

Note

Cerebral lateralization of face-sensitive areas in left-handers: Only the FFA does not get it right

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ARTICLE INFO

Article history:

Received 2 August 2012

Reviewed 13 September 2012

Revised 2 January 2013

Accepted 15 May 2013

Action editor Paolo Bartolomeo

Published online 14 June 2013

Keywords:

Face localizer

fMRI

Left-handedness

FFA

Brain asymmetry

ABSTRACT

Face perception is highly lateralized to the right hemisphere (RH) in humans, as supported originally by observations of face recognition impairment (prosopagnosia) following brain damage. Divided visual field presentations, neuroimaging and event-related potential studies have supported this view. While the latter studies are typically performed in right-handers, the few reported cases of prosopagnosia with unilateral left damage were left-handers, suggesting that handedness may shift or qualify the lateralization of face perception. We tested this hypothesis by recording the whole set of face-sensitive areas in 11 left-handers, using a face-localizer paradigm in functional magnetic resonance imaging (fMRI) (faces, cars, and their phase-scrambled versions). All face-sensitive areas identified (superior temporal sulcus, inferior occipital cortex, anterior infero-temporal cortex, amygdala) were strongly right-lateralized in left-handers, this right lateralization bias being as large as in a population of right-handers (40) tested with the same paradigm (Rossion et al., 2012). The notable exception was the so-called 'Fusiform face area' (FFA), an area that was slightly left lateralized in the population of left-handers. Since the left FFA is localized closely to an area sensitive to word form in the human brain ('Visual Word Form Area' – VWFA), the enhanced left lateralization of the FFA in left-handers may be due to a decreased competition with the representation of words. The implications for the neural basis of face perception, aetiology of brain lateralization in general, and prosopagnosia are also discussed.

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1. Introduction

The right-hemispheric dominance for face recognition is well established. It originates from the observation that a large proportion of patients suffering from prosopagnosia – the inability to recognize faces following brain damage – present with clinical signs indicating a lesion in the right posterior hemisphere (i.e., left superior quadrant visual field defects; Hécaen and

Angelergues, 1962; Meadows, 1974). The view that right unilateral lesions are sufficient to cause prosopagnosia was challenged by Damasio et al. (1982) on the basis of postmortem evidence and computerised tomography (CT) data obtained in a number of cases (see also Meadows, 1974). However, since then, tens of cases with right unilateral damage have been reported (e.g., Barton, 2008a; Busigny et al., 2010; De Renzi, 1986; De Renzi et al., 1991; Landis et al., 1988; Sergent and Signoret, 1992; Wada and

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<http://dx.doi.org/10.1016/j.cortex.2013.05.002>

Yamamoto, 2001). Although bilateral lesions may possibly lead to more severe impairments in face recognition than unilateral damage (Barton, 2008a), and although an additional posterior left hemisphere (LH) lesion appears to be necessary to cause prosopagnosia in some patients (Ettlin et al., 1992; Iwanaga et al., 2011), the view that right unilateral posterior brain damage can often be sufficient to cause prosopagnosia is now largely accepted. Studies using tachistoscopic stimulation in split-brain patients or normal observers later confirmed the right-hemispheric dominance for face recognition (Heller and Levy, 1981; Levy and Nagylaki, 1972; Parkin and Williamson, 1987), which is now firmly validated by neuroimaging studies of the healthy human brain (e.g., Kanwisher et al., 1997; Sergent et al., 1992), and electrophysiological recordings on the scalp (e.g., Bentin et al., 1996; Rossion et al., 2003).

The view that a right unilateral lesion is *necessary* to cause prosopagnosia has been challenged only by the reports of five cases of prosopagnosia following a left unilateral lesion. Strikingly, four of these patients were left-handed (Barton, 2008b; Eimer and McCarthy, 1999; Mattson et al., 2000; Tzavaras et al., 1973). Regarding the only right-handed patient, functional damage might have been also present in the right hemisphere (RH) due to inter-hemispheric spreading of epileptic seizures (Wright et al., 2006). In light of these observations, it is reasonable to test the hypothesis that lateralization of face perception depends on handedness, as language does (Corballis, 2009; Knecht et al., 2000).

Two recent neuroimaging studies supported this view. Badzakova-Trajkov et al. (2010) reported a smaller proportion of left-handers (73%) than right-handers (94%) with a right-hemispheric dominance in blood-oxygen-level-dependent (BOLD) signal across the whole brain for a simple face task (detection of repetition of video-clips). Willems et al. (2010) found that a middle fusiform gyrus face-sensitive area, the so-called 'Fusiform face area' (FFA, Kanwisher et al., 1997) was bilateral in size in left-handers. However, these studies were limited in their conclusions. Badzakova-Trajkov et al. (2010) used unconventional stimuli (facial expressions compared to nonbiological motion of objects) and compared the global activation of each hemisphere to the other, without defining face-sensitive areas. In contrast, the study of Willems et al. (2010) focused only on the FFA. Thus, given that the perception of faces is subtended by a widely distributed set of well-defined face-sensitive areas (e.g., Ishai, 2008; Sergent et al., 1992; Weiner and Grill-Spector, 2010; Rossion et al., 2012), the question of a differential lateralization of this function in left-handers remains largely open.

This issue was addressed here by presenting to a group of left-handed participants a whole-brain face localizer that has been used in several of our previous studies with right-handed participants (Jiang et al., 2009, e.g., 2011; Ramon et al., 2010; Rossion et al., 2011; see Rossion et al., 2012 for a large-scale analysis).

2. Methods

2.1. Participants

The study had 11 healthy participants [age = 23.10 ± 2.55 ; 9 females; left-handed according to the Edinburgh Inventory (Oldfield, 1971), who gave their informed written consent prior

to the experiment]. The laterality quotient of the left-handed participants is provided in Supplementary Table 1. The study was conformed to the Declaration of Helsinki of 1964 and was approved by the Biomedical Ethical Committee of the University.

2.2. Task and stimuli

The whole-brain face-localizer experiment has been fully described previously (Rossion et al., 2012) and will be only summarized here. Four categories of stimuli, corresponding to 4 conditions, were used (43 pictures by category): colour photographs of faces (F), cars (C), and their respective phase-scrambled versions (SF and SC respectively; see Rossion and Caharel, 2011; for all details about the stimuli).

Participants performed two runs of 11 min. In each run, 6 blocks of each of the 4 conditions were presented in random order, for a total amount of 144 stimuli per condition and per run. Each block lasted 18 sec during which 24 stimuli of the same condition were presented for 750 msec. All blocks had a 9 sec interval with a cross fixation as baseline condition. The stimuli and the fixation cross were presented centrally, but stimulus location varied randomly in *horizontal* (6%, 5.5° of visual angle) and in *vertical* (8%, 6.2°) directions at each presentation (average location centred). Participants performed a one-back task with 2 or 3 consecutive repetitions of the exact same stimulus in each block (target trials). Performance was at ceiling ($96.93\% \pm 1.43\%$), with mean response times of $510 \text{ msec} \pm 42 \text{ msec}$.

2.3. Imaging acquisition parameters

Imaging data was collected at the University of Maastricht (Faculty of Psychology and Neuroscience) using a 3 T head scanner (Siemens Allegra, Siemens AG, Erlangen, Germany) with repeated single-shot echo-planar imaging: echo time (TE) = 50 msec, flip angle (FA) = 90° , matrix size = 64×64 , field of view (FOV) = $224 \times 224 \text{ mm}^2$, slice order descending and interleaved, slice thickness = 3.5 mm, 36 slices, and repetition time (TR) = 2250 msec. A three-dimensional T1-weighted data set encompassing the whole brain was acquired to provide detailed anatomy (1 mm^3) thanks to a Alzheimer's Disease Neuroimaging Initiative (ADNI) sequence (TR = 2250 msec, TE = 2.6 msec, FA = 9° , matrix size = 256×256 , FOV = $256 \times 256 \text{ mm}^2$, 192 slices, slice thickness = 1 mm, no gap, total scan time = 8 min 5 sec).

2.4. Data analysis

MR data analysis was performed using BrainVoyager QX (Version 1.9.10, Brain Innovation, Maastricht, Netherlands). Preprocessing consisted in applying a linear trend removal to exclude scanner-related signal, a temporal high-pass filtering (cut-off: <3 cycles per run), a correction for the difference between the scan times of the different slices, and a correction for small interscan head movements by a rigid body algorithm (sinc interpolation) allowing rotating and translating each functional volume in 3D space. The data was not smoothed spatially. Anatomical and functional volumes were spatially normalized to compare the locations of activated brain region

across individual brains (Talairach and Tournoux, 1988). Computed statistical maps were overlaid to the 3D T1-weighted scans. Functional data were analyzed and modelled using a multiple regression model (General Linear Model – GLM) with predictors corresponding to the particular experimental conditions of the experiment. The predictor time courses of all experimental visual stimulations were computed on the basis of a linear model of the relation between neural activity and haemodynamic response (Boynton et al., 1996).

Statistical analyses were done as in the study of Rossion et al. (2012). First, we performed a whole-brain group analysis and used the conjunction contrast [(F–SF) and (F–C)] to identify face-sensitive areas where each voxel had to exceed threshold on both contrasts. For the group analysis, we used the same statistical threshold of the right-handed group ($t = 3.38$; $p = .00703$). For individual subject analysis, we were faced with the common issue that using a conservative statistical threshold would not allow observing all areas in all individual brains, while using a less severe threshold would cause some areas to merge with others in some individual brains. For this reason, and in line with Fox et al. (2009) and our previous study (Rossion et al., 2012), we used a common criterion for all subjects by fixing the size of the area that is the easiest to identify (i.e., the right FFA). Hence, a size of right ‘FFA’ the closest possible to 200 mm^3 was used in each individual (see Rossion et al., 2012; see also Fox et al., 2009; for a similar approach using a 50 mm^3 cluster size of right FFA).

3. Results

3.1. Group analysis

Fourteen face-sensitive areas were identified in the whole-brain group analysis: 8 were in the RH, and 6 in the LH. These clusters include the FFA, occipital face area (OFA), posterior superior temporal sulcus (pSTS), amygdala, and the precentral gyrus bilaterally, the hippocampus, perirhinal cortex, and the parieto-occipital junction only in the RH and the cuneus only in the LH (see Fig. 1 and Table 1 for a full description). Overall, there is a right-hemispheric dominance of the face perception network, with 62% of significant voxels located in the RH. Moreover, all areas identified bilaterally were larger in the right than the LH, with the important exception of the FFA, a region that had only 37% of the voxels in the RH (162 vs 272 in the LH).

3.2. Individual subject analysis

At a threshold of $\sim 200 \text{ mm}^3$ for the right FFA, we considered the extent of right lateralization of the face-sensitive network and its three core areas: the FFA, the OFA, and the pSTS (Table 2). The percentage of voxels significantly activated in the RH was expected to be higher than 50%, revealing a right-hemispheric dominance.

1. At the level of the whole face-sensitive network, 64.78% of the activated voxels are in the RH, which is significantly more than 50% [$t(10) = 2.55$, $p = .014$].

2. When considering only the FFA, only 48.04% of the voxels are in the RH. Hence, the FFA is not right-lateralized [$t(10) = .27$, $p = .395$]. In terms of sizes of the right and left FFA, there is actually a trend for a larger left FFA (326.90 ± 296.48) than a right FFA [209.18 ± 13.56 ; $t(10) = 1.67$, $p = .067$].
3. Regarding the other regions of the core face network, the OFA has more activated voxels in the RH than 50% ($67.83\% \pm 33.71$); which is marginally significant [$t(10) = 1.75$, $p = .055$]. Even though no cluster could be found in the pSTS in two participants, this region has significantly more than 50% of activated voxels in the RH [$t(8) = 3.24$, $p = .006$] and appears to be the most right-lateralized ($78.72\% \pm 26.59$) area of the entire set.
4. If we consider that an area is bilateral at the individual level when the proportion of voxels in each hemisphere is between 45% and 55% (arbitrary criterion), then only 27% of left-handers are characterized by a bilateral FFA, although there is a substantial proportion left-handers who present with a larger FFA in the left than in the RH (Fig. 2).

In summary, both the group analysis and the individual subjects analysis indicate that the face-sensitive areas are right-lateralized in left-handed subjects, with the notable exception of the FFA.

3.3. Comparisons between left- and right-handers

We also compared the left-handers to the larger group of right-handers reported in our previous study (Rossion et al., 2012; 40 participants, 31 females; mean age of 25.8 ± 5.55 ; see Supplementary Table 2 for a list of face-preferential areas in right-handers, at the group level). Both groups had a majority of female participants, with no difference in the proportion of females between groups ($31/40 = 77.5\%$; $X^2(2, N = 51) = .95$, $p = .758$).² Age was also matched [$t(49) = 1.560$, $p = .125$].

When considering the percentages of voxels in the RH for the whole face-sensitive cortical network, the OFA and the pSTS, there is no difference between right- and left-handed participants. The only exception is the FFA, which is on average bi-lateralized in left-handed participants rather than being right-lateralized as in right-handed participants (Table 2). The proportion of individuals having an FFA with more than 55% of the voxels in the RH (i.e., right dominant) is different between the two groups, $X^2(2, N = 47) = 7.220$, $p = .027$. Specifically, a right dominant FFA is found in 72% of the right-handers whereas only 27% of the left-handers show a right-hemispheric dominance (Fig. 2). In contrast, the proportions of participants who have a right-hemispheric dominance do not differ between left- and right-handers for any of the other areas (network: 73% vs 75%, OFA: 58% vs 60%, STS: 78% vs 78%, respectively; all p 's $> .8$).

² Note also that in our previous study with right-handers, there was no evidence that females and males differed in their pattern of lateralization, neither for the FFA [$t(34) = .184$, $p = .855$], nor for the other areas of interest [Network: $t(34) = .538$, $p = .594$; OFA: $t(29) = .992$, $p = .329$; STS: $t(25) = .703$, $p = .488$].

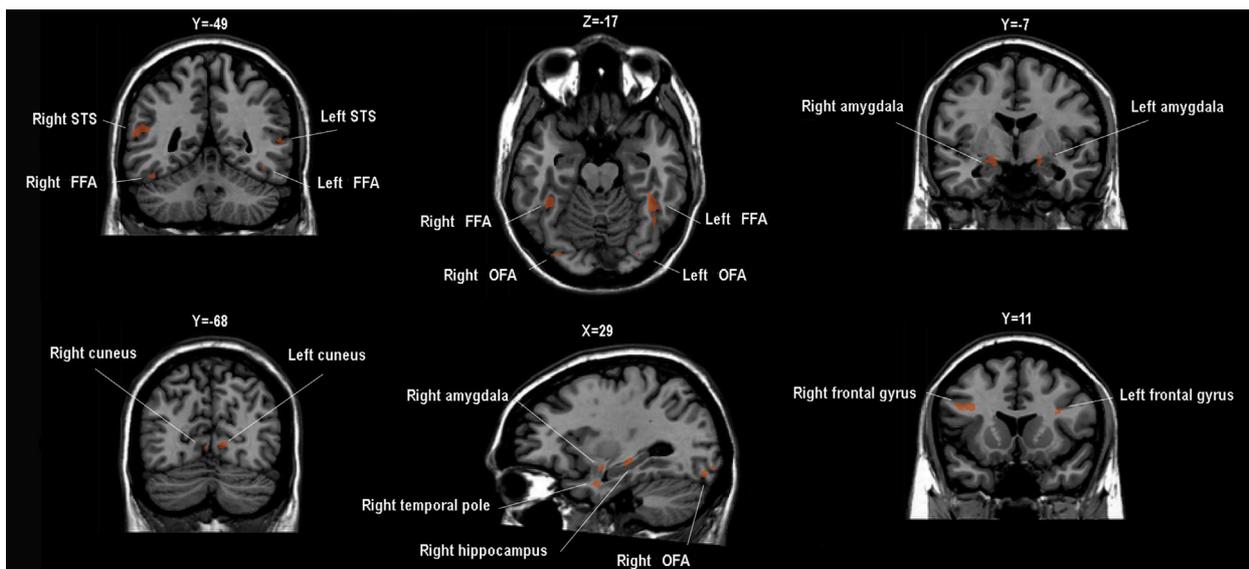


Fig. 1 – Activation maps of the face-sensitive areas found at the group level among left-handers (at decreased threshold for illustrative purpose only). See Figure 4 of Rossion et al. (2012) for a comparison of activated areas in right-handers.

In summary, the only difference between right- and left-handers concerns the FFA, a functional area that is not right-lateralized among left-handers, considered at the population level. The other areas of the face-sensitive cortical network are right-lateralized in both groups.

4. Discussion

We assessed the degree of lateralization of the whole set of areas responding preferentially for faces in left-handers, and found a

Table 1 – Face-sensitive areas among the left-handers at the group level.

Area	BA	x	y	z	Size	Peak
					Voxels	z-Score
T-value = 3.38						
Right fusiform gyrus = right 'FFA'	37	36	-42	-20	162	4.663
Left fusiform gyrus = left 'FFA'	37	-41	-44	-16	272	5.193
Right inferior occipital gyrus = right 'OFA'	18	24	-89	-10	37	4.050
Left inferior occipital gyrus = left 'OFA'	18	-25	-90	-15	3	3.017
Right pSTS	22	50	-50	14	48	4.183
Left pSTS	22	-55	-50	6	5	3.864
Right amygdala		21	-6	-10	169	5.160
Left amygdala		-19	-10	-9	42	4.801
Right precentral gyrus	6	32	7	26	96	3.971
Left precentral gyrus	6	-32	10	21	2	3.298
Right hippocampus		29	-25	-7	39	4.910
Right perirhinal cortex and fusiform gyrus	38	27	0	-24	28	4.127
Right parieto-occipital junction	31	2	-71	24	6	3.331
Left cuneus	17	-11	-70	-1	34	4.106

clear right-hemispheric dominance in this group (65% of the volume activated on average). Overall, this proportion is not very different than the right-hemispheric superiority observed in right-handed brains (68% in our previous study in a larger sample of participants, Rossion et al., 2012) and is in agreement with the observations of Badzakova-Trajkov et al. (2010).

As noted in the introduction, the human RH superiority in face perception has been long evidenced by lesion studies (Hécaen and Angelergues, 1962; Meadows, 1974), studies using divided visual hemifield presentations (e.g., Heller and Levy, 1981), neuroimaging (e.g., Kanwisher et al., 1997; Sergent et al., 1992), and ERPs (e.g., Bentin et al., 1996; Rossion et al., 2003). The reason(s) of this right lateralization of face perception in humans remain(s) largely unknown. It has been related to the holistic versus analytic processing dichotomy of the RH and LH respectively, faces being considered as a typical example of a visual stimulus requiring holistic/configural perception (Sergent, 1988). Further studies have shown that the RH superiority for faces is related to the processing of low-spatial frequency information (de Schonen and Mathivet, 1989; Woodhead et al., 2011), which supports holistic face perception (Goffaux and Rossion, 2006; Sergent, 1986). Accordingly, the dominance of the RH to process holistic/configural spatial relations has been consistently evidenced (see Hellige, 1996; Jager and Postma, 2003; for reviews). In line with this view, neuroimaging studies have shown that when holistic perception of faces is required, or enhanced, the RH superiority increases significantly, in particular at the level of the FFA (e.g., Schiltz and Rossion, 2006). Even though recent fMRI studies of the monkey brain rather report bilateral activations (Tsao et al., 2008), there is also evidence of such a right lateralization of face perception in non-human primates (Perrett et al., 1988; Zangenehpour and Chaudhuri, 2005) and other mammals (Peirce and Kendrick, 2002), in line with the view that hemispheric asymmetries in humans are inherited from common ancestors (Ocklenburg and Güntürkün, 2012).

Table 2 – Lateralization indices of face-sensitive voxels within the FFA, OFA, and STS among the left- and right-handers at the individual level.

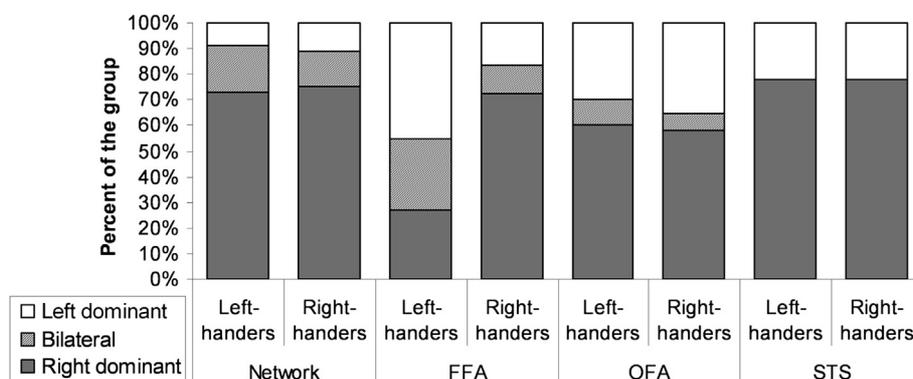
	Network		'FFA'		'OFA'		pSTS	
	M	SD	M	SD	M	SD	M	SD
<i>Left-handers</i>								
Voxels in RH	852	513	209	14	306	336	191	288
Voxels in LH	696	829	327	296	173	266	115	237
% in RH	64.78	19.18	48.04	23.91	67.83	33.71	78.72	26.59
<i>Right-handers</i>								
Voxels in RH	648	657	215	32	140	274	152	294
Voxels in LH	472	778	151	218	113	358	50	144
% in RH	68.45	18.32	71.02	25.83	61.50	38.79	76.85	36.28

Is this right lateralization of face perception related to the left lateralization of language (Broca, 1861; Gaillard et al., 2004; Knecht et al., 2000; or conspecific communication signals in other species, e.g., Böye et al., 2005; Ocklenburg et al., 2013)? At first glance, the present study does not support this view since language is more often right lateralized in left-handers than right-handers (25% vs 5%, Bethmann et al., 2007), yet there was a similar overall right lateralization of face-sensitive responses between our groups of left- and right-handers (for whom lateralization of language was not tested). However, there was one notable exception to the right lateralization of the face-sensitive areas in left-handers: at the group level, the FFAs of left-handers is bilaterally distributed, with a slight advantage of the LH (see also Willems et al., 2010). This observation supports the relationship between language and face lateralization, for two reasons.

The first is that the FFA is not more bilateral in left-handers considered as individuals. Rather, some left-handers present with a clear right-hemispheric dominance of the FFA, while others present with a clear left hemispheric dominance. Thus, although our sample of participants was limited, our study does not support bi-laterality of the FFA as a general pattern of left-handedness and rather suggests a more heterogeneous pattern of FFA lateralization in left-handed than in right-handed brains. This higher heterogeneity of left-handers' FFA

goes in line with the higher heterogeneity of language lateralization found in this population (Annett, 2002; McManus, 2004).

The second and most important reason is that the left FFA is located next to the so-called "Visual Word Form Area" (VWFA), a region of the middle fusiform gyrus associated with the representation of abstract letter identities invariant for parameters such as spatial position, size, font or case (e.g., Cohen and Dehaene, 2004; Dehaene and Cohen, 2011). According to electrophysiological (Allison et al., 2002) and neuroimaging (Cantlon et al., 2010; Dehaene et al., 2010) evidence, there is a competition between the visual representation of words and faces, in particular at level of the left fusiform gyrus. This competition would contribute to the right lateralization for faces (Dundas et al., 2013; Plaut and Behrmann, 2011). Under this view, a plausible interpretation of our data is that in some left-handers at least, the competition of word to face representation is reduced in the left fusiform gyrus, leading to an increased left FFA response. In contrast, given that the other face-sensitive areas [i.e., 'OFA', pSTS, anterior inferotemporal cortex (AIT), ...] do not have to compete with a potential representations of words in a neighbouring area, they are free to express their right-hemispheric dominance, even in left-handers. To make it clear, we do not claim that the right lateralization of face perception is only, or even primarily, a consequence of the left lateralization of language.

**Fig. 2 – Relative hemispheric dominance for the different face-sensitive areas and the whole network.**

However, in human adults, the emergence of language may increase the right dominance of the representation of faces, in particular in the middle fusiform gyrus (Cantlon et al., 2010; Dundas et al., 2013). Some left-handers presenting with a complete or partial right lateralization of language functions would be the exception to this rule. Whether literacy and handedness play a role as interacting factors in the lateralization pattern of the FFA needs to be investigated and could provide a better understanding of prosopagnosia.

Finally, our observations have implications on the medical prognosis of prosopagnosia after posterior cerebral lesion or surgery among left-handers. Neuropsychological data has so far informed that a RH lesion was both necessary and sufficient to cause prosopagnosia. However, among the tens of cases of prosopagnosia following right unilateral damage reported in the literature, we were not able to identify a single left-hander. Although this could be taken as evidence that a right unilateral lesion is not sufficient to cause prosopagnosia in this population, our data rather suggests that a right unilateral lesion to other face-sensitive areas than the middle fusiform gyrus (e.g., the right OFA) should lead to prosopagnosia even in left-handers.³ Interestingly, the left-handed prosopagnosic patients with unilateral brain damage (Barton, 2008a, 2008b; Eimer and McCarthy, 1999; Mattson et al., 2000; Tzavaras et al., 1973) all presented with lesions concerning the cortical territory of the left middle fusiform gyrus. This observation completes the present neuroimaging findings to suggest that in a proportion of left-handers at least, the left FFA is not only relatively increased in size but may also have become a critical component of their cortical face network.

Acknowledgements

We thank Corentin Jacques for the making of the stimuli. LD was supported by a PAI grant. HB, BH and BR are supported by the Belgian National Foundation for Scientific Research (FNRS). We thank two anonymous reviewers for their helpful comments on a previous version of this paper.

Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.cortex.2013.05.002>.

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³ We thank an anonymous reviewer of a previous version of this paper for this suggestion.

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