



Research Report

A meta-analytical account of the functional lateralization of the reading network



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ABSTRACT

The observation that the neural correlates of reading are left-lateralized is ubiquitous in the cognitive neuroscience and neuropsychological literature. Still, reading is served by a constellation of neural units, and the extent to which these units are consistently left-lateralized is unclear. In this regard, the functional lateralization of the fusiform gyrus is of particular interest, by virtue of its hypothesized role as a “visual word form area”. A quantitative Activation Likelihood Estimation meta-analysis was conducted on activation foci from 35 experiments investigating silent reading, and both a whole-brain and a bayesian ROI-based approach were used to assess the lateralization of the data submitted to meta-analysis. Perirolandic areas showed the highest level of left-lateralization, the fusiform cortex and the parietal cortex exhibited only a moderate pattern of left-lateralization, while in the occipital, insular cortices and in the cerebellum the lateralization turned out to be the lowest observed. The relatively limited functional lateralization of the fusiform gyrus was further explored in a regression analysis on the lateralization profile of each study. The functional lateralization of the fusiform gyrus during reading was positively associated with the lateralization of the precentral and inferior occipital gyri and negatively associated with the lateralization of the triangular portion of the inferior frontal gyrus and of the temporal pole. Overall, the present data highlight how lateralization patterns differ within the reading network. Furthermore, the present data highlight how the functional lateralization of the fusiform gyrus during reading is related to the degree of functional lateralization of other language brain areas.

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1. Introduction

1.1. Functional localization and lateralization of reading in the brain

The dominance of the left cerebral hemisphere (LH) over the right one (RH) for reading has been evident in Cognitive Neuroscience since the earliest anatomic-clinical descriptions dating back to the second half of the 19th century (Dejerine, 1891, 1892; Skwartzoff, 1881). In these seminal descriptions, clinical cases were reported of patients who had suffered brain lesions to posterior regions in the LH and displayed acquired reading disorders. The concomitant sparing of the RH in these patients made neuropsychologists conclude not only that posterior cortices are involved in reading, but also that the function of reading is left-lateralized.

While in the first anatomic-clinical descriptions reading was depicted as a somewhat monolithic entity, contemporary cognitive psychology considers this function as a set of concatenated and interwoven computations (Coltheart et al., 2001; Harm & Seidenberg, 2004; Paulesu et al., 2021; Ziegler et al., 2014), mirrored by the involvement of a relatively widespread set of brain areas. More specifically, the left ventral occipito-temporal (vOT) cortex/posterior fusiform gyrus has been associated to pre-lexical orthographic analysis, more anterior parts of the left fusiform gyrus to lexical orthographic and semantic processing, the inferior parietal lobule to grapheme/phoneme conversion, the inferior frontal gyrus (IFG), the insula and precentral cortex to phonological analysis and output processes and the left middle temporal gyrus (MTG) and angular gyrus to phonological lexicon and/or semantic processing (Cattinelli et al., 2013; Jobard et al., 2003; Price, 2012; Taylor et al., 2013; Turkeltaub et al., 2002). In this work, we conceived reading as grounded on the activity of a wide set of different neural units, of which we explored the functional lateralization pattern.

Despite the more fine-grained level of analysis, contemporary accounts agree with the earliest neuropsychological observations in attributing little (if any) functional role to the RH in the extraction of meaning and/or sound from written words. Yet, there is still little understanding on the extent to which functional lateralization is identical across all neural centres that serve the function of reading. Earlier frameworks that formalized the neurocognitive underpinnings of reading and language in general (see for instance Ellis, 2004; Ellis et al., 1988; Luzzatti, 2003; Luzzatti et al., 1998; Price, 2012) implicitly assume a consistent degree of functional lateralization across the involved cognitive components and underlying neural centres, and provide no information on variability across brain areas; conversely, Parker et al. (2022) advocate that some degree of variability exists in how the activity of areas within the middle cerebral artery territory lateralizes in different language sub-tasks. In other words, there seems to be variability in the lateralization of the language network while being engaged in different language sub-processes. In analogy with this view, it is possible to hypothesize that – within a given language task (in this case, reading) – some degree of

variability exists in the functional lateralization of different brain areas involved in information processing.

A critical neurocognitive hub to consider for reading is the so-called “Visual Word-Form Area” (VWFA). The notion that visual representations for written words could be encoded in a specific brain area was introduced by classical neuropsychological models (Dejerine, 1891, 1892; Lichtheim, 1885), according to which a VWFA was located in the “pli courbe” (i.e., the angular gyrus). Since the early 2000s, the term VWFA has instead been used to refer to brain activity detected in left vOT cortices (specifically, in a part of the left fusiform gyrus) during reading tasks (Cohen et al., 2000, 2002; Dehaene et al., 2002). This evidence is in line with neuropsychological literature suggesting the association between Pure Alexia and a lesion and/or disconnection of the left fusiform gyrus (see for instance Bonandrini et al., 2020; Epelbaum et al., 2008; Montant & Behrmann, 2000; Ripamonti et al., 2014). This observation, together with the lack of descriptions of a “crossed” version of Pure Alexia (i.e., selectively associated to a RH lesion), suggests a prominent left functional lateralization of the vOT cortices for reading.

However, the neuropsychological literature indicates that, even in case of acquired reading disorders due to left vOT lesions, some residual reading abilities can be observed. This evidence suggests that the RH can contribute to compensate the deficit induced by left-sided brain lesions (Bonandrini et al., 2020; Coltheart, 1980; Saffran & Coslett, 1998; Saffran et al., 1980). Along this line, it was also shown that, in patients who first suffered a LH brain lesion producing an acquired reading deficit, a second brain lesion occurring in the RH further worsened reading performance (Bartolomeo et al., 1998; Bartolomeo & Thiebaut de Schotten, 2016). In addition, literature provides evidence of RH reading in patients who underwent callosotomy, i.e., the surgical transection of the corpus callosum (“split brain” patients”; Baynes et al., 1992; Gazzaniga & Hillyard, 1971; Levy & Trevarthen, 1977; Reuter-Lorenz & Baynes, 1992; Zaidel, 1983) when asked to read words presented in isolation to the left visual field/right hemisphere. This evidence points towards a more nuanced view of the functional lateralization of the reading system, that leaves room for the possibility that the RH might be able to contribute (at least to some extent) to orthographic processing.

This position is compatible with Pierre Marie’s (1897) intuition that it is unlikely that the neural correlates of reading (whose evolutionary origins and diffusion as a mass phenomenon is relatively recent) are biologically anchored to anatomical landmarks (see also Price & Devlin, 2003). Also, recent proposals suggest that the lateralization of the visual word form system is *graded* (Behrmann & Plaut, 2015; Plaut & Behrmann, 2011). Accordingly, such lateralization would represent the result of a process progressively binding newly formed orthographic representations (that are initially bilateral) with pre-existing linguistic ones derived from spoken language, which would be already left-lateralized before reading development (Dehaene-Lambertz et al., 2002; Sowman et al., 2014).

This position complements and parallels another theory on the development of reading lateralization, known as the *phonological mapping theory* (Maurer & McCandliss, 2007; McCandliss & Noble, 2003), which identifies in phonological processing the key cognitive mechanism linking spoken language processing (and its lateralization) to the lateralization of reading. The corollary of these proposals is that, if mechanisms of reading depend on more general cognitive mechanisms involved in spoken language processing, then the lateralization of reading should be largely dependent on that of spoken language.

The available literature provides some support for this framework. In an EEG study, Cai et al. (2008) reported that, for both LH and RH-language dominant participants, brain activity during a divided visual field reading task co-lateralized with brain activity during a verb generation task. A significant positive correlation was also observed between the activity in the IFG during word generation and the activity in the vOT during lexical decision in an fMRI study (Cai et al., 2010). In a similar way, the lateralization of brain activity during a word generation task proved to be significantly positively correlated with the behavioural lateralization pattern in a divided visual field word naming task (i.e., difference in reaction times between words projected to the right and left visual fields; Gerrits et al., 2019; Van der Haegen et al., 2011), as well as with the lateralization of brain activity in the vOT during a lexical decision task with words presented centrally (Van der Haegen et al., 2012) and during a word recognition task (Gerrits et al., 2019). More recently, behavioural performance lateralization in a divided visual field reading task proved to be positively correlated with performance lateralization in a dichotic listening task (Van der Haegen & Brysbaert, 2018).

Yet, although the corpus of data supporting the association between the functional lateralization of reading and that of spoken language is progressively expanding, the extent to which this finding can be reliably observed across studies is open to question. Meta-analyses of functional imaging data could contribute to this endeavour. To the best of our knowledge, no study has attempted to explore these phenomena at a meta-analytical level, nor has it adopted a meta-analytical standpoint from which to describe the lateralization of the different areas subserving the function of reading. More broadly, it still remains unclear whether the neural correlates of reading are strongly left-lateralized, or rather the pattern of lateralization is nuanced, with the functional lateralization of the vOT cortices during reading being associated to that of other language-related areas.

1.2. A meta-analytical look at the functional lateralization of reading

Although their functional significance is often overlooked, RH activation foci often emerge in neuroimaging studies of reading, as testified by previous meta-analytical evidence (Cattinelli et al., 2013; Jobard et al., 2003; Murphy et al., 2019; Taylor et al., 2013; Turkeltaub et al., 2002). This suggests that the lateralization of the reading network can be profitably

described from a meta-analytical standpoint. However, to do so, meta-analytical frameworks must be combined with specific techniques of analysis capable of describing different functional lateralization patterns between brain regions. In this regard, existing literature provides some suggestions.

In their meta-analytical work, Vigneau et al. (2011) explored the lateralization of different linguistic components (namely phonological, semantic and text processing). They found that lexical-semantic processing was associated with bilateral clusters in the pars opercularis of the IFG and in the insula/pars orbitalis of the IFG. However, activation foci were *a priori* divided into unilateral and bilateral, and separate analyses were run for unilateral and bilateral datasets. Furthermore, hierarchical clustering was adopted, which, although particularly useful in the case of a limited number of studies (Berlingeri et al., 2019), does not provide direct assessment of the significance of the spatial convergence across studies.

More recently, Trettenbrein et al. (2021) conducted a meta-analytical assessment of the neural correlates of sign language. To do so, they adopted an Activation Likelihood Estimation (ALE) approach (Eickhoff et al., 2009, 2012; Turkeltaub et al., 2002, 2012). This technique provides voxel-wise information on the spatial convergence across studies, offering hints about the localization of the phenomenon under examination. In order to explore its lateralization, they used ALE images as input and computed a laterality index (LI) see (Matsuo et al., 2012, 2021) in a set of Regions of Interest (ROIs). Although this method provides a quantitative measure of lateralization, still the spatial resolution is limited to the spatial extent of the chosen ROIs.

A different stream of research focused on providing a voxel-wise measure of functional lateralization. Similarly to an fMRI study (Liégeois et al., 2002) that compared standard-oriented functional brain images with the same images flipped along the posterior–anterior axis resulting in a left–right inversion (see also Berlingeri et al., 2013), Turkeltaub and Coslett (2010) compared the results of a standard-oriented ALE analyses with one in which the x coordinates (indicating left [$x < 0$] and right [$x > 0$] positioning in the standard stereotactic space) were flipped (see also Hoffman & Morcom, 2018; Rice et al., 2015). However, it is worth noting that although this method provides a direct and statistically testable measure of meta-analytic functional lateralization at the voxel level, it suffers from two major limitations. On the one hand, it cannot provide a direct quantitative measure of lateralization (like a laterality index would do). On the other hand, this method implicitly assumes perfect structural symmetry between hemispheres, so that, in principle, any voxel can be directly compared with its contralateral homologue in a meaningful manner. This assumption may be a source of error in light of data showing anatomical differences between the left and right cerebral hemispheres in some critical regions like, for example, those around the Sylvian fissure (Duboc et al., 2015; Kong et al., 2018; Toga & Thompson, 2003).

One possibility to overcome these limitations is to complement an ALE-based voxel-wise lateralization analysis with a ROI-based approach capable of exploring the functional

lateralization in different brain regions without a-priori assumptions of perfect symmetry at a voxel level (i.e., by comparing the left/right ratio with a target value of 50% with a binomial test). In addition, an “anatomy-weighted” analysis could be run to compare the probability for an activation focus to fall on the left or the right side with a theoretical probability determined by the size ratio of contralateral homologous areas (instead of 50%). Indeed, if for a given brain region the left area is twice the size of the right area, then an activation focus has twice the probability of falling randomly in the left area relative to the right homologue one. In this case, we would be looking at a functional lateralization phenomenon that could be accounted for in terms of structural asymmetries. On the other hand, if in the same set of regions (with the left area being twice the size of the right area) most peaks fall in the RH, then we can be confident that a functional lateralization phenomenon took place, whose intensity is stronger than what pure anatomical lateralization would anticipate. Such “anatomy-weighted analysis” could also potentially highlight functional lateralization patterns that would appear irrelevant otherwise. Indeed, it might be that the activation of a given area looks of little relevance in functional terms if the anatomy is not taken into account (i.e., at a purely phenomenal level). However, if considered in light of the different size of homologous contralateral areas, the same activation might provide insightful information on the functional lateralization of that region.

1.3. Aims and predictions

In this study we re-assessed the issue of whether and to what extent the reading network shows a significant and meaningful lateralization. We explored whether reading is consistently left-lateralized across the involved brain areas, or rather if some degree of variability in its lateralization exists. We anticipated different outcomes to our investigation. One scenario entailed the possibility that, in line with implicit assumptions of earlier frameworks modelling the neural correlates of reading – and language in general – (see for instance Ellis, 2004; Ellis et al., 1988; Luzzatti, 2003; Luzzatti et al., 1998; Price, 2012), there is substantial consistency in the functional lateralization of the reading network. An alternative possibility was that some degree of variability exists in the functional lateralization of the reading network, in analogy with the observation that the language system shows different lateralization patterns when engaged in different language sub-tasks (Parker et al., 2022, 2024).

We also had some specific anatomical questions in mind. For example, we explored the extent to which any functional lateralization of fusiform gyrus (which is meant to contain the VWFA) is driven by the lateralization of the rest of the language system or some specific parts of it. In this regard, the possibility that the lateralization of the fusiform gyrus during reading can be predicted by the lateralization of areas involved in spoken language would support the hypothesis of the *graded* functional lateralization of the visual word form system (Behrmann & Plaut, 2015; Plaut & Behrmann, 2011); an alternative scenario would speak in favour of a relative functional autonomy of the fusiform gyrus in the context of reading.

To answer these questions, we complemented an ALE lateralization meta-analysis with the computation of laterality indices, and we compared the relative proportion of left and right foci with a binomial distribution for each ROI. To this end, we used as a reference value either 50% (to explore at a phenomenal level the functional lateralization of reading in each brain area), or the size ratio of the homologous areas (to correct for structural brain asymmetries). Bayesian binomial tests were used to compare (by using the Bayes Factor) the likelihood of the null hypothesis (either the 50% distribution of left/right peaks or the distribution of peaks complying with anatomical differences) with the alternative hypothesis of functional lateralization. By doing so, we were able to quantify the extent to which there is evidence supporting the hypothesis that there is some degree of lateralization in a given area, relative to the null hypothesis (i.e., lack of functional lateralization). In a subsequent analysis, laterality indices were computed (separately for each study included in the meta-analysis) for the brain areas involved in reading. The extent to which the functional lateralization of the fusiform gyrus in reading was predicted by the functional lateralization of the other areas of the reading network was then estimated. In addition, we estimated the extent to which functional lateralization patterns during reading differ between word and sentence/text level processing.

2. Materials and methods

The present meta-analytic study was carried out following the PRISMA guidelines (Moher et al., 2009; Page et al., 2021). The PRISMA flowchart of the paper selection process is shown in [Supplementary Fig. S1](#); Müller et al. (2018)'s checklist is reported in [Supplementary Table S1](#). We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

2.1. Database construction

We entered the following queries in PubMed: “reading” AND “fMRI”; “reading” AND “functional magnetic resonance imaging”; “reading” AND “PET”; “reading” AND “positron emission tomography”. These keywords provided 1701, 960, 980, and 519 results, respectively. After the removal of double entries (1103 out of the 4160 initial results), the data set was reduced to 3057 results. From the initial set of 3057 records, we removed 1656 results as they were not related to reading. Among the discarded results, there were also two additional double entries and a paper whose full text could not be found online. At this stage, the data set consisted of 1401 records. We then removed two additional sets of 88 non-fMRI or non-PET experiments and 73 reviews or meta-analyses of already published articles. At this stage the data set consisted of 1240 records. We discarded 387 studies that did not include data from healthy literate adult subjects, studies that explicitly investigated elderly subjects only, as well as single case studies. An additional set of 140 records was discarded since it included data from a non-consistently right-handed sample

or did not explicitly report subjects' handedness.¹ We further discarded 86 records since they reported data from multilingual subjects only. An additional set of 109 records was discarded since the experiments did not report univariate analyses performed with an analytical pipeline composed of pre-processing, 1st and 2nd-level general linear model. We subsequently removed 126 records since the experiments reported only ROI-based analyses or data using small-volume corrections; during this stage, we also excluded papers that did not provide whole-brain coverage. At this point, the data set consisted of 392 records. We further restricted our research to 137 silent reading tasks (i.e., we excluded overt reading and lexical decision experiments) and – in particular – to 70 studies that reported contrasts from a silent reading task compared to a low-level baseline (resting, implicit, or visual non-linguistic baselines such as: fixation cross, checkerboards, lines patterns, geometric shapes, or pseudo-font strings). The use of a relatively low-level baseline was chosen to consider the reading network in the broadest possible sense, without *a-priori* limiting our analysis to lexical, semantic, phonemic, or grapheme-phoneme conversion mechanisms. We also excluded 8 experiments whose sample included less than 10 subjects (Tahmasian et al., 2019). Also, as age has been extensively shown to modulate the degree of functional brain lateralization (see for instance Berlinger et al., 2010; Cabeza, 2002), we considered average age in included studies (if only the age range was provided, the average between the extreme values was used) and excluded 2 additional studies reporting an average age greater than 40 years. At this point, we also discarded another set of 8 records using scripts different from the Latin alphabet. An additional set of 17 experiments was discarded because of the presence of tasks, baselines or analytical pipeline not complying with the above criteria. The final database consisted of 35 articles, 642 participants and 575 foci, with average sample size being 18.64 (sd = 8.03) and average age being 25.75 (sd = 3.41). Details of the included articles are reported in Table 1. We included activation foci that exceeded the statistical thresholds defined in each study. The only exception is constituted by Stowe et al. (1999), for which the statistical threshold was set to a lenient $p < .1$. In this case, we only included foci that survived the .001 threshold at peak level. No part of the study procedures was pre-registered prior to the research being conducted. No part of the study analyses was pre-registered prior to the research being conducted.

¹ The choice of including only data from right-handed participants stems from the classical observation by Branch et al. (1964) that adextral subjects show greater variability than right-handers in the lateralization of language functions. This is also mirrored by recent evidence from our lab (Bonandrini et al., 2023) suggesting that left-handed participants show a comparatively smaller visual field effect than right-handed participants in a visual-half-field reading task. Since – to the best of our knowledge – there is no available evidence suggesting that the reduced functional lateralization for reading in adextrals involves all portions of the reading network to the same extent, we chose to exclude data from non-consistently right-handed samples to avoid introducing a potential source of variability in the laterality estimates.

2.2. Activation Likelihood Estimation analyses

Our ALE analyses were performed using GingerALE (Eickhoff et al., 2009, 2012; Turkeltaub et al., 2002, 2012), version 3.0.2 (www.brainmap.org). In order to minimize the cumulative effects of foci coming from the same experimental groups, we organized our data according to subject groups (Turkeltaub et al., 2012). All the coordinates reported in the Talairach space were converted into the MNI space by means of the “SPM” method implemented in GingerALE. The more conservative (smaller) grey matter mask was used.

First, the ALE meta-analysis was conducted on activation foci in a standard orientation (“Standard dataset”). Significant peaks resulting from this analysis were labelled according to the AAL3v1 template (Rolls et al., 2020). Subsequently, coordinates in the “standard dataset” were flipped along the posterior–anterior axis (resulting in a left–right inversion), by multiplying x coordinates by -1 . An ALE meta-analysis was conducted on activation foci in the flipped orientation (“Flipped dataset”). For both analyses, a Family-Wise Error (FWE) cluster-corrected threshold of $p < .05$, p value $< .001$ and 1,000 threshold permutations, was adopted. After merging the standard and the flipped data sets through GingerALE, a subtraction (contrast) analysis was performed between the two maps, with the contrast of interest being “Standard > Flipped”. A threshold of $p < .01$, with 100,000 permutations and a minimum volume of 300 mm³, was adopted.² These analyses allowed us to directly compare, in a voxel-wise fashion, the convergence of the ALE maps within the two hemispheres, and to evaluate which portions of the brain were more consistently reported as active in just one hemisphere.

2.3. ROI-based Bayesian Binomial analyses

The location of all foci in the standard dataset was determined by means of the AAL3v1 template (Rolls et al., 2020). Only foci falling into the areas that were included in significant clusters within the “standard” ALE analysis were taken into consideration. For each area, the 50% Bayesian binomial test was carried out by using .5 as the test value and a flat prior (Beta prior with a and b equal to 1). For the “anatomy-weighted” analyses, the same prior was used. However, the test value was set depending on the ratio of voxels – for each given area – on the left side divided by the sum of voxels of the two contralateral areas. In this regard, a value ranging from 0 to .5 indicates a greater number of voxels in the right side compared to the left side. A value ranging from .5 to 1 indicates more voxels in the left side compared to the right side. For all analyses, the number of left activation peaks was considered as the number of “success trials” for binomial tests. All Bayesian binomial analyses were carried out in Jasp (v 0.16). Bayes Factors (BFs) were interpreted as in Lee and

² The cluster FWE-corrected threshold of $p < .05$ was chosen as it maximizes the possibility of observing “true” results, while minimizing false positives (Eickhoff et al., 2016). We used 100,000 permutations a minimum volume of 300 mm³ instead of 10,000 and 200 mm³ minimum volume (standard in GingerALE) to increase the robustness of our analyses.

Table 1 – Details of included studies. Studies included in the meta-analysis, listed by year of publication; the sum of all the subjects equals 642, while the sum of all the foci equals 575. “Foci” indicates the number of significant foci from each study that were included in the present meta-analysis. Abbreviations: Ws = words; PWs = pseudowords; CSs = consonants; PLs = pseudoletters.

Reference	Method	Participants	Language	Stimuli	Baseline	Stereotaxic space	Foci	Foci source
Stowe et al. (1999)	PET	12	Dutch	Ws; sentences	Fixation asterisk	Talairach	9	Tab. 6, 7
De Nil et al. (2000)	PET	10	English	Words	X strings	Talairach	5	Tab. 2
Dehaene et al. (2001)	fMRI	15	French	Words	Blank screen	Talairach	15	Tab. 1
Longcamp et al. (2003)	fMRI	11	French	Letters	Symbols; PLs	Talairach	10	Tab. 1
Mechelli et al. (2003)	fMRI	20	English	Ws; PWs	Fixation cross	MNI	10	Tab. 2
De Nil et al. (2003)	PET	10	English	Words	X strings	Talairach	6	Tab. 3
Rapp et al. (2004)	fMRI	15	German	Sentences	Blank screen	Talairach	23	Tab. 1
Hauk et al. (2004)	fMRI	14	English	Words	Fixation cross	MNI	15	Tab. 1
Vigneau et al. (2005)	fMRI	23	French	Words	Fixation cross	MNI	39	Tab. 2
Mechelli et al. (2005)	fMRI	22	English	Words	Pseudoletters	MNI	6	Tab. 1
Pulvermüller and Hauk (2006)	fMRI	14	English	Words	Hashes strings	Talairach	4	Tab. 1
Powell et al. (2006)	fMRI	10	English	Sentences	Pseudoletters	MNI	3	Tab. 1
Ryan and Schnyer (2007)	fMRI	12	English	Words	Symbols	Talairach	8	Tab. 2
Vinckier et al. (2007)	fMRI	12	French	Words	Fixation dot	MNI	10	Tab. 1
Bahlmann et al. (2007)	fMRI	12	German	Sentences	X strings	MNI	5	Tab. 2
Hauk et al. (2008)	fMRI	21	English	Words	Hashes strings	MNI	11	Tab. 1
Buchweitz et al. (2009)	fMRI	12	Portuguese	Sentences	Fixation cross	MNI	13	Tab. 2
Assadollahi et al. (2009)	fMRI	20	German	Words	Fixation cross	Talairach	25	Tab. S1
Boulenger et al. (2009)	fMRI	18	English	Sentences	Hashes strings	MNI	11	Tab. 2
Purcell et al. (2011)	fMRI	17	English	Words	Checkerboards	MNI	9	Tab. 2
Vartiainen et al. (2011)	fMRI	15	Finnish	Ws; PWs; CSs	Resting	Talairach	11	Tab. S4
Rapp and Lipka (2011)	fMRI	10	English	Ws; CSs	Checkerboards	MNI	9	Tab. 1
Benjamin and Gaab (2012)	fMRI	13	English	Sentences	Resting	MNI	23	Tab. 1
Danelli et al. (2013)	fMRI	28	Italian	Ws; PWs	Lines strings	MNI	28	Tab. 2
Shah et al. (2013)	fMRI	28	German	Text	Fixation cross	MNI	35	Tab. S1
Choi et al. (2014)	fMRI	31	English	Texts	Fixation cross	Talairach	52	Tab. 2, 3, 4
Humphreys and Gennari (2014)	fMRI	17	English	Sentences	Fixation cross	MNI	8	Tab. 3
Moseley and Pulvermüller (2014)	fMRI	18	English	Words	Hashes strings	MNI	31	Appendix C
Danelli et al. (2015)	fMRI	20	Italian	Words	Lines strings	MNI	48	Tab. 2
Henderson et al. (2015)	fMRI	23	English	Text	Implicit	Talairach	24	Tab. 2
Danelli et al. (2017)	fMRI	23	Italian	Pseudowords	Lines strings	MNI	25	Tab. sr-1
Pomp et al. (2018)	fMRI	18	German	Sentences	Fixation cross	MNI	6	Tab. B1
Purcell and Rapp (2018)	fMRI	30	English	Ws; PWs; CSs	Checkerboards	MNI	26	Tab. 2
Hsu et al. (2019)	fMRI	46	English	Text	Implicit	MNI	7	Tab. 1
Weber et al. (2020)	fMRI	22	English	Sentences	Lines strings	MNI	5	Tab. S5

Wagenmakers (2014).³ These analyses represent a Bayesian implementation of the Binomial Cluster Composition Analysis technique included in the Clustering the Brain (Clu-B) toolbox (Berlinger et al., 2019). For each ROI, 50% and anatomy-weighted frequentist binomial tests were also carried out.

2.4. Computation of the LIs (full dataset)

Activation Likelihood estimation and Bayesian Binomial analyses were complemented by a computation of a LI in all 14 areas of which we explored the functional lateralization during reading. To do so, we used the unthresholded ALE map of the “standard” ALE meta-analysis and we computed (for each

region) the LI by using the AveLI toolbox (Matsuo et al., 2012, 2021) similarly to Trettenbrein et al. (2021). The AveLI represents the magnitude of functional lateralization across the full range of statistical thresholds. In order to match the dimensions of the ALE maps, ROIs were extracted by means of the AAL3 with a spatial resolution of 2 mm³.

2.5. Meta-analytical lateralization of the fusiform gyrus with respect to the rest of the reading network

In order to quantify the relationship between the functional lateralization of the fusiform gyrus and the rest of the reading network at a meta-analytical level, we proceeded as follows. We initially divided the standard meta-analytical dataset into 35 sets, each one corresponding to one of the studies included in the full database. We then used GingerALE to model activation foci, thus producing one unthresholded ALE map for each study. For each map, and for each area included in significant clusters within the “standard” ALE analysis (as for Binomial analyses), we computed the LI by using the AveLI toolbox. The AveLI extracted across studies from the fusiform

³ $BF_{10} < 1/100$: Extreme evidence for H_0 ; $1/100 \leq BF_{10} < 1/30$: Very strong evidence for H_0 ; $1/30 \leq BF_{10} < 1/10$: Strong evidence for H_0 ; $1/10 \leq BF_{10} < 1/3$: Moderate evidence for H_0 ; $1/3 \leq BF_{10} < 1$: Anecdotal evidence for H_0 ; $BF_{10} = 1$: No evidence; $1 < BF_{10} < 3$: Anecdotal evidence for H_1 ; $3 \leq BF_{10} < 10$: Moderate evidence for H_1 ; $10 \leq BF_{10} < 30$: Strong evidence for H_1 ; $30 \leq BF_{10} < 100$: Very Strong evidence for H_1 ; $BF_{10} \geq 100$: Extreme evidence for H_1 .

gyrus was then used as dependent variable in a multiple regression in which the AveLIs from all other reading areas constituted the independent variables. Due to the skewed distribution of the functional lateralization of the fusiform gyrus, a generalized linear model with gamma distribution and logarithmic link function was adopted. As the original range of the AveLI measures (–1 to 1) did not comply with a Gamma distribution due to the presence of negative values, all laterality measures were converted to a [1 2] scale, in which 1 corresponds to a complete left lateralization and 2 to a complete right lateralization. Given the relatively high number of predictors (13) relative to the available data-points (35), we ran a Bayesian-Information-Criterion(BIC)-informed model selection procedure whereby the initial model including all predictors was progressively simplified until the simplest “winning” model was detected. More specifically, at each step N of the model selection procedure we excluded from the model the predictor with the smallest effect (i.e., the minimum absolute t value) and kept the simpler model as long as the Δ BIC between model N–1 and model N was greater than 2 (Fabozzi et al., 2014).

2.6. Lateralization of the reading system across different processing levels

Data from the analysis outlined in paragraph 2.5 was subsequently used as an input in an analysis focussing on the lateralization of the reading system across different

processing levels. In particular, we classified the studies included in the meta-analysis according to the pre-lexical versus word versus sentence/text level of processing depending on the stimuli used in the contrast as reported in Table 1. We only considered studies in which only one stimulus type was used. This yielded 2 studies in the pre-lexical level, 14 in the word level and 13 in the sentence/text level. Given the scarcity of pre-lexical data and the substantial imbalance of the dataset ($\chi^2(2) = 9.600, p = .008$), we focused on the comparison between word and sentence/text level. In this regard, a series of two-samples Wilcoxon tests (this non-parametric test was chosen due to the non-gaussian distribution of data) was performed on the AveLI data of each ROI. Analyses described in Sections 2.5 and 2.6 were conducted in R (v 4.0.3).

3. Results

3.1. “Standard” ALE analysis

This analysis assessed the replicability of the reading networks as “simple effects” and revealed seven clusters of significant spatial convergence across studies (Table 2, Fig. 1).

In particular, the first cluster was left lateralized, and it included the precentral and postcentral gyri, the triangular, opercular and orbital portions of the IFG, the insula and the superior temporal pole. The second left-lateralized cluster

Table 2 – Results of the “Standard” ALE analysis. BA = Brodmann Area. Frontal_Inf_Tri = IFG (triangular portion); Frontal_Inf_Oper = IFG (opercular portion); Frontal_Inf_Orb = IFG (orbital portion); Temporal_Pole_Sup = superior temporal pole; Occipital_Inf = inferior occipital gyrus; Temporal_Mid = middle temporal gyrus; Supp_Motor_Area = supplementary motor area; Parietal_Sup = superior parietal gyrus; Parietal_Inf = inferior parietal gyrus.

Cluster #	x	y	z	ALE	p	Z	AAL3 label	side	BA
1	–46	4	32	.047	<.001	7.083	Precentral	L	44
1	–50	–10	42	.042	<.001	6.550	Postcentral	L	3
1	–50	28	0	.039	<.001	6.259	Frontal_Inf_Tri	L	45
1	–48	14	22	.032	<.001	5.348	Frontal_Inf_Oper	L	–
1	–48	20	18	.029	<.001	4.992	Frontal_Inf_Tri	L	–
1	–40	30	–6	.027	<.001	4.769	Frontal_Inf_Orb	L	47
1	–32	20	4	.027	<.001	4.746	Insula	L	–
1	–52	12	–4	.024	<.001	4.395	Temporal_Pole_Sup	L	38
1	–48	–2	56	.021	<.001	3.949	Precentral	L	6
2	–38	–48	–22	.051	<.001	7.582	Fusiform	L	37
2	–36	–80	–10	.044	<.001	6.831	Occipital_Inf	L	19
2	–40	–56	–18	.035	<.001	5.752	Fusiform	L	37
2	–22	–88	–10	.030	<.001	5.134	Occipital_Inf	L	18
2	–38	–72	–20	.027	<.001	4.796	Cerebellum_Crus1	L	–
2	–40	–66	–18	.026	<.001	4.642	Fusiform	L	19
2	–26	–96	–8	.019	<.001	3.598	Occipital_Inf	L	18
3	–56	–24	–2	.030	<.001	5.161	Temporal_Mid	L	21
3	–56	–28	–2	.030	<.001	5.147	Temporal_Mid	L	21
3	–54	–44	2	.026	<.001	4.596	Temporal_Mid	L	21
3	–48	–36	8	.020	<.001	3.856	Temporal_Mid	L	22
4	–2	2	62	.033	<.001	5.585	Supp_Motor_Area	L	–
4	6	10	52	.019	<.001	3.604	Supp_Motor_Area	R	6
5	28	–90	–4	.035	<.001	5.749	Occipital_Inf	R	18
5	26	–98	–2	.018	<.001	3.579	Occipital_Inf	R	18
6	–28	–60	52	.026	<.001	4.678	Parietal_Sup	L	7
6	–28	–64	42	.022	<.001	4.162	Parietal_Inf	L	7
7	32	20	6	.026	<.001	4.634	Insula	R	–

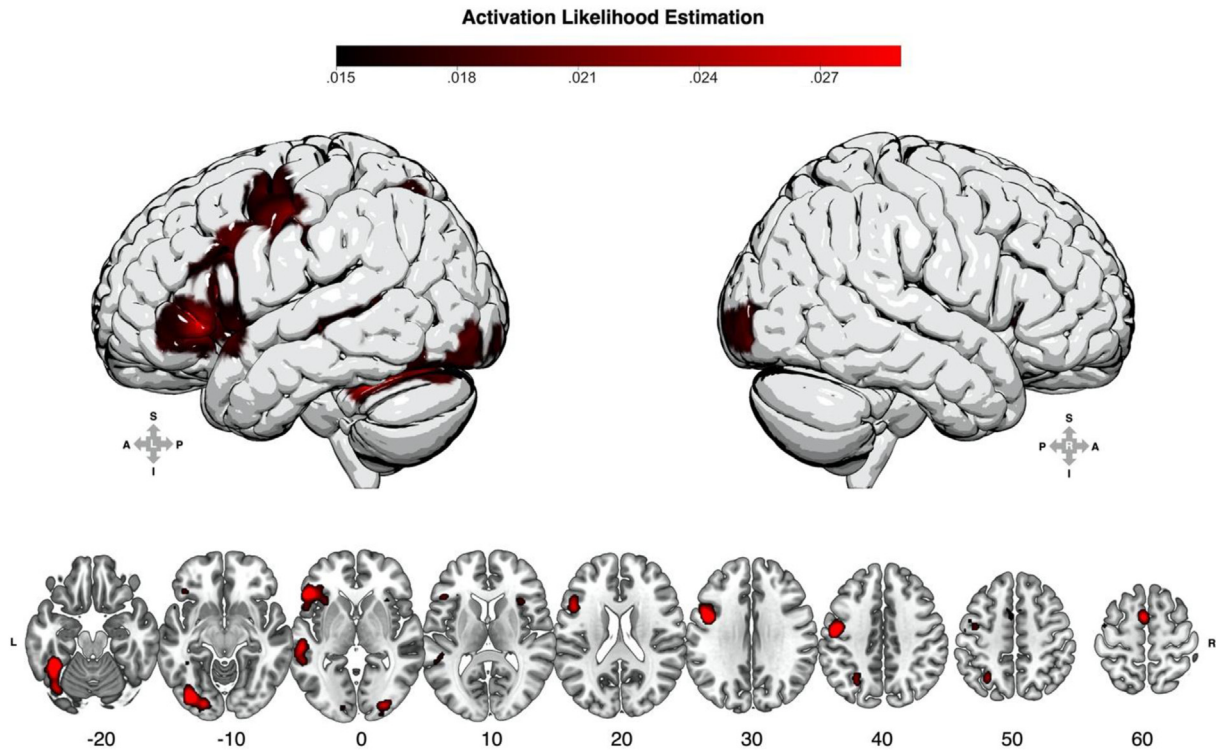


Fig. 1 – Results of the “Standard” ALE analysis. A = anterior; P = posterior; L = left; R = right; S = superior; I = inferior. The numbers located in proximity of the 2D rendering indicate the coordinate along the inferior–superior (z) axis corresponding to the distance in mm from the horizontal origin of the MNI space.

involved the fusiform gyrus, the inferior occipital gyrus and the cerebellum. The third cluster was also left lateralized and it was located in the middle temporal gyrus. The fourth cluster was formed by activation foci located in both the left and right supplementary motor area (SMA). The fifth cluster was located in the right inferior occipital gyrus. The sixth was located in the left superior and inferior parietal gyri, while the seventh cluster was located in the right insula.

3.2. “Standard > Flipped” ALE analysis

The results of the “Flipped” ALE analysis, as well as those of the conjunction analysis between the “Standard” and “Flipped” datasets are reported in [Supplementary Tables S2 and S3](#).

The “Standard > Flipped” analysis revealed 8 significant clusters ([Table 3](#), [Fig. 2](#)): one located in the left precentral/postcentral gyri, one in the left triangular, opercular and orbital portions of the IFG, one located in the left inferior temporal gyrus, one located in the left middle temporal gyrus, one in the left inferior occipital gyrus, one in the left opercular and triangular portions of the IFG, one in the right middle occipital gyrus, and one in the left inferior parietal gyrus.

3.3. ROI-based Bayesian Binomial analyses and LIs

For what concerns analyses that used 50% distribution of L/R foci as a test value for the Bayesian Binomial tests, apart for the insula and the cerebellum (in which anecdotal evidence for a non-lateralized functional pattern was observed), in all other ROIs left lateralization was observed. In particular,

extreme evidence for a left dominance was observed in precentral and postcentral regions, very strong evidence for a left dominance was observed in the triangular portion of the IFG, in the middle temporal gyrus and in the inferior parietal gyrus, strong evidence for a left dominance in the SMA, moderate evidence in the superior temporal pole, and anecdotal evidence in the orbital and opercular portions of the IFG, in the superior parietal gyrus, fusiform gyrus, and in the inferior occipital gyrus.

Bayesian Binomial “anatomy-weighted” analyses (in which the test value was the proportion – for each ROI – of left voxels over the total of left and right voxels) revealed the following results. Once again, the insula and the cerebellum were associated with anecdotal evidence for a non-lateralized functional pattern. Extreme evidence in favour of a left functional lateralization was observed in the precentral and postcentral gyri; very strong evidence for a left functional lateralization was detected in the middle temporal gyrus; strong evidence in the SMA and in the opercular portion of the IFG; moderate evidence in the triangular portion of the IFG, in the fusiform gyrus, in the superior temporal pole, and in the inferior occipital gyrus, and anecdotal evidence in the orbital portion of the IFG, superior and inferior parietal gyri.

The 50% and “anatomy weighted” analyses yielded similar results. However, it is worth noting that, when anatomy was taken into account, evidence towards functional lateralization strengthened in the opercular portion of the IFG, in the inferior occipital gyrus, and in the fusiform gyrus and weakened in the triangular portion of the IFG and in the inferior parietal gyrus.

Table 3 – Results of the “Standard” > “Flipped” ALE analysis. BA = Brodmann Area. Temporal_Inf = inferior temporal gyrus; Occipital_Mid = middle occipital gyrus.

Cluster #	x	y	z	p	Z	AAL3 label	Side	BA
1	-48	-13	48	<.001	4.417	Postcentral	L	–
1	-49	-11	42	<.001	4.265	Postcentral	L	–
1	-50	-14	36	<.001	3.891	Postcentral	L	3
1	-44	2	30	.001	3.056	Precentral	L	44
1	-38	8	30	.001	3.054	Precentral	L	44
1	-42	6	30	.001	3.026	Precentral	L	44
2	-48	36	2	.001	3.253	Frontal_Inf_Tri	L	45
2	-40	28	4	.002	2.948	Frontal_Inf_Tri	L	47
2	-50	10	0	.002	2.896	Frontal_Inf_Oper	L	–
2	-50	16	4	.002	2.891	Frontal_Inf_Tri	L	–
2	-40	34	2	.003	2.788	Frontal_Inf_Tri	L	47
2	-38	34	-6	.004	2.683	Frontal_Inf_Orb	L	47
3	-48	-48	-20	<.001	4.107	Temporal_Inf	L	20
3	-44	-50	-16	<.001	4.013	Temporal_Inf	L	37
4	-54	-42	2	.001	3.279	Temporal_Mid	L	22
4	-50	-42	10	.001	3.230	Temporal_Mid	L	21
5	-38	-82	-10	.002	2.888	Occipital_Inf	L	57
5	-34	-76	-10	.002	2.847	Occipital_Inf	L	57
6	-50	12	12	<.001	3.346	Frontal_Inf_Oper	L	44
6	-44	20	22	<.001	3.339	Frontal_Inf_Tri	L	–
7	30	-92	2	.001	3.179	Occipital_Mid	R	18
8	-30	-66	40	.002	2.811	Parietal_Inf	L	7

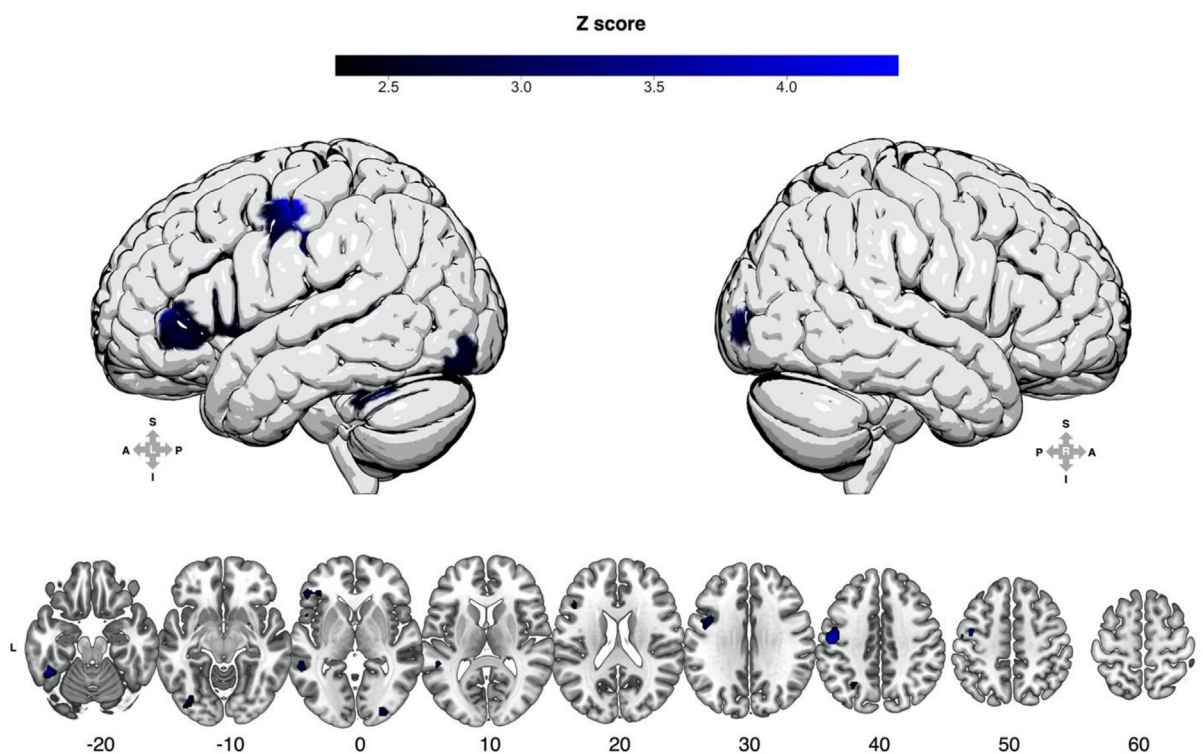


Fig. 2 – Results of the “Standard” > “Flipped” ALE analysis. A = anterior; P = posterior; L = left; R = right; S = superior; I = Inferior. The numbers located in proximity of the 2D rendering indicate the coordinate along the inferior–superior (z) axis corresponding to the distance in mm from the horizontal origin of the MNI space.

Results of the ROI-based Bayesian Binomial analyses, complemented by computation of the AveLI, can be seen in Table 4. In Fig. 3, the BFs (log-transformed, to ease visualization) of the ROI-based Bayesian binomial analyses have been projected onto relevant AAL3 areas.

3.4. Meta-analytical lateralization of the fusiform gyrus with respect to the rest of the reading network and lateralization of the reading system across different processing levels

As Table 5 shows (see also Fig. 4), the multiple regression analysis on the selected model (see Supplementary Table S5 for details on model selection) revealed a significant positive association between the meta-analytical lateralization of the fusiform gyrus during reading and that of the inferior occipital gyrus ($t = 4.403$, $p < .001$) and precentral gyrus ($t = 3.702$, $p = .001$). In addition, a significant negative association was found with the triangular portion of the IFG ($t = -2.883$, $p = .007$) and with the temporal pole ($t = -2.493$, $p = .019$).

To exclude the positive association with the precentral gyrus to be related to spurious activity in the primary motor cortex, we repeated the regression analysis while omitting four studies in which no explicit subtraction of motor activity (i.e., a button press) was present in the contrast of interest. Results (see Supplementary Table S6 for details on model selection and Supplementary Table S7 for results) confirmed the significant association between the functional lateralization of the fusiform gyrus and that of the precentral gyrus ($t = 3.518$, $p = .002$), the inferior occipital gyrus ($t = 5.726$, $p < .001$) and the triangular portion of the IFG ($t = -3.173$, $p = .004$), while the association with the functional lateralization of the temporal pole was no longer significant ($t = -1.679$, $p = .106$).

Descriptive statistics for the meta-analytical laterality measures as used in multiple regressions predicting the functional lateralization of the fusiform gyrus during reading are reported in Supplementary Table S8. Maximum Cook's distance (measuring the impact of outliers in model fit) and Kullback–Leibler R^2 for the models with and without control for hand movements are reported in Supplementary Table S9.

The analysis on the lateralization of the reading system across different processing levels highlighted no significant difference in the functional lateralization pattern during reading between the word and the sentence/text level in any of the ROIs (see Supplementary Table S10).

4. Discussion

The present study was conducted with the aim of characterizing the functional lateralization profile of the reading network. To do so, we first conducted a meta-analytical study on neuroimaging evidence on covert reading in alphabetic languages. In line with previous experimental (see for instance Cohen et al., 2000; Cohen et al., 2002; Howard et al., 1992; Small et al., 1996) and meta-analytical evidence (Cattinelli et al., 2013; Taylor et al., 2013; Turkeltaub et al., 2002; Vigneau et al., 2011), we found a vast set of brain

regions involving an extensive frontal cluster (spanning from the IFG to the more dorsal peri-rolandic cortices, and including the superior Temporal Pole) a vOT cluster (trespassing into cerebellar areas), a parietal cluster, a temporal cluster, and an inferior occipital cluster.

To explore functional lateralization effects at the voxel level, we used the method proposed by Turkeltaub and Coslett (2010), which consists of the comparison between meta-analytical results of the standard dataset with a further meta-analysis in which the x values are flipped after multiplication of x coordinates by -1 (resulting in a left-right inversion). A voxel-wise comparison of the standard versus the flipped meta-analyses returns voxels in which there is a more consistent spatial convergence across studies in one hemisphere compared to the other. This analysis revealed significant results within various left-brain regions: the IFG, the peri-rolandic cortices, middle and inferior temporal cortices, the vOT cortex, and the parietal cortex; in the RH, also a middle occipital cluster was more consistently active than its contralateral counterpart. In order to overcome limitations in voxel-wise comparisons between hemispheres due to latent uncontrolled structural differences (Kong et al., 2018; Toga & Thompson, 2003), we also used a ROI approach to compare the amount of activation foci in the LH and RH, among the set of regions that proved to be consistently activated across studies during reading. This was done by defining the lack of functional lateralization either as a perfect 50% distribution of foci between left and right homologous brain areas, or as a distribution of foci between the LH and RH matching with the size ratio of each pair of contralateral homologous areas. Results of these ROI-based analyses (complemented by the computation of the LIs) unveiled two main aspects of the functional lateralization of the reading network. First, they confirmed that the reading network is broadly left-lateralized; second, they revealed that the brain areas involved in this network are lateralized to a different degree. Of course, given that the present data are based on studies on right-handed participants, the extent to which this lateralization pattern can be found in asexual participants as well is an empirical question that will have to be addressed by future studies.

Still notably, all the present data agree in emphasizing a high degree of left functional lateralization for reading in the IFG and in peri-rolandic cortices. Conversely, a relatively limited left functional lateralization emerged in the fusiform gyrus. Although a few studies exist invoking a potential role for the right fusiform gyrus in reading (Bonandrini et al., 2020; Chu & Meltzer, 2019; Rauschecker et al., 2012) this result looks surprising in light of the role of the VWFA, systematically identified to be in the left fusiform gyrus (see for instance Cohen et al., 2000; Cohen et al., 2002), and accompanied by an equally consistent absence of its RH homologue in formal neural models of reading (Taylor et al., 2013). One possible reason behind this result is the idea that the lateralization of the fusiform gyrus is the result of the interaction between this area and other brain regions involved in language processing (Behrmann & Plaut, 2015; Plaut & Behrmann, 2011). To explore this scenario, a multiple regression analysis was conducted to explore the extent to which the meta-analytical lateralization

Table 4 – Results of the Bayesian Binomial tests conducted on the 14 ROIs. #foci L = number of foci in the left area; #foci R = number of foci in the right area; AveLI = magnitude of functional lateralization across the full range of statistical thresholds (Matsuo et al., 2012, 2021), which ranges from –1 (complete right lateralization) to 1 (complete left lateralization); BF_{10} = Bayes Factor₁₀ (likelihood ratio between the lateralization [H1] and the non-lateralization [H0] hypothesis); $\text{Log}(BF_{10})$ = log-transformed BF_{10} ; anatomical L/(L + R) = proportion of voxels in the left hemisphere for each brain region, according to the AAL3 template. SMA = supplementary motor area. The number of foci indicates how many peaks of activation included in the input database for the “standard” ALE meta-analysis (i.e., after pooling activation foci from all studies in the same dataset) fall in the left and right area of each ROI in the AAL3 atlas. The “anatomical L/(L + R)” value reported for each ROI indicates the ratio between the dimension of the left area and the overall size of the ROI across hemispheres. Values above 50% indicate that the left area is bigger than its right homologue. Values below 50% indicate that the left area is smaller than its right homologue. This metric provides a measure of structural asymmetries and it is used as test value in the anatomy-driven ROI-based binomial tests; Binomial $p_{(\text{uncorrected})}$ = uncorrected p value of the frequentist binomial test; Binomial $p_{(\text{Bonferroni})}$ = p value of the frequentist binomial test after Bonferroni correction for multiple comparisons.

		Frontal Inf Orb	Frontal Inf Tri	Frontal Inf Oper	Insula	SMA	Precentral	Temporal pole sup
Test value: 50%	#foci L	9	32	14	10	20	29	8
	#foci R	3	11	5	5	6	7	1
	AveLI	.735	.802	.689	.268	.472	.673	.774
	BF_{10}	1.432	34.755	2.254	.682	10.796	222.491	5.689
	$\text{Log}(BF_{10})$.359	3.548	.813	–.383	2.379	5.405	1.739
	Interpretation	Anecdotal evidence for H1	Very Strong evidence for H1	Anecdotal evidence for H1	Anecdotal evidence for H0	Strong evidence for H1	Extreme evidence for H1	Moderate evidence for H1
	Binomial $p_{(\text{uncorrected})}$.146	.002	.064	.302	.009	<.001	.039
	Binomial $p_{(\text{Bonferroni})}$	1.000	.028	.896	1.000	.126	.004	.546
Test value: anatomy-driven	Anatomical L/(L + R)	.482	.540	.426	.512	.475	.510	.490
	BF_{10}	1.786	7.310	10.663	.607	22.328	141.302	6.565
	$\text{Log}(BF_{10})$.580	1.989	2.367	–.499	3.106	4.951	1.882
	Interpretation	Anecdotal evidence for H1	Moderate evidence for H1	Strong evidence for H1	Anecdotal evidence for H0	Strong evidence for H1	Extreme evidence for H1	Moderate evidence for H1
	Binomial $p_{(\text{uncorrected})}$.083	.009	.009	.304	.003	<.001	.019
	Binomial $p_{(\text{Bonferroni})}$	1.000	.126	.126	1.000	.042	.005	.266
		Temporal Mid	Postcentral	Parietal Sup	Parietal Inf	Fusiform	Occipital Inf	Cerebellum Crus
Test value: 50%	#foci L	29	20	6	15	27	23	6
	#foci R	8	3	2	2	13	10	3
	AveLI	.732	.733	.715	.746	.503	.439	.343
	BF_{10}	93.680	197.360	1.016	53.542	2.229	2.729	.610
	$\text{Log}(BF_{10})$	4.540	5.285	.016	3.980	.802	1.004	–.494
	Interpretation	Very Strong evidence for H1	Extreme evidence for H1	Anecdotal evidence for H1	Very Strong evidence for H1	Anecdotal evidence for H1	Anecdotal evidence for H1	Anecdotal evidence for H0
	Binomial $p_{(\text{uncorrected})}$.001	<.001	.289	.002	.038	.035	.508
	Binomial $p_{(\text{Bonferroni})}$.011	.007	1.000	.028	.532	.490	1.000
Test value: anatomy-driven	Anatomical L/(L + R)	.528	.504	.482	.645	.478	.488	.496
	BF_{10}	30.018	169.679	1.183	2.317	4.244	3.810	.626
	$\text{Log}(BF_{10})$	3.402	5.134	.168	.840	1.446	1.338	–.468
	Interpretation	Very Strong evidence for H1	Extreme evidence for H1	Anecdotal evidence for H1	Anecdotal evidence for H1	Moderate evidence for H1	Moderate evidence for H1	Anecdotal evidence for H0
	Binomial $p_{(\text{uncorrected})}$.002	<.001	.166	.043	.017	.022	.340
	Binomial $p_{(\text{Bonferroni})}$.028	.007	1.000	.602	.238	.308	1.000

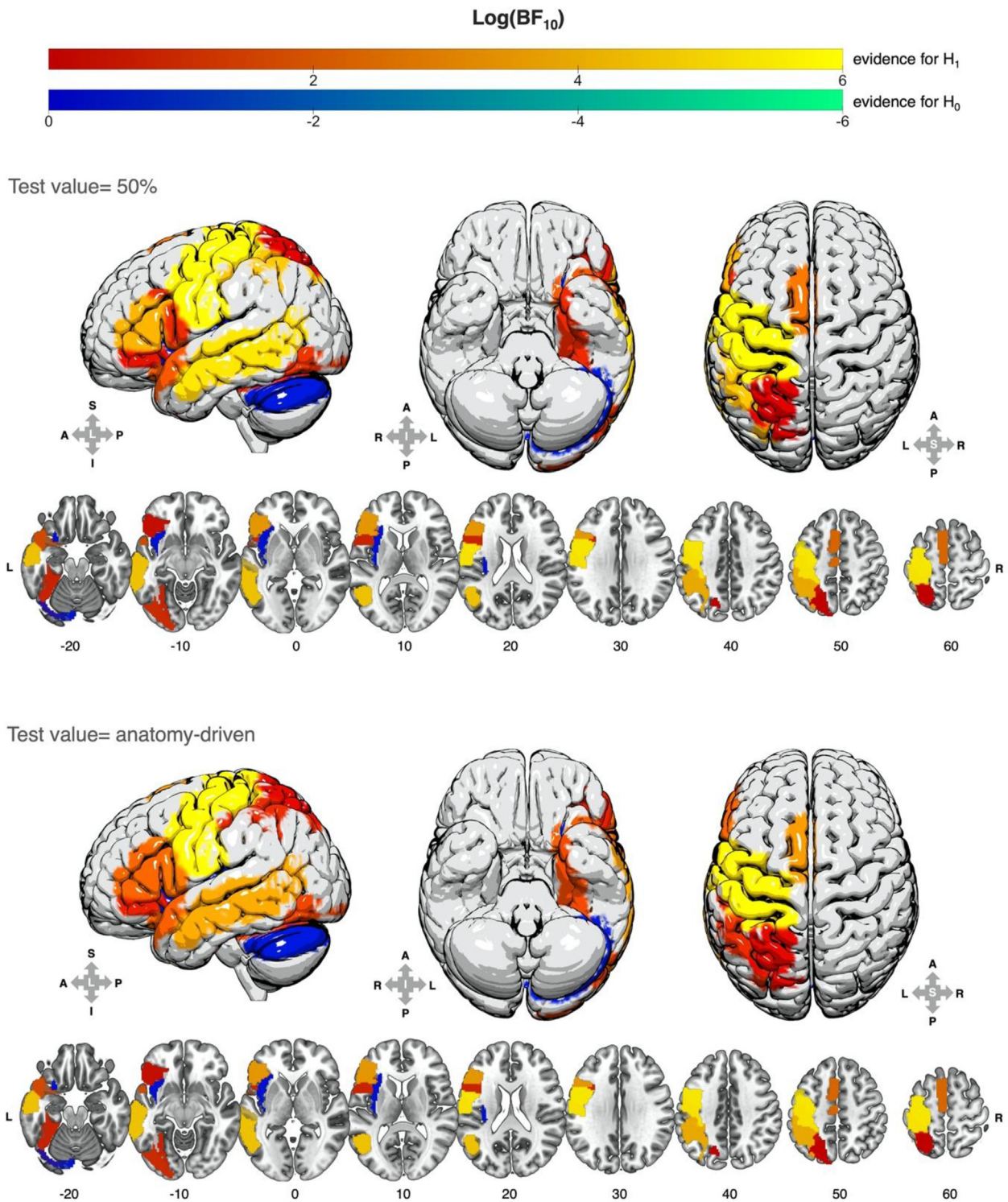


Fig. 3 – Log(BF₁₀) of the 50% (upper row) and “anatomy-weighted” (lower row) Bayesian binomial analyses. The first column shows the left view, the second column shows the inferior view, and the third column shows the superior view of the brain. A = anterior; P = posterior; L = left; R = right; S = superior; I = inferior. The numbers located in proximity of the 2D rendering indicate the coordinate along the inferior–superior (z) axis corresponding to the distance in mm from the horizontal origin of the MNI space.

Table 5 – Results of the multiple regression analysis on the meta-analytical lateralization of the fusiform gyrus during reading.

	Estimate	Std. error	t value	Pr (> t)
(Intercept)	-.698	.226	-3.089	.004
IFG triangular	-.444	.154	-2.883	.007
Inferior occipital	.418	.095	4.403	<.001
Inferior parietal	.319	.164	1.951	.061
Precentral	.610	.165	3.702	.001
Middle temporal	.152	.085	1.784	.085
Temporal pole	-.295	.118	-2.493	.019

of the fusiform gyrus during reading can be predicted by the functional lateralization of the other brain areas included in the reading network. Results from this analysis indicate that, during silent reading, the functional lateralization pattern of the fusiform gyrus is positively associated to that of the inferior occipital gyrus and the precentral gyrus, and negatively associated to that of the triangular portion of the IFG and of the temporal pole.

4.1. The heterogeneous lateralization pattern of the reading network

The most immediate conclusion that can be derived from the present data is the confirmation that (in line with classical and contemporary accounts) the reading network is overall left lateralized. However, our methodology allowed us to go beyond this observation, and report substantial variability in the lateralization patterns of the regions involved in reading. In what follows each degree of lateralization refers to the 50% binomial benchmark (50BB) and to the anatomically-driven (AD) reference values respectively.

In particular, the IFG was associated with an overall mild left-lateralization for both indexes, although with substantial differences between different portions: the orbital portion, which previous literature linked to semantic processing (Binder et al., 2009; Mechelli et al., 2007), yielded only anecdotal evidence towards its lateralization. The triangular portion, instead, turned out to be very strongly lateralized in the 50BB analysis and moderately left-lateralized in the AD analysis. The activity of this portion of the IFG has been interpreted as related to semantic processing (see for instance

Binder et al., 2009; Mechelli et al., 2005; Price, 2012), although not all accounts agree in this interpretation (see for instance Taylor et al., 2013). The opercular portion, instead, was associated with anecdotal (50BB analysis) and strong evidence (AD analysis) towards left-lateralization, respectively. This portion of the IFG, for its part, has been reliably associated with phonological processing (Cattinelli et al., 2013; Fiebach et al., 2002; Mechelli et al., 2005; Paulesu et al., 1993; Vigneau et al., 2006), as well as with the processing of hierarchical and syntactic structures. In particular, the opercular part of the IFG seems to be capable of differentiating between finite state grammars and phrase structure grammars (Friederici, Bahlmann, et al., 2006; Tettamanti et al., 2002), and to be crucial for syntactic operations (Friederici, Fiebach, et al., 2006). Despite the relative anatomical vicinity to the IFG, the insula, often associated with phonological and articulatory coding (Binder et al., 2005; Carreiras et al., 2009; Fiebach et al., 2002; Mechelli et al., 2007; Paulesu et al., 1993), achieved only anecdotal evidence towards a lack of lateralization.

Peri-rolandic areas and the SMA overall showed a very strong left-lateralization, although the “Standard > Flipped” analysis revealed no lateralization in the SMA at the voxel-level. The involvement of motor and premotor regions is not novel in the reading literature and is meant to be related to the preparation of output motor responses (Cattinelli et al., 2013; Price, 2012; Taylor et al., 2013; Turkeltaub et al., 2002).

As for temporal areas, the temporal pole, which is known to be involved both in sentence and semantic processing, showed moderate evidence for left lateralization, while the middle temporal gyrus, involved in phonological, semantic and sentence processing (Cattinelli et al., 2013; Pollack & Ashby, 2018; Price, 2012; Tan et al., 2005; Taylor et al., 2013; Vigneau et al., 2006), was very strongly lateralized.

For what concerns the parietal areas, the superior parietal cortex, whose activation during reading has been interpreted as related to coping with attentional demands (Cattinelli et al., 2013), turned out to be associated only with an anecdotal lateralization pattern. The inferior parietal gyrus, involved in phonological processing and phoneme–grapheme conversion (Cattinelli et al., 2013; Taylor et al., 2013), showed evidence towards a very strong left-lateralization, but only in the 50% binomial analysis.

The fusiform gyrus, which is regarded as a crucial gateway towards orthographic processing (Cohen et al., 2000, 2002; Dehaene et al., 2002) only showed moderate evidence for left

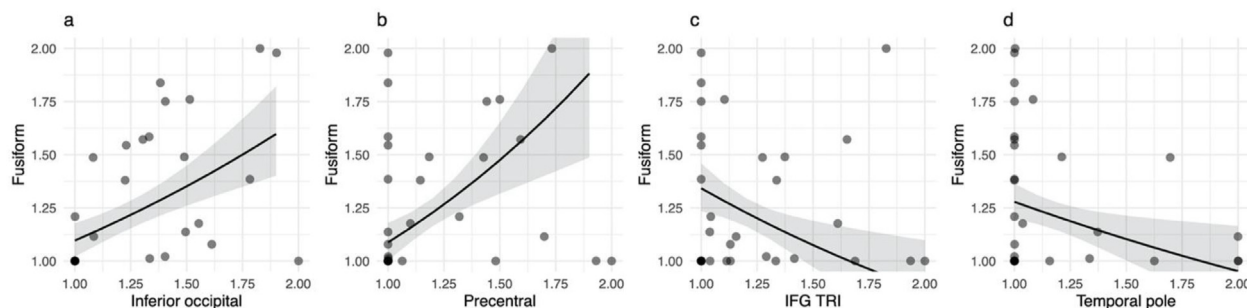


Fig. 4 – Results of the multiple regression analysis: modelled association between the lateralization of the fusiform gyrus and (a) the inferior occipital gyrus; (b) precentral gyrus; (c) triangular portion of the inferior frontal gyrus; (d) temporal pole.

lateralization in the anatomy-weighted binomial analysis. A similar result was observed in the inferior occipital gyrus, that previous literature regards as an area primarily involved in visual analysis (Fiebach et al., 2002; Jobard et al., 2003).

Overall, these findings complement existing models on the neurocognitive underpinnings of reading in the two cerebral hemispheres (see for instance Ellis, 2004; Ellis et al., 1988; Luzzatti, 2003; Luzzatti et al., 1998; Price, 2012), by showing that the lateralization of the reading network is fundamentally heterogeneous (for a similar proposal on language in general, see Parker et al., 2022; 2024).

4.2. RH and reading

In the “Standard” analysis, two right clusters were detected: one in the inferior occipital gyrus and one in the insula. In the “Standard > Flipped” analysis, a right-lateralized cluster was observed only in the middle occipital gyrus. Of course, one trivial possibility would be that the right sided lateralized areas were found only because of irreducible anatomical morphological differences not corrected by the stereotactic normalization. There are no means to exclude this possibility *a priori*, a possibility that is made more plausible by the fact that a right-hemispheric lesion model of the reading process is lacking altogether, if not for the case of neglect dyslexia syndrome typically associated with right parietal lesions. Leaving aside this fundamental reservation, our results seem to suggest that the processes involved in reading do not take place in the LH only, starting from occipital cortices. Previous reading meta-analyses failed to integrate RH activations into an organic description of the functional lateralization of the reading network: either they refrained from proposing any functional significance for these clusters (Jobard et al., 2003; Turkeltaub et al., 2002), or, in the case of fronto-parietal RH clusters, they proposed an explanation of their involvement related to coping with attentional and/or executive task demands (Cattinelli et al., 2013; Murphy et al., 2019; Taylor et al., 2013). This interpretation seems to assume a functional compensation standpoint for the RH involvement during reading, whereby the RH would be engaged during particularly challenging computations to facilitate the job of the LH (see also Reuter-Lorenz & Cappell, 2008). In this case other interpretations might be adopted, depending on alternative assumptions on the nature of RH brain activity during an fMRI reading study. A possibility in this regard might be that RH activations mirror its specific competence for a processing step that is unnecessary in the LH, such as the active inversion of the visual acuity gradient to allow visual processing of letters in an ordered fashion (Whitney, 2001, 2008; Whitney & Lavidor, 2005).⁴ Another possible alternative interpretation of RH activations during reading is one of “challenge-related hyperactivation”. In this case, the RH is considered to be less proficient than the LH in carrying out a specific computation, which is mirrored by greater neural labour in the RH than in the LH. This is in line with recent evidence suggesting that the RH is less proficient than the LH in selectively activating lexical/semantic nodes on the basis of sub-lexical orthographic

cues (Bonandrini et al., 2023). As a final attempt to try and find a latent justification for the right-lateralized clusters, we revised the studies that contributed to them and yet we could not find any specific latent cause (see Supplementary Table S11).

In summary, the present data is insufficient to point towards one specific interpretation for right-lateralized clusters. Most probably, all three frameworks (i.e., compensation, specific competence, challenge-related hyperactivation) contribute to the explanation of RH activations during reading, although differences in their explanatory power may exist across tasks, cognitive operations and brain areas. Future experimental studies focussing on the relationship between RH activation and stimuli features (as well as overall performance) will be able – we believe – to shed further light on this issue.

4.3. Functional lateralization beyond structural lateralization

In order to overcome potential interpretative limitations to our ALE analyses due to hemispheric differences in structural anatomy, we ran two complementary analyses. In particular, we carried out two different sets of analyses to explore functional lateralization patterns at the phenomenal level (test value = 50%), and functional lateralization patterns once size differences between homologue contralateral regions are considered (test value being anatomically driven). Indeed, an apparent functional lateralization phenomenon might be completely accounted for in terms of structural asymmetries. Conversely, a functional lateralization pattern could emerge regardless of structural asymmetries.⁵ It is worthy to note that in most areas the 50% and the anatomy-weighted analyses provided similar results. This suggests that almost all lateralization patterns that can be observed at a phenomenal level (i.e., while not accounting for structural lateralization) are not a mere epiphenomenon of anatomical differences between the two hemispheres. Interestingly, in a few areas the lateralization pattern changed between 50% and anatomy-weighted analyses. Indeed, evidence towards functional lateralization was stronger in anatomy-weighted than in 50% analyses in the opercular portion of the IFG, in the inferior occipital gyrus, and in the fusiform gyrus. This evidence suggests that – if brain areas are considered as functional units regardless of their size – their lateralization is actually stronger than pure observation at the phenomenal level would anticipate. Conversely, weaker evidence for left-lateralization in the triangular portion of the IFG and in the inferior parietal gyrus suggests that functional lateralization patterns described in these areas during reading at the phenomenal level could be – at least partially – explained by anatomical asymmetries.

⁵ It is worthy to note that the relationship between anatomical and functional effects is considered here in adult participants, when the process of acquisition of reading had already terminated. Potential mutual influences between structure and function during the acquisition of reading should not be excluded, but as far as the present data are concerned, they remain unaccounted for.

⁴ For a different interpretation of RH-specific pre-lexical processing during reading, see Ellis (2004) and Ellis et al. (1988).

Results in the fusiform gyrus are of particular interest. Indeed, our data suggest that left lateralization in this area is relatively limited. Of course, we cannot *a priori* exclude that the apparent lack of functional lateralization of the fusiform gyrus is due to the partial inability of the studies included in the present meta-analysis to fully capture – within the anatomical boundaries of the fusiform gyrus – the exact location of the VWFA, which shows wide spatial variability across subjects (Glezer & Riesenhuber, 2013). Still, the observation of a stronger lateralization pattern when anatomical differences between the left and right area are taken into account suggests that the magnitude of the lateralization process occurring in this area is still notable.

To the best of our knowledge, this is the first meta-analytical account of functional lateralization that has tried to disentangle phenomena that can be accounted for in terms of anatomical differences from those that are independent from structural laterality. Yet, the interpretation of the present results can vary depending on how the relationship between structure and function in the brain is conceived.

One possibility in this direction is to consider a given function as “predicted by” its underlying structure (see for instance Honey et al., 2010). The corollary of this view might be that structural asymmetries come first, and functional asymmetries follow. In line with this view, brain areas whose functional lateralization gain strength when structural asymmetries are accounted for (i.e., their effect is ruled out) could indicate a lateralization process more rooted in functional interactions than in anatomy. This interpretation, if applied to the lateralization pattern of the fusiform gyrus, is directly related to Pierre Marie (1897)’s observations, suggesting that the visual word form system develops as a result of functional interactions, rather than being biologically determined (Dehaene et al., 2015).

However, the assumption of “structure predicting function” appears intuitively simplistic. Available literature indicates genetic influences on both structural and functional asymmetries (Duboc et al., 2015), with both structural and functional asymmetries being observable since early development (Bisiacchi & Cainelli, 2022). Also, research on adult participants suggests a dynamic interplay between structure and function (see for instance Draganski et al., 2004; Maguire et al., 2000). In light of this evidence, a more parsimonious interpretation entails that brain areas whose functional lateralization gain strength when structural asymmetries are accounted for (as in the case of the fusiform gyrus) indicate a lateralization process that is independent from the interactions between anatomy and function that determine structural differences between hemispheres.

Regardless of the type of assumption adopted to interpret the different results of the 50% and the anatomy-weighted analyses, it is evident that the functional lateralization of the fusiform gyrus during reading is more related to a dynamic interplay with other brain regions, than to structural asymmetries. To further explore the functional interactions between the lateralization of the fusiform gyrus and other areas in the reading network, evidence from the regression analysis will be discussed below.

4.4. The (graded) functional lateralization of the fusiform gyrus

The involvement of the left fusiform gyrus in reading has been extensively described (see for instance Montant & Behrmann, 2000), and interest towards this area surged after the description of a part of this anatomical structure as the “visual word form area” (Cohen et al., 2000, 2002; Dehaene et al., 2002). This region, which is part of the ventral visual stream, is also known to be involved in object recognition (Fiebach et al., 2002; Price & Devlin, 2003), Braille reading (Büchel et al., 1998; Reich et al., 2011), and in the processing of signed language (Emmorey et al., 2011, 2016; Trettenbrein et al., 2021).

For this reason, its apparent specialization and lateralization has captured the interest of neuroscientists. It has been argued that the specialization of the fusiform gyrus represents the outcome of a process through which neurocognitive resources originally supporting other processes, are *adapted* or *recycled* in order to carry out orthographic processing (Dehaene & Cohen, 2007; Marie, 1897). This view is also supported by the observation that illiterate adults can still efficiently learn to read and write at any time during their life; that is to say, the acquisition of reading is not constrained by developmental windows such as for certain aspects of spoken language (Dehaene et al., 2010). In ontogenetic terms, it has been proposed that the lateralization of the fusiform cortex may depend on the progressive association between visual processes (which have, in principle, little reason to be lateralized) and language-specific modules (which tend to be already left-lateralized before reading is acquired; see for example Dehaene-Lambertz et al., 2002). This would lead to a *graded* lateralization of the fusiform gyrus, due to the progressive lateralization of all the chain of sub-processes necessary to efficiently decode a written string (Behrmann & Plaut, 2015; Plaut & Behrmann, 2011). The evidence from our regression analysis is compliant with this hypothesis: the functional lateralization of the fusiform gyrus during reading turned out to be positively associated with the lateralization of the precentral and inferior occipital gyri. In addition, a negative association was found between the functional lateralization of the fusiform gyrus and that of the triangular portion of the IFG and of the temporal pole. The precentral gyrus is known to be involved in motor/articulatory processes (Price, 2012; Ripamonti et al., 2018). This qualifies the precentral gyrus as an ideal candidate to guide the *graded* lateralization of the reading network. Still, the precentral gyrus also hosts the primary motor cortex, so it could be that such association simply represents spurious motor activity in the precentral gyrus. In this regard, to exclude that motor activity could explain this effect, we repeated the regression analysis while omitting four studies in which no explicit subtraction of motor activity (i.e., a button press) was present in the contrast of interest. Results were identical, with the only exception of the temporal pole, whose association with the functional lateralization of the temporal pole turned out to be no longer significant.

The inferior occipital gyrus is known for its involvement in visual processing (Fiebach et al., 2002; Jobard et al., 2003). Yet, caution is needed when considering the relationship between

the functional lateralization of the fusiform gyrus and that of the inferior occipital gyrus. Indeed, the activation of these two areas across studies converges in the same meta-analytical cluster (see Table 2) and the present data are insufficient to discern functional association from the mere spatial vicinity.

For what concerns the negative association between the functional lateralization of the fusiform gyrus and that of the triangular portion of the IFG and of the temporal pole, we interpreted this apparently puzzling finding as related to the possibility that – for the sake of the efficiency of the reading network – the computations (i.e., semantic processing; Binder et al., 2009; Price, 2012) run by these areas benefit from a distributed, bilateral pattern of activation (e.g., Coslett & Saffran, 1992; Luzzatti, 2003; Luzzatti et al., 1998; Rice et al., 2015). This result suggests that the transition between orthographic and semantic processing is characterized by hemispheric redundancy. Yet, although it cannot be excluded that this result is due to complex hemispheric inhibition versus cooperation patterns related to the involvement of different commissures (i.e., the callosum and the anterior commissure, that connects the temporal poles; Catani & Thiebaut De Schotten, 2008), we believe that this result will need to be explored in depth by future studies. This is particularly true for what concerns the temporal pole, whose effect on the functional lateralization of the fusiform gyrus turned out to be no longer significant after controlling for possible hand movements.

More broadly, it is important to consider that our data do not allow inferences on whether the influences on the functional lateralization of the fusiform gyrus reflect the endpoint of the process with which reading is acquired (and therefore are relatively static within each participant), or rather they mirror online feedback and feedforward processes of cross-talk between regions. If the former scenario were true, then the functional lateralization of the reading system might potentially be regarded as a fingerprint of the ontogenetic development of the language system in the brain. If the latter case were true instead, then it's possible to hypothesize that the temporary modulation of the activity of one region could affect the performance of participants in lateralized reading tasks. Future brain stimulation studies may contribute to shed light to these issues, as well as to explore a causal link between the lateralization of the brain areas described above.

It is worth noting that in our analysis on the lateralization of the reading system across different processing levels no significant difference in the functional lateralization pattern during reading between the word and the sentence/text level was detected in any of the ROIs. This finding would suggest that the functional lateralization of the regions involved in the reading network is relatively stable regardless of the type of processing level. Still, we cannot exclude that this ancillary analysis may lack statistical power. This possibility, paired with the data from Vigneau et al. (2011) suggesting variability in lateralization profiles for lexical/semantic and text/sentence processing across a variety of tasks, and data suggesting differences in lateralization of orthographic processing in natural and fixed-gaze conditions (e.g., Nárai et al., 2022; Weiss et al., 2022) call for a very cautious interpretation of this finding. With particular reference to the effect described by Weiss et al. (2022), it is possible that neuroimaging techniques

may not be best suited to capture it. Yet, potential lateralization effects related to the presence versus absence of eye movements during reading should be considered carefully in future studies.

Still, given the bias towards maximising spatial resolution at the expense of temporal resolution of functional neuroimaging techniques, the question remains as to whether the results presented here in the spatial domain can be mirrored by similar meta-analytical findings in the time domain. In this regard, data from invasive, EEG and MEG recordings (see for instance Schwartz et al., 1996; Nárai et al., 2022; Barca et al., 2011; Chu & Meltzer, 2019) – and in particular meta-analytical work – could complement the present findings by providing details on the temporal underpinnings of reading-related lateralization effects.

As a final remark, it is worth highlighting that although the present meta-analysis is based on data from healthy participants, results may inform novel research exploring the lateralization of reading in the case of acquired and developmental dyslexia. Available evidence has suggested the involvement of the RH in reading after a LH brain insult (Bartolomeo et al., 1998; Bartolomeo & Thiebaut de Schotten, 2016; Bonandrini et al., 2020; Coltheart, 1980; Saffran & Coslett, 1998; Saffran et al., 1980), in lateralized reading after surgical disconnection of the corpus callosum (Baynes et al., 1992; Gazzaniga & Hillyard, 1971; Levy & Trevarthen, 1977; Reuter-Lorenz & Baynes, 1992; Zaidel, 1983), as well as reduced functional lateralization relative to healthy participants in developmental dyslexia (Brambati et al., 2006; Helenius, 1999; Mahé et al., 2012, 2013; Paulesu et al., 2001; Paz-Alonso et al., 2018; Richlan et al., 2009, 2011; Weiss et al., 2022), partially assumed to be due to RH compensatory processes (e.g., Liu et al., 2021). Although the exact underlying mechanisms are still unclear, the functional lateralization pattern described in the present meta-analysis allows to speculate that a rightward shift in brain involvement during reading in the case of reading difficulties is most likely to take place in regions showing a relatively limited functional lateralization (i.e., occipital areas, fusiform gyrus), as in these regions a relatively low degree of competition with the contralateral homologous area must be resolved.

5. Conclusions

Reading relies on a collection of left-lateralized areas. The present meta-analytical evidence suggests that the degree of lateralization of these areas varies considerably: the functional lateralization of perirolandic areas is prominent, while that of the fusiform cortex (often regarded as the gateway to the reading system) is more elusive.

Overall, the present data highlight how lateralization patterns differ within the reading network. Furthermore, the results of a regression analysis indicate that the functional lateralization of the fusiform gyrus during reading is associated with that of the precentral gyrus, inferior occipital gyrus, temporal pole, and the triangular portion of the IFG. This brings support to the hypothesis that the functional lateralization of the fusiform gyrus during reading might be positively related to the degree of functional lateralization of

visual input areas and phonological output areas. Our results further complement this framework, by suggesting that the lateralization of the temporal pole and of the triangular portion of the IFG (which are involved in semantic processing) is inversely related to that of the fusiform gyrus.

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Data availability statement

The data and materials used in this study are available at: <https://osf.io/f85t9/>.

Open practices

The study in this article has earned Open Data badge for transparent practices. The data studies are available at: <https://osf.io/f85t9/>.

CRedit authorship contribution statement

R. Bonandrini: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis. E. Gornetti: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. E. Paulesu: Writing – review & editing, Writing – original draft, Supervision.

Declaration of competing interest

The authors declare no competing interests.

Supplementary data

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