The asymmetry of the fusiform face area is a stable individual characteristic that underlies the left-visual-field superiority for faces

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1. Introduction

Recognition of faces is better when faces are presented in the left than right-visual-field. Furthermore, this perceptual asymmetry is a stable individual characteristic. Although it has been commonly assumed that the right hemispheric dominance for face processing underlies this left-visual-field superiority in face recognition, this neural–behavioral association has never been directly demonstrated. Here we applied functional MRI (fMRI) to measure the magnitude of the asymmetric response to faces for each subject. To determine whether the asymmetric neural response to faces is stable across sessions, subjects returned for a second fMRI session. In addition, subjects performed a behavioral experiment outside the scanner where they had to recognize centrally presented chimeric faces, which presented different identities in the right- and left-visual-field. This task yielded a measure of the magnitude of the left-visual-field bias for each subject. Our findings show that the magnitude of the asymmetry of the face-selective area in the fusiform gyrus (FFA) is highly consistent for each individual across scans. We then show that the behavioral left-visual-field asymmetry, measured outside the scanner, was strongly and specifically correlated with the asymmetry of the FFA across subjects, but not with other face-specific or nearby object-general regions. Our findings provide the first empirical evidence for the prevalent idea that perceptual asymmetries in face recognition are associated with the well-known hemispheric asymmetry for faces. We conclude that the FFA asymmetry is a highly stable individual characteristic that underlies the well-established left-visual-field superiority for face recognition.

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Serger, 1982), in particular for visual matching of unfamiliar faces and when faces cannot be recognized based on a single feature (Rhodes, 1985; Sergent & Bindra, 1981). Studies with split-brain patients reported similar results. Levy et al. (1972) briefly presented faces that were composed of right and left halves of two different identities (chimeric faces) at the center of the visual field and asked split-brain patients to point to the face that matched the briefly presented faces. Results showed that patients matched the face that was presented in the left-visual-field on over 90% of trials. Interestingly, the split-brain patients were not aware of the chimeric nature of the stimuli but perceived a consistent face that was composed of the half-face presented in the left-visual-field. Recently, Yovel, Paller, and Levy (2005) reported a similar phenomenon with normal participants, with a novel paradigm that we adopted in the current study. Taken together, these findings suggest that facial information presented in the left-visual-field dominates the perception of the full face under most task conditions.

Whereas the laterization method was the major procedure to study the role of the two hemispheres in face processing in the 1970s and 1980s, in the past decade neuroimaging techniques, such as event-related potentials (ERP) and functional MRI (fMRI) allow us to directly study the role of each hemisphere in face processing. Consistent with brain damage and laterization studies, neuroimaging studies have consistently revealed right hemisphere dominance for faces presented in the center of the visual field. ERP studies have reported an early face-selective ERP component (N170) that is larger over the right than left occipital–temporal cortex for centrally presented faces (Bentin, Allison, Puce, & Perez, 1996; Campanella et al., 2000; Rossion, Joyce, Cottrell, & Tarr, 2003; Yovel, Levy, Grabowecky, & Paller, 2003). Similarly, positron emission tomography (PET) and functional MRI studies have consistently revealed larger face-selective regions over the right than the left hemisphere for centrally presented faces (Kanwisher, McDermott, & Chun, 1997; Kanwisher & Yovel, 2006; Sergent, 1991). Surprisingly, it is not known yet whether these hemispheric asymmetries revealed with neuroimaging methods are associated with the well-established perceptual asymmetries for faces.

To the best of our knowledge, no previous studies assessed the correlation between neural and behavioral asymmetries for faces. A few studies did assess the correlation between lateralized perceptual linguistic abilities and related neural asymmetries. For example, Zatorre (1989) found a correlation between ear advantage in the fused dichotic word task and the lateralization of speech representation as determined by carotid sodium amytal test in epileptic patients. The majority of subjects with left hemisphere speech lateralization showed right ear advantages, and all subjects with right hemisphere lateralization displayed left ear advantages (Zatorre, 1989). Moffat, Hampson, and Lee (1998) measured the size of the planum temporal and used the fused dichotic word task to measure ear advantage but only found a non-significant trend for a correlation between the asymmetry of ear advantage and the asymmetry of planum temporal size. All subjects with a right ear advantage had a larger left planum temporal size, but only approximately half of the subjects with a left ear advantage had larger right planum temporal volumes (Moffat et al., 1998). Recently, Dorsaint-Pierre et al. (2006) found a correlation between the lateralization of speech representation in epileptic patients (determined by carotid sodium amytal test) and the asymmetry of the inferior frontal gyrus, but not for the planum temporal and Heschl’s gyrus (Dorsaint-Pierre et al., 2006). Overall, these studies provide evidence for some associations between anatomical and behavioral asymmetries in the language domain. None of these studies has examined the relationship between functional brain activations and behavioral asymmetries, which may provide further information about the associations between the neural and perceptual laterality measures.

Despite wide agreement that the left-visual-field superiority is mediated by the right hemispheric dominance for faces, and the robust right hemisphere dominance that is found in neuroimaging studies, the association between these behavioral and neuroimaging measures has never been demonstrated directly. To find out whether these two well-known effects are associated, we examined the correlations between the neural and behavioral effects across individuals. Previous studies have shown that the left-visual-field asymmetry is a stable individual characteristic (Levy et al., 1983a; Luh et al., 1991). In other words, the magnitude of the asymmetry was stable across different sessions for each individual. In the current study we were particularly interested in exploring this stable aspect of perceptual and neural asymmetries for faces. Thus, we first asked whether the neural asymmetry for centrally presented faces is a stable characteristic of each individual across sessions. We then explored whether this neural asymmetry for faces is correlated with the behavioral laterality effect for faces, which we obtained on a different session outside the scanner. Specifically, subjects underwent a functional MRI scan to measure their face-selective regions in the right and left temporal–occipital cortex. In a different session, subjects completed a behavioral face recognition task, which yielded a measure of their left-visual-field bias for faces. To assess whether hemispheric asymmetry for face regions is a stable characteristic, a subset of our subjects underwent a second scan and we examined the correlations between the magnitude of their asymmetry during the first and second sessions. To find out whether the behavioral and neural asymmetry measures are associated, we examined the correlation across subjects between the behavioral laterality measure and the asymmetry of activation to centrally presented faces in the temporal–occipital lobe. Finally, to determine whether the relationship between the right and left hemispheres and correlated asymmetry index with the behavioral left-visual-field bias.

2. Materials and methods

2.1. Subjects

Seventeen right-handed individuals (11 females, ages: 17–46) participated in a functional MRI scan and a separate behavioral experiment. To determine the stability of the neural measure across time, a subset of our sample (N = 11) volunteered to participate in a second scan (1–19 months later), in which they underwent exactly the same procedures as in the original scan. All participants completed a 9-item handedness questionnaire and indicated that they preferred their right hand (1 [right hand]) and 5 (left hand) on each of its items [mean = 1.26, S.D. = .26]. Informed consent was obtained for all subjects separately for the behavioral and the functional MRI experiments.

2.2. Behavioral experiment

The behavioral experiment was conducted outside the scanner 2 days to 19 months following the functional MRI scan.

2.3. Stimuli and apparatus

Frontal views of faces of six young males were selected from the University of Stirling face database (http://pics.psych.stir.ac.uk/). We divided the faces into their right and left halves. For each face we randomly chose either its left or right half (not both) to generate 30 inconsistent (chimeric) faces, which were comprised of the combinations of each half-face with the half-face of each of the other five faces. A white vertical midline strip of 0.2° horizontal visual angle was included to conceal the inconsistency between the two half faces (Yovel et al., 2005).

The choice set was comprised of six consistent faces, which were made of the half-face that was chosen to make the chimeric faces combined with its mirror image (Fig. 1). Each face subtended 3.2° of visual angle horizontally. The midline strip was also added to the faces in the choice stimuli. Subjects were not informed that they were presented with inconsistent faces, and expressed no knowledge
Fig. 1. The behavioral task: on each trial a chimeric face was briefly presented at the center of the visual field followed immediately by a pattern mask. Then a choice set of six faces was presented at the lower part of the screen. Subjects were asked to press a key which corresponded to the face that matched their representation of the briefly presented chimeric face. The white stripe was used to prevent subjects from noticing that the chimeric faces were composed of inconsistent identities. All subjects were not aware that the briefly presented face was chimeric and reported perceiving a consistent face that was composed of either the right face (correct-right) or the left face (correct-left) or neither face (incorrect choice) during debriefing of the inconsistency in the stimuli. Stimuli were presented on a 17 in. monitor (85 Hz) using Psychtoolbox implemented in MATLAB (Brainard, 1997; Pelli, 1997) and viewed from a distance of 45 cm, which was controlled by a chin rest.

2.4. Procedure

A trial sequence included a fixation plus sign for 1000 ms, a central inconsistent face stimulus for 59 ms (5 refresh rates) and a symmetrical rectangular pattern mask of scrambled facial features (4.3° high by 3.4° wide) for 200 ms. After the mask disappeared, the six choice faces were presented (Fig. 1). Subjects chose the face they thought matched the centrally presented face by pressing the corresponding key (1–6) on the computer keyboard. Each chimeric face matched two of the six faces in the choice set. Thus, on each trial subjects either correctly chose a face that matched the left side of the chimeric face, the right side of the chimeric face, or were incorrect. Subjects were instructed to fixate on the cross and maintain their gaze at the center of the screen throughout the task. It is unlikely that subjects moved their eyes away from fixation to the right or the left of the visual field during the presentation of the face because subjects were unaware that the centrally presented faces were chimeric and the stimuli were presented very briefly (59 ms), before eye movements could be initiated. The task began with a practice block, which included 18 unmasked consistent faces (3 repetitions of each of the 6 faces) to familiarize subjects with the 6 target faces. The experimental task consisted of 120 trials (4 repetitions of each of the 30 chimeric faces) presented in a random order that were divided into 3 blocks of 40 trials each.

2.5. Functional MRI experiment

2.5.1. fMRI data acquisition

Scanning was done on a Siemens 3.0-T research scanner at the MGH-NMR Center in Charlestown, MA. For the anatomical scan we collected 128 sagittal slices (TR = 11 ms; TE = 4 ms; FOV = 256). For the functional scans, twenty-eight contiguous 4 mm thick axial slices (matrix size: 64 × 64) were oriented parallel to the temporal lobe and covered the entire brain. A Gradient Echo pulse sequences with TR 2 s; TE 30 ms; flip angle 90°; resolution 3.1 mm × 3.1 mm × 4 mm were used.

2.5.2. Localizer scan

The localizer scan consisted of four stimulus categories including faces, objects, scrambled images of objects and scenes. The object images included a variety of familiar objects (e.g., ball, sofa) and the scrambled images were generated by dividing an object image to 20 × 20 squares and then scrambling them. Five subjects were also presented with an additional 5th block of bodies (a five-category localizer—see Yovel & Kanwisher, 2004). The scene and body categories were not included in the analyses. All stimuli were presented at the center of the screen. Each block lasted 16 s and consisted of 20 stimuli from one of the categories. Each image was presented for 300 ms followed by a blank interval for 500 ms. Each scan included three fixation blocks (16 s) for the five-category localizer (total scan 208 s) or five fixation blocks (16 s) for the four-category localizer (total scan time 272 s). Importantly, in both types of localizers, each stimulus block was repeated eight times across all scans. Eighty different images were presented for each category across the different scans. The serial position of the categories was counterbalanced within and across scans. To ensure that subjects were alert and attentive, they were instructed to press a key whenever they noticed two images repeated in a row (one-back task). This happened twice per block.

2.5.3. fMRI data analysis

Data were analyzed separately for each subject using Fslfast (http://surfer.nmr.mgh.harvard.edu/). Motion correction was conducted using the AFNI motion correction algorithm (Cox & Jesmanowicz, 1999) to align all the images to the first time image of the first run; all corrections were performed prior to data analysis. The data were spatially smoothed with a Gaussian filter (full width half maxi-
mum = 5 mm). A gamma function with delta = 2.25 and tau = 1.25 was used to model the hemodynamic response for each condition.

2.5.4. ROI analysis

For each subject, voxels that responded significantly more to faces than objects (t-test, p < 10^{-4}) in the localizer scan were defined as face-selective regions. This threshold has been commonly used in previous reports and has been shown across tens of testing sessions to generate reliable face-activating activations across all of our subjects that we have tested so far (over 150 individuals). An ROI tool, fROI (http://froi.sourceforge.net/), was used to define face-selective voxels in the right and left fusiform gyrus (FFA), right and left lateral occipital cortex (OFA), and regions in the right and left superior temporal sulcus (STS). Voxels that responded more to objects than scrambled images of objects (t-test, p < 10^{-4}) were defined as object-general regions (Malach et al., 1995). These regions were composed of a lateral occipital object-general region (LO) and a ventral object-general region (posterior fusiform—pFs). For each subject we measured the volume (# of voxels × 3.1 mm × 3.1 mm × 4 mm) and extracted the hemodynamic response for each of these regions.

3. Results

3.1. Behavioral

For each subject we measured the proportion of correct matches to the right side and the left side of a chimeric face (see Fig. 1) (chance level = 16.6%). Performance level was significantly higher than chance for left-visual-field matches [t(16) = 5.8, p < 0.001, two-sided, paired Student’s t-test] and for right-visual-field matches [t(16) = 4.22, p < 0.001]. Consistent with the left-visual-field superiority for face recognition, a higher proportion of correct matches were made to the left side of the chimeric face (26%) than the right side of the chimeric face (22%). Paired comparisons revealed a marginally significant effect of visual field [t(16) = 1.95, p = .07]. It is noteworthy that the same task did yield a significant left-visual-field bias in a study by Yovel et al. (2005). We therefore believe that the marginally significant effect reflects sampling error rather than a problem related to the task. More important for the current study were the individual differences across subjects in this visual field asymmetry measure, which we tried to account for by examining the correlations between the behavioral asymmetry of each subject and his/her hemispheric asymmetry for faces measured with functional MRI.

3.2. Functional MRI

We identified face-selective brain regions (voxels that showed a significantly higher response to faces than objects—p < 10^{-4}, uncorrected) for each subject. We then measured the volume of each of the face-selective regions separately for the right and left hemispheres. Table 1 shows the proportion of subjects who showed face-selective activations in the right and left fusiform face area (FFA), lateral occipital cortex (OFA) and the posterior portion of the superior temporal sulcus (STS). Consistent with prior studies we found a larger activation for faces over the right than the left hemisphere for all three face-selective regions. We performed t-tests for each region for subjects who showed bilateral activations. The right FFA (1.84 cm^3) of 16 out of 17 subjects who showed bilateral FFA activations, was larger than the left FFA (0.89 cm^3) [t(15) = 4.26, p < 0.001] and the right OFA (1.54 cm^3) of 10 out of 15 subjects who showed bilateral OFA activations, was larger than the left OFA (0.87 cm^3) [t(9) = 3.45, p < 0.01]. The STS face-activative activation was found only in the right hemisphere (0.96 cm^3) in 9 of our 10 subjects who showed this face-activative activation in the STS. Table 1 shows the average volume of all subjects who showed face-selective activation in each of the three regions within each hemisphere (regardless of the volume of the other hemisphere).

We performed similar analyses on the peak response to faces in the face-selective regions. The response to faces in the right FFA (percent signal change: 0.77) was marginally significantly larger than in the left FFA (percent signal change: 0.65) [t(15) = 1.8, p = 0.09]. There was no significant difference between the response to faces in the right OFA (percent signal change: 0.96) than the left OFA (percent signal change: 0.91). Thus, the laterality of the magnitude of the response to faces of face-selective regions is not as robust as the laterality of their volume.

Eleven subjects returned for a second session where we ran exactly the same localizer. The data we obtained in the second session was very similar to findings from the first session. All 11 subjects showed a face-selective fusiform activation that was larger over the right hemisphere (rFFA volume = 1.48 cm^3) than the left hemisphere (lFFA volume = .7 cm^3) [t(10) = 2.73, p < 0.05]. Eight subjects showed bilateral face-selective activations in the lateral occipital cortex, which was larger over the right hemisphere (rOFA volume = 1.48 cm^3) than the left hemisphere (lOFA volume = 0.88 cm^3) [t(7) = 2.18, p = .06]. Five subjects showed face-selective activation in the right STS (1.15 cm^3) and no subjects showed face-selective activation in the left STS. Paired t-tests between the volumes that we obtained during the first and second sessions revealed no significant differences.

3.3. Correlation analyses

3.3.1. Is hemispheric asymmetry for faces a stable individual characteristic?

Previous behavioral studies have shown a high test–retest reliability measure of the left-visual-field superiority for faces (Heller & Levy, 1981; Levy et al., 1983b). Here we examined whether the fMRI asymmetry measures are also stable across time. To that effect, 11 of our subjects volunteered to participate in a second scanning session that took place 1–19 months after the first scan. We calculated an asymmetry index for each face-selective region. A positive brain asymmetry index reflects a larger volume of face-activative activation over the right than left hemisphere right − left/right + left. A

Table 1

<table>
<thead>
<tr>
<th>Face-selective areas</th>
<th>rFFA</th>
<th>lFFA</th>
<th>rOFA</th>
<th>lOFA</th>
<th>rSTS</th>
<th>lSTS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean volume (cm^3)</td>
<td>1.84</td>
<td>0.89</td>
<td>1.54</td>
<td>0.87</td>
<td>0.96</td>
<td>0.15</td>
</tr>
<tr>
<td>No. of subjects (percent out of N = 17)</td>
<td>17 (100%)</td>
<td>16 (94%)</td>
<td>15 (88%)</td>
<td>10 (59%)</td>
<td>9 (53%)</td>
<td>1 (6%)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Object-general areas</th>
<th>rpFS</th>
<th>lpFS</th>
<th>rLO</th>
<th>lLO</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean volume (cm^3)</td>
<td>3.97</td>
<td>4.88</td>
<td>2.41</td>
<td>3.21</td>
</tr>
<tr>
<td>No. of subjects (percent out of N = 17)</td>
<td>15 (88%)</td>
<td>15 (88%)</td>
<td>14 (82%)</td>
<td>12 (71%)</td>
</tr>
</tbody>
</table>

Note that the sample size may differ for different analyses (see Section 3). Paired t-tests were performed only on subjects that showed activations in both hemispheres. The correlations for each region were ran across all subjects that showed activation on at least one of the hemispheres and therefore include more subjects than the paired comparison.

a Only 14 individuals showed activations in both the right and left pFs. On each side an additional subject showed a unilateral activation.
laterality score of 1 or −1 reflects an exclusive activation in only one hemisphere. Because 90% of our subjects showed only right hemisphere face-selective activation in the STS, we did not include this measure in the correlation analysis.

We then calculated the Pearson’s correlation coefficients between the asymmetry measures in the first and second sessions for the FFA $r_{FFA} - l_{FFA} / r_{FFA} + l_{FFA}$ and OFA $r_{OFA} - l_{OFA} / r_{OFA} + l_{OFA}$. All 11 subjects showed bilateral face-selective activation in the fusiform gyrus and 10 showed bilateral face-selective activation in the occipital cortex. Our findings show a strong correlation between the asymmetry of the FFA across the two scans ($r(9) = .69$, $p < .02$) (Fig. 2A) but a weak and non-significant correlation for the OFA asymmetry measure ($r(8) = .15$, $p = .67$). These findings suggest that our measure of OFA asymmetry is less reliable and therefore is less likely to contribute to the stable individual differences in the asymmetric processing of faces, whereas our measure of FFA asymmetry is highly reliable and stable across measurements.

A similar analysis was conducted on the peak response to faces in the FFA. We computed a difference between the response to faces in the right and the left FFA for the first and the second scans. Our findings show a relatively low test–retest reliability score, which suggests that unlike the volume laterality of the FFA, this measure does not remain stable across different scans ($r(9) = .32$, $p = .35$).

### 3.3.2. The relationship between the behavioral left-visual-field bias for faces and the asymmetry of face-selective brain regions

To examine whether hemispheric asymmetry for faces is correlated across subjects with the behavioral asymmetry measure, we computed a normalized behavioral index for each subject. A positive behavioral asymmetry index reflects better left-visual-field than right-visual-field matching rate $LVF - RVF / LVF + RVF$. We then assessed the correlation between the behavioral asymmetry index and the brain asymmetry index for each face-selective region that we measured on the first scan of each subject.

A Pearson’s correlation analysis showed a significant positive correlation between the asymmetry of the FFA volume and the behavioral left-visual-field asymmetry ($r(15) = .49$, $p < .05$) (Fig. 3A). In other words, individuals who showed a stronger bias for left than right face matching in the behavioral task that we conducted outside the scanner had a larger face-selective activation over the right hemisphere.

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**Fig. 2.** A large correlation between the asymmetry measures: (A) FFA and (B) OFA across two scans that took place several weeks to months apart indicates a strong test–retest reliability for the FFA suggesting that the FFA asymmetry is a stable characteristic.

**Fig. 3.** Scatterplots display the correlation across subjects between the behavioral visual field laterality index and fMRI laterality measures that were collected using different tasks and on different sessions. (A) A large positive correlation between hemispheric asymmetry of the FFA volume $r_{FFA} - l_{FFA} / r_{FFA} + l_{FFA}$ and the magnitude of perceptual asymmetry $LVF - RVF / LVF + RVF$. (B) A weak positive correlation between hemispheric asymmetry of the OFA volume $r_{OFA} - l_{OFA} / r_{OFA} + l_{OFA}$ and the magnitude of the left-visual-field asymmetry: performance level.
than left fusiform gyrus. Fig. 3A shows that out of the six subjects who showed a right field bias, two showed a larger contralateral left FFA than right FFA. One subject who showed no perceptual asymmetry bias, also showed no difference between right and left FFA activations. Finally, all nine subjects who showed a left side bias had a larger contralateral right than left FFA. The correlations between perceptual and FFA asymmetries for the subset of nine subjects who showed a left side bias was \( r(7) = .68, p < .05 \).

Notably, the asymmetric face-selective activations were revealed on a different task in which faces and objects are presented at the center of the visual field. Thus, the behavioral and fMRI measures were collected on different sessions and under different experimental tasks. These findings suggest that the FFA and behavioral asymmetry measures are stable individual characteristics (see test–retest reliability analyses above). In contrast to the FFA asymmetry, we found no correlation between the asymmetry of the OFA and the behavioral measure (\( r(13) = .15, p = .6 \)) (Fig. 3B).

The face-selective STS was exclusively found in the right hemisphere for 90% of our subjects who showed face-selective activation in the STS (9 out of 10). Thus, we were unable to assess the association of its asymmetry with the lateralized behavioral measure. However, we can still ask whether the behavioral asymmetry is correlated with the overall face-selective asymmetry across all face-selective areas, rather than just the FFA asymmetry. To that end, we computed the sum of the volumes of face-selective regions (FFA + OFA + STS) over the right and left hemispheres and measured the correlation of this overall face-selective asymmetry measure with the behavioral asymmetry, as well as their partial correlations when the FFA or OFA were held constant. The zero order correlation of the overall face-selective asymmetry and the behavioral asymmetry was as large as the correlation with the FFA only (\( r(15) = .49, p < .01 \)). The partial correlation when the FFA was held constant was smaller and not significant (\( r(15) = .31, p = .28 \)). The partial correlation between the overall face-selective asymmetry measure when the OFA was held constant was high and positive (\( r(12) = .58, p < .05 \)). Taken together, these findings suggest that among the three face-selective regions, the variance in the FFA asymmetry is the main source of variance in the behavioral face asymmetry.

The data reported above is based on data we obtained for each subject on the first scanning session. Face-selective activations were re-assessed in 11 out of our 17 subjects on a second session. Because data on the second session was very similar in magnitude to the first session and highly correlated with it (see above), the average volume across the two sessions serves as a more reliable asymmetry measure than data obtained on one session. We therefore computed the volume of each of the face-selective regions in each individual, using the average volume for subjects who underwent two scans and the first session volume for subjects that were scanned once. The significant positive correlation between the behavioral asymmetry and the FFA asymmetry (\( r(15) = .57, p < .05 \)) was larger than the correlation we revealed with data collected only on the first session. A similar analysis for OFA volume revealed no significant correlation with the behavioral asymmetry (\( r(13) = .25 \)).

Finally, in addition to the volume laterality measure we also assessed whether the laterality of the magnitude of the response to faces in face-selective regions may be associated with the behavioral laterality. Consistent with the low test–retest reliability of this measure, we did not find a correlation between the laterality of the magnitude of the response to faces in the FFA and the behavioral left–visual-field superiority (\( r(15) = .33, p = .25 \)). Similarly, the laterality of the response to faces in the right and left OFAs was not correlated with the left–visual-field superiority (\( r(8) = .38, p = .27 \)). These low correlations may reflect the relatively low test–retest reliabilities as well as the relatively weaker laterality effects of the magnitude of the response to faces in face-selective regions.

### 3.3.3. No relationship between the behavioral left–visual-field bias for faces and the asymmetry of object-general brain regions

Our findings show that only the FFA asymmetry accounted for individual differences in the behavioral left–visual-field asymmetry. Here we asked whether nearby regions that are not face-selective may also be associated with the behavioral left–visual-field bias. These general object regions (lateral occipital complex—LOC) are typically defined as areas that show a higher response to objects than scrambled images of objects and differ from face-selective regions in that they respond similarly to faces and objects. To assess whether the asymmetry of object-general regions is associated with the behavioral asymmetry for faces, we measured the volume of object-general regions in the occipital–temporal cortex for each subject. Such regions are typically found in the posterior fusiform gyrus (pFIs), near the FFA, and in the lateral occipital (LO) cortex, near the OFA (Grill-Spector & Malach, 2004). In contrast to face-selective regions that are larger over the right than left hemisphere, paired t-tests of the volumes of object-selective regions over the right and left hemispheres showed no hemispheric asymmetry for LO (for the 12 subjects that showed bilateral LO activations, right: 2.62 cm³, left: 3.21 cm³) (\( t(11) = 1.33, p = .21 \)) or pFIs (for the 14 subjects that showed bilateral pFIs activations, right: 4.06 cm³, left: 5.15 cm³) (\( t(13) = 1.68, p = .12 \)). Nonetheless, there are individual differences in these measures that may be associated with the behavioral asymmetry for faces. Although the asymmetry of the pFIs was significantly correlated with the asymmetry of the nearby FFA (\( r(13) = .56, p < .05 \)), only the FFA asymmetry correlated significantly with the behavioral asymmetry. Neither the asymmetry of the object-general LO (\( r(11) = .10, p = .76 \)) nor the asymmetry of the pFIs (\( r(13) = .17, p = .54 \)) correlated significantly with the behavioral face asymmetry. Taken together, our findings suggest that the behavioral left–visual-field bias for faces is only associated with the face-selective region in the fusiform gyrus.

### 4. Discussion

The left–visual-field superiority for faces is a well-established behavioral phenomenon. Although it has been commonly assumed that this behavioral effect is due to the well-known right hemispheric dominance for faces, our study provides the first empirical support for this prevalent idea. In particular, we found that the asymmetry of the volume of the fusiform face area (FFA) was correlated with the magnitude of the left–visual-field bias that was measured on a behavioral task outside the scanner. Another important feature of our findings is that the FFA asymmetry is a stable trait of each individual. In particular, a subset of our sample underwent a second fMRI scan in which we again measured the asymmetry of the volume of their face-selective regions. We found a strong correlation between the asymmetry of the face-selective response in the fusiform gyrus across the two sessions that took place 1–19 months apart. Furthermore, the fMRI asymmetry measure and the behavioral asymmetry measures in our study were also obtained on different tasks and different sessions that took place 2 days to 19 months apart, which also confirms the stability of both the neural and the behavioral asymmetry measures.

Stable individual differences in perceptual asymmetries have been reported in several studies (Levine, Banich, & Koch-Weser, 1984; Levy et al., 1983a; Luh, Redl, & Levy, 1994; Luh et al., 1991). Whereas early reports suggested that the group mean asymmetry reflects face-specific effects and the variance reflects a general leftward attentional bias (Levy et al., 1983a), later work has established that individual differences in perceptual asymmetry for faces contain a unique face-specific component that is not shared by non-face tasks that generate a leftward attentional bias (Luh et al., 1991).
Thus, individual differences in perceptual asymmetries for faces reflect a unique face-specific asymmetry and a unique leftward attentional bias. Our finding that the FFA asymmetry accounted for 25% of the variance in perceptual asymmetries is likely to reflect the face-specific component of the task. The unexplained variance may reflect reliable individual differences in leftward attentional bias, which our task was not designed to measure, as well as unreliable variance.

Why was the correlation with perceptual asymmetries for face recognition specific to the FFA? Previous functional MRI studies have assessed the different roles of face-selective regions in face processing. In particular, Haxby, Hoffman, and Gobbini (2000) suggested that the occipital face area (OFA) is responsible for early stages of face processing, the fusiform face area is associated with extraction of face identity, and the fSTS with expression and gaze. In our behavioral task subjects were asked to match faces based on their identity. Thus, the relationship we found between the behavioral task and the FFA is consistent with prior research, which implicate the role of the fusiform face area in the processing of face identity (Grill-Spector, Knouf, & Kanwisher, 2004; for review see Kanwisher & Yovel, 2006; Rotstein, Henson, Treves, Driver, & Dolan, 2005; Yovel & Kanwisher, 2005). The absence of a correlation between the left-visual-field superiority for face recognition with the asymmetry of the OFA is consistent with the idea that the OFA is sensitive to physical differences rather than to identity differences between faces (Rotstein et al., 2005). In addition, unlike the FFA, the OFA and the fSTS responses are not correlated with the well-established behavioral face inversion effect (better recognition of upright than inverted faces) (Yovel & Kanwisher, 2005). The current study adds to these findings by showing that only the FFA is associated with another unique behavioral face recognition phenomenon, the left-visual-field superiority for face recognition. Importantly, however, a left-visual-field bias was also reported on face expression tasks (Levy et al., 1983b; Luh et al., 1991). Given the role of the face-selective STS in social aspects of face processing, such as gaze and expression (Engell & Haxby, 2007; Winston, Henson, Fine-Goulden, & Dolan, 2004), future studies may examine whether the left-visual-field superiority for facial expression is mediated primarily by the strong right hemisphere lateralization of the face-selective region in the STS and/or the amygdala.

Whereas group mean perceptual asymmetries for faces are reported in many studies that have used various methodologies, they are more likely to be generated under some tasks (e.g., unfamiliar faces, sequential matching) than others (e.g., famous faces, simultaneous matching) (Rhodes, 1985; Sergent & Bindra, 1981). We believe that the correlation between the FFA asymmetry and perceptual asymmetries for faces may also be task specific. It is possible that the FFA asymmetry may account for perceptual asymmetry only in tasks that involve visual face identification but not on other face tasks (e.g., naming, part-based face recognition) that do not rely on right hemisphere face identification processes.

Our study also assessed whether the left-visual-field superiority is associated with non-face-selective responses in the fusiform gyrus and occipital cortex. Studies have identified object-general regions (the lateral occipital complex) that are primarily composed of two regions located near face-selective regions in the lateral occipital (LO) and the posterior fusiform (pFS) cortex (Grill-Spector & Malach, 2004). These nearby object-general regions respond as highly to faces as face-selective regions, but their response to faces is similar to their response to objects. Thus, we also examined individual differences in brain asymmetry of the non-face-selective lateral occipital complex. Our correlation analyses showed that despite the fact that the face-selective asymmetry in the fusiform gyrus was correlated with the asymmetry of the nearby object-general region (pFS), only the FFA asymmetry was associated with the behavioral left-visual-field superiority for faces. Thus, the variance in the behavioral measure is not explained by general asymmetric activation in the occipital–temporal cortex, but is only associated with the asymmetry of face-selective brain regions and in particular with the asymmetric activation of face-selective regions in the fusiform gyrus.

What is the functional significance of the asymmetric brain response to faces? Levy (1988) has suggested a general principle for the evolution of lateralization for cognitive operations. “The presence of cerebral asymmetry . . . can be explained by a parallel evolution in response to common selective pressures for an efficient use of neural space, in which different neural programs that serve different functions are organized in opposite sides of the brain (p. 157)” (Levy, 1988). The importance of face recognition for humans, together with the complexity of the computations that are needed for efficient discrimination of the many faces we encounter during our life, probably resulted in the development of a lateralized neural mechanism. Similar to language and handedness that show strong brain lateralization and involve highly specialized mechanisms to allow complex cognitive and motor computations, respectively, face recognition is a highly complicated perceptual function that is essential for normal functioning of social creatures as humans. In particular, in addition to part-based processing (i.e., representation of the shape/color of parts) and first-order relational processing (i.e., representation of the relative location of parts) that we apply for recognition of both faces and objects, faces also uniquely engage holistic processing mechanisms, which represent faces as non-decomposable wholes (Farah, Wilson, Drain, & Tanaka, 1998). Thus, in contrast to object recognition that is processed similarly by the left and right hemispheres, faces are processed differently by the two hemispheres and uniquely engage holistic mechanisms that are localized in the right hemisphere (Rhodes, 1985; Rossion et al., 2000; Slutz & Rossion, 2006; Sergent, 1984). All in all, face lateralization reflects the importance of face recognition and the uniqueness of the computations that are required for efficient discrimination of a large number of highly similar visual stimuli such as faces.

In summary, our findings provide the first empirical evidence for the prevalent assumption in the face processing literature that the left-visual-field superiority for face processing is mediated by the right hemispheric dominance for faces. Importantly, we found that this asymmetry is a stable individual characteristic. Furthermore, only the FFA rather than any other face-selective or object-general activation in the occipital–temporal cortex, was associated with the left-visual-field superiority. We hope that our findings will encourage future studies to assess the extent to which this stable neural asymmetry is associated with other face processing abilities that individuals reliably differ on as well as the correlation between neural and perceptual asymmetries of other lateralized cognitive functions.

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