



# Is human face recognition lateralized to the right hemisphere due to neural competition with left-lateralized visual word recognition? A critical review

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## Abstract

The right hemispheric lateralization of face recognition, which is well documented and appears to be specific to the human species, remains a scientific mystery. According to a long-standing view, the evolution of language, which is typically substantiated in the left hemisphere, competes with the cortical space in that hemisphere available for visuospatial processes, including face recognition. Over the last decade, a specific hypothesis derived from this view according to which neural competition in the left ventral occipito-temporal cortex with selective representations of letter strings causes right hemispheric lateralization of face recognition, has generated considerable interest and research in the scientific community. Here, a systematic review of studies performed in various populations (infants, children, literate and illiterate adults, left-handed adults) and methodologies (behavior, lesion studies, (intra)electroencephalography, neuroimaging) offers little if any support for this reading lateralized neural competition hypothesis. Specifically, right-lateralized face-selective neural activity already emerges at a few months of age, well before reading acquisition. Moreover, consistent evidence of face recognition performance and its right hemispheric lateralization being modulated by literacy level during development or at adulthood is lacking. Given the absence of solid alternative hypotheses and the key role of neural competition in the sensory–motor cortices for selectivity of representations, learning, and plasticity, a revised language-related neural competition hypothesis for the right hemispheric lateralization of face recognition should be further explored in future research, albeit with substantial conceptual clarification and advances in methodological rigor.

**Keywords** Neural competition · Faces · Words · FFA · VWFA

## The right hemispheric lateralization of human face recognition

Face recognition, defined here as *the reliable production of selective responses to faces*,<sup>1</sup> is extremely important for social interactions in the human species. We rely on facial cues to readily and automatically recognize, and sometimes act upon, someone's emotion, direction of attention through eye gaze and head orientation, gender, age, ethnical origin and identity, as well as to make social judgments of, e.g., dominance, attractiveness and trustworthiness (Bruce and

Young 1998; Perrett 2012; Todorov 2017). This facial recognition ability evolves during development without formal training (i.e., it is a *naturally developed* ability) and ultimately constitutes what is arguably the richest (visual) recognition function in neurotypical human adults.

The dominance of the right hemisphere (RH) in human face recognition was initially evidenced by lesion studies, showing that *prosopagnosia*, a category-selective

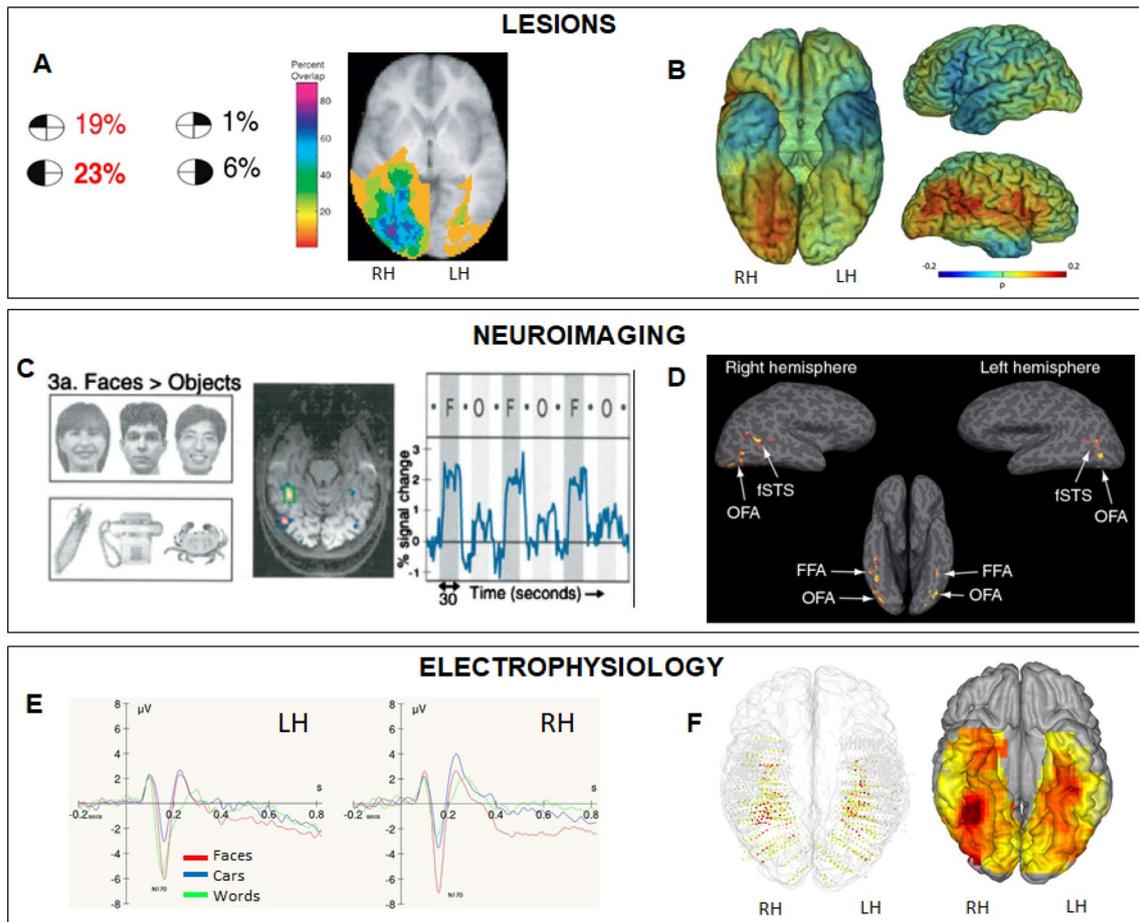
<sup>1</sup> In psychology, the term “recognition” is often used to refer to the judgment of previous occurrence (specifically “*the ability to identify information as having been encountered before*”, APA Dictionary of Psychology; see also Mandler 1980). In psychological research on human faces, the term is even often restricted to the judgment of a previous occurrence of specific *identities* of faces (i.e., familiar faces). Here it is used in a more general biological sense as the reliable production of selective (i.e., differential) responses to sensory inputs at different levels, ranging from the recognition of a visual stimulus as a face (“generic face recognition”) to its specific identity (“face identity recognition”) or its emotional expression (“emotional facial expression recognition”).

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**Fig. 1** Various illustrations of the RH dominance in human face recognition, with lesions studies (**A**, **B**), neuroimaging (**C**, **D**) and electrophysiology (**E**, **F**). **A** Left: there is a higher percentage of patients with prosopagnosia associated with left as compared to right visual field defects (19 vs. 1% in the upper visual field; 23 vs. 6% in both the upper and lower visual fields), indicating predominant lesions in the right as compared to the left VOTC (original observation by Hecaen and Angelergues 1962; here from the sample of Bouvier and Engel 2006); Right: overlap of lesions causing prosopagnosia, from Bouvier and Engel 2006; see also Cohen et al. 2019). **B** Probability maps associated with deficits at matching pictures of unfamiliar faces in a classical neuropsychological test (201 brain-damaged participants; Tranel et al. 2009; Positive (negative) values in the color bar indicate a greater (lower) proportion of participants with a lesion and a deficit among those with a deficit. Note the larger involvement of right as compared to left VOTC structures, but also for the lateral

neurological deficit of face identity recognition (FIR) (Bodamer 1947; see Rossion 2018a for a recent review) was most commonly associated with left upper visual field defects, typical of a right ventral occipito-temporal lesion (Hécaen and Angelergues 1962; Meadows 1974; Bouvier and Engel 2006; Fig. 1A). Although bilateral lesions are most commonly observed in cases of prosopagnosia (Damasio et al. 1982), damage to the RH is necessary, and can be sufficient, to cause the impairment (e.g., Landis et al. 1986; De Renzi

occipito-temporo-parietal junction around the posterior temporal sulcus. **C** Face-selective responses in fMRI are larger in the RH than the LH. Illustration of the so-called “Fusiform Face Area” (FFA), from Kanwisher et al. 1997, usually identified by comparing blocks of face stimuli (F) to object (O) stimuli. **D** Illustration of the network of face-selective regions in the VOTC and superior temporal sulcus (STS), from Kanwisher and Yovel (2006). **E** ERP findings illustrating the larger N170 amplitude in the RH for faces and in the LH for written words. Hemispheric asymmetry is not observed for pictures of cars (from Rossion et al. 2003). **F** Mapping of selective responses to faces measured with a frequency-tagging approach in intracerebral recordings in a large sample of individuals, showing a larger amplitude (red color) to faces in the RH, in particular the right lateral section of the middle fusiform gyrus (from Jonas et al. 2016; see also Hagen et al. 2020)

et al. 1991; Sergent and Signoret 1992; Bouvier and Engel 2006; Barton 2008; Cohen et al. 2019). Besides these rare cases of prosopagnosia,<sup>2</sup> group studies of brain-damaged

<sup>2</sup> The definition of prosopagnosia used here does not include cases of developmental disorders at FIR in the absence of neurological history, which are often referred to as *developmental prosopagnosia* or *congenital prosopagnosia* (Behrmann and Avidan 2005; Duchaine and Nakayama 2006), but more correctly as *prosopodysgnosia* (Rossion 2018b; Sorensen and Overgaard 2018).

patients have generally shown that lesions in the posterior region of the RH often disrupt FIR (as typically tested with tasks requiring the discrimination and matching of unfamiliar faces for their identity), while a similar lesion in the left hemisphere (LH) usually leaves this function intact (Benton and Van Allen 1968; De Renzi 1986; Newcombe et al. 1989; Tranel et al. 2009; Fig. 1A, B). Following lesion studies, behavioral experiments performed in neurotypical individuals with lateralized visual stimulation, including chimeric stimuli made of two left or right halves of the same face identity, have also shown RH advantage in FIR (Rizzolatti et al. 1971; Levy et al. 1972; Gilbert and Bakan 1973; Kolb et al. 1983; Hillger and Koenig 1991; Yovel et al. 2003; Brederoo et al. 2020).

From the 1990s, functional neuroimaging (initially positron emission tomography, PET; then functional magnetic resonance imaging, fMRI) studies of the human brain revealed bilateral occipito-temporal activity, with a larger amplitude in the RH than LH, to the presentation of face stimuli and to the difference in signal between faces and other visual forms (i.e., face-selective responses; Sergent et al. 1992; Puce et al. 1996; Kanwisher et al. 1997; McCarthy et al. 1997; for more recent studies: Rossion et al. 2012; Zhen et al. 2015; Frassle et al. 2016; see also Yovel et al. 2008 for a link between behavioral and neural right hemispheric dominance) (Fig. 1C, D).

Initial electroencephalographic (EEG) studies did not report RH advantage of selective event-related potentials (ERPs) to faces (Bötzel and Grüsser 1989; Jeffreys 1989; although see Srebro 1985), probably for methodological reasons (e.g., linked mastoid references, lack of low temporal electrodes and a focus on central electrodes for analysis; see Joyce and Rossion 2005). However, subsequent ERP studies consistently identified a face-selective occipito-temporal potential, the N170, which is generally larger in the RH than LH (Bentin et al. 1996; for review: Rossion and Jacques 2011) (Fig. 1E). More recently, electrophysiological studies using fast periodic visual stimulation (frequency-tagging<sup>3</sup>) have objectively isolated and quantified face-selective responses (Rossion et al. 2015) or FIR responses (Liu-Shuang et al. 2014; Rossion et al. 2020) in the EEG frequency domain, systematically showing a right

hemispheric advantage in terms of amplitude over occipito-temporal brain regions.

In the same vein, initial intracranial, electrophysiological, low-frequency-band responses (“local field potentials”) to faces in patients with epilepsy refractory to medication were also described in occipito-temporal regions of both hemispheres, without any report of hemispheric lateralization (Allison et al. 1994; Halgren et al. 1994; see also e.g., Vidal et al. 2010 for bilateral face-selective broadband high frequency ‘gamma’ activity). However, more recent intracranial recordings of large samples of individual brains with a frequency-tagging approach have also now demonstrated larger face-selective responses in the right as compared to the left ventral occipito-temporal cortex (VOTC) (Jonas et al. 2016; Hagen et al. 2020; Jacques et al. 2020) (Fig. 1F). Finally, causal studies with transcranial magnetic stimulation (TMS) (Pitcher et al. 2007) and especially intracranial electrical stimulation (Jonas et al. 2012; Rangarajan et al. 2014) have corroborated the RH dominance of face recognition. Strikingly, up till now, cases of transient impairment in FIR following intracerebral electrical stimulation have been observed in various VOTC regions, but only in the RH (Jonas and Rossion 2021).

According to this brief summary, decades of observations across a wide variety of methodologies have provided overwhelming evidence for the RH advantage in (category-selective) response to faces, or to FIR measures, in the human adult brain. In some studies, this RH lateralization has been quantified, showing for instance a 2.3-fold increase of face-selective amplitude in intracerebral recordings of the lateral section of the middle fusiform gyrus of the RH as compared to the LH (Jonas et al. 2016; Fig. 1F).

Despite the long-standing scientific interest in hemispheric lateralization of function (Broca 1865; Gazzaniga 1967; Geschwind and Levitsky 1968; Bradshaw and Nettleton 1981) and the biological and social importance of face recognition for humans, the factors driving the RH lateralization of this latter function remain largely mysterious. In the present review, we focus specifically on a current, influential hypothesis according to which the RH lateralization of face recognition is due to neural competition in the left hemisphere with the representation<sup>4</sup> of letter strings (Behrmann and Plaut 2015, 2020; Dehaene et al. 2010, 2015).

<sup>3</sup> Fast periodic visual stimulation or “frequency-tagging” in EEG is a technique in which stimuli are presented at a (usually fast) periodic rate, leading to neural responses expressed in the EEG frequency spectrum (Regan 1966). This technique has considerable advantages in terms of sensitivity and objectivity of measurement (see Norcia et al. 2015; Rossion et al. 2020 for reviews).

<sup>4</sup> The term ‘representation’ as used here refers merely to (a pattern of) activity in the neural system that has a systematic relationship with a sensory stimulus of the environment. Although the term ‘representation’ has sometimes been used in neuroimaging in the restrictive context of multivariate pattern analysis (Kriegeskorte et al. 2008), the neural activity does not have to be distributed across spatial units such as voxels (e.g., larger neural activity to faces than non-face stimuli in the right lateral middle fusiform gyrus as a whole “represents” face stimuli).

In the next section (Sect. 2), we briefly put this hypothesis in context and summarize the key principles upon which it rests. Next, evidence in favor or against this hypothesis is evaluated in depth (Sect. 3), before briefly discussing complementary or alternative views of RH lateralization of faces and directions for future research on this scientific issue (Sect. 4).

## Is human face recognition right-lateralized due to left language lateralization?

Why is face recognition right-lateralized in the human brain? While various hypotheses have been advanced, usually in terms of dichotomies of preferential stimuli or processes between the LH and RH (e.g., verbal vs. pictorial; local vs. global; analytic vs. holistic; high vs. low spatial frequencies; coordinate vs. categorical spatial relationships, respectively; see Bradshaw and Nettleton 1981; also Sergent 1988; Farah 1990 and Sect. 3 of the present review), it has long been proposed that right-lateralized functions of the human brain, such as face recognition, occur merely as a consequence of the well-established LH lateralization of the language function (Lhermitte et al. 1972; Gazzaniga and Ledoux 1978; Corballis and Morgan 1978; Ellis 1983). For instance, LeDoux (1983) explicitly proposed that visuospatial skills in the occipito-temporo-parietal junction could be primarily mediated by brain areas of the right hemisphere because of the opposite left hemispheric region being taken over by language in humans (i.e., Wernicke's area). According to this view, many right hemispheric advantages, including face recognition, are mere consequences of invasion of the left hemisphere by language (and praxis) skills in humans (Ellis 1983; Corballis 1983, 1991; see also Gotts et al. 2013).

Regarding face recognition, this view appears to be supported at a general level by contrasting observations of RH lateralization between humans and other animal species, which are devoid of language. Indeed, while there are a few reports of RH lateralization in the behavioral processing of face stimuli in non-human animal species (e.g., in macaque monkeys: Hamilton and Vermeire 1983, 1988; Vermeire et al. 1998; in sheep: Peirce et al. 2001; in chimpanzees: Dahl et al. 2013), the data are weak and rather controversial (Overman and Doty 1982; Doty et al. 1999). Moreover, evidence for RH lateralization of face recognition at the neural level in non-human species is very weak (in sheep: Peirce and Kendrick 2002), contradictory (e.g., in macaques: Perrett et al. 1988 vs. Zangenehpour and Chaudhuri 2005) and more often non-existent (see also Chance et al. 2013, showing microstructural asymmetry in the middle fusiform gyrus of humans but not chimpanzees). In particular, the macaque monkey, widely considered in the neuroscientific community as the best available animal model to understand human

visual recognition, including face recognition (DiCarlo and Cox 2007; but see Rossion and Taubert 2019), shows no sign of RH lateralization in terms of face-selective responses as recorded in fMRI (e.g., Tsao et al. 2008) or in neurophysiology (Perrett et al. 1988). As put forward already in an early review of RH lateralization of human face recognition "... this suggests that lower primates may be entirely bilateral in their processing of faces, and provide circumstantial evidence for the idea that any symmetry found in human subjects may have arisen as a result of language development in the dominant hemisphere. The evolution of a language processor situated usually in the left hemisphere may have reduced the available space in that hemisphere for processing visuospatial information, including faces" (Ellis 1983, p. 58).

Building upon these initial views, a more specific language-related hypothesis has been advanced over the last decade regarding the RH lateralization of human face recognition: that it is due to neural competition with the selective visual representation of letters and words in the LH, in particular in the left VOTC (Dehaene et al. 2010, 2015; Behrmann and Plaut 2015, 2020). That is, during reading acquisition, populations of neurons in the left VOTC, essentially in the left middle fusiform gyrus, would become selective to letter strings,<sup>5</sup> because of spatial constraints due to proximity with other language functions in the left hemisphere in the majority of humans (Posner and Carr 1992; Jacobs and Jordan 1992; Behrmann and Plaut 2015), preferential connectivity to language-related structures (Saygin et al. 2016; Stevens et al. 2017; Bouhali et al. 2014; Li et al. 2020; Hanagan et al. 2015; Lerma-Usabiaga et al. 2018; Ekstrand et al. 2020; Bedny 2017), high-resolution foveal representation (Hasson et al. 2002; Gomez et al. 2018), and/or because of initial tuning of this brain tissue for sensitivity to line junctions and high spatial frequencies<sup>6</sup> (Szwed et al. 2011). Due to competition for cortical space, selectivity to faces initially supported by both left and right homologous VOTC regions, would be reduced in the LH, therefore relying increasingly on RH structures (Dehaene et al. 2010; Behrmann and Plaut 2020). Hence, reading acquisition would

<sup>5</sup> In the remainder of the text, we will typically use the term 'letter strings' as a general term that encompasses words (e.g., familiar written forms), non-words (unmeaningful strings of letters), or even consonant strings. The distinction is relevant given the debate of whether the visual word form area (VWFA) processes only pre-lexical (McCandliss et al. 2003) or also lexical representations (Glezer et al. 2009, 2015; Kronbichler et al. 2004).

<sup>6</sup> Note that the spatial frequency hypothesis is not supported by training studies on reading acquisition with atypical visual shapes (such as faces or houses) differing greatly from the natural script characteristics, but also revealing the left middle fusiform gyrus as the site of learning effects (Moore et al. 2014; Hirshorn et al. 2016; Martin et al. 2019).

directly *cause* RH lateralization for faces. Here, we will refer to this hypothesis as the reading-induced Lateralized Neural Competition hypothesis (the reading-LNC hereafter).

Besides the long-standing language-related view for a right hemispheric advantage in non-language functions including face recognition (Gazzaniga and LeDoux 1978; Corballis and Morgan 1978; Ellis 1983; Corballis 1991) and empirical evidence from experiments that have been designed to test it specifically (as reviewed in the next section), this currently influential reading-LNC hypothesis, according to which right hemispheric lateralization for face recognition would have emerged only over the past thousands of years in *Homo sapiens*, rests on four key principles. First, the well-established evidence that, in line with the language function in general, the LH is dominant in visual recognition of letters and words in most adult individuals (Gazzaniga et al. 1965; Newcombe et al. 1989; Rizzolatti et al. 1971; Farah 1990; early neuroimaging evidence: Petersen et al. 1988; Puce et al. 1996; EEG: Salmelin et al. 1996; Tarkiainen et al. 1999; Rossion et al. 2003; lesion studies: Déjerine 1891; Hillis et al. 2001; Hillis et al. 2005; but see Olulade et al. 2020 for fluctuations of hemispheric lateralization of language during development). Second, the relatively more recent definition of neighboring category-selective representations of visual letter strings and faces in the adult VOTC, in particular in the middle fusiform gyrus of the LH, where a brain region responding selectively to letter strings, the so-called Visual Word Form Area (VWFA) is found in the vicinity of the left FFA (usually slightly laterally; Cohen et al. 2002; Cohen and Dehaene 2004; McCandliss et al. 2003; Kronbichler et al. 2004; Devlin et al. 2006; Davies-Thompson et al. 2016; Kubota et al. 2019) (Fig. 2). Third, that face and visual word recognition would share important functional characteristics, such as the requirement of high-resolution foveal representations (Hasson et al. 2002) as well as both part-based and holistic representations (e.g., Martelli et al. 2005; Wong et al. 2019). Fourth and finally, neural competition as a general principle of brain function, namely the view that sensory inputs (or motor outputs) sharing functional characteristics compete for the same populations of neurons in the cerebral cortex (Edelman and Finkel 1985; Edelman 1987), this competition being mediated by synaptic excitation and inhibition, and forming the basis of selectivity, learning and cortical plasticity (Merzenich et al. 1988; Zhang et al. 2003).

## A systematic evaluation of the lateralized neural competition hypothesis

The main prediction of the reading-LNC hypothesis is that there is a causal, unidirectional, link between LH lateralization for letter strings in the VOTC and RH lateralization

for faces (Dehaene et al. 2010, 2015; Behrmann and Plaut 2015, 2020). That is, RH lateralization for faces would emerge because of the LH specialization for letter strings in the VOTC, and would be further modulated during development and across the lifetime by reading acquisition and improvement.

A secondary prediction is that face recognition would *change* with letter-string selectivity. On the one hand, this change would be expressed at a *quantitative* level, i.e., a diminution in performance. Specifically, the ability to recognize letter strings (literacy) would cause “small losses in perceptual and cognitive abilities due to competition of the new cultural ability with the evolutionarily older function in relevant cortical regions” (Dehaene and Cohen 2007). On the other hand, under the view that the right and left hemispheres differ in terms of the types of processes/representations involved in visual recognition (e.g., holistic vs. analytic, respectively; de Moraes et al. 2014; Farah 1990; Ivry and Robertson 1998; Sergent 1982a, b), there should be a *qualitative* alteration of face recognition (e.g., increase in holistic representation).

Below, we evaluate the data supporting the first prediction (RH shift of face recognition) and the second prediction in turn.

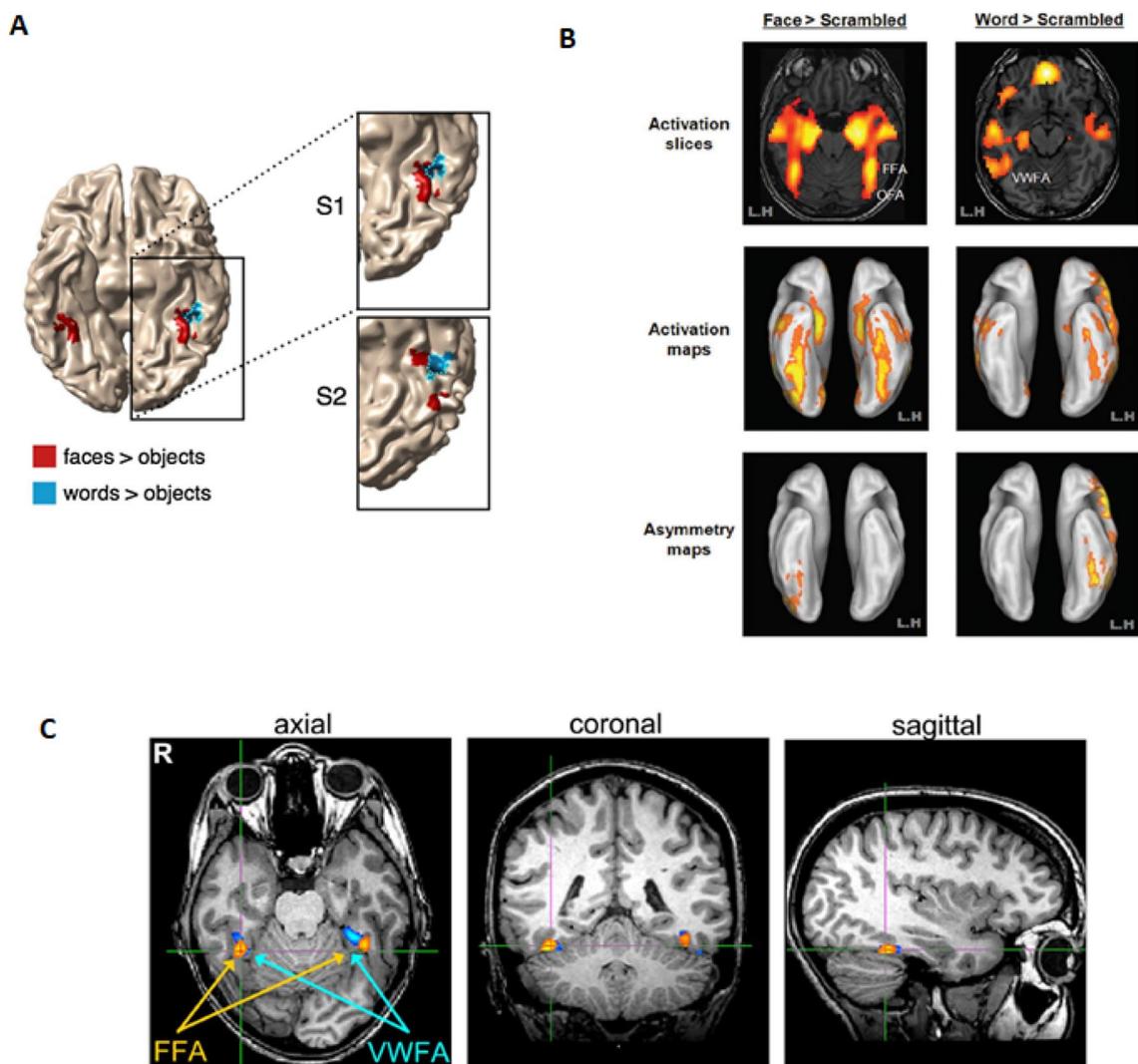
## Does letter-selectivity in the left hemisphere cause the right lateralization of face-selective responses?

### Impact of variable literacy levels at adulthood

At the root of the reading-LNC hypothesis, an influential fMRI study compared groups of Portuguese and Brazilian illiterate adults, ex-illiterate (who learnt to read at adulthood) and literate adults, reporting a larger LH specialization for letter strings in the left fusiform gyrus with increasing levels of literacy (Dehaene et al. 2010). Since this effect was accompanied by a relatively smaller response to faces in the same region in literates (Dehaene et al. 2010), the headline of that study, which has generated substantial experimental studies and reviews, was that “the gain of function appeared to occur at a cost—the area in the temporal cortex devoted to face processing shrank” (Dehaene et al. 2010)<sup>7</sup>. Critically, a relatively larger response to faces was also reported in the RH in literates compared to illiterates (Dehaene et al. 2010), providing apparent support for the hypothesis evaluated in the present review.

While literacy undoubtedly causes profound changes in brain structure and connectivity beyond neural responses to print (Castro-Caldas et al. 1999; Carreiras et al. 2009; Skeide et al. 2017; Thiebaut De Schotten et al. 2014) and

<sup>7</sup> <https://science.sciencemag.org/content/330/6009/1359>.



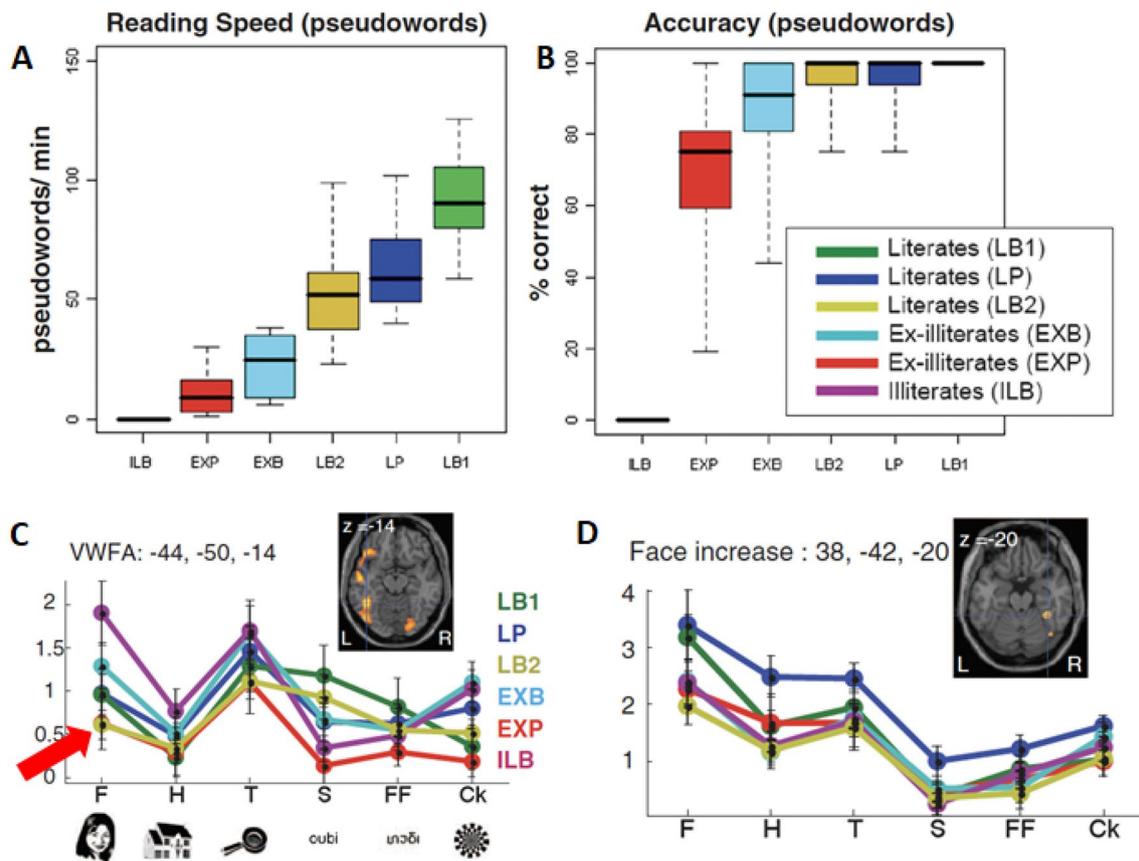
**Fig. 2** Illustration of the respective localizations of the VWFA and FFA in fMRI. **A** Selective responses to faces and written words in Kubota et al. (2019), showing a slightly more lateral selective response to written words than faces in the middle fusiform gyrus; **B** Brain regions responding to faces and words against scrambled stimuli are represented as activation slices (top row), projected on

an inflated brain (middle row), with an illustration of the asymmetry between hemispheres in the bottom row (from Pinel et al. 2015). **C** Axial, coronal and sagittal views of regions responsive to words and faces in a single individual (against their scrambled control stimuli) in Davies-Thompson et al. (2016)

may enhance early visual responses to non-linguistic stimuli (Pegado et al. 2014a, b), a careful analysis indicates that the right hemispheric shift of neural face representation claimed in the fMRI study of Dehaene et al. (2010) does not rest on solid evidence. First, as the authors themselves acknowledged, the lower response to faces in literates induced by the expansion of orthographic representations in the left fusiform gyrus was ‘small’ (abstract) or ‘modest’ (p. 1361), given that the results of the regression with reading performance (assessed by the number of words read per minute) measured independently was actually marginal (Dehaene et al. 2010). Second, this decrease did not occur at the peak of the FFA but only on the weakest face-selective voxels

at the edge of the region (e.g., a 6–8 voxel radius). Third, the decrease was not specific to faces: it was also observed for another type of stimuli, houses (Dehaene et al. 2010, Fig. S6 of the study). Fourth, the decrease of response to faces in the LH was unrelated to reading performance (e.g., besides illiterates, a group of ex-illiterates with the lowest reading performance had the lowest response to faces in the left fusiform (VWFA); Dehaene et al. 2010; Fig. 3 and Fig. S2 of that study; see Fig. 3 below).

Finally, and perhaps most importantly, as also acknowledged by the authors, the relative increase in the RH (shown by positive correlations between reading scores and RH responses) was not specific to faces (i.e., occurred also for



**Fig. 3** (Adapted from Dehaene et al. 2010). Above **A**, **B**: reading performance of the six groups of participants (Literates are from Brazil (LB) or Portugal (LP), differentiated according to their socio-economic status: LB1 are not matched while LB2 are matched to Illiterates (ILB). Ex-illiterates (EX) who learned to read at adulthood and are distinguished per country (B or P). Illiterates (ILL) are all from Brazil; see also supplementary material S1 of the original study). Note the relatively low performance of Portuguese ex-illiterates (EXP) who, accordingly, also had the lowest neural response to letter strings (S) and false fonts (FF) in the defined left VWFA (in **C**).

houses) and was related to the type of living neighborhood (rural/urban) rather than to literacy: “Notably, however, face and house increases were found neither when we compared illiterates with their socio-economic status-matched literate group” (Fig. 3) (Dehaene et al. 2010, p. 1362). This finding is in line with subsequent evidence that being exposed to larger hometowns population size affects not only performance in face-learning tasks (Balas and Saville 2017) but also face-selectivity of the N170 (Balas and Saville 2015), thereby showing the influence of experience with faces—rather than literacy—on behavioral and neural face recognition.

In summary, a careful look at the study of Dehaene et al. (2010), which included only 10 complete illiterates with important differences in their demographic characteristics or attempts to attend alphabetization classes (Huettig and

Despite this, their response to faces was among the lowest in this region (see also supplementary Fig S2. of the original study), against the hypothesis of reading-induced lateralized neural competition. **D** The increase to faces in the right hemisphere was found mainly in the right anterior fusiform gyrus, in a more anterior and medial region than the FFA, and essentially concerned participants living primarily in urban areas (in blue and green) regardless of their schooling and reading scores. Illiterates do not differ from the other three groups of literates tested

Mishra 2014) does not provide evidence that literacy causes a RH shift or increase of face-selective representation in the VOTC.

Subsequently, a smaller sample of the participants from the fMRI study was tested in EEG by Pegado et al. (2014a), also claiming for an increase of RH lateralization for faces in proportion to the participants’ reading ability. Despite this, the relationship between literacy and the face-selective N170 lateralization was non-significant (and in the opposite direction as predicted,  $r = -0.07$ ) and there was no hemispheric difference on the amplitude of this component between literates and illiterates. Instead, the authors’ conclusion was based a source space analysis of EEG data, showing a non-significant marginal increase of responses to faces with literacy in the RH ( $r = 0.23$ ) at around 168 ms post-stimulus onset, as well as a decrease in the LH ( $r = -0.25$ ),

leading to a trend for a relationship between literacy scores and RH lateralization for faces ( $r = -0.28$ ) at this latency. However, literacy also led to a large *enhancement* for faces in the same localized region in the LH only at a later time-course (Fig. 4 of Pegado et al. 2014a, b), and whether these effects were due to increased visual experience with faces rather than literacy as in Dehaene et al. (2010) was not evaluated. In line with these two studies, a longitudinal fMRI single-case study over the course of literacy acquisition (Braga et al. 2017) reported a slight decrease in face-selective responses near the VWFA site in the LH, but there was no correlation between time (i.e., reading improvement) and activation to faces in either of the two hemispheres, and no observable increase for faces in the RH.

Most recently, a recent large-scale fMRI study compared neural responses of illiterate/literate adults to letter strings and faces, reaching a different conclusion than Dehaene and colleagues (Hervais-Adelman et al. 2019). This latter study included 91 participants of different literacy backgrounds (31 of them being completely illiterate), finding no evidence for hemispheric displacement of selective responses to other categories (including faces). In contrast, while literacy enhanced responses in the left fusiform gyrus for letter strings, it also enhanced visual responses to other categories, including faces. In fact, literacy correlated significantly with increased *left-lateralized* responses to faces (Hervais-Adelman et al. 2019). Admittedly, the acquisition of an alphasyllabic script in this study, which is more complex at the visuo-spatial level than the alphabetic script used in the studies of Dehaene et al. (2010) and Pegado et al. (2014a, b), may have played a role in these results (since responses to reading are more bilateral). However, while literacy indeed increased neural responses both in the left VWFA and its homolog region in the right hemisphere, correlation with literacy was significant only in the left hemisphere. Moreover, and importantly, there was no negative correlation between literacy and the extent of voxels responding to faces or other visual stimuli, thereby showing no shrinkage—and no displacement—of neural tissue responding to those other categories with reading acquisition.

Overall, we conclude from our critical evaluation of studies comparing literate and illiterate adults that they do not support the reading-LNC hypothesis of RH lateralization of face recognition.

### Infant studies

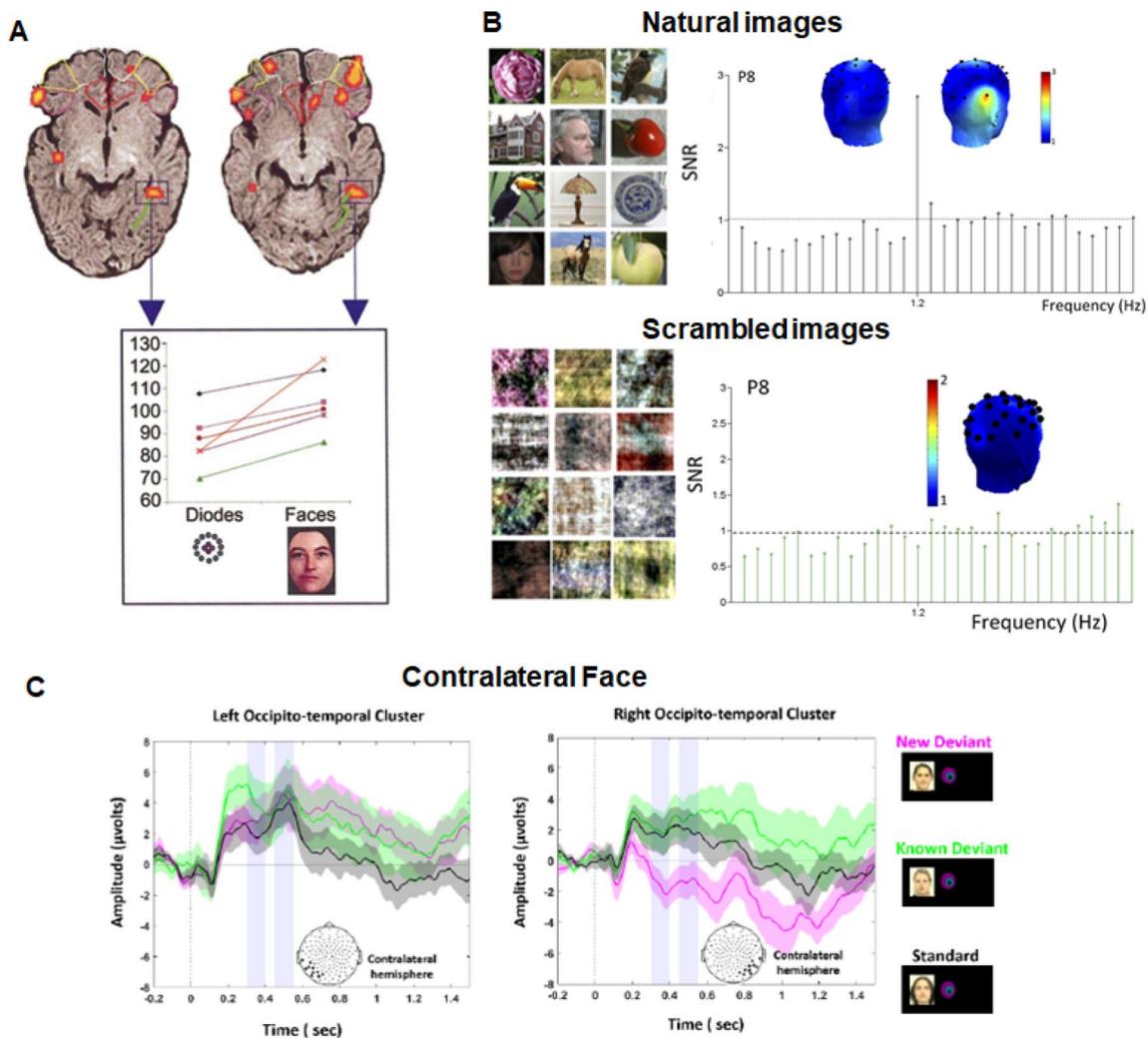
While cognitive neuroscience studies contrasting illiterates to literates are very interesting, some illiterate adults have been exposed to print in specific contexts throughout lifetime (mainly in urban areas), potentially leading to (proto-)specialization of cortical responses for these stimuli. This is much more unlikely for young infants, who show sensitivity

from birth to the general visual characteristics of face stimuli (Goren et al. 1975; Johnson et al. 1991; Turati and Simion 2002) and are intensely exposed to faces during the first months of life (Sugden et al. 2014). Therefore, a key question is whether there is evidence of RH lateralization for faces in infants, well before exposure to print and reading acquisition.

On the one hand, EEG studies using a standard event-related potential (ERP) approach have not reported hemispheric differences to face stimulation, or differences in responses to faces with other visual stimuli (cars, toy pictures), in infants of a few months old (de Haan and Nelson 1999; Gliga and Dehaene-Lambertz 2007). For instance, the N290 component evoked by faces and often considered to be a precursor of the adult N170, is associated with a medial occipital (rather than lateralized, occipito-temporal) scalp topography. In the same vein, a latter face-sensitive N400 component in infants is not lateralized (de Haan et al. 2003, for review). More recently, Deen et al. (2017) studied face and non-face stimuli in 4–6-month-old infants with fMRI, claiming to identify category-selective regions with a spatial organization similar to adults but with no hint of a RH lateralization for face stimuli. However, with the use of only a few uncontrolled (movie) stimuli in that study, no clear face-selective responses were recorded in the infant VOTC (possibly due to a low quality of fMRI signal, with only 9/22 infants displaying sufficient low-motion for inclusion in the analyses), making it not reliable enough to assess the question at stake.

On the other hand, against the prediction of the lateralized neural competition hypothesis, several observations relying on lateralized visual stimulation suggest that the RH lateralization for faces is already present in a few months old infants. For instance, 4–9 months of age children saccade faster towards their mother's face than a stranger's face when these pictures are presented in the left visual field (LVF) but not in the right visual field (RVF), and they also learn to recognize unfamiliar faces faster in the left than the right hemifield (de Schonen et al. 1986; de Schonen and Mathivet 1990). Also, in 1- to 5-month-old infants, new/deviant faces inserted in a stream of standard faces are discriminated (as attested by larger N290 and weaker N400 EEG amplitudes) only when face stimuli appear in the LVF (Adibpour et al. 2018; Fig. 4C). In line with these observations, early deprivation of visual input for several months (between 6 weeks and 3 years) to the right but not the left hemisphere causes atypical FIR at adulthood (Le Grand et al. 2003).

With neuroimaging, a positron emission tomography (PET) study of six 2- to 3-month-old infants looking at unknown female faces reported a significantly larger response to faces than a simple visual control stimulus in the right but not in the left middle fusiform gyrus (Tzourio-Mazoyer et al. 2002; Fig. 4A). Moreover, functional



**Fig. 4** **A** Results from Tzourio-Mazoyer et al. (2002). In a PET-study, 2–3-month-old infants show greater responses to faces than simple control stimuli in the middle fusiform gyrus of the RH and not in the LH. **B** Results from the EEG study of de Heering and Rossion (2015). 4–6-month-old infants viewed 20 s sequences of stimulation where images were presented at 6 Hz. Highly variable images of faces occurring every five stimuli generate a category-selective response at 1.2 Hz in the RH only. The EEG spectrum and 3D scalp topography of the frequency-tagged response for faces (i.e., generic face recognition) are displayed on the top panel (experiment 1 of the original study), a response that is not driven by low-level cues

near-infrared spectroscopy (fNIRS) studies have shown a significant RH advantage for faces over other visual stimuli in 5- to 8-month-old infants (e.g., Otsuka 2014; for review). Unfortunately, while these observations support the view that the RH lateralization for faces occurs at an early age, they are generally limited since they do not measure face-selective (i.e., differential) neural activity, or do so using inappropriately matched control stimuli (e.g., Tzourio-Mazoyer et al. 2002; Fig. 4A).

as shown by its absence (below) for phase-scrambled versions of the stimuli (experiment 2). Note that the 1.2 Hz response for natural images is already face-selective, with the common visual response to faces and non-face objects appearing at a 6-Hz base rate frequency in the EEG spectrum over bilateral medial occipital sites (not shown here; see e.g., de Heering and Rossion 2015). **C** Results from Adibpour et al. (2018). In 2.5–5-month-old infants, ERP responses to the detection of a new deviant face presented in the contralateral hemisphere generate an individual discrimination response only in the right hemisphere

In this context, the report of a face-selective EEG response predominantly over the right occipito-temporal cortex already at 4–6 months of age (de Heering and Rossion 2015; Fig. 4B) arguably constitutes the strongest evidence to date against the reading-induced lateralized neural competition hypothesis evaluated here. Indeed, thanks to the frequency-tagging approach used in that study (see also Fig. 5A, “Generic Face Recognition” sequence), the robust face-selective response is isolated from a common bilateral response to faces and objects. Moreover, the potential

contribution of low-level visual cues as contained in the amplitude spectrum of the highly variable natural images is ruled out by the absence of face-selective response to phase-scrambled versions of these images (Fig. 4B; de Heering and Rossion 2015). The strong right lateralization of the face-selective response over occipito-temporal channels obtained in 27 infants across two experiments in the original study has been replicated in three recent studies of 4 months old tested with a different stimulus set (Leleu et al. 2020; Rekow et al. 2020, 2021), providing consistent data in more than 100 infants tested in total. Importantly, in all these studies, the common neural activity to face and non-face objects that is frequency-tagged at a base rate of 6 Hz leads to a *bilateral* medial occipital response in infants, ruling out an alternative account of the RH lateralization of the face-selective response in terms of general advantage to all visual stimuli at that age due to, e.g., attentional factors or a spatial frequency bias (Behrmann and Plaut 2020).

Overall, even considering that hemispheric lateralization from EEG responses on the scalp cannot be inferred with certainty,<sup>8</sup> the findings in infancy described above cast strong doubt on the view that human RH lateralization of face recognition is (initially) *caused* by neural competition with letter strings in the LH. However, providing that the RH lateralization of face-selective response in infancy is not permanent, they do not rule out a subsequent *modulation* of RH lateralization with active exposure to print (i.e., reading acquisition) at later stages of development. This issue is reviewed and discussed in the next section.

### Developmental studies in kindergartners and school-aged children

**Lateralization of face-selectivity** Interestingly, the very same EEG frequency-tagging paradigm as used in infant studies above elicits a completely *bilateral* face-selective response in preschool children (Lochy et al. 2019, 2020) (Fig. 5C) and even in 8–12-year-olds (Vettori et al. 2019; Fig. 5C). Likewise, there is no significant hemispheric lateralization of the N170 in response to faces in children of various age groups until late adolescence (Dundas et al. 2014; Kuefner et al. 2010).

<sup>8</sup> Technically, a response recorded over EEG electrodes positioned over the RH could potentially be generated from sources in the LH, although this is unlikely for the focal occipito-temporal response as displayed in Figs. 4 and 5

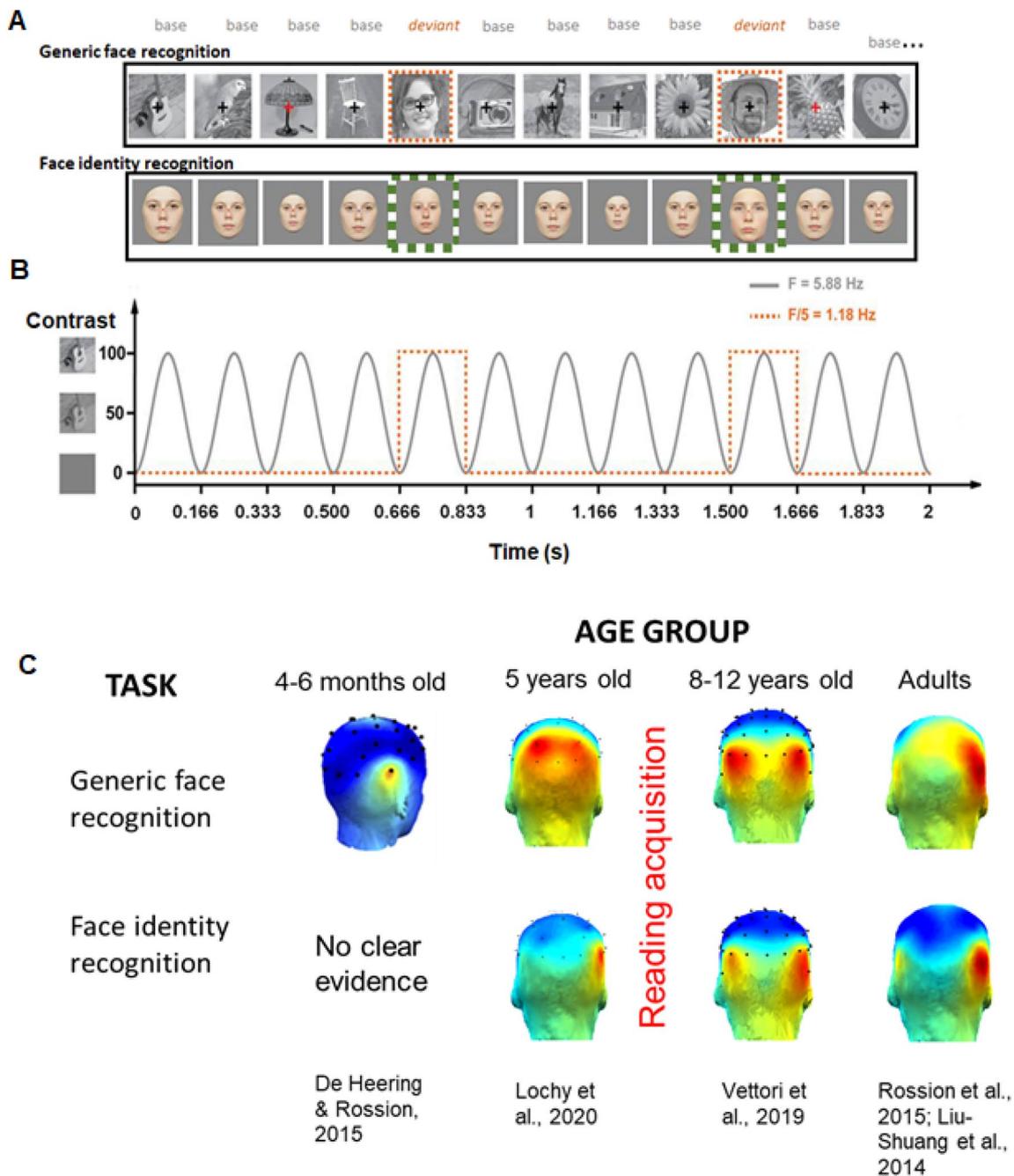
. Due to the undetermined inverse problem in EEG (or MEG), source localization algorithms applied to such data would not enable substantial progress on this issue. However, testing an adapted frequency-tagging paradigm with functional near-infrared spectroscopy (e.g., slowing down the face stimulation frequency as in fMRI, see Gao et al. 2019), recording neural signals under the sampled area, could provide decisive evidence.

These EEG results are in line with strictly bilateral face-selective fMRI responses observed in 5–9-year-old children (Golarai et al. 2007; Scherf et al. 2007; Natu et al. 2016; Hildesheim et al. 2020). In older children, face-selective regions in the VOTC (and superior temporal sulcus, STS) progressively enlarge with small, if any, right lateralization effects (7–11 years old, Gathers et al. 2004; Golarai et al. 2007; Peelen et al. 2009; Natu et al. 2016) that become clear only at adolescence (Cohen Kadosh et al. 2011; Joseph et al. 2011). While these observations are usually taken as supporting a (slow, gradual) effect of literacy on RH lateralization for face recognition (Behrmann and Plaut 2015, 2020), a number of fMRI studies report RH dominance for faces already in young children (4 years old: Cantlon et al. 2011; 6 years old: Centanni et al. 2018; Dehaene-Lambertz et al. 2018; Fig. 6; Feng et al. 2021; 8–10 years old: Monzalvo et al. 2012).

In the same vein, experimental findings in children tested with divided visual field stimulation are inconsistent across studies. For instance, while relatively recent divided visual field presentation studies reported no LFV/RH advantage for face recognition in children (7–9 years old) or teenagers (Dundas et al. 2012, 2014), early studies with this technique reported RH lateralization for faces already at the earliest age tested (5 years old), without any evidence of an increase of this effect at later stages of development (Ellis 1983 for review).

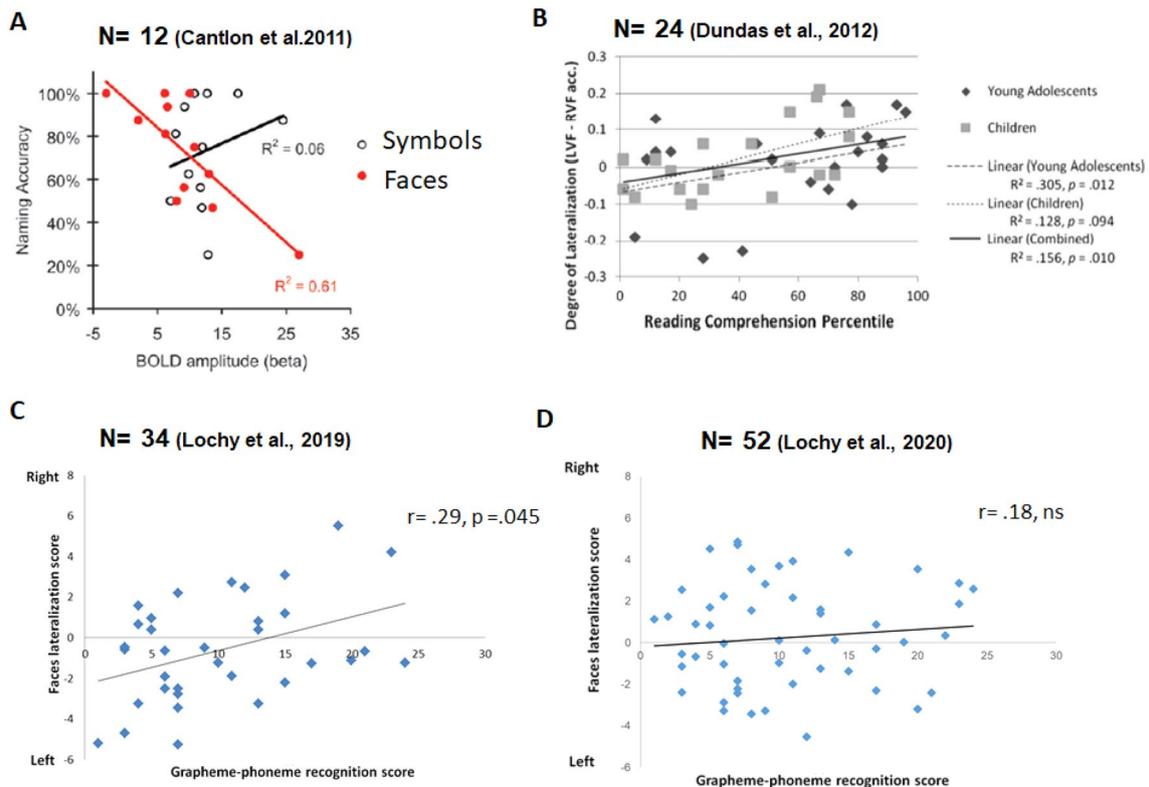
**Correlations between face- and word-selective neural responses** The reading-LNC hypothesis predicts a *positive* correlation during development between LH lateralization for words and RH lateralization for faces, with a negative correlation between faces and words in the LH. Surprisingly, few studies have directly addressed these predictions, with mixed outcomes. Specifically, a fMRI study in 6-year-old children reported a reduction in the volume of face-selective responses in the left VOTC ( $r = -0.34$ ) with increased selective responses to letter strings (Centanni et al. 2018). However, since neural category-selectivity is defined in that study by directly contrasting faces and letter strings (Faces > Letters and Letters > Faces), this result is trivial and cannot be taken as supporting the competition hypothesis. Indeed, if responses to letters increase, the contrast Faces > Letters will automatically lead to weaker responses to faces. In any case, the increase in “letter-selectivity” in the LH did not lead to a significant increase of “face-selectivity” in the RH (Centanni et al. 2018).

With EEG recordings, Li et al. (2013) reported a strong negative correlation between the word N170 left-lateralization (amplitude left–right) and the face right-lateralization (amplitude right–left) ( $r = -0.51$  with  $N = 81$ ): the more left-lateralized word N170, the *less* right-lateralized face N170. While the authors interpreted this observation in favor of the



**Fig. 5** Frequency-tagging paradigms for face recognition and scalp topographies of responses across different age groups. **A** Example of visual stimulation sequences. Top row: Generic face recognition, where base stimuli are constituted of non-face objects, interspersed every 5 items with highly variable images of faces (various identities, viewpoints, ...) (from de Heering and Rossion 2015; Rossion et al. 2015). Second row: face identity recognition, where a base unfamiliar face identity is repeated throughout the sequence with random variations of size, and different identities are inserted every five stimuli. **B** Stimuli flicker on the screen at 6 Hz (6 stimuli per second) with

a sinusoidal contrast modulation, with faces or different identities inserted every 5 stimuli (1.2 Hz). **C** Topographical representation of selective responses on the back of the head in different age groups across studies. Top row: generic face recognition with RH responses in infants (De Heering and Rossion 2015), and bilateral responses at 5 years old (Lochy et al. 2019, 2020) and 8–12 year-old children (Vettori et al. 2019). Bottom-row: face identity recognition, with no clear evidence identified in infants so far in this paradigm, but RH dominant responses found from 5 years old onwards (Lochy et al. 2020; Vettori et al. 2019; Liu-Shuang et al. 2014)



**Fig. 6** Relationships between reading abilities and lateralization for faces. **A** The results from Cantlon et al. (2011), in 4–5-year-olds, show a negative relationship between naming accuracy (single letters and digits) and the BOLD response for faces in the LH. The correlation is based on 12 data points only, with a clear outlier on the bottom right driving the significant effect. **B** Dundas et al. (2012) found a small correlation in teenagers ( $N=25$ ) between RH lateralization

for faces derived from accuracy in divided visual field stimulation and reading comprehension percentile. In **C**, **D** Lochy et al. (2019, 2020) tested generic face recognition with EEG frequency-tagging in 5-year-old children, finding a small positive correlation between reading score and lateralization score with 34 children. However, the correlation was no longer significant when adding participants to reach a sample of 52 children (2020)

lateralized neural competition hypothesis, from our understanding, it actually goes against the view that the emergence of LH lateralization for words would *increase* RH lateralization for faces. Finally, in another fMRI study using a classifier approach, there was no relationship between the word classification in the left VOTC and the face classification in the right VOTC, or between their laterality indexes, suggesting independent development of category-selective neural responses to faces and written words in this region (Nordt et al. 2021).

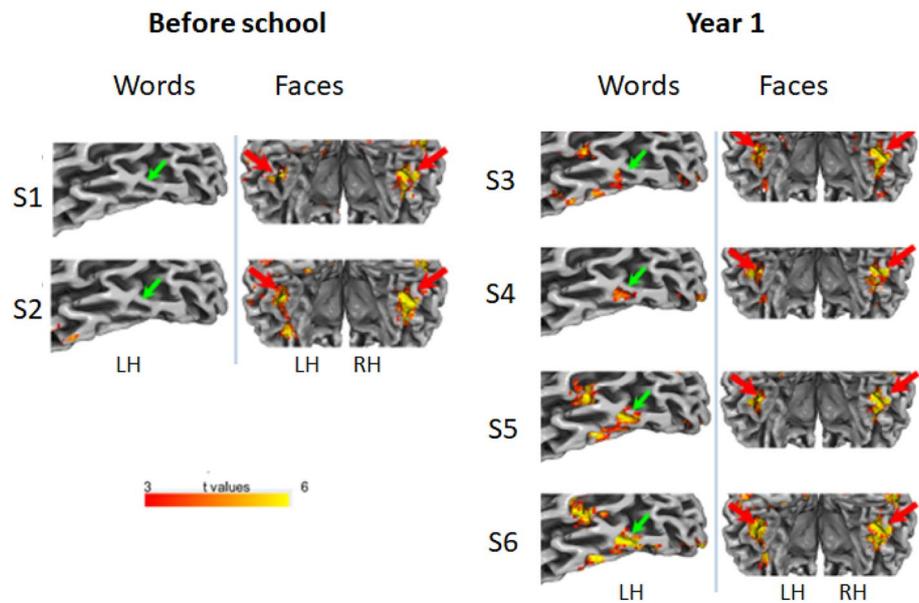
**Correlations between reading ability and face-selective responses** Significant correlations of reading scores with lateralization to faces have been reported in a handful of studies, in apparent support of the reading-LNC hypothesis. For instance, Li et al. (2013) contrasted the N170 amplitude to faces in 5–6-year-old children with higher and lower reading abilities, claiming to find support for the reading-LNC hypothesis (Fig. 1 of that paper). However, as reported by the authors in their text and another illustration, higher word reading abilities in 5–6 years old children correlated

*negatively* ( $r = -0.27$ ) with the right-lateralization of the N170 for faces, a result that we interpret again against the hypothesis.<sup>9</sup>

In very young children (4–5 years old), a negative relationship between the fMRI response to faces in the left VOTC and reading abilities (naming single characters) has been found ( $r = -0.78$  in Cantlon et al. 2011; Fig. 6A), as well as a signal increase for faces near the right FFA correlating with reading speed in 6 years old (Dehaene-Lambertz et al. 2018). On the other hand, Dundas et al. (2012) reported RH lateralization scores for faces in divided visual field studies that significantly correlated with behavioral reading performance ( $r = 0.55$ ) only in teens and not in children (Fig. 6B). Moreover, with the exception of Li et al. 2013 ( $n = 81$ ), in all of these studies, several correlation coefficients are computed without correcting p values, and

<sup>9</sup> To the best of our understanding, this negative correlation interpreted in support of the hypothesis cannot be due to the negative polarity of the N170 component.

**Fig. 7** Evolution of responses to letter strings and to faces in a longitudinal study over testing sessions (S1 to S6) (adapted from Dehaene-Lambertz et al. 2018). Illustrated here are the results of one child, from the summer before school started [2 months before (S1) and 10 days before (S2)] and during the first year of primary school (from S3 to S6, approximately every 2 months). The RH dominance for face-selective neural responses is present from the start of the study and, while impressive changes occur at the VWFA location for words, is remarkably stable across testing sessions



the sample sizes are small for correlation analyses ( $n = 12$ ,  $n = 10$ ,  $n = 24$ , respectively). The importance of this latter factor is highlighted by the following comparison: while Lochy et al. (2019) also reported a significant correlation ( $r = 0.29$ ) between reading performance and RH lateralization of a face-selective frequency-tagged responses, this effect disappeared entirely when the population of children tested increased from 34 to 52 (Lochy et al. 2020; Fig. 6C, D). Moreover, in the most recent fMRI study testing this hypothesis in a large sample ( $N = 60$ , 6–9 years old) and with left VOTC activation for words positively correlating with reading level, RH activation for faces correlated with age independently of reading level (Feng et al. 2021).

**Developmental dyslexia** A number of developmental studies have also explored the impact of a disorder in learning to read (developmental dyslexia) on the RH lateralization for faces, again with mitigated evidence. Here, the rationale is that since dyslexia is associated with weaker activation and specialization of the VWFA to print (Martin et al. 2015; Richlan 2012), there should be *less* competition with faces in the LH. Therefore, developmental dyslexics should show a *reduced* RH lateralization for faces.

Weaker activation and volume of the right FFA in dyslexics compared to typical readers have indeed been found in some studies (Monzalvo et al. 2012), but not in others (Perrachione et al. 2016). Moreover, while the specificity of an atypical neural representation for faces in dyslexia is claimed by some authors (Gabay et al. 2017), a more general disorder of the left ventral stream, generalizing across several categories has been found (Sigurdardottir et al. 2015; Perrachione et al. 2016). Overall, the conclusions that can be drawn from studies with this population have to be taken

with great caution: dyslexia is a neurodevelopmental disorder with abnormalities in brain maturation and function that are not limited to the reading network, the LH, and even less to the specialization of the VWFA for letters (see Martin et al. 2015; Richlan 2020).

**Summary of children studies** In our view, the studies in children reviewed above do not provide much empirical evidence for the proposed causal influence of reading acquisition and specialization of the left VOTC for print on the RH lateralization for faces in this region.

First, the brief review above shows that RH lateralization for faces may be related to reading abilities in some studies, but their results are limited by the use of particularly small samples and/or confounding effects of age. Second, RH lateralization is not significantly linked to LH lateralization for letter strings, even though there is surprisingly little direct evaluation of this prediction. In this context, the longitudinal study of Dehaene-Lambertz et al. (2018), in which 6-year-old children were tested in fMRI at 6–7 time points during their first year of schooling, is particularly interesting (Fig. 7). In that study, face-selectivity is already found in the RH (around the MidFusiform gyrus, i.e., FFA) 2 months before formal reading acquisition (again against the view that this RH lateralization emerges only due to selectivity to print in the LH). Following reading acquisition, word-selective responses in the left OT regions (i.e., VWFA) emerge significantly.

Crucially, a retrospective analysis of the initial selectivity of those voxels that became selective to letter strings shows that they were *not* face-selective initially, as suggested earlier by Saygin et al. (2016), and in fact,

in full agreement with a fair evaluation of the adult study of Dehaene et al. (2010). Based on these observations, Dehaene-Lambertz et al. (2018) suggest that new visual categories, such as letter strings, invade only weakly specified cortex, while leaving face-selective cortical responses unchanged (see also the most recent fMRI study of Nordt et al., 2021). Unless one can demonstrate that further expansions of category-selective responses to faces at later developmental stages are *specifically* blocked in the LH, increasing RH dominance of face recognition even further, such findings speak directly against even a weak version of the reading-LNC hypothesis.

Third, while RH lateralization is inconsistently reported in young child studies, it cannot be ignored. Indeed, the fact that group-level face responses are either bilateral or RH lateralized, in particular in fMRI, *but never LH lateralized*, points to a genuine RH lateralization that may not be systematically captured due to the various methods, stimuli, paradigms and measures (i.e., absolute responses to faces, faces vs. rest, faces vs. letter strings, faces vs. non-face objects (including letter strings or not ...) used across studies (see Sect. 4).

Here, the issue of the level of face recognition/categorization (e.g., generic face recognition vs. FIR), which is usually neglected in all of these studies, may be crucial. To illustrate its importance, Lochy et al. (2020) recently compared RH lateralization to face stimuli in 52 preschool children with two frequency-tagging paradigms measuring different recognition levels. While, as already mentioned, strictly *bilateral* responses for the discrimination between faces and nonface stimuli were found (i.e., category-selective face responses), clear *right-lateralized* responses were observed for (unfamiliar) FIR measures obtained in the very same sample (Fig. 5). These findings show that incorrect conclusions regarding the (absence of) right lateralization of face recognition in early development, and of its relationship to reading acquisition, could be drawn due to the use of a limited set of measures, in particular regarding the specific face recognition function sampled.

#### Inter-individual variability in literate adults, concurrent stimulation and handedness

Hemispheric lateralization for letter strings and faces can vary substantially among neurotypical literate human adults (Badzakova-Trajkov et al. 2010; Cai et al. 2008). This inter-individual variability allows evaluating a corollary to the lateralized neural competition hypothesis, namely that hemispheric lateralization for letter strings and faces should correlate across individuals: if competition induces a reduction of the face-selective response in the LH, then responses to faces and words should negatively correlate

in that hemisphere. Moreover, this could lead to a compensatory increase of face-selectivity in the RH, such that a positive correlation should emerge across hemispheres between selective responses to letter strings (LH) and faces (RH). Consequently, under the lateralized neural competition hypothesis, the greater the left lateralization ( $LH - RH$ , or  $(LH - RH)/(LH + RH)$ ) for letter strings, the greater the right lateralization ( $RH - LH$ , or  $(RH - LH)/(LH + RH)$ ) for faces across individuals. With divided visual field stimulation, Brederoo et al. (2020) indeed recently showed a significant correlation ( $r = 0.29$ ) between RH-lateralization at a face processing task and LH-lateralization for word processing as measured in response speed. However, this issue has been most deeply explored in a number of fMRI studies that have used a variety of indices (raw signals per hemisphere, extent of responsive voxels, difference between hemispheres, normalized indices, ...) to examine the above-predicted correlations.

Pinel et al. (2015) tested a large cohort ( $N = 64$ ) of individuals, reporting higher reading speed of pseudowords related to a decrease of face-related activity in the left FFA. However, there was no correlation between category-selective responses in the right FFA (faces) and left VWFA (letter strings). Davies-Thompson et al. (2016,  $N = 26$ ) found no correlation for the number of voxels in the right FFA for faces and left VWFA for letter strings, but a positive correlation for the peak MR response, which was even stronger when fusiform cortical thickness and cortical volume were considered. While this last result apparently supports the reading-LNC hypothesis, there were also positive correlations between the peak MR responses for faces in the right FFA and those in the left FFA, and for letter strings between the right and left VWFA. Thus, as the authors conclude, the positive correlations between words and faces across hemispheres merely reflect the fact that subjects with greater activation for faces also had greater activation for letter strings, a typical confound in the direct interpretation of correlation coefficients between two measures across individuals (e.g., Dundas et al. 2014). As for hemispheric lateralization indexes (computed left-wise for both categories,  $(LH - RH)/(LH + RH)$ ) between the response to faces in the FFA and for letter strings in the VWFA, the direction of the significant correlation—which fell below threshold after removal of an outlier—was against the reading-LNC hypothesis and in line with the general conclusion of the authors.

Using explicit tasks in fMRI, Gerrits et al. (2019;  $N = 27$ ) found a significant negative correlation in terms of fMRI signal in a large pre-defined section of the fusiform gyrus between face recognition and language-lateralization assessed by a word production task. However, there was no significant correlation in this region between lateralization indexes for face and written word recognition. Finally, in the most recent fMRI study of Canário et al. (2020), there

was again no significant correlation between lateralization indexes for the VWFA (letter strings) and the FFA (faces) across the 58 individuals tested, for any of three measures of fMRI signal. Overall, while the relationship between neural activity to speech in the LH and right hemispheric lateralization of the FFA is worth mentioning, the results of these fMRI studies clearly go against a major prediction of the reading-LNC hypothesis, namely that an increase in LH lateralization for letter strings in the VOTC causes an increase in RH lateralization for faces in the same region (and in general).

At the behavioral level, Robinson et al. (2017) used an attentional blink paradigm (with central presentation) claiming to find interfering effects between words and face processing in favor of the reading-LNC hypothesis. However, contrary to the predictions of this hypothesis, words presented at T1 did not produce larger short-lag deficits for face T2 discrimination than pictures of glasses (in 2 experiments). Moreover, words T2 discrimination was more affected by faces than by words, a result which cannot be explained under the assumption that the paradigm used in that study is adequate to measure competition between functionally similar representations.

Using an ERP paradigm initially developed to test concurrent competition between different face stimuli (Jacques and Rossion 2004) and objects of visual expertise with faces (Rossion et al. 2004, 2007), Fan et al. (2015) showed a decrease in the amplitude of the N170 evoked by lateral face stimulation when concurrently processing known characters centrally. However, this competition effect was not stronger when faces were presented in the LVF than in the RVF, contrary to the prediction of the reading-LNC hypothesis. Moreover, while the N170 is clearly left-lateralized for the Latin alphabet (Maurer et al. 2006; Rossion et al. 2003), Chinese characters bear several similarities with faces (uniqueness, configuration, processed at an individual level, shape) and they have been shown to induce bilateral responses both in fMRI (Tan et al. 2005; Fu et al. 2002; Bolger et al. 2005; Liu et al. 2008; Wu et al. 2012) and EEG/MEG (Kim et al. 2004; Zhang et al. 2011). Finally, such neural competition effects in the same paradigm can be observed (even more strongly) for familiarization of non-letter string stimuli, such as “Greebles” and pictures of cars in car experts (Rossion et al. 2004, 2007, respectively), indicating that they are not specific to letter strings.

An important aspect to take into consideration in inter-individual differences studies is the *handedness* of participants. Indeed, among the only four reported cases of

prosopagnosia with a left unilateral lesion, three of these patients were left-handed (Tzavaras et al. 1973; Eimer and McCarthy 1999; Mattson et al. 2000),<sup>10</sup> whereas functional damage might have been also present in the right hemisphere of the only right-handed patient (Wright et al. 2006). While the lateralization of language in these cases was unknown, their left handedness makes them more likely to be right language-dominant than right-handed people (Knecht et al. 2000; although see Packheiser et al. 2020), suggesting a systematic opposite relationship between hemispheric lateralization of language (in general) and face recognition.

In line with these observations, EEG and fMRI studies have suggested that the VWFA co-lateralizes with the language-dominant hemisphere (i.e., being right-lateralized when language is lateralized to the right hemisphere, as more often the case in left-handed people, Cai et al. 2008, 2010; Van der Haegen et al. 2012). fMRI studies have reported a smaller proportion of left-handed (73%) than right-handed (94%) people, with a right hemispheric dominance for a simple face task across the whole brain (Badzakova-Trajkov et al. 2010). Moreover, the FFA is bilateral or even slightly left-lateralized overall in left-handed people (Willems et al. 2010; Bukowski et al. 2013; Frässle et al. 2016b; Dundas et al. 2015; Gerrits et al. 2019).

Building upon these observations, a recent fMRI study attempted to relate language dominance to written letter strings and face lateralization in left-handed people characterized by a typical LH or atypical RH language dominance (Gerrits et al. 2019). There was a positive correlation between lateralization indexes of language and word recognition (0.65) and a negative correlation between language and FIR performance ( $-0.62$ ) (but see Van der Haegen and Brysbaert 2018 for an absence of correlation in performance at lateralized behavioral tasks). However, against the reading-LNC hypothesis, written words and face recognition did not inversely correlate, neither in terms of the direction nor the strength of lateralization of the response recorded in fMRI (Gerrits et al. 2019). This latter observation contradicts the findings of the EEG study of Dundas et al. (2015) who reported a negative relationship ( $r = -0.65$ ) between the left N170 to words and the right lateralization for faces  $((RH - LH)/(RH + LH))^* - 1$  independently of handedness.

In summary, if anything, the most convincing sources of evidence of a relationship between hemispheric lateralization of the two domains in adults come from observations in left-handed people who, more often than those who are right-handed, show atypical hemispheric lateralization for

<sup>10</sup> As also noted by an anonymous reviewer of this manuscript, the prosopagnosic patient reported by Barton (2008) was ambidextrous and had in fact a bilateral VOTC lesion and is therefore not considered here.

both faces and letter strings. However, these data offer at best only indirect evidence of neural competition between reading acquisition in the VOTC and right hemispheric lateralization of face recognition. This is also the case for the— notable—finding of Pinel et al. (2015) in which the increase in RH lateralization for faces in the FFA was positively related to left lateralization for speech in the posterior STS.

Other than that, behavioral and neural measures exploiting inter-individual variability in lateralization and performance in neurotypical adults with correlation analyses offer little to no direct support for the reading-LNC hypothesis. Admittedly, both for child and adult studies, these correlation analyses are complicated by the use of highly variable dependent measures (i.e., absolute amplitude/magnitude of brain response to faces or letter strings, category-selective responses, lateralization indexes through subtraction with or without normalization, etc.) in different and differently defined brain regions, requiring clarification and systematicity for further progress on this issue (see Sect. 5 below).

### Does an increase in letter-selectivity decrease face recognition performance?

As mentioned above, the reading-LNC hypothesis predicts at least a small drop of face recognition performance with literacy (Dehaene and Cohen 2007). This prediction can also be evaluated in behavioral developmental studies, and in adult studies comparing behavioral performance of literates to illiterates.

#### Developmental studies of face recognition

Young human infants, even newborns, show selective behavioral and neural responses to face stimuli (Goren et al. 1975; Johnson et al. 1991; de Heering and Rossion 2015). However, face identity recognition (FIR) appears very limited at an early age and develops slowly until adulthood, maybe peaking as late as 30 years of age (Germine et al. 2011). Whether this protracted development is due to the progressive maturation of face recognition processes specifically (presumably through extensive experience with faces) or could be explained by the development of more general cognitive or task-related factors, is debated.

On the one hand, McKone et al. have argued that holistic recognition of facial identities, considered as hallmark of the specificity of the function, reaches maturity early in development, i.e., by 5–7 years of age at the latest (Crookes and McKone 2009; McKone et al. 2012). This would leave little or no room for reading acquisition to negatively affect FIR. On the other hand, a number of behavioral studies have failed to find significant reduction of FIR performance with inversion of face stimuli, i.e., a face inversion effect in children (e.g., 6–8 y.o.: Carey and Diamond 1977; Hills and

Lewis 2018; Schwarzer 2000), this effect being extremely robust in adults and also considered as a hallmark of face specificity and expertise (Yin 1969; see Rossion 2008 for review). Other studies have reported a reduced effect as compared to adults (Carey 1981; de Heering et al. 2012; Sangrigoli and De Schonen 2004), with the effect increasing over childhood and adolescence (Carey and Diamond 1977; Itier and Taylor 2004; de Heering et al. 2012; Hills and Lewis 2018). Behavioral studies in participants of Korean origin who were adopted in a French-speaking European environment after up to 9 years of age have also provided evidence of a reversal of their “other-race” face effect (Sangrigoli and de Schonen 2004; see also de Heering et al. 2010), suggesting that the face recognition system retains a great deal of experience-contingent plasticity during development for FIR.

Overall, neuroimaging investigations are consistent with such a progressive specific development of face (identity) recognition, showing an increase in face-selective responses in the fusiform gyrus from 7 years of age to adulthood (Golarai et al. 2007; Scherf et al. 2007). Under this latter view, i.e., if face recognition progressively and specifically improves during development, a dip in performance in this function, or at least a slowing down of this improvement, might be observed when children start schooling, as predicted by the reading-LNC hypothesis (Kühn et al. 2021). While there is no evidence of such a performance dip,<sup>11</sup> a major difficulty to investigate this question lies in the confounding factors that may affect face recognition performance, such as the increase of general cognitive abilities with age. Most importantly, schooling usually corresponds with an increase in socialization and thus of quantitative and qualitative experience with variable face identities, these factors playing an important role in FIR performance (Balas and Saville 2017) and the magnitude of face-selective VOTC responses (Dehaene et al. 2010; see also Balas and Saville 2015).

#### Adult studies of illiterates/literates

To our knowledge, there is no study in adults showing detrimental effects of literacy on face recognition performance. On the contrary, several studies show that illiterate adults perform worse than literate adults in recognizing, detecting, and naming visual objects, although these effects are not specific to any category (Huettig and Mishra 2014). In face recognition tasks of various difficulty, literates also perform

<sup>11</sup> Early developmental studies of face recognition have instead argued in favor of a dip of performance at a later age, at around 11 years old (Carey 1992), but this has not been supported by subsequent studies.

better than illiterates (Orihuela et al. 2013). Thus, rather than competing with shared visual processes for faces, literacy appears to boost face recognition, by fine-tuning object recognition mechanisms (Hervais-Adelman et al. 2019; van Paridon et al. 2020), and improving the detection, segmentation and interpretation of visual information (Huettig et al. 2018; Kolinsky et al. 2011). For instance, a positive association between literacy scores and face/object recognition was found in memory tasks (97 participants, from illiterate to highly literate) (Van Paridon et al. 2020) suggesting that older abilities are *enhanced* rather than impaired by the acquisition of new related abilities.

Let us note, however, the inherent difficulty in behavioral studies comparing literates to illiterates. Most often, these two groups of participants, even when they are well-matched in terms of rural/urban environment or socio-economic backgrounds, differ in other cognitive measures related to schooling, testing habits, etc. For instance, in the above-mentioned study, participants with high-reading scores also displayed more general perceptual reasoning abilities, as well as higher digit-span, complicating the interpretation of the results (Van Paridon et al. 2020). The observation of a mere quantitative improvement in performance for face (identity) recognition in literates compared to illiterates could thus also rely on general cognitive abilities, better exemplar discrimination across domains (Pegado et al. 2014a, b), or familiarity with testing conditions, than literacy per se.

### Is face recognition qualitatively modified by letter string sensitivity?

Assessing whether face recognition changes qualitatively with letter string sensitivity is complicated by the lack of scientific agreement about the nature of face representations (e.g., holistic vs. feature-based; shape or surface-based) and the most adequate paradigms to measure holistic face recognition (Rossion 2013). Perhaps for this reason, so far, the qualitative hypothesis has been tested only in a handful of studies comparing literate and illiterate adults.

At a general level, literacy is thought to change basic visual principles, such as mirror-invariance (Kolinsky and Fernandes 2014; Pegado et al. 2014a, b; Pegado et al. 2014a, b; Fernandes et al. 2016, 2021), and to enhance qualitatively analytic, part-based processing, therefore improving performance in visual search tasks (Malik-Moraleda et al. 2018). In line with this prediction, Ventura et al. (2013) claimed that literacy induces a reduction of holistic processing of faces in a composite face task (albeit with a Stroop-based version of the paradigm; see Rossion 2013). However, this hypothesis is at odd with the assumption that if face recognition is shifted towards the RH with literacy, then greater holistic processing should be found, not the reverse. Moreover, Cao et al. (2019) showed greater

sensitivity to face orientation in literates, as well as better performance in detecting differences due to spatial configuration not only for faces, but also for houses, thus suggesting a general improvement with literacy at detecting spatial relations between components. More generally, the above-cited fMRI study of Hervais-Adelman et al. (2019) showed a representational similarity increase between text and faces in the VWFA in trained illiterates as compared to literates, in favor of the view that tuning to orthographic stimuli does not involve a loss of responsiveness to faces but may in fact induce an increase in shared aspects of the representation between text and faces.

### Summary

To summarize, the reviewed scientific literature in development, in illiterate adults, or assessing inter-individual differences, does not offer much empirical support in favor of a causal influence of VOTC specialization for reading in the LH on the RH lateralization of face recognition (i.e., the reading-LNC hypothesis as referred here). The strongest arguments advanced in the literature lie in some positive correlations between reading abilities and RH lateralized face-selective responses, but the results are inconsistent and often suffer from (very) small sample sizes. Also, there is no evidence to date of a negative impact of literacy on performance for face recognition, acknowledging that the evaluation of this hypothesis is complicated by confounding factors of general cognitive abilities increase (due either to age or to schooling). Finally, the few studies that have examined left-handed participants or inter-individual variability, relating language dominance and face lateralization, offer some support to the idea that LH language lateralization in general—rather than letterstrings selectivity in the VOTC specifically—could contribute to RH face lateralization (Pinel et al. 2015; Gerrits et al. 2019). This possibility is discussed further in the last section of the review.

### Alternatives and perspectives

If the reading-LNC hypothesis is incorrect, i.e., if RH lateralization of face recognition, which appears to be specific to the human species, is not due to neural competition with the representation of letter strings in the VOTC of the LH when learning to read, what are the alternative views? Although a full survey of these alternative accounts is beyond the scope of the present review, they are briefly discussed below.

## What is right?

### Global/local and holistic/analytic dichotomies

Ever since the LH has been considered as the (main) seat of verbal function, a number of dichotomies in terms of processing modes have been proposed to contrast it to the RH, invading the popular culture: the LH is seen as the logical, analytical, serial, rational, digital mind, while the RH as the spatial, analogic, holistic, synthetic, parallel, intuitive and artistic mind (e.g., Bogen 1969; Springer and Deutsch 1981; Bradshaw and Nettleton 1981). Beyond these caricatural dichotomies, the hypothesis that the RH is well predisposed for the processing of *global* aspects of the visual world, whereas the LH is well suited for processing its *local* aspects has been more thoroughly explored with visual stimuli.

Evidence collected in brain-damaged patients with unilateral RH or LH lesions tested with hierarchical ‘Navon’ stimuli (i.e., large letters made of congruent or incongruent small letters; Navon 1977) provides some support for this view (Delis et al. 1986; Robertson et al. 1988; Lamb et al. 1989; see Hellige 1993 for review) although the results of studies in neurologically intact individuals tested with divided visual field stimulation, as often, are more equivocal (e.g., Sergent 1982a, b; Boles 1984; Van Kleeck 1989; although see Brederoo et al. 2020). Most importantly, the tasks performed in these experiments often concern visuospatial attention rather than visual recognition processes per se. Indeed, rather than key regions of the ventral occipitotemporal cortex involved in object recognition, the lesions of the patients leading to such hemispheric asymmetries in global vs. local processing concern the posterior superior temporal gyrus (Lamb et al. 1990; see also Busigny and Rossion 2011 for intact processing of hierarchical Navon letters in a well-defined case of prosopagnosia). In short, a hemispheric dichotomy in terms of global vs. local visual processes may be partly valid, but does not appear to provide direct evidence to account for the RH lateralization of human face recognition, at least regarding ventral occipitotemporal brain structures.

It is this global/local dichotomy that probably inspired a subsequently proposed hemispheric dissociation, based on neuropsychological studies, between stimuli that can or cannot be decomposed in parts during visual recognition (Levine and Calvanio 1989; Farah 1991). According to this proposal, all visual forms are recognized by a combination of part-based and holistic processes across the two hemispheres: while the part-by-part analysis would be

preferentially accomplished by the LH VOTC, corresponding regions of the RH would process visual objects holistically/configurally.<sup>12</sup> On the one hand, written words provide the clearest example of objects that are decomposed into simpler unit parts (i.e., letters). On the other hand, there is overwhelming evidence that a face is processed holistically, i.e., as a single unit rather than a collection of independent parts (one eye, a mouth, etc.) (Sergent 1984; Young et al. 1987; Tanaka and Farah 1993; see Rossion 2013 for review). Therefore, according to this view, faces would be primarily recognized through holistic processes in the RH, while written words would be mainly handled in the LH (Farah 1991).

Importantly, and although there is considerable confusion at this level in human face recognition research, this holistic/analytic dichotomy is fundamentally different than the global/local dichotomy discussed above. That is, “holistic processing” does not imply that individual parts (or features) of the visual stimulus are not important, or that the whole stimulus needs to be physically present: it is a *processing mode* through which the individual parts of the stimulus are not represented independently from one another, i.e., there is no part-decomposition (Farah et al. 1998; Rossion 2013). This does not mean that the parts of a face (e.g., one eye, a mouth, etc.) are not important for face recognition (as often misinterpreted), but that there is no *category-selective* representation of independent parts (i.e., there is no neural functional unit, e.g., a cortical minicolumn, responding only and specifically to one eye, a mouth, etc.) (see Rossion 2009, 2013 for extensive discussion of this issue).

While the study of visual (object) agnosia in neurological patients provided the impetus for this proposed hemispheric dissociation in terms of holistic/RH vs. analytic/LH recognition processes (Levine and Calvanio 1989; Farah 1991), studies with the divided visual field approach in neurologically intact participants do not provide strong support for it, with the advantages found for the RH or the LH usually depending more on the type of visual categories and tasks performed than on holistic vs. analytic modes of processing (Sergent 1983; although see Hillger and Koenig 1991).

Moreover, Farah (1991)’s influential proposal of a hemispheric dissociation between on the one hand RH/holistic representation/faces and LH/analytic representation/words coincided with the advent of functional neuroimaging, high-density EEG and other techniques in cognitive neuroscience, which have allowed its deeper evaluation. Over three decades of research since this initial proposal, it is fair to say that it has received only limited support. While the RH is often dominant over the LH in terms of holistic

<sup>12</sup> The terms ‘holistic’ and ‘configural’ are sometimes used to refer to different concepts in human face recognition research, but they are used as synonyms here (as proposed and discussed extensively in Rossion 2009, 2013).

processing of faces (e.g., divided visual field studies: Parkin and Williamson 1987; Hillger and Koenig 1991; neuroimaging: Rossion et al. 2000; Schiltz and Rossion 2006; Harris and Aguirre 2010; EEG: Jacques and Rossion 2009), this difference seems to be more quantitative (i.e., a reduced face-selective activity in the RH coinciding with a reduced holistic representation) than qualitative (see also Meng et al. 2012; for review: Yovel 2016). Specifically, there is no evidence that face-selective neural populations in the LH represent the parts of a face independently.

Most importantly, going beyond lesion studies, functional neuroimaging and EEG studies point to a fundamental contradiction between the holistic/analytic view of hemispheric lateralization and the respective representation of faces and words across the two hemispheres that was not apparent in lesion studies. That is, while representation of faces in the VOTC is *bilateral* with a RH dominance, representation of letter strings is much more lateralized (to the left hemisphere) in this region. In particular, the so-called FFA is typically identified in both hemispheres while the VWFA is strongly left-lateralized in readers of alphabetic writing systems, and is sometimes identified *only* in the LH (e.g., Cohen et al. 2000; McCandliss et al. 2003; Davies-Thompson et al. 2016; Canario et al. 2019; Kubota et al. 2019; Fig. 2). Likewise, the N170 ERP component is often only slightly right-lateralized for faces, but much more left-lateralized for printed letter strings (e.g., Rossion et al. 2003; Fig. 1E).

Following the holistic/analytic account of hemispheric lateralization for faces, this would imply that these latter stimuli are processed both holistically and analytically (with an advantage for holistic processes), while letter strings would be processed essentially analytically. Yet, if anything, the opposite is true: while, as mentioned above, faces may be represented only holistically/configurally, *both* part-based and holistic representations are important for written words. That is, in alphabetic systems, recognition needs to operate both at the single letter level, each letter being associated with a specific sound during most formal acquisition procedures (which may enhance an analysis of component features of the stimulus, Perfetti 1992; Yoncheva et al. 2010, 2015) and at the level of the whole stimulus (as evidenced by phenomena such as the word superiority effect, Reicher 1969; see also e.g., Martelli et al. 2005; Wong et al. 2019). Hence, following this logic, selective representations of faces should be almost only limited to the RH while those of familiar orthographic letter strings should be bilateral: the exact opposite to what is observed. In summary, the holistic/analytic dichotomy does not appear to provide a satisfying explanatory account of the right hemispheric lateralization of face recognition.

## From spatial frequencies to resistance to degradation

According to another influential hypothesis originating in the 1980s, face recognition would be lateralized to the RH because it would depend essentially on coarse variations of luminance across the stimulus, i.e., low spatial frequencies (LSF). In contrast, the recognition of letter strings would essentially rest on the processing of edges, i.e., high spatial frequencies (HSF). The connection between SF and hemispheric asymmetries in high-level processing was put forward by the late Justine Sergent (1982a, b), who reported a number of theoretical and empirical contributions to this hypothesis, testing it with face stimuli in particular (e.g., Sergent 1983, 1985, 1987; Sergent and Hellige 1986). According to Sergent's hypothesis (see also Ivry and Robertson 1998) applied to vision, whereas early processes unfold symmetrically in the two hemispheres, the RH preferentially operates on the low-frequency outputs of the visual channels, and the LH is more adept at operating on higher spatial frequencies. The fact that low frequencies are more resistant to degradation, and more easily resolvable at low contrast, far away or during motion, may give the RH a critical role in face recognition when the prevailing conditions prevent the resolution of HSF. The contribution of the LH would increase when fine visual operations are required (perhaps driven by reading acquisition, Ossowski and Behrmann 2015), but this hemisphere would also be more vulnerable to reduction in the redundancy of incoming information (Sergent 1985). This hemispheric balance across SF bands is also considered to account for the early infant bias towards the LVF for their mother's face, thought to be the result of the faster maturation rate of the RH at a time at which the infants' visual system mainly extracts LSF from facial inputs (de Schonen and Mathivet 1989).

However, as for the holistic/analytic hemispheric dichotomy described above, the hypothesis of a differential sensitivity to SF to account for the RH dominance in face recognition has received little empirical support. In divided visual field stimulation studies, differences between visual recognition of complex stimuli in the LVF and RVF are also more susceptible to the effect of task and stimulus category than to SF per se (Sergent 1985; Sergent 1987; see Hellige 1993). While other techniques in cognitive neuroscience generally support Sergent (1986)'s view of a coarse-to-fine accumulation of evidence for face recognition, they do not appear to support RH/LH imbalance in processing LSF/HSF, respectively (Goffaux et al. 2011; Quek et al. 2018). In fact, the RH merely appears to be more sensitive or more resistant to degradation of visual inputs than to LSF per se, again pointing to a quantitative rather than a qualitative difference between hemispheres at this level (Peterzell 1991, 1997).

Finally, also in common with the holistic/analytic dichotomy, there is a fundamental contradiction between the

relative use of facial cues available at different frequency ranges for visual recognition and the RH lateralization for faces. With respect to faces, LSF essentially convey information about the general shape, outer contour, and hairline of a face while HSF carry information concerning inner features, such as texture elements and the specific shape of the eyes, nose, and mouth (Sergent 1986; Morrison and Schyns 2001). Accordingly, recognizing a stimulus as a face can be achieved based on very coarse cues (Sergent 1986; e.g., as low as 4.22 cycles per image for face-selective responses, see Quek et al. 2018) while the recognition of its identity (FIR) depends on cues available at higher SF ranges (Sergent 1986; Morrison and Schyns 2001; Näsänen 1999; Yan et al. 2020). Yet, compared to generic face recognition, it is FIR (even when based only on internal features) that is associated with an enhanced RH lateralization (Lochy et al. 2020; Jacques et al. 2020; Fig. 5).

### What is left? Conceptual and methodological considerations for a revised lateralized neural competition account

The brief survey above suggests that there is no strong alternative in the scientific literature to the view that the RH lateralization for faces in the human brain is directly or indirectly caused by neural competition with letter string sensitivity in the left VOTC. The lack of solid alternative may partly explain why this read-LNC hypothesis is currently influential and very actively tested. Yet, in the present review, we have provided an extensive critical analysis of this hypothesis, demonstrating that it is not well supported. An intriguing possibility emerging from this analysis is that the long-standing view of RH lateralization for faces being due to cortical competition with LH lateralized functions, language in particular (Ellis 1983; Corballis 1983, 1991), is correct, but that this competition is not initiated and operated at the level of the VOTC. Instead, the (early) specialization for phonological and semantic aspects of language in the occipito-parieto-temporal junction and perisylvian area (Dehaene-Lambertz et al. 2002; Rosselli et al. 2014 for review) may be the driving factor for an initial RH lateralization of face-selective regions in the middle and posterior sections of the human STS. In turn, due to spatial proximity and efficiency of connectivity, VOTC regions would become preferentially selective for faces in the RH as compared to the LH. Such a revised account of the hypothesis would agree with the fact that the right hemisphere is less lateralized in general (Corballis 1991; Gotts et al. 2013), with observations made in left-handed individuals (Sect. 3, e.g., Gerrits et al. 2019) as well as significant correlations between left pSTS/mSTS responses to speech and right FFA activity for faces (Pinel et al. 2015). It would also be in line with the strong, human-specific, RH lateralization at

the level of these regions of the pSTS/mSTS (Fig. 1A, B), and with the relative developmental immaturity of the main function of the VOTC cortical face network, i.e., face identity recognition, compared to face recognition functions carried out at the level of the STS (i.e., recognition of dynamic aspects of faces, such as head orientation, gaze direction or to a lesser extent facial expression; Haxby et al. 2000; Duchaine and Yovel 2015). Beyond the need to include (the development of) this ‘dorsal’ cortical face network (or the ‘third pathway’ specialized in social perception, see Pitcher and Ungerleider 2021) and the functions that it subtends, we conclude this review below by proposing a number of conceptual clarifications and methodological improvements for a proper evaluation of any language-related lateralized neural competition hypothesis in future research.

### Acknowledging and clarifying functional differences between faces and words

Similarities between the processing of written words and faces (e.g., holistic processing, foveal bias ...) are often emphasized by proponents of the reading-LNC hypothesis. While this is interesting, we think that it is important to acknowledge at the outset the clear differences between these types of stimuli and the nature of the respective recognition functions that they are associated with. Faces are 3D dynamic stimuli, predominately curved, and made of parts that do not stand alone. In contrast, written words are 2D shapes, containing edges and junctions, and letters may recombine for other meanings. Face recognition is acquired incidentally and improves from birth to adulthood, while learning to read requires an effortful, explicit learning process starting usually only after a few years of development. While faces convey a great deal of social cues leading to many types of recognition functions (e.g., identity, expression, gender, head orientation, etc.) and may be associated with names and both verbal and nonverbal semantic information, words are strongly linked to phonology, to language production, and more generally to semantics.

In the time-scale of the evolution of the species, word recognition is a recently acquired skill (5000 years) and until a few hundred years ago, only a small proportion of the population could read. In fairness, human face recognition has also certainly experienced significant changes in most human populations over the last 5000 years (i.e., since the emergence of early civilizations and populations of thousands of individuals living in a city, changing forever the status of an unfamiliar face). Yet, it is arguably an older evolutionary skill which, unlike word recognition, is shared partly by other animal species (although with important differences even compared to non-human primates, e.g., in terms of face identity recognition; see Rossion and Taubert 2019).

Reading is built on the pre-existence of speech, as it puts in relation speech segments (phonemes, syllables or words, depending on the system) to arbitrary written symbols, that involve a strong serial processing component in alphabetic languages. According to most reading acquisition methods, words are initially processed with an analytic visual strategy, and the issue of whether orthographic learning (of frequent words) allows them to be processed entirely holistically is an open question. In contrast, while parts/features of faces are the building blocks of recognition, part-based processes are largely inefficient in face recognition, as evidenced in neurological patients with prosopagnosia who are left to rely on this processing mode (Farah 1990; Van Belle et al. 2010). Acknowledging and characterizing in depth these fundamental differences from the outset is key to define the conditions under which faces and visual words/letter strings could truly overlap and/or compete for cortical representations and processes in the human brain.

### Relying on independent, controlled, measures of category-selectivity

A major issue for the reading-LNC hypothesis is that studies do not, or rarely adequately, isolate category-selectivity, which is at the core of the (visual) recognition process, according to the definition adopted at the beginning of the present review. Instead, “raw” or “absolute” neural responses to faces (e.g., N170 amplitude to faces, Dundas et al. 2014), or responses to faces compared to basic visual stimuli that are not matched for low-level visual cues (e.g., Fig. 4) are sometimes measured. Moreover, in several studies, the approach used to define regions of selectivity to faces or words is problematic. For instance, the FFA is sometimes defined by the contrast faces—letter strings (Centanni et al. 2018). In these conditions, responses to letter strings and faces are not defined independently of each other (even if an independent functional localizer is used), and any increase in the response to letter strings in the LH will lead to a decrease in the “selective” response to faces, erroneously interpreted in favor of the reading-LNC hypothesis. This methodological confound also plagues a number of fMRI studies that include letter strings among other stimuli in their definition of face-selective response (i.e., faces vs. other categories; e.g., Dehaene-Lambertz et al. 2018). In our opinion, it is necessary to define face-selectivity completely independently of responses to letter strings, to measure its degree of hemispheric lateralization and size, and then test whether letter-selectivity affects this lateralization.

As for the definition of letter-selective brain regions, the same methodological issue stands (e.g., the definition of the VWFA by contrasting letter strings to faces in Centanni et al. 2018). Moreover, depending on the contrasted material (checkerboards, pseudofonts, or symbols), the location

of the area with greater selectivity for letter strings can vary substantially (e.g., Fig. 2) from the “classical” VWFA with posterior coordinates (Talairach atlas:  $y = -54$ ; Cohen et al. 2000) to more anterior VOTC regions ( $y = -42$ ; Olulade et al. 2013; Turkeltaub et al. 2003; see also Martin et al. 2015). Further, depending on the tasks and contrasts used, this region is sometimes considered as being exclusively pre-lexical (Vinckier et al. 2007; Vogel et al. 2012) or lexical (Glezer et al. 2009, 2015), while its true selectivity to letter strings over object shapes can even be debated (see Fig. 3 above, from Dehaene et al. 2010, in which the “VWFA” response to pictures of tools is larger than to letter strings in all groups tested; see also Price and Devlin 2003; Starfelt and Gerlach 2007). Future studies addressing a lateralized neural competition hypothesis should clarify these issues and develop more standard protocols, preferably with implicit tasks, in terms of the visual stimuli that are used to define selectivity, both for faces and letter strings.

### Defining the face recognition functions and levels that are evaluated

Another important issue is that different techniques evaluating the LNC hypothesis measure different face recognition functions. Usually, behavioral measures during divided visual field stimulation evaluate face *identity* recognition (FIR), whereas neural measures (at best) reflect generic face recognition, i.e., category-selective responses to faces. Thus, the *type* and *level* of facial recognition functions assessed are different across different methodologies. This is unfortunate because, in line with the early and consistent neuropsychological observations that RH lesions are dominant in causing a deficit in *identity* recognition, not the ability to recognize faces as faces (e.g., Rossion et al. 2011), this factor is key in evaluating RH lateralization for faces, as shown perhaps most clearly in the children study of Lochy et al. 2020. In that study, as already mentioned, strictly bilateral responses for the discrimination between faces and non-face stimuli were found (category-selective face responses), but clear right-lateralized responses were observed for identity recognition (of unfamiliar faces) in the exact same sample of children (Fig. 5). This is also the case in human intracerebral recordings, where the RH advantage in the VOTC is substantially larger when measuring (unfamiliar) face identity recognition (Jacques et al. 2020) than the recognition of faces among other objects (Jonas et al. 2016; Hagen et al. 2020).

Note that while such observations point to a qualitative difference between hemispheres (i.e., an interaction with the face recognition level), they could also be accounted for by a quantitative difference: if the RH contains larger populations of neurons involved in face recognition, then the difference between hemispheres is particularly salient when testing for

the most difficult recognition level, i.e., FIR. This quantitative difference between hemispheres in terms of neural face representation could also explain why VOTC lesions, or electrical intracerebral stimulation in these regions, cause FIR impairments more often when they occur in the RH than in the LH (Bouvier and Engel 2006; Jonas and Rossion 2021). In short, before drawing conclusions about the hemispheric lateralization of the face recognition function in a given individual or at the population level, we recommend to explore it at least both at the level of category-selectivity and of individual recognition of face exemplars.

### Using implicit neural measures of the face recognition

The study of hemispheric lateralization of visual recognition has traditionally been based on behavioral measures collected in neuropsychological patients (including split-brain patients, e.g., Gazzaniga and Ledoux 1978) or neurologically intact individuals tested with divided visual field stimulation (see Bradshaw and Nettleton 1981). In contrast, studies performed in the past three decades have provided a flurry of direct and indirect neural measures in/over the two hemispheres, which have often been difficult to reconcile with these behavioral measures. On the one hand, the permanent or transient impairment of a specific behavioral ability such as FIR (i.e., in prosopagnosia) can be spectacular and represent an invaluable source of information to understand the critical contribution of a hemisphere or a specific brain region (Jonas and Rossion 2021). On the other hand, explicit behavioral measures of face recognition collected in neurotypical individuals during divided visual field stimulation are often difficult to interpret because they reflect a mixture of numerous sensory, cognitive and motor processes.

For this reason, comparing literates and illiterates in explicit behavioral tasks (of face recognition) is confounded by many factors that have nothing to do with the visual recognition process per se (e.g., understanding of task instructions), often leading to superior performances in literate populations (e.g., Hervais-Adelman et al. 2019). Moreover, behavioral responses during divided visual field stimulation can reflect the outcome of many higher-level processes that are not necessarily lateralized, or lateralized according to the stimulation side, making the interpretation of such studies often difficult (see Sergent 1982a, b). Neural measures are therefore invaluable to evaluate a lateralized neural competition hypothesis, not only because they provide more information in terms of spatial and temporal localization of the processes of interest, but also because they can be collected in the absence of an explicit task. In particular, since frequency-tagging (or fast periodic visual stimulation) studies provide valid, objective, sensitive, and reliable quantifiable measures of face recognition in a frequency-domain EEG representation, usually

in a few minutes of testing (see the recent review Rossion et al. 2020), they may have a major role to play in future studies evaluating any revised lateralized neural competition hypothesis. In addition, this approach also generates sensitive left-lateralized measures of letter strings recognition in adults and children (Lochy et al. 2015, 2016, 2018), providing an invaluable tool to implicitly measure and compare the evolution of lateralization of function for both face and letter string processing during development (Fig. 5), and between illiterate and literate individuals in future studies.

### Acknowledging the distributed cortical network for face (and word) recognition

Neuroimaging studies investigating the reading-LNC hypothesis often focus exclusively on face-selective responses in the lateral middle section of the fusiform gyrus, i.e., the FFA. While this region typically presents with the largest face-selective activity in fMRI (e.g., Kanwisher et al. 1997; Gao et al. 2018) and intracerebral EEG (Jonas et al. 2016; Hagen et al. 2020) and appears to be critical for FIR (as also shown by recent lesion overlap analyses of cases of prosopagnosia; Cohen et al. 2019), there are many clusters of voxels with significantly higher neural activation to pictures of faces than non-face visual stimuli in the VOTC, up to the temporal pole (as well as in the Superior Temporal Sulcus (STS) (e.g., Rossion et al. 2012; Zhen et al. 2015; Gao et al. 2018; for reviews see Duchaine and Yovel 2015; Grill-Spector et al. 2017; Fig. 1D, F). These face-selective cortical clusters are usually considered as discrete components, i.e., processing stages, of a well-defined neuro-functional network in the human brain, with a definite pattern of anatomo-functional connectivity (Pyles et al. 2013; Elbich et al. 2019). They tend to all show RH lateralization and, contrary to the FFA, remain lateralized at the group level to the RH in left-handed individuals (Bukowski et al. 2013).

Although apparently less distributed, letter string representations have also been identified in several subregions in a postero-anterior axis (Vinckier et al. 2007; Grill-Spector and Weiner 2014), with selective responses to letters independently of their organization rather localized in the inferior occipital gyrus, and higher-level selective responses to words/pseudowords in more anterior ventro-temporal regions of the mid-fusiform gyrus (Thesen et al. 2012; Lochy et al. 2018). A proper evaluation of any revised language-related lateralized neural competition hypothesis needs to consider not only the region of the lateral Mid-Fusiform gyrus, but at least the whole network of (VOTC) face-selective and word-selective regions.

## Defining representation overlap and competition at the neuronal level

Finally, for significant progress in evaluating a language-related lateralized neural competition hypothesis, substantial revision of this hypothesis at the conceptual level may be required.

A key issue is whether neural competition implies *overlap of representation* or not, i.e., whether a neural population in the VOTC may truly respond selectively to *both* faces and letter strings (i.e., vs. their respective control stimuli). While neural competition is typically conceptualized as the driving factor for a neat separation of VOTC representation for different categories, such as faces and letter strings, an apparent partial overlap in representation (e.g., between the FFA and VWFA Fig. 2; see Davies-Thompson et al. 2016) even in the adult brain is in fact also considered in support of the reading-LNC hypothesis (Nestor et al. 2013; Robinson et al. 2017; Behrmann and Plaut 2020). Thus, without clarification at this level, the reading-LNC hypothesis appears unfalsifiable.

In this context, a recent human intracerebral study with a large sample identified a moderate degree of overlap in the VOTC between category-selective responses to faces and words (i.e., 30% of recorded electrode contacts). Moreover, there was no (positive or negative) correlation of face-selective and word-selective amplitude at these overlapping locations, suggesting that these overlapping contacts recorded spatially distinct populations of neurons for the two visual categories (Hagen et al. 2021). A clear theoretical framework of a language-related lateralized neural competition hypothesis in terms of overlap of representation is necessary to avoid that such findings are taken by some in support of the neural competition hypothesis and by others against it.

Directly related to this issue, the reading-LNC hypothesis evaluated here has been often defined as reflecting a form of “neuronal recycling” (Dehaene and Cohen 2007), a terminology adopted by a number of authors but avoided deliberately in the present review since it is misleading at many levels. For a start, the term “recycling” usually refers to the *process* by which used (waste) material is converted into (usually) new material, not the novel use/repurposing of this material per se. An analogy at the neural level would imply that the neural representations are somehow transformed, and do not simply become tuned to a different type of sensory inputs. Moreover, recycling would seem to imply the re-use of neural representations that have been already (completely) used for another function. However, face (identity) recognition undergoes a long developmental process until adulthood (Hills and Lewis 2018), characterized by a progressive increase in VOTC representation (Golarai et al. 2007; Scherf et al. 2007; Natu et al. 2016). Therefore, if letter string selectivity

invades cortical regions that are not yet selective to faces (or any category) during development (Dehaene-Lambertz et al. 2018), or only weakly selective, the term “recycling” is also incorrect at this level and should not be revised (or recycled indeed) once again, but abandoned.

Also against the notion of “neuronal recycling”, there is no evidence that regions that end up responding selectively to letter strings in the left VOTC of literate adults were predetermined genetically (i.e., selected in evolution) to respond selectively to faces. Indeed, despite gross anatomical constraints driving, e.g., the localization of these regions to the lateral rather than the medial fusiform gyrus (Grill-Spector et al. 2017), there is a large amount of variability in the location of face-selective VOTC regions across individuals (e.g., Zhen et al. 2015).

Finally, while “neuronal recycling” is a loaded and (in this case) misleading terminology, *neural competition* is, in contrast, ubiquitous in the central nervous system and appears fundamental for neural plasticity and selectivity (Edelman 1987; Merzenich et al. 1988). For instance, competition for representation has been well characterized in different animal species at the level of the somatosensory cortex (e.g., for inputs from different fingers; Merzenich et al. 1988), the primary auditory cortex (e.g., for different frequency sounds; Zhang et al. 2003) and the primary visual cortex (e.g., visual field and ocular dominance; Antonini and Stryker 2003; El-Boustani et al. 2018). Collectively, these studies have shown that sensory inputs that are actively enhanced (due to extensive experience/training) or suppressed (due to denervation for instance), increase or shrink in terms of cortical representations relative to competing sensory inputs with similar functional properties. Importantly, this neuronal competition depends on inherent overlap of terminating neuronal fibers and a fine balance of inhibitory-excitatory connections between cortical columns (Buanomano and Merzenich 1998). Despite the unconvincing evidence reviewed here at a large-scale level in support of direct neural competition between faces and letter strings in the human VOTC, it would be extremely exciting if such fundamental neural competition principles could be generalized to high-level visual representations in these cortical regions in future research.

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