dominant for face recognition. In addition, we will explore any associations in the strength of lateralization between language, face recognition, and reading.

2. Methods

2.1. Participants

Participant recruitment was restricted to left-handers, as they have significantly higher rates of RLD compared to right-handers (± 7 to 27% in left-handers vs. ± 4% in right-handers) (Knecht, et al., 2000; Mazoyer, et al., 2014). Most participants were recruited from previous large-scale behavioral studies in left-handers (Van der Haegen, Cai, Seurinck, & Brysbaert, 2011; Van der Haegen & Brysbaert, submitted). Specifically, inclusion in the present study was based on their performance on a word and picture visual half field (VHF) task. Briefly, during these VHF tasks, pictures or words were presented either to the left or the right field. Participants were instructed to name out loud the target as quickly and accurately as possible. Language dominance can then be determined using the between-field difference in verbal reaction time. As stimuli presented in the left visual field (LVF) arrive first in the right hemisphere, and vice versa, shorter reaction times to targets in the LVF are indicative of RLD, whereas better performance on targets in the RVF is suggestive of LLD. All participants with an LVF reaction time advantage were invited to participate in the current study to increase the probability of including a sizeable number of individuals with RLD. Doing so, a total of 27 left-handers were included in the present study (17 females, 10 males; age range = 20 to 39 years with mean age = 26.1 years). All participants were receiving or completed higher education, were native Dutch speaking and had normal or corrected-to-normal vision. A priori written informed consent was obtained from each participant in accordance with the guidelines of the Ethics Committee of the Ghent University Hospital.

2.2. MRI data acquisition

The results reported in the present study are based on a bigger study on object recognition. All participants completed the following MRI protocol consisting of a T1-weighted anatomical scan and 3 functional paradigms: a verbal fluency task, a localizer task probing visual and auditory object recognition and a spatial frequency task. The latter two tasks were divided in 2 runs and were alternated with each other following the word generation task.

All MRI data were collected on a 3-T Siemens Trio scanner (Siemens Medical Systems, Erlangen, Germany) with a 32-channel head coil. A high-resolution anatomical image of the whole brain was obtained using a T1-weighted MPRAGE sequence [TR/TE = 2250/4.18 ms, matrix size = 256 x 256, flip angle = 9°, isotropic voxel size=1mm. Functional images were acquired using a T2*-weighted multi-band EPI sequence with TR/TE = 1500/30.8 ms, matrix size = 128 x 128, FOV = 192, flip angle = 90° and voxel size of 1.5 x 1.5 x 2.5 mm. A total of 271 and 561 volumes were collected for the word generation and visual localizer task respectively. During functional imaging, stimuli were projected onto a translucent screen at the back of the magnet bore, which participants viewed via a mirror attached to the head coil.

2.3. Tasks

All tasks were programmed and administered using Presentation (NeuroBehavioral Systems, CA, USA).

2.2.1. Letter verbal fluency task

Dominance for word production - hence referred to as language dominance - was determined using a letter verbal fluency task adapted from previous studies (Van der Haegen, et al., 2011; Van der Haegen, et al., 2012). Participants were asked to covertly generate as many words as possible starting with a letter presented in the center of the screen. Eight letters were selected based on a pre-test with Flemish-Dutch participants to exclude letters for which only a few words could be produced and included *b,d,k,m,p,r,s* and *t*. In the control task, the meaningless but pronounceable letter string 'baba' was presented in the middle of the screen and participants were instructed to silently repeat this non-word until it disappeared. Including this control task allowed to subtract activity associated with covert articulation and orthographic processing. Task and control blocks were separated by rest blocks during which participants passively viewed a short line displayed on the screen. Each block lasted 12s and was repeated eight times, resulting in a total acquisition time of 6m24s. All stimuli were presented in white on a black background. The trial structure is visualized by Figure 1A.

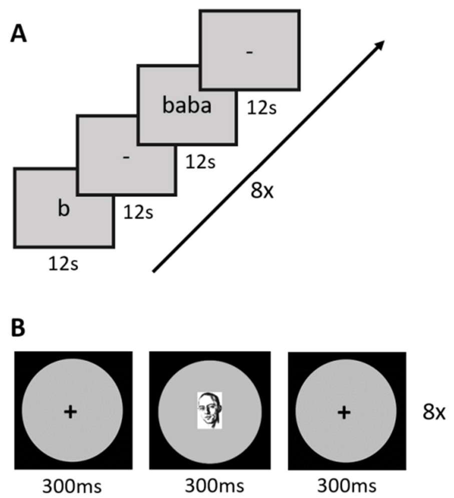

Figure 1: Trial structure of the word generation task (A) and visual localizer task (B).

2.2.2. Visual localizer task

Laterality for reading and face recognition was determined using a perceptual matching task (one-back task) administered as part of a bigger study on visual and auditory recognition. This task has been used previously to investigate object recognition (e.g.: Amalric & Stanislas, 2016). Participants were instructed to press a response button each time the same stimulus was displayed twice in a row. Stimuli belonged to one out of ten categories, including written words, faces, numbers, equations, houses, tools, bodies, checker boards, auditory words and auditory noise. All visual stimuli were static grey scale pictures presented in the middle of the screen in a grey disk on a black background. Twelve different stimuli were created for each category. Written words were existing Dutch nouns (7/12) or verbs (5/12) consisting of six letters of which half were presented in full upper case and the remaining half in full lower case. All faces were cropped to display only the neck and head, were forward-facing or slightly lateral facing and were balanced for gender.

A block design was used for this task, with each block consisting of eight randomly chosen stimuli belonging to the same stimulus category. Stimuli were presented for 300ms following a black fixation cross displayed for 300ms in a grey disc on a black background. The trial structure and a sample stimulus are shown in Figure 1B. The inter-block interval was determined at random and could last either 2.4s, 3.6s or 4.8s. After every ten blocks, a 10-second rest period was presented. The task was split up in two runs of about 7 minutes, each consisting of 4 blocks per stimulus category, which yielded a total of 8 blocks per category.

2.4. fMRI data analysis

fMRI data analysis was performed with SPM12 (Wellcome Trust Centre for Neuroimaging, London, UK) implemented in Matlab2016b (MathWorks, Massachusetts, USA). The first five volumes of each participant were discarded to obtain magnetic saturation. Subsequent preprocessing consisted of (1) motion correction by ridged realignment; (2) coregistration of the functional images to the participant’s anatomical image using the mean functional image; (3) normalization to the ICBM European brains T1 template in MNI space; and (4) spatial smoothing using a Gaussian kernel with a full width at half maximum of 3 mm. In order to further optimize data quality, outlier volumes were detected and repaired using the toolbox ArtRepair, version 5b (Mazaika, Hoeft, Glover, & Reiss, 2009). This toolbox identifies volumes which deviate strongly from the average global image intensity (threshold: 1.3%) or have excessive scan-to-scan motion (threshold: 0.5mm/TR) and subsequently repairs them by means of linear interpolation from the nearest non-outlier scans.

Next, first-level analyses were conducted with each participant’s preprocessed volumes. Experimental conditions were modeled by convolving the canonical hemodynamic response function (Friston, Jezzard, & Turner, 1994) with a boxcar function. Six estimated head motion parameters were included as nuisance variables in the general linear model. An autoregressive AR(1) model was applied during the parameter estimation to account for serial correlations in the functional time series. For each task, contrasts of interest were obtained by comparing task-related activity against activation in a control condition: word generation>repeating baba (language), written words vs all other visual categories (orthography) and faces vs all other visual categories (face recognition).

LI’s were computed for each participant following a region of interest (ROI) based approach. For the word generation task, the ROI consisted of the pars opercularis (Brodmann area 44) and pars triangularis (Brodmann area 45) in the AAL template (Tzourio-Mazoyer, et al., 2002). Laterality for the two remaining functions was determined using an MFG mask, adapted from Van der Haegen, et al. (2012), which encompasses the middle-posterior fusiform gyrus. By assessing laterality for written word and face recognition in a relatively large part of the fusiform gyrus, the inter-individual variability in the localization of the VWFA and FFA is accounted for (Glezer & Riesenhuber, 2013). LI's were calculated in an established multi-step procedure (Fernandez, et al., 2001; Jansen, et al., 2006). First, a threshold was determined by selecting voxels with activity stronger than the mean t-value of the 5% most active voxels/2 over the combined left and right ROI. Next, all voxels with t-values above this threshold were summed separately within the left and right ROI and used as input the calculate the LI:

$$LI = \frac{\text{Sum T values}_{\text{Left ROI}} - \text{Sum T values}_{\text{Right ROI}}}{\text{Sum T values}_{\text{Left ROI}} + \text{Sum T values}_{\text{Right ROI}}}$$

Positive LI's thus indicate relative leftward lateralization, whereas negative LI's are indicative of relative rightward lateralization.

2.5. Participant classification and statistical analysis

For each of the three lateralized functions measured, the participants were classified as left lateralized, right lateralized or bilateral by thresholding their LI with a cut-off of ±0.15. Associations between direction of asymmetry for language, reading and face recognition were investigated by computing correlations between their laterality indices. Next, the mean and distribution of the LI's for reading and face recognition were compared between left-handers with LLD and RLD. Finally, associations between the strength of laterality were assessed by computing correlations between the absolute values of the LI's. Assumptions of normality and homoscedasticity were checked based on visual inspection. All statistical analyses were performed in R, version 3.3.1 implemented in RStudio, version 1.1.453.

3. Results

3.1 Group level fMRI results

Participants were classified as being left lateralized, right lateralized or bilateral for language dominance by thresholding their LI's obtained from the word generation fMRI task. Doing so, we identified 12 participants with LLD (44.4%), 12 participants with RLD (44.4%) and 3 with bilateral activation (11.1%) for language. Figure 2 shows the activation maps for all three fMRI tasks separately for the LLD and RLD groups. Peak locations and coordinates of all three tasks can be found in the appendix (Table A1). Sites of peak activation in the word generation task included the insula, superior/inferior frontal gyrus, the superior/middle temporal gyrus and the cerebellum ($p = 0.01$, uncorrected, cluster size ≥ 40 voxels). The reading and face recognition tasks activated the fusiform gyrus and inferior/middle occipital gyrus among other sites (reading: $p = 0.02$, uncorrected, cluster size ≥ 40 voxels; face recognition: $p = 0.03$, uncorrected, cluster size ≥ 40 voxels).

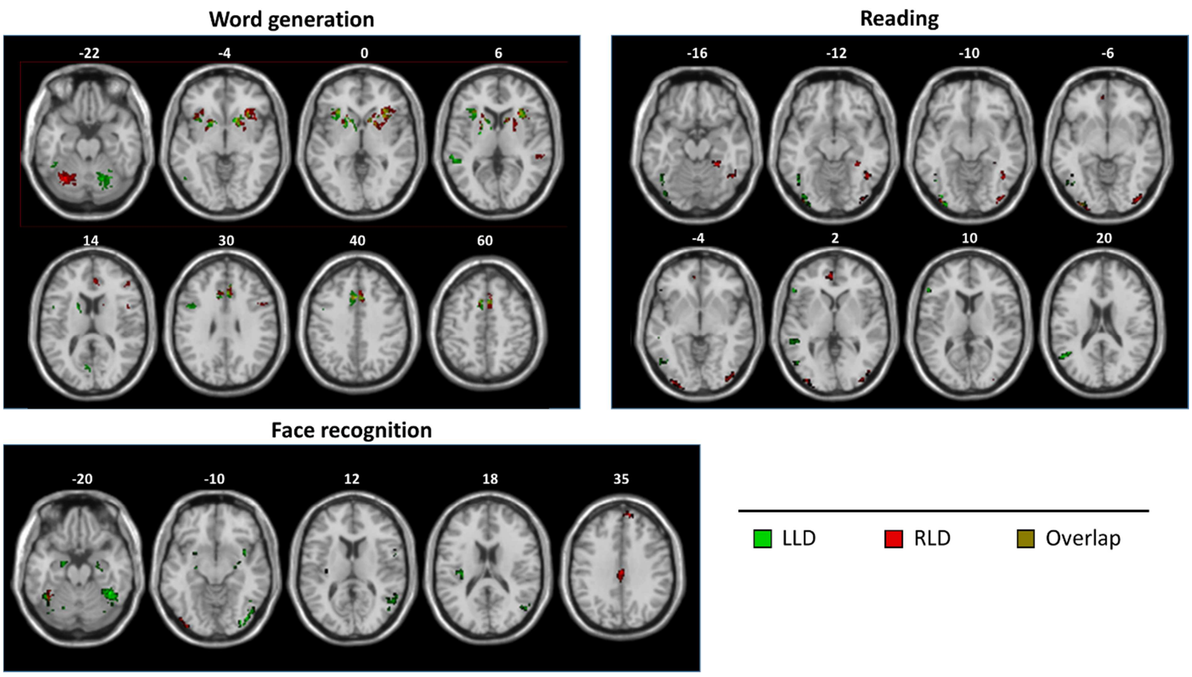

Figure 2: Group-level activation maps of the word generation, reading and face recognition task for the left (green, LLD) and right (red, RLD) language dominant participants. Overlapping activation between the participant groups is indicated in yellow. The z-coordinate is displayed above each slice.

3.2 Associations in direction of asymmetry

To assess relationships between asymmetries for language, reading and face recognition, first spearman rho correlations between the LI's were calculated. A significant positive correlation between language and reading ($\rho = 0.648$, $p < 0.001$) as well as a significant negative correlation between language and face recognition ($\rho = -0.620$, $p = 0.001$) was revealed. However, the correlation between reading and face recognition failed to reach significance ($\rho = -0.360$, $p = 0.065$). Repeating the analysis without participants with bilateral language dominance yielded similar results. Again, the correlations were significant for language and reading ($\rho = 0.655$, $p = 0.001$) as well as language and face recognition ($\rho = -0.641$, $p = 0.001$), but not for reading and face recognition ($\rho = -0.388$, $p = 0.061$).

Next, we split the participants in clearly LLD (N=12) and clearly RLD (N=12) sub-groups - thus omitting participants with bilateral dominance - and determined the distribution of the LI's for reading and face recognition in each group separately, as visualized by Figure 3. Mann-Whitney U tests revealed statistically significant between-group differences in the median LI of reading ($Median_{LLD}$=0.22, $Median_{RLD}$=-0.33, W=98, p=0.003) and face processing ($Median_{LLD}$=-0.30, $Median_{RLD}$=0.04, W=102, p=0.006).

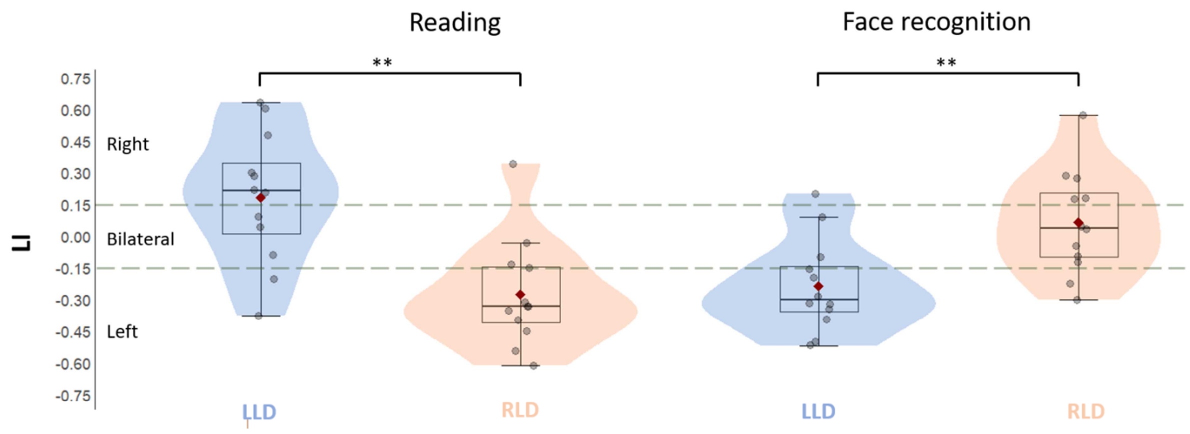

Figure 3: Raw Data, Descriptive and Inferential plots for reading and face recognition laterality in the LLD and RLD groups. The boxplot's bold lines and diamonds represent the median and mean LI respectively. Whiskers denote interquartile ranges. Within-group proportions of rightward, leftward and bilateral laterality are displayed in the left-hand side of the corresponding violin plot. Significance of the Mann-Whitney U test is indicated by asterisks (**: $p < 0.01$).

Finally, we determined the proportions of leftward lateralization, rightward lateralization and bilateral organization for reading and faces in LLD and RLD subgroups, as shown by Table 1. Using two-sided Fisher's exact tests, we revealed significant between-group differences in these proportions for both reading ($p = 0.022$) and face recognition ($p = 0.028$). To identify which cells contribute the most to these significant results standardized residuals were calculated. This follow-up residual analysis indicates that the effect for reading is equally due to a difference in the rates of left as right VWFA dominance between LLD and RLD participants. In line with our hypothesis, participants with LLD have higher rates of left and lower rates of right dominance for reading, while participants with RLD show the opposite pattern. No difference in the proportion of bilateral activity was found. For face recognition, the effect is predominantly driven by a difference in proportion of right FFA dominance, which is the most common direction of dominance in the LLD subgroup, but the least common in the participants with RLD. The latter subgroup demonstrates leftwards dominance and bilateral activation for faces more often than left-handers with LLD.

Table 1: Participant classification conditioned on direction of language dominance

	Reading			**Face recognition**		
	Left	*Bilateral*	*Right*	*Left*	*Bilateral*	*Right*
LLD (N = 12)	58% (7)	25% (4)	8% (1)	8% (1)	17% (2)	75% (9)
	2.6	*0*	*-2.5*	*-1.9*	*-1.3*	*2.9*
RLD (N = 12)	17% (2)	25% (4)	67 (8)	42% (5)	42% (5)	17% (2)
	-2.6	*0*	*2.5*	*1.9*	*1.3*	*-2.9*

Percentage (number) and *adjusted residuals* of participants showing left hemisphere (LHD), right hemispheric (RHD) or bilateral dominance for written word recognition task (Reading) and face recognition task (Faces) within the left language dominant (LLD) and right language dominant (RLD) subgroups.

Similar results were obtained when the analysis was repeated omitting participants with bilateral dominance for reading or face recognition (Reading: $p = 0.015$; Face recognition: $p = 0.035$). In both groups, we observed crossed dominance between word generation and reading (LLD: 2/12; RLD: 1/12) as well as hemisphere crowding of word generation and face recognition (LLD: 1/12; RLD: 2/12).

3.3 Associations in strength of laterality

In addition to direction of laterality, we explored potential effects of strength of laterality, defined as the absolute value of the LI. To assess whether language, reading, and face recognition were associated in terms of strength of laterality, spearman Rho correlations were computed based on the whole sample. A statistically significant positive correlation was found between strength of laterality between language and reading ($\rho = 0.58$, $p = 0.001$). None of the other correlations reached statistical significance (language and face recognition: $\rho = 0.17$, $p = 0.406$; reading and face recognition: $\rho = 0.10$, $p = 0.615$). Repeating the analyses excluding participants with bilateral language dominance revealed similar findings (language and reading: $\rho = 0.548$ $p = 0.017$; language and face recognition: $\rho = 0.06$, $p = 0.80$; reading and face recognition: $\rho = 0.02$, $p = 0.923$). Next, we compared the strength of laterality between LLD and RLD participants. This comparison did not yield any statistically significant difference, as shown in Table 4A of the appendix.

4. Discussion

4.1. Lateralization for language, reading, and face recognition covaries

The present study compared lateralization for face recognition and reading in left-handers with LLD or RLD. Replicating previous studies, we show that language measured in the IFG and reading measured in the MFG typically colateralize (Cai, Paulignan, Brysbaert, Ibarrola, & Nazir, 2010; Van der Haegen, et al., 2012). Moreover, they are also associated in terms of the strength of their asymmetries. Taken together, these findings suggest a strong relationship between laterality for word production (language) and reading. This relationship likely reflects a facilitated interaction between regions specialized for reading, like the VWFA, and language regions, due to their colateralization. Considering that the establishment of language asymmetry predates that of reading both ontogenetically and phylogenetically, language dominance can be taken as an important determinant of reading dominance. However, the observation of hemispheric segregation between reading and language in several participants, as has been reported previously (Van der Haegen, et al., 2012), suggests language dominance may not be the only factor that influences reading asymmetry.

This study further demonstrates that language laterality is associated with face recognition laterality in terms of the direction of asymmetry. While the vast majority of LLD participants showed a clear right MFG dominance for face processing, participants with RLD were only rarely right lateralized for faces and had higher rates of left face dominance compared to left-handers with LLD. Different accounts could explain the observed segregation between language and face recognition. First, the competition hypothesis proposes that it arises because of competition for neural resources within the fusiform gyrus between reading and face recognition during reading acquisition (Plaut & Behrmann, 2011; Ventura, 2014). Specifically, this hypothesis suggests that learning to read relies on repurposing neurons previously devoted to face recognition for recognizing written words. As this recycling process predominantly takes place in the language dominant hemisphere, face recognition is increasingly forced to rely more heavily on the opposite, non-language dominant hemisphere, thus giving rise to its hemisphere asymmetry. While the association between language and face recognition asymmetry predicted by this hypothesis is supported by our study, the lack of a relationship in both direction and strength of asymmetry between reading and face recognition may argue against the competition hypothesis.

A second account for the segregation between language and face recognition assumes that there exists an innate mechanism which predisposes them to lateralize. Support for this view is provided by the observation that both functions are already lateralized in (preliterate) infants

(Dehaene-Lambertz, Hertz-Pannier, & Dubois, 2006; Dubois, et al., 2009; Vannasing, et al., 2016; Adibpour, Dubois, & Dehaene-Lambertz, 2017). Their segregation may then follow from the brain's general drive to establish an optimal pattern of functional division to enhance neural processing efficiency. Note that this account and the competition hypothesis are not mutually exclusive, as competition between reading and face recognition may further strengthen a pre-existing asymmetry for face recognition.

While language and face recognition appear generally lateralized to opposite hemispheres in the present study, these functions crowed to the same hemisphere in several participants (3/24, 12.5%). The alleged role of functional segregation in terms of conflict prevention of duplicate functional regions, enhancement of parallel processing, and higher neural capacity by eliminating redundant duplication, predicts that individuals with crowding of complementary functions within the same hemisphere might show reduced performance on cognitive tasks probing these functions (Vingerhoets, Gerrits, & Bogaert, 2018). This prediction remains to be tested in future research. Regardless, these findings do suggest that some individuals lack whichever bias pressures language and faces to segregate.

4.2 Segregation between language and face recognition is less clear in RLD

We predicted that left-handers with RLD would also be reversed for reading and face recognition. In line with this hypothesis, the distribution of LI's for reading in RLD almost exactly mirrors the one found for LLD. However, the same does not hold for face recognition. While rates of right hemisphere dominance for faces were substantially lower in left-handers with RLD compared to left-handers with LLD, they did not have a correspondingly strong increase in left hemisphere dominance for faces. Rather, the rates of bilateral activation and leftwards lateralization for face recognition was surprisingly found to be equal within the RLD group. Put differently, in comparison to left-handers with LLD, more participants with RLD lack a clear asymmetry for faces (LLD: 16.7% vs RLD: 41.7%) and less of them show the expected hemisphere segregation between language and faces (LLD: 75% vs RLD: 41.7%).

Several explanations can account for these findings. First, absence of asymmetry for face recognition in RLD may be the outcome of a competition between two different biases. On the one hand, there may be pressure to maintain the typical pattern of functional segregation, which 'pushes' face recognition to the left hemisphere in RLD. On the other hand, there might also exist a simultaneous pressure preventing hemisphere reversal of face recognition, as this might represent an evolutionary inferior solution. As a consequence of these conflicting pressures, several participants with RLD may fail to develop an outspoken asymmetry for face recognition in either direction. An alternative explanation is that individuals with RLD might use different strategies to process faces which involves both hemispheres more equally compared to individuals with LLD. For example, it has been suggested that the left FFA takes a featural approach to face recognition as opposed to the holistic face processing strategy of the right FFA (Meng, Cherian, Singal, & Sinha, 2012; Frässle, Krach, Paulus, & Jansen, 2016). The increased bilateral activation for face recognition observed in participants with RLD thus might reflect a stronger reliance on feature-based strategies to process faces in these individuals. Future work is needed to assess whether individuals with RLD employ different strategies to recognize faces.

4.3 Face recognition in left-handers: same or different mechanisms?

Most research on lateralized cognition is based on right-handers (Willems, Van der Haegen, Fisher, & Francks, 2014). However, it has become increasingly apparent that functional asymmetries behave differently in left-handers. For instance, studies on face recognition usually report more bilateral face representations in the FFA of left-handers (Willems, Peelen, &

Hagoort, 2007; Badzakova-Trajkov, Haberling, Roberts, & Corballis, 2010; Dundas, Plaut, & Behrmann, 2015). A recent study attributed this symmetric activation pattern to an elevated left FFA recruitment and suggested that left-handers may engage different neural mechanisms, and putatively use differential processing strategies, to recognize faces (Frässle, et al., 2016). Specifically, based on differential face processing mechanisms indicated for the left and right FFA - that is face semblance and face/non-face judgements respectively (Meng, Cherian, Singal, & Sinha, 2012)- they suggest that left-handers might recruit more low-level feature-based processes to recognize faces and therefore activate the left FFA more strongly than right-handers.

In contrast to the findings of Frässle, et al. (2016), our results suggest that most left-handers with LLD, which constitutes the majority of the left-handed population, have a rightward dominance for faces in the FFA rather than bilateral activation, similar to right-handers. In fact, the LI distribution for face recognition we found in left-handers with LLD almost exactly matches the one previously reported for right-handers, of whom ± 70% were right lateralized, ± 20% were bilateral and ± 10% were left lateralized (Bukowski, Dricot, Hanseeuw, & Rossion, 2013). The typical group-level observation of an increased bilateral activation in the FFA of left-handers may have resulted from the higher prevalence of RLD in this population, who, as the present study shows, are more likely to be left lateralized or bilateral than right lateralized for faces in the MFG. By including left-handers with LLD alongside left-handers with RLD, the rightward asymmetry for faces in the former group is dragged down, resulting in an overall activation pattern which is more bilateral relative to right-handers. This study thus argues against an inherent difference in the neural implementation of face recognition in most left-handers.

Acknowledgements

We thank Ruth Seurinck for her input on the preprocessing of the fMRI data and Prof. Stanislas Dehaene for kindly providing us the visual localizer paradigm. In addition, we want to express our gratitude to all participants who participated in the present study.

Funding: This work was supported by the Fonds Wetenschappelijk Onderzoek-Vlaanderen (Research Council Flanders) by grant n° G2916N and G0114.16N.

References

Adibpour, P., Dubois, J., & Dehaene-Lambertz, G. (2017). Right but not left hemispheric discrimination of faces in infancy. *Nature Human Behaviour*, https://doi.org/10.1038/s41562-017-0249-4.

Amalric, M., & Stanislas, D. (2016). Origins of the brain networks for advanced mathematics in expert mathematicians. *PNAS, 113*(18), 4909-4917.

Badzakova-Trajkov, G., Haberling, I., Roberts, R., & Corballis, M. (2010). Cerebral asymmetries: Complementary and independent processes. *PLoS One, 5*, e9682.

Barton, J., Press, D., Keenan, J., & O'Conner, M. (2002). Lesions of the fusiform face area impair perception of facial configuration in prosopagnosia. *Neurology, 58*(1), 71-8.

Bukowski, H., Dricot, L., Hanseeuw, B., & Rossion, B. (2013). Cerebral lateralization of face-sensitive areas in left-handers: only the FFA does not get it right. *Cortex, 49*(9), 2583-9.

Cai, Q., Paulignan, Y., Brysbaert, M., Ibarrola, D., & Nazir, T. (2010). The left ventral occipito-temporal response to words depends on language lateralization but not on visual familiarity. *Cerebral Cortex, 20*(5), 1153-63.

Cai, Q., Van der Haegen, L., & Brysbaert, M. (2013). Complementary hemispheric specialization for language production and visuospatial attention. *Proceedings of the National Academy of Sciences of the United States of America, 110*(4), E322-E330.

Cohen, L., Dehaene, S., Naccache, L., Lehericy, S., Dehaene-Lambertz, G., Henaff, M., & Michel, F. (2000). The visual word form area: spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. *Brain, 123*(2), 291-307.

Davies-Thompson, J., Johnston, S., Tashakkor, Y., Pancarogly, R., & Barton, J. (2016). The relationship between visual word and face processing lateralization in the fusiform gyri: A cross-sectional study. *Brain Research, 1644*, 88-97.

Dehaene, S. (2005). Evolution of Human Cortical Circuits for Reading and Arithmetic: The "Neuronal Recycling" Hypothesis. In S. Dehaene, J.-R. Duhamel, M. Hauser, & C. Rizzolatti, *From Monkey Brain to Human Brain: A Fyssen Foundation Symposium* (pp. 133-152). Cambridge: MIT Press.

Dehaene, S., & Cohen, L. (2007). Cultural recycling of cortical maps. *Neuron, 56*, 384–398.

Dehaene, S., & Cohen, L. (2011). The unique role of the visual word form area in reading. *Trends in Cognitive Sciences, 15*(6), 254-262.

Dehaene-Lambertz, G., Hertz-Pannier, L., & Dubois, J. (2006). Nature and nurture in language acquisition: anatomical and functional brain-imaging studies in infants. *Trends in Neurosciences, 29*(7), 367-373.

Dubois, J., Hertz-Pannier, L., Cachia, A., Mangin, J., Le Bihan, D., & Dehaene-Lambertz, G. (2009). Structural asymmetries in the infant language and sensori-motor networks. *Cerebral Cortex, 19*(2), 414-23.

Dundas, E., Plaut, D., & Behrmann, M. (2015). Variable Left-hemisphere Language and Orthographic Lateralization Reduces Right-hemisphere Face Lateralization. *Journal of Cognitive Neuroscience, 27*(5), 913-925.

Fernandez, G., de Greiff, A., von Oertzen, J., Reuber, M., Lun, S., & P., K. (2001). Language mapping in less than 15 minutes: real-time functional MRI during routine clinical investigation. *Neuroimage, 14*, 585-94.

Frässle, S., Krach, S., Paulus, F., & Jansen, A. (2016). Handedness is related to neural mechanisms underlying hemispheric lateralization of face processing. *Scientific Reports, 6*, 27153.

Friston, K., Jezzard, P., & Turner, R. (1994). Analysis of functional MRI time-series. *Human Brain Mapping, 1*(2), 153-171.

Glezer, L., & Riesenhuber, M. (2013). Individual Variability in Location Impacts Orthographic Selectivity in the “Visual Word Form Area”. *The Journal of Neuroscience, 33*(27), 11221-26.

Jansen, A., Deppe, M., Schwindt, W., Mohammadi, S., Sehlmeyer, C., & Knecht, S. (2006). Interhemispheric dissociation of language regions in a healthy subject. *Archives of Neurology, 63*, 1344-46.

Kanwisher, N., & Yovel, G. (2006). The fusiform face area: a cortical region specialized for the perception of faces. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences , 361*(1476), 2109-2128.

Knecht, S., Dräger, B. D., Bobe, L., Lohmann, H., Floël, A., Ringelstein, E., & Henningsen, H. (2000). Handedness and hemispheric language dominance in healthy humans. *Brain, 123*, 2512-8.

Mazaika, P., Hoeft, F., Glover, G., & Reiss, A. (2009). Methods and Software for fMRI Analysis for Clinical Subjects. Poster presented at Human Brain Mapping conference*.* San Francisco, CA.

Mazoyer, B., Zago, L., Jobard, G., Crivello, F., Joliot, M., Perchey, G., . . . Tzourio-Mazoyer, N. (2014). Gaussian Mixture Modeling of Hemispheric Lateralization for Language in a Large Sample of Healthy Individuals Balanced for Handedness. *PLoS One*, e101165.

Meng, M., Cherian, T., Singal, G., & Sinha, P. (2012). Lateralization of face processing in the human brain. *Proceedings of the Royal Society B, 279*(1735), 2052-2061.

Mercure, E., & Cohen Kadosh, K. J. (2011). The n170 shows differential repetition effects for faces, objects and orthographic stimuli. *Frontiers in Human Neuroscience, 5*(6).

Parr, L. (2011). The Evolution of Face Processing in Primates. *Philosophical Transactions of the Royal Society B, 366*(1571), 1764-77.

Plaut, D., & Behrmann, M. (2011). Complementary neural representations for faces and words: a computational exploration. *Journal of Cognitive Neuropsychology, 28*(3-4), 251-75.

Robotham, R., & Starrfelt, R. (2017). Face and Word Recognition Can Be Selectively Affected by Brain Injury or Developmental Disorders. *Frontiers in Psychology, 8*, Article 1547.

Rossion, B., Joyce, C., Cottrell, G., & Tarr, M. (2003). Early lateralization and orientation tuning for face, word, and object processing in the visual cortex. *Neuroimage, 20*(3), 1609-24.

Simion, F., & Di Giorgio, E. (2015). Face perception and processing in early infancy: inborn predispositions and developmental changes. *Frontiers in Psychology, 6*(969).

Sorger, B., Goebel, R., Schiltz, C., & Rossion, B. (2007). Understanding the functional neuroanatomy of acquired prosopagnosia. *NeuroImage, 35*(2), 836-852.

Starrfelt, R., & Shallice, T. (2014). What's in a name? The characterization of pure alexia. *Cognitive Neuropsychology, 31*(5-6), 367-377.

Szwed, M., Dehaene, S., Kleinschmidt, A., Eger, E., Valabrègue, R., Amadon, A., & Cohen, L. (2011). Specialization for witten words over objects in the visual cortex. *Neuroimage, 56*(1), 330-334.

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., . . . Joliot, M. (2002). Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *Neuroimage, 15*(1), 273-89.

Van der Haegen, L., Cai, Q., & Brysbaert, M. (2012). Colateralization of Broca's area and the visual word form area in left-handers: fMRI evidence. *Brain & Language, 122*, 171-178.

Van der Haegen, L., Cai, Q., Seurinck, R., & Brysbaert, M. (2011). Further fMRI validation of the visual half field technique as an indicator of language laterality: A large-group analysis. *Neuropsychologia, 49*(10), 2879-88.

Vannasing, P., Florea, O., González-Frankenberger, B., Tremblay, J., & Paquette, N. S. (2016). Distinct hemispheric specializations for native and non-native languages in one-day-old newborns identified by fNIRS. *Neuropsychologia, 84*, 63-9.

Ventura, P. (2014). Let's face it - reading acquisition, face and word processing. *Frontiers in Psychology, 5*, 787.

Vingerhoets, G., Alderweireldt, A.-S., Vandemaele, P., Cai, L., Van der Haegen, L., Brysbaer, M., & Achten, E. (2013). Praxis and language are linked: evidence from co-lateralization in individuals, with atypical language dominance. *Cortex, 49*(1), 173-183.

Vingerhoets, G., Gerrits, R., & Bogaert, S. (2018). Atypical brain functional segregation is more frequent in situs inversus totalis. *Cortex, 106*, 12-25.

Willems, R., Peelen, M., & Hagoort, P. (2007). Cerebral Lateralization of Face-Selective and Body-Selective Visual Areas Depends on Handedness. *Cerebral Cortex, 20*, 1719-1725.

Willems, R., Van der Haegen, L., Fisher, S., & Francks, C. (2014). On the other hand: including left-handers in cognitive neuroscience and neurogenetics. *Nature Reviews Neuroscience, 15*, 193-201.

Appendix

Table A1: Location and coordinates of peak activation in the word generation task for the LLD and RLD groups.

LLD group

Region	BA	x	y	z	Peak T	Cluster size
Left hemisphere						
Superior frontal gyrus	6/8	-3	0.5	70	11.50	565
Putamen		-22.5	-4	5	7.55	384
Insula		-27	24.5	0	7.45	368
Inferior frontal gyrus	6/44	-42	6.5	27.5	7.29	184
Fusiform gyrus	37	-48	-47.5	-20	6.74	165
Inferior occipital gyrus	18	-12	-73	12.5	6.52	50
Middle temporal gyrus	21	-58.5	-34	5	6.41	80
Cerebellum		-6	-56.5	-12.5	5.20	50
Right hemisphere						
Cerebellum		39	-67	-27.5	9.32	571
Insula		33	24.5	2.5	8.81	205
Putamen		15	14	-5	7.60	265
Superior frontal gyrus	8	9	21.5	32.5	6.25	260

RLD group

Region	BA	x	y	z	Peak T	Cluster size
Left hemisphere						
Cerebellum		-30	-62.5	-22.5	9.04	241
Putamen		-21	2	-7.5	7.19	229
Insula	13	-30	23	-2.5	6.16	148
Right hemisphere						
Insula	13	31.5	18.5	10	8.66	877
Superior frontal gyrus	6/8	6	18.5	35	6.98	730
Inferior frontal gyrus	44	46.5	8	17.5	5.80	79
Anterior cingulate	32	0	20	40	5.51	182
Superior temporal gyrus	22	58.5	-32.5	5	4.63	42
Inferior frontal gyrus	46	43.5	35	15	4.39	42

Table A2: Location and coordinates of peak activation in the reading task for the LLD and RLD groups.

LLD group

Region	BA	x	y	z	Peak T	Cluster size
Left hemisphere						
Inferior occipital gyrus	18	-33	-94	-7.5	6.80	60
Inferior parietal lobe	39	-43.5	-55	20	6.07	71
Fusiform gyrus	37	-43.5	-62.5	-12.5	5.25	51
Inferior frontal gyrus	45	-52.5	30.5	10	4.87	40
Middle temporal gyrus	21	-57	-37	2.5	4.21	54
Middle occipital gyrus	19	-43.5	-65.5	-5	3.41	43

RLD group

Region	BA	x	y	z	Peak T	Cluster size
Left hemisphere						
Inferior occipital gyrus	18	-34.5	-94	-5	4.93	78
Right hemisphere						
Fusiform gyrus	37	28.5	-40	-15	6.65	45
Inferior occipital gyrus	18/19	45	-83.5	-7.5	4.71	117
Fusiform gyrus	37	48	-55	-12.5	3.77	57

Table A3: Location and coordinates of peak activation in the reading task for the LLD and RLD groups.

LLD group

Region	BA	x	y	z	Peak T	Cluster size
Right hemisphere						
Inferior occipital gyrus	18	37.5	-89.5	-10	7.69	191
Putamen		30	-8.5	-15	7.04	143
Fusiform gyrus	37	42	-47.5	-20	6.62	347
Inferior frontal gyrus	44	58.5	8	5	5.50	62
Middle occipital gyrus	19	52.5	-68.5	17.5	5.25	66
Insula	13	40.5	6.5	-10	4.25	98
Caudate		10.5	18.5	-2.5	4.19	46
Cingulate	32	7.5	-4	47.5	3.99	43
Middle occipital gyrus	19	55.5	-58	12.5	3.69	64
Left hemisphere						
Putamen	18	-25.5	5	-7.5	6.25	68
Cingulate	24	-4.5	-5.5	50	5.13	44
Insula	13	-33	-23.5	20	5.00	52
Middle occipital gyrus	19	-43.5	-71.5	-17.5	4.39	51
Cerebellum		-46.5	-58	-27.5	4.37	75
Parahippocampal gyrus	54	-19.5	-10	-20	3.91	50
Cerebellum		-22.5	-68.5	-25	3.83	44

RLD group

Region	BA	x	y	z	Peak T	Cluster size
Right hemisphere						
Cingulate	23/24	1.5	-19	37.5	6.38	113
Middle frontal gyrus	9	10.5	56	35	5.45	52
Left hemisphere						
Inferior occipital gyrus	18	-37.5	-91	-10	3.66	74
Fusiform gyrus	37	-39	-53.5	-20	3.32	55

Table 4A: Strength of laterality in LLD and RLD subgroups

	LLD	RLD	W	P
Language	0.59 (0.18)	0.75 (0.43)	132	0.300
Reading	0.25 (0.33)	0.34 (0.25)	137	0.453
Faces	0.30 (0.22)	0.18 (0.23)	120	0.083

Median (inter-quartile range) of strength of laterality for the word generation task (Language), written word recognition task (Reading) and face recognition task (Faces) in participants with LLD and RLD. W = Wilcoxon W, p = p-value of Mann-Whitney U test used to compare LLD and RLD participants.