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BRIEF REPORT

On handedness and the lateralization of fusiform face area(s)

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Abstract

In the human cerebral cortex, the right hemisphere dominance of face processing has been well-established across age groups and in different clinical populations. Nevertheless, the role of handedness in this lateralization remains unclear as previous studies have yielded inconclusive results due to small sample sizes and the fact that they did not consider recent results identifying multiple face-selective regions on the fusiform gyrus (FG) that are anatomically and functionally distinct in over 1000 individuals. To address these parallel concerns, we investigated the relationship between handedness and the structural, functional, and connectivity properties of manually defined FG face-selective regions using multimodal neuroimaging data from a large sample of non-right-handers ($N = 124$)—a sample size which is 5–11 times the size of previous studies. Our careful, manual delineations of FG face-selective regions—in the spirit of "precision imaging" in the broader cognitive neuroscience and human brain mapping fields—revealed that pFus-faces/FFA-1 is more selective in the right, compared to the left, hemisphere in non-right handers, which is not the case for mFus-faces/FFA-2. Subsequent analyses relating handedness to network properties or anatomical features did not reveal any significant effects. The combination of these findings provides a foundation for implementing a precision imaging approach that is ideal for building strategies for case studies and the treatment and intervention of neurological disorders that include issues with either face perception, handedness, or both—as well as evolutionary and theoretical insights regarding hemispheric specialization of cortical function.

Keywords Handedness · Fusiform face area(s) · Lateralization · Precision imaging · Multimodal magnetic resonance imaging

Introduction

In extended fields integrating higher-level cognition, biology, brain mapping, development, aging, evolution, and functional specialization, the Fusiform Face Area is likely the most popular region studied across these fields - indeed, the original paper (to date and to our knowledge) is the most cited paper in the *Journal of Neuroscience* (Kanwisher et al. 1997). Despite this great interest and the well-known right hemisphere dominance for face processing (which has been known for decades from both neuroimaging and patient studies), there are inconclusive results regarding the role of handedness in this lateralization (Bukowski et al. 2013; Frässle et al. 2016; Rossion et al. 2012; Thome et al. 2022; Willems et al. 2010; Zhen et al. 2015), especially since only about 10% of the population identify as left-handed, which limits sample sizes.

Handedness aside, over two dozen studies published over the last decade have identified two anatomically and

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functionally distinct FFA(s) – most recently in over 1000 participants (Chen et al. 2023). Leveraging these manually identified functional regions, we had the rare opportunity to revisit the relationship among handedness and the lateralization of the structural and functional (including network) properties of the two anatomically and functionally distinct face-selective regions on the FG in a sample size 5–11 times the size of previous studies (124 non-right-handers and 124 well-matched right-handers).

We found that pFus-faces/FFA-1 is more selective (measured as the difference in BOLD fMRI signal between faces and objects) in the right, compared to the left, hemisphere in non-right handers, which is not the case for mFus-faces/FFA-2. Nevertheless, there was not a significant hemisphere × group × region interaction indicating that the influence of handedness on face selectivity is small as indicated in the largest sample size of manually defined FFA(s) currently available in the present study. Further, we did not identify handedness effects for other anatomical, functional, or network properties of FFA(s). The present findings, in combination with control and group analyses outside the FG, provide a foundation for implementing a precision imaging approach that is ideal for building strategies for case studies and the treatment and intervention of neurological disorders that include issues with cognition, handedness, or both.

Methods

Participants

The study sample was part of the Human Connectome Project-Young Adult dataset (HCP-YA, S1200 release, 2017), which comprises behavioral and multimodal MRI data from 1206 healthy young adults. The 1053 participants (575 females) who completed structural MRI (sMRI), resting-state functional MRI (rfMRI), and task functional MRI (tfMRI) scans (Van Essen and Glasser 2018) were selected. The data collection was approved by multiple Institutional Review Boards (IRBs) led by Washington University in St. Louis and the University of Minnesota.

Table 1 Demographic information of participants

	Non-right-handed	Right-handed	*p* value
Number of subjects	124	124	
Gender; male/female	57/67	62/62	n.s.($p=0.611$)
Average age	28.48(3.72)	28.65(3.65)	n.s.($p=0.729$)
Average standard handedness score	0.53(0.31)	0.57(0.31)	n.s.($p=0.349$)

Participants' handedness was defined based on the score of Edinburgh Handedness Inventory, which ranges from −100 to 100, with higher score indicating a stronger preference for right-handedness. According to previous research (Labache et al. 2023), participants with a score less than and equal to 30 were considered as non-right-handers, thus defining non-right-handed scores as ranging from −100 to 30, and right-handed scores as ranging from 30 to 100. The sample contained 124 non-right-handed participants (57 females) and 929 right-handed participants (518 females). A control sample of 124 right-handers tightly matched with the 124 non-right-handers in terms of gender, age, and standardized handedness scores within each group was selected from the 929 right-handed participants to isolate the effect of handedness from potential confounds as much as possible using Propensity Score Matching (IBM SPSS Statistics) (Table 1).

MRI acquisition

MRI data were acquired on the HCP's customized 3T Siemens Skyra scanner using a 32-channel head coil. T1-weighted (T1w) images were acquired using a 3D MPRAGE sequence (TR = 2400 ms, TE = 2.14 ms, voxel size = 0.7 mm isotropic, iPAT = 2). T2-weighted (T2w) images were acquired with a 3D SPACE sequence (TR = 3200 ms, TE = 565 ms, voxel size = 0.7 mm isotropic, iPAT = 2). Functional data were collected using gradient-echo EPI sequence (TR = 720 ms, TE = 33.1 ms, voxel size = 2 mm isotropic, MB = 8). Each participant underwent four resting-state fMRI (rfMRI) scans, each lasting approximately 15 min. The task fMRI scans we used included the working memory (2 runs, each lasting 4 min) and emotion tasks (2 runs, each lasting 2 min). The description for the fMRI tasks can be found in the Supplementary Materials. More detailed information on the HCP-YA MRI acquisition protocol can be found in previous publications (Barch et al. 2013; Glasser et al. 2013; Smith et al. 2013; Uğurbil et al. 2013).

MRI preprocessing

The MRI data from HCP-YA were preprocessed using the HCP minimal preprocessing pipelines (Glasser et al. 2013). T1-weighted (T1w) and T2-weighted (T2w) images were used to reconstruct individual cortical surfaces, estimate the T1w/T2w ratio as a myelination proxy, and measure cortical thickness. These surfaces and maps were registered to the standard fsLR surface using the MSM algorithm (Glasser et al. 2016; Robinson et al. 2014).

The functional MRI data underwent motion correction, high-pass temporal filtering (2000 s for rfMRI; 200 s for tfMRI), and spatial denoising with the ICA+FIX approach (rfMRI only). The data were then registered to the standard CIFTI grayordinate fsLR space using MSM. Preprocessed task fMRI data were analyzed using a general linear model (GLM) to estimate activity at each vertex/voxel with FSL (Barch et al. 2013). BOLD responses were modeled with a boxcar function convolved with a double gamma hemodynamic response function and its temporal derivative. Linear contrasts estimated effects of interest (e.g., faces vs. others for the working memory task; faces vs. shapes for the emotion task), and fixed-effects analyses determined average effects across runs within participants.

Definition of face-selective ROIs

When examining functional brain areas, functional regions of interest (ROIs) can be defined at the individual or group level. Individual ROIs that are defined based on independent fMRI localization tasks within each participant preserve individual specificity and improve statistical power. In contrast, group-level ROIs are defined based on statistical summaries of functional activations from an independent group of subjects, providing stable and generalizable regions across participants, which enhances statistical power. However, the latter approach might be less sensitive to individual differences. Here, we employed both individual and group ROI approaches to investigate the lateralization of face-selective areas, balancing large N and precision imaging approaches. Specifically, the working-memory task (faces vs. others) was used to define FFAs, while the emotion task (faces vs. shapes) was employed to assess their face selectivity. This approach ensures unbiased estimation of ROI selectivity, and enhances both the validity and generalizability of our findings.

Individual FFA definition

Individual FFAs were defined for each participant. Specifically, according to the macroanatomical landmarks of the fusiform gyrus and mid-fusiform sulcus, pFus-faces/FFA-1 and mFus-faces/FFA-2 were manually delineated on individual activation maps (face vs. others, $p < 0.05$, uncorrected) from the working memory task. More details can be found in Chen (2023).

Group face-selective ROI definition

Group-level face-selective ROIs were manually delineated on the thresholded probabilistic activation maps (threshold = 0.25) which were generated from the face-selective activation maps (faces vs. others, $p < 0.05$, uncorrected) of 805 right-handed participants who were not selected as controls for non-right handers (Zhen et al. 2015).

Characteristics of FFA(s)

Functional characteristics of FFA(s)

Face selectivity was measured by the average z-value of the face vs. shape contrast from the emotion processing task, which were independent of the definition of ROIs, thereby guaranteeing complete analytical separation and eliminating any circularity.

Structural characteristics of FFA(s)

Cortical thickness and myelination were used to characterize the structural properties of the FFA(s). For each participant, the average myelination and cortical thickness values, as well as total surface area, of each ROI was calculated.

Connectivity characteristics of FFA(s)

Resting-state functional connectivity (RSFC) was used to characterize the connectivity of pFus-faces/FFA-1 and mFus-faces/FFA-2. For each ROI, the Pearson correlation coefficients between the average resting-state time series of the ROI and 12 functional networks (Cole et al. 2010) were calculated to obtain 12 functional connectivity features.

Impact of handedness on the lateralization of structural and functional features of the FFA(s)

We used a 2 × 2 mixed ANOVA to test the effects of hemisphere (left hemisphere, right hemisphere; within-subjects) and handedness (non-right-handed, right-handed; between-subjects) on measures characterizing the function, structure, and connectivity of pFus-faces/FFA-1 and mFus-faces/FFA-2.

Results

Definition of individual face-selective ROIs

At the individual-level, we manually defined pFus-faces/FFA-1 and mFus-faces/FFA-2 for each participant based on their face-selective activation maps from the working memory task (Fig. 1A). In the 124 non-right-handed participants, 118 participants had identifiable pFus-faces/FFA-1 and mFus-faces/FFA-2 in both hemispheres, while in 124 right-handed participants, 116 participants had identifiable pFus-faces/FFA-1 and mFus-faces/FFA-2 in both hemispheres.

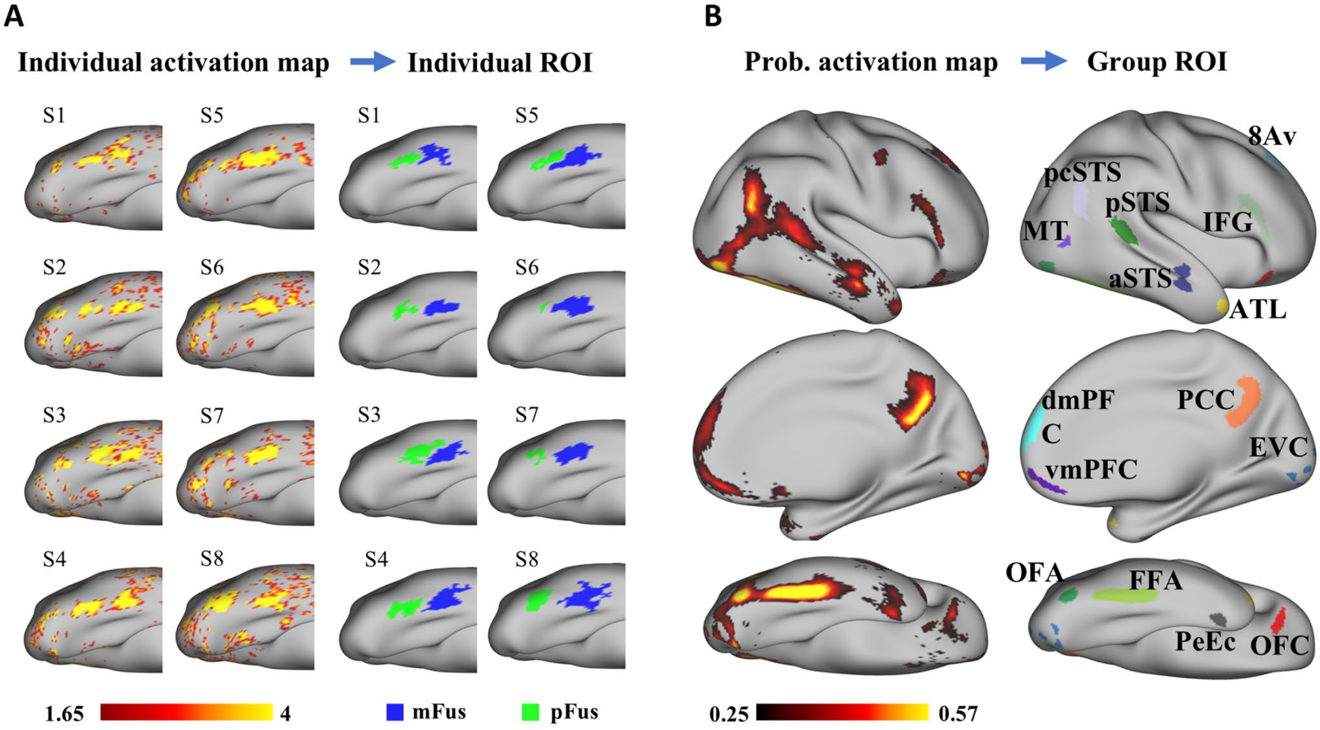


Fig. 1 Defining individual and group face-selective ROIs. **A** Two individual FG face-selective regions (mFus-faces/FFA-2, blue; pFus-faces/FFA-1, green) were manually delineated on individual activation maps. **B** Sixteen group ROIs were defined on the thresholded probabilistic activation map constructed from the HCP working memory task. The ROI name was adopted from the HCP multi-modal parcellation (Glasser et al. 2016). Prob. activation map: probabilistic activation map

Definition of group-level face-selective ROIs

At the group-level, probabilistic activation maps were first constructed from the working memory task based on 805 right-handed participants. A set of face-selective ROIs was then manually defined on the probabilistic map (Fig. 1B), including both fusiform face-selective regions, lateral orbitofrontal cortex (OFC), anterior superior temporal sulcus (aSTS), anterior temporal lobe (ATL), inferior frontal gyrus (IFG), dorsal and ventral parts of dorsolateral frontal area 8 A(8Ad, 8Av), ventromedial prefrontal cortex (VMPFC), dorsomedial prefrontal cortex (DMPFC), middle temporal area (MT), occipital face area (OFA), early visual cortex (EVC), posterior continuation of the superior temporal sulcus (pcSTS), posterior superior temporal sulcus (pSTS), perirhinal-entorhinal cortex (PeEc), and the posterior cingulate cortex (PCC) (Supplementary Fig. S1).

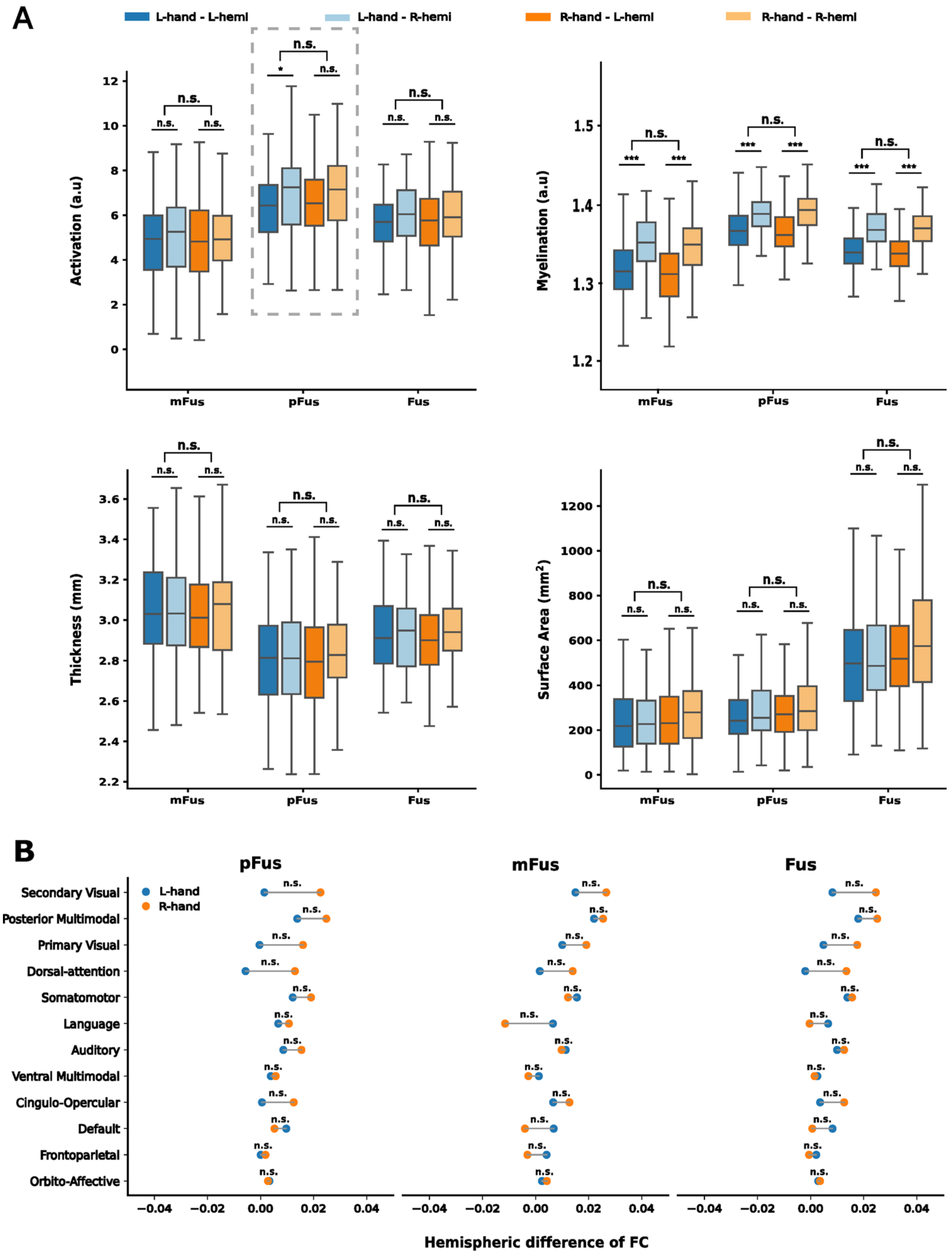
Lateralization of face selectivity of FFA(s) is independent of handedness

The face-selective responses were quantified as the average face-selective response from the independent HCP emotion processing task (faces vs. shapes). A two-way ANOVA with hemisphere and handedness as factors was conducted to test the effects of handedness on the laterization of the structural and functional properties of each face-selective region.

Surprisingly, pFus-faces/FFA-1 was more selective in the right hemisphere in non-right-handed individuals ($F(1,182) = 6.49$, $p = 0.012$, Bonferroni corrected), but not right-handed individuals ($F(1,212) = 3.30$, $p = 0.071$, Bonferroni corrected; Fig. 2A, upper left). These findings indicate a benefit of our approach of defining face-selective regions separately on the middle and posterior portions of the FG in individual participants – a finding that would have been missed if these regions were lumped together. To evaluate this effect more rigorously, a three-way ANOVA was performed (Nieuwenhuis et al. 2011). However, the interaction among region, hemisphere, and handedness did not reach statistical significance ($F(1, 212) = 0.034$, $p = 0.792$, Bonferroni corrected, see Supplementary Table 2 for more details), which we attribute potentially to limited statistical power arising from the current sample size.

We further examined the handedness effect on the structural properties of face-selective regions on the FG: no handedness effects on the lateralization of anatomical features were found including myelin content, cortical thickness and cortical surface area measured by structural MRI data (Fig. 2A). Moreover, we examined the handedness effect on resting-state functional connectivity (RSFC) between each

Fig. 2 pFus-faces/FFA-1, but not mFus-faces/FFA-2, is more selective in the right compared to the left hemisphere in non-right handers, but not right handers, in the largest sample size to date ($N = 124$). **A** Structural (cortical thickness, myelination, and surface area) and functional properties (selectivity) of fusiform face-selective regions from non-right- and right-handed participants. As indicated by the boxplots, pFus-faces/FFA-1, but not mFus-faces/FFA-2, is more selective in the right compared to the left hemisphere in non-right handers compared to right handers (upper left, middle, dotted gray rectangle). **B** Interhemispheric differences of resting-state functional connectivity (RSFC) between fusiform face-selective areas and 12 resting-state networks. The data is obtained by subtracting the functional connectivity strength of the left hemisphere from that of the right hemisphere ROI within a specific network. n.s., non-significance; *$p<0.05$; **$p<0.01$; ***$p<0.001$, Bonferroni corrected. L-hand: non-right-handed; R-hand: right-handed; L-hemi: left hemisphere; R-hemi: right hemisphere; mFus: mFus-faces/FFA-2; pFus: pFus-faces/FFA-1; Fus: FFA (the two areas together)



face-selective region and 12 functional networks (Cole et al. 2010) and again, found no handedness effects on the lateralization of RSFC (Fig. 2B).

Moreover, while we implemented a "precision imaging" approach by conducting analyses in individually defined regions on the FG (496 manually defined functional regions in total), we also tested handedness effect on the group-level FFA. We found no effect of handedness on the lateralization of face selectivity and structure in the group analyses of the FFA. A two-way ANOVA with hemisphere and handedness as factors indicated a significant main effect of hemisphere on face selectivity in the group-level FFA ($F(1, 218) = 28.866$, $p < 0.001$, Bonferroni corrected), with greater activation in the right hemisphere than the left. However, there were no significant main effects of handedness or interactions between hemisphere and handedness ($ps > 0.83$, Bonferroni corrected).

Finally, we examined the effect of handedness on the lateralization of other face-selective areas outside the FG using group ROIs, including: OFC, aSTS, ATL, IFG, 8Ad, 8Av, VMPFC, DMPFC, MT, OFA, EVC, pcSTS, pSTS, PeEc and PCC. No significant main effect of handedness or interaction on face selectivity and structure of these ROIs was identified (see Supplementary Fig. 1). However, several areas showed significant main effects of hemisphere (see Supplementary Table 1).

Discussion

In summary, our results indicate that pFus-faces/FFA-1 is more selective in the right, compared to the left, hemisphere in non-right handers, which is not the case for mFus-faces/FFA-2 – emphasizing the utility of defining separate face-selective regions on the FG. These results are a product from the largest sample to date to test the role of handedness on the selectivity, anatomy, and functional connectivity after manually defining separate face-selective regions on the FG. In parallel, probabilistic analyses outside the FG showed null results, indicating the benefit of the targeted "precision imaging" approach of the FG implemented here.

Zooming out, these findings contribute to a broader ongoing discussion regarding the theoretical implications of sample size and effect size in neuroscience and biology regarding precision imaging vs. large N studies (Marek et al. 2022). Additionally, as the role of Yakovlevian anticlockwise torque (also referred to as *occipital bending*) has previously been proposed to play a role in functional brain asymmetry (Toga and Thompson 2003), which has recently been tested and linked to (i) handedness, (ii) underlying genetics, (iii) sociodemographic factors, (iv) physical and mental health, and (v) cognitive function (Kong et al. 2021; Zhao et al. 2022), future studies can test how the results reported here are related to these identifying factors more broadly, as well as in neurocognitive models of face processing within and outside the FG.

The present findings provide an important quantitative benchmark for subsequent studies – whether targeting the FG or outside the FG. For example, we hypothesize that future studies exploring the effect of handedness and FG face-selective regions implementing a precision imaging approach will replicate our effects in the same sample size included here - or larger. While we did find that pFus-faces/FFA-1 was more selective in the right, compared to the left, hemisphere in non-right-handed participants, but not right-handed participants, we acknowledge the limitation that this was in just one task and one set of stimuli. Further, since our exploratory analyses leveraged probabilistic face-selective regions, it's an open question if individually-defined face-selective regions outside of the FG may show an effect of handedness. Altogether, the present findings not only deepen our understanding regarding the complex relationship between cognitive function and lateralization of face processing, but also provide a foundation for implementing a precision imaging approach that is ideal for building strategies for case studies and the treatment and intervention of neurological disorders that include issues with either face perception, handedness, or both.

The differential impact of handedness on the lateralization of pFus-faces/FFA-1 and mFus-faces/FFA-2 offers insights into the functional organization of face processing, suggesting the distinct components of the face processing system (facial identity processing in pFus-faces/FFA-1and processing facial expressions in mFus-faces/FFA-2) are differentially influenced by factors like handedness, highlighting the need to consider individual differences in neurocognitive models of face perception.

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Data availability All data generated or analysed during this study are included in this published article (and its supplementary information files).

Declarations

Competing interests The authors declare no competing interests.

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