

# Defining face perception areas in the human brain: A large-scale factorial fMRI face localizer analysis

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## ARTICLE INFO

### Article history:

Accepted 1 January 2012

Available online 12 February 2012

### Keywords:

Face localizer

fMRI

FFA

OFA

Right hemisphere

## ABSTRACT

A number of human brain areas showing a larger response to faces than to objects from different categories, or to scrambled faces, have been identified in neuroimaging studies. Depending on the statistical criteria used, the set of areas can be overextended or minimized, both at the local (size of areas) and global (number of areas) levels. Here we analyzed a whole-brain factorial functional localizer obtained in a large sample of right-handed participants (40). Faces (F), objects (O; cars) and their phase-scrambled counterparts (SF, SO) were presented in a block design during a one-back task that was well matched for difficulty across conditions. A conjunction contrast at the group level {(F–SF) and (F–O)} identified six clusters: in the pulvinar, inferior occipital gyrus (so-called OFA), middle fusiform gyrus (so-called FFA), posterior superior temporal sulcus, amygdala, and anterior infero-temporal cortex, which were all strongly right lateralized. While the FFA showed the largest difference between faces and cars, it also showed the least face-selective response, responding more to cars than scrambled cars. Moreover, the FFA's larger response to scrambled faces than scrambled cars suggests that its face-sensitivity is partly due to low-level visual cues. In contrast, the pattern of activation in the OFA points to a higher degree of face-selectivity. A BOLD latency mapping analysis suggests that face-sensitivity emerges first in the right FFA, as compared to all other areas. Individual brain analyses support these observations, but also highlight the large amount of interindividual variability in terms of number, height, extent and localization of the areas responding preferentially to faces in the human ventral occipito-temporal cortex. This observation emphasizes the need to rely on different statistical thresholds across the whole brain and across individuals to define these areas, but also raises some concerns regarding any objective labeling of these areas to make them correspond across individual brains. This large-scale analysis helps understanding the set of face-sensitive areas in the human brain, and encourages in-depth single participant analyses in which the whole set of areas is considered in each individual brain.

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## 1. Introduction

The perception and recognition of faces are the objects of intense research in Cognitive Neuroscience. In particular, the localization of this complex function in the human brain is highly investigated. Investigation of the neural basis of face recognition started in the middle of the 19th century, with the reports of patients presenting difficulties at face recognition following brain damage (Quaglino & Borelli, 1867; Wigan, 1844). This neurological syndrome, prosopagnosia (Bodamer, 1947), has for long been the only source of information about the neural basis of face recognition. Correlation between, on the one hand, the behavioral difficul-

ties at recognizing faces and, on the other hand, the localization of lesion causing prosopagnosia, offered the first opportunity to identify cortical areas and white matter tracts considered to be important for face recognition. Patients with prosopagnosia present with either bilateral or unilateral right hemisphere damage, in different areas of the ventral occipital and temporal cortices, in particular the lingual, fusiform and parahippocampal gyri, as well as the anterior temporal pole (Barton, 2008a; Bouvier & Engel, 2006; Damasio & Van Hoesen, 1982; Fox, Iaria, & Barton, 2009; Hecaen & Angelergues, 1962; Meadows, 1974; Sergent & Signoret, 1992; Sorger, Goebel, Schiltz, & Rossion, 2007). Hence, neuropsychological investigations of patients with prosopagnosia revealed early on the dominance of the right hemisphere in face recognition (Hecaen & Angelergues, 1962), and pointed to a critical role of multiple occipito-temporal cortical areas for this function (Sergent & Signoret, 1992). However, for a number of reasons (e.g., large size and variability of the lesions, potential effects of these lesions on the function of other areas), the precise definition of the (sub)cortical areas

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involved in normal face recognition in humans, their function, and whether these areas are uniquely devoted to the processing of faces remained largely unclear before the advent of functional neuroimaging studies of the healthy brain.

Starting with the seminal work of Justine Sergent and colleagues (1992) using positron emission tomography (PET), a wealth of neuroimaging studies have since been carried out, mainly with functional magnetic resonance imaging (fMRI), allowing a definition of the brain areas particularly responsive to face stimulation in the human healthy brain. Even though there were already a number of published neuroimaging studies of face perception at that time, both with PET and fMRI (e.g., Haxby et al., 1994; Puce, Allison, Gore, & McCarthy, 1995 respectively), a landmark paper in this field is the fMRI study reported by Kanwisher, McDermott, and Chun (1997). That study introduced the (face) localizer approach in neuroimaging, comparing the presentation of (blocks of) faces vs. nonface objects while keeping task constant. The authors focused on a single cluster of voxels in the middle section of the right ventral occipito-temporal cortex (fusiform gyrus) that responded the most, and the most consistently across participants, to pictures of faces as compared to other objects. Both the approach and the cluster identified in most individual brains, the so-called “fusiform face area” (FFA) (Kanwisher et al., 1997), have enjoyed a special status in the field of face processing over the past 15 years (e.g., see the reviews of Berman et al. (2010) and Kanwisher and Yovel (2006)). Currently, in many neuroimaging studies of face perception, researchers conduct an independent experiment to localize an FFA in each individual brain. Once an FFA is defined, its response properties can then be tested in another experiment by manipulating face stimuli and tasks of interest.

However, as pointed out early on by Tovee (1998) the FFA certainly needs “a little help from its friends” to carry a complex function such as face perception, in agreement with evidence collected in the above-cited studies on acquired prosopagnosia (see Rossion, 2008). Indeed, it is now widely acknowledged in the neuroimaging community of this field that in each individual human brain there are *many* clusters, of different sizes and distributed across the whole brain, that respond more to faces than to nonface visual stimuli (e.g., Fox et al., 2009; Haxby, Hoffman, & Gobbini, 2000; Ishai, Schmidt, & Boesiger, 2005; Rajimehr, Young, & Tootell, 2009; Rossion et al., 2003a; Tovee, 1998; Tsao, Moeller, & Freiwald, 2008; Weiner & Grill-Spector, 2010; see also Allison, McCarthy, Nobre, Puce, and Belger (1994), Allison, Puce, Spencer, and McCarthy (1999), and Barbeau et al. (2008) for converging evidence from intracranial recordings in epileptic patients). Specifically, these clusters are localized in the posterior part of the inferior occipital cortex (one of them being termed the “Occipital Face area”, OFA, e.g., Gauthier et al., 2000a; see Pitcher, Walsh, and Duchaine (2011a) for a review), and of the superior temporal sulcus (pSTS, e.g., Puce, Allison, Bentin, Gore, & McCarthy, 1998), the anterior infero-temporal cortex or temporal pole (AIT) as reported mainly in PET studies (e.g., Sergent et al., 1992) but also more recently in fMRI studies (Kriegeskorte, Formisano, Sorger, & Goebel, 2007; Rajimehr et al., 2009) and the amygdala (e.g., Morris et al., 1996). Interestingly, recent fMRI studies carried out in the monkey brain also point to a set of areas responding more to faces than nonface visual stimuli, and distributed in the occipital, temporal and prefrontal cortices (Pinsk et al., 2009; Tsao, Freiwald, Tootell, & Livingstone, 2006; Tsao et al., 2008; see e.g., Desimone, 1991; Gross, Rocha-Miranda, & Bender, 1972; Perrett, Rolls, & Caan, 1982; Rolls, 1992; for earlier evidence coming from single-cell recording studies in non-human primates).

Considering these observations, the community of researchers inside or outside this field may be under the impression that the question of localization of face perception in the human brain is largely solved: there is a set of well identified clusters particularly activated following face presentation, and one should now focus

entirely on defining the respective functions of these localized areas, as well as how they interact anatomically and functionally. However, even if one acknowledges the interest of such a face localizer approach to clarify the neural substrates of human face perception (see the debate by Friston, Rotshtein, Geng, Sterzer, and Henson (2006) and Saxe, Brett, and Kanwisher (2006)), there are a number of important methodological issues that need to be considered and resolved because they can greatly influence the definition of the area(s) involved in face perception, and hence our understanding of the functional neuro-anatomy of this function. More precisely, there are at least four main, and non-independent, methodological issues that arise when defining such a functional face localizer.

First, the *kind of stimuli* that are compared to faces in a functional localizer vary in different studies: objects from multiples categories (chair, table, apple, ball, ...), or (phase-)scrambled faces, or yet exemplars from a single nonface object category (e.g., pictures of different houses). Usually, only one of these three comparisons is performed, and the three kinds of comparisons have been performed in different face localizer studies (e.g., Haxby et al., 1999; Ishai et al., 2005; Kanwisher et al., 1997 respectively). Yet, these different comparisons can lead to highly different definitions (i.e., localization, magnitude and extent) of an FFA and of other areas responding preferentially to faces (see Berman et al., 2010; Wiggett & Downing, 2008).

Second, the *task* that participants have to perform in the face localizer should be considered. Most of the time either passive viewing or a one-back task (detecting immediate repetition of the exact same stimulus in a train of stimuli) is used. Berman and colleagues (2010) recently concluded that the task performed was not a major factor accounting for localization of the human FFA. However, this claim might not be valid for other face-preferential clusters. Moreover, the task cannot be considered as being independent of the kind of stimuli that are compared to faces. Indeed, when using objects from multiple categories to compare to faces, the greater visual homogeneity of the face class implies that a one-back task is much more difficult to perform for faces than objects. For instance, in a typical size group of 15 right-handed participants taken from a previous study of our group (Dricot, Sorger, Schiltz, Goebel, & Rossion, 2008), there was a highly significant difference in accuracy at the one-back task between faces and objects, participants performing much better for objects than faces ( $t_{14} = 5.12$ ,  $p < 0.0002$ ). Such a difference in task difficulty may cause an increase of attention for faces as compared to objects in the face localizer, and therefore an increase of the level of activation and size of the FFA (e.g., Gentile & Jansma, 2010; Wojciulik, Kanwisher, & Driver, 1998) or even possibly in the number of clusters above statistical threshold that would be erroneously defined as reflecting face-selective voxels. This issue has been largely neglected in neuroimaging studies using face localizer paradigms, for which, most of the time, behavioral data is not even reported.

A third issue is whether the whole brain, or only a portion of it (as in the original Kanwisher et al. (1997) study), should be considered. While scanning the whole brain allows identification of preferential response to faces without a priori localization constraints, it requires a relatively long recording time and is thus potentially less sensitive to disclose and characterize such local preferential response to faces (i.e., in the middle fusiform gyrus), also increasing the severity of corrections for multiple statistical tests.

Fourth, the statistical criteria used to define the voxels presenting a larger response to faces than comparison stimuli have a huge impact on the outcome of a face localizer. For instance, contrary to previous neuroimaging studies (e.g., Puce et al., 1995; Sergent et al., 1992), Kanwisher and colleagues (1997) focused on a single cluster only whose response was larger for faces than control

stimuli. To do that, these authors restricted their recording to a small portion of the brain and used a statistical threshold that singled out the area showing the most significant difference of activation between visual presentation of faces and objects. Using a less conservative threshold allows disclosing many more clusters responding preferentially to faces in the ventral stream, but may inflate the size of the FFA so that it encompasses voxels whose preferential response to faces is weak relative to the center of activation in this area. This raises the important issue of whether the same criterion should be used to define all the brain areas presenting a preferential response to faces. Ideally, the response to this question should be positive. According to our experience, reviewers of an fMRI study that relies on an independent face localizer often request that the same statistical criterion is used to define clusters responding more to faces than control stimuli across the whole brain, and across individuals of a given study. However, the shape and height of the hemodynamic response (HDR) to neural activity measured with blood oxygen level dependent (BOLD) fMRI varies greatly across regions of the brain and across individual brains (e.g., Aguirre, Zarahn, & D'Esposito, 1998; Handwerker, Ollinger, & D'Esposito, 2004). So does the signal-to-noise ratio, with the signal in some brain regions (e.g., the medial temporal lobe and temporal pole) being affected more by magnetic susceptibility artifacts than other regions. Therefore, there is no reason to expect that the magnitude of a difference between conditions should be equal in all brain regions. This makes it practically impossible to use the same statistical criterion to define all functional brain areas in all participants of a study. When using a common conservative statistical threshold, not only the amount of overlap between the voxels identified in the localizer and the experimental task may be relatively low (Duncan, Pattamadilok, Knierim, & Devlin, 2009), but many important functional areas may not be identified at all in the localizer. In contrast, using a liberal threshold may lead to distinct functional areas being merged with each other, or certain areas like the FFA to be artificially over-extended. One recently proposed procedure to resolve this issue is to fix the size of the area that is usually the most significant when comparing faces and objects, namely the right FFA (rFFA), and define the other areas at that cluster size-defined threshold (Fox et al., 2009). However, this procedure implies that there is somehow a constant relationship between the size of the rFFA, and the size of the other areas identified, across individual brains. This assumption has never been tested. If it is not the case, fixing the size of the FFA may lead to the identification of many other areas in one individual brain, while the same procedure may lead to very few areas disclosed in another individual brain. More generally, should the same statistical criterion be used for all individual participants of a given study to define their FFA and other clusters responding preferentially to faces? To complicate matters further, the issue of which statistical threshold to use is certainly not independent of the kind of comparison that is performed (e.g., faces vs. scrambled faces or faces vs. objects), and of the brain volume tested (i.e., a correction for multiple comparisons is more severe with a large than a small volume).

In the present paper, we combined fMRI data of a face localizer collected in several recent studies of our group (Jiang et al., 2011, 2009; Ramon, Dricot, & Rossion, 2010a; Rossion, Dricot, Goebel, & Busigny, 2011) and the same recordings made on a new group of participants to perform a large-scale analysis (40 participants in total) in order to shed light on the issues raised above – and draw their theoretical implications. The face localizer used in these recent studies has several interests. First, it is a factorial design, in which faces are compared to a familiar nonface object category (cars) and to phase-scrambled versions of both faces and cars. The face and car stimuli are controlled for global luminance (Rossion & Caharel, 2011), but not for other low-level visual cues

that differ between faces and objects and which can potentially be used to detect faces, such as spatial frequencies (Keil, 2008) and color (see Rossion & Caharel, 2011). Control of these low-level visual cues is provided by phase-scrambling of the two categories of stimuli. Therefore, the present face localizer allows assessing the degree to which a larger response to face stimuli in a given area is truly face-specific (i.e., the area does not respond to nonface objects at all) or face-preferential (i.e., the area responds both to faces and objects, but relatively more to faces). It also allows assessing whether a larger response to faces is driven entirely by the information associated with the phenomenological experience of a face (the phase), that is face perception, or if there is a contribution of low level visual cues to the larger response to faces (i.e., the area responds more to scrambled faces than scrambled cars) (see also Andrews, Clarke, Pell, & Hartley, 2010). Clarifying this issue was one of the main goals of the present large-scale analysis. Another interest of this report is that the factorial face localizer was performed on a large sample of participants, measuring differences of activation between faces and other stimuli in their whole brain. Hence, the large-scale analysis allowed a global overview of the set of areas responding more to faces than other visual stimuli, not only in terms of their sensitivity to faces, but also in terms of their degree of lateralization, variability in localization and level of activation across participants, to inform about all the issues raised above. Finally, the large sample of participants allowed us to tentatively compare the time-course of activations across areas by calculating for each of them the bold estimation of the onset time of the response (Formisano & Goebel, 2003) to the first face in each block of faces (432 trials in total) and provide potentially relevant information concerning the functional dynamics of activation within the set of areas responding more to faces than other visual stimuli in the human brain (see Rossion, 2008).

## 2. Materials and methods

### 2.1. Participants

The data of 40 right-handed participants [age =  $25.8 \pm 5.55$ ; 31 females; Edinburgh Inventory (Oldfield 1971)] was included: 7 participants from the study of Jiang, Dricot, Blanz, Goebel, and Rossion (2009), 10 participants from Ramon et al. (2010a), 4 participants from Rossion et al. (2011), and 11 participants from Jiang et al. (2011). We selected the data of the right-handed participants only in these studies, who were all presented with the exact same stimulation (black background for the stimuli). In these studies, and for the eight remaining participants, the face localizer runs were performed before the other experiments, so that the outcome of the face localizer studies could not have been differentially influenced by the other studies performed. None of the participants had a history of neurological or vascular disease, head injury or alcohol abuse, nor did they display cognitive complaints. The study was conformed to the Declaration of Helsinki and was approved by the Ethical Committee of the Medical Department of the University of Louvain. Written informed consent was obtained from all participants prior to the fMRI experiment, following procedures approved by University of Maastricht where all imaging took place.

### 2.2. Experimental procedures

#### 2.2.1. Stimuli

Four categories of stimuli were used: photographs of Faces, Cars, and their phase-scrambled versions: Scrambled Faces and Scrambled Cars (Fig. 1).

The Face condition consisted of 43 pictures of faces (22 females) cropped so that no external features (hair, etc.) were revealed. All



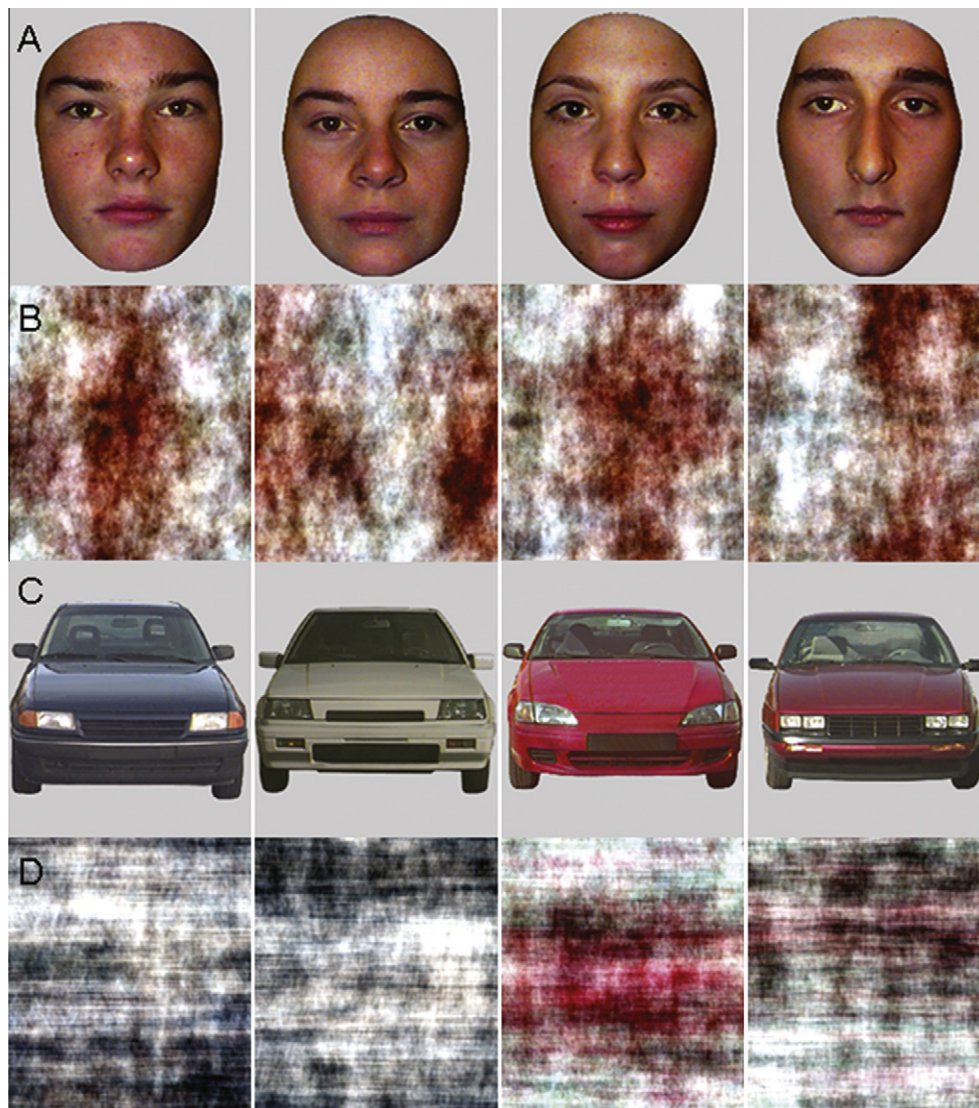
faces were shown in frontal view. They were inserted in a gray rectangle (Fig. 1). Similarly, the Car condition consisted of 43 pictures of different cars in a full-front view also embedded in a gray rectangle. Faces and cars were presented in color and equalized in overall luminance (see Rossion and Caharel (2011) for full details about the stimuli). However, they were not equalized for pixel intensity in each color channel (RGB), and in spatial frequencies, because such variations are potentially used to categorize faces as compared to other stimuli, and are controlled by the phase-scrambling procedure. The scrambled stimuli were made using a Fourier phase randomization procedure [FFT with phase replaced by phase of a uniform noise (amplitude conserved in each frequency band (see e.g., Sadr & Sinha 2004)] that yields images preserving the low-level properties of the original image (i.e. luminance, contrast, spectral energy, etc.), while completely degrading any category-related information (Fig. 1). Pictures of faces/cars and the phase scrambled face/car pictures subtended equal shape, size and contrast against background.

Rather than using multiple object categories mixed up in a block, as performed in many studies including previous experiments of our group (see e.g., Table 1 in Berman et al. (2010)), here a single object category – cars – was used to compare to faces.

**Table 1**Behavioral data of the functional localizer experiment (one-back task). Mean  $\pm$  SD.

	Faces	Scrambled Faces	Objects	Scrambled objects
Accuracy rates (%)	98.8 $\pm$ 0.02	96 $\pm$ 0.018	97.3 $\pm$ 0.015	95.5 $\pm$ 0.018
Correct RTs (ms)	559 $\pm$ 72	557 $\pm$ 56	515 $\pm$ 52	547 $\pm$ 64

Pictures of cars were used as the single object category, for several reasons: cars are a set of mono-oriented objects, they form a highly familiar and visually homogenous category, and they have multiple parts, just like faces (“internal”: lights, radiator grill, window, bumper; “external”: mirrors, wheels, etc.). Also, pictures of cars have been used as control stimuli of faces in numerous behavioral (e.g., Yin, 1969) and neuroimaging studies (e.g., Gauthier, Skudlarski, Gore, & Anderson, 2000b; Grill-Spector & Malach, 2004), and these pictures in particular have been used in several of our previous studies (Busigny, Graf, Mayer, & Rossion, 2010; Rossion & Caharel, 2011; Rossion & Curran, 2010; Schiltz et al., 2006). Here, pictures of cars will be referred to as objects (O) in contrast to faces (F), and their scrambled versions (SF, SO).



**Fig. 1.** Examples of stimuli used in the face localizer (4 examples in each condition, 43 stimuli by condition in total). From top to bottom (A–D): Faces, phase-scrambled faces, cars, and phase-scrambled cars. All details about the stimuli can be found in Rossion and Caharel (2011).

### 2.2.2. Paradigm

Participants performed two runs of 11 min duration each. In each run, there were 6 blocks of 18 s duration for each of the 4 types of stimuli. Blocks were separated by a baseline condition (cross fixation) of 9 s. In each block, 24 stimuli of the same condition were presented (750 ms per stimuli, no ISI) on a black background screen, with two or three consecutive repetitions of the exact same stimulus in each block (target trials in the one-back task). This gave a total amount of 144 stimuli per category per run. The stimuli and the fixation cross were presented centrally, but stimulus location varied randomly in  $x$  (6%) and in  $y$  (8%) direction at each presentation ( $5.5^\circ$  and  $6.2^\circ$  as visual angle degrees in the  $x$  and  $y$  direction, average location is centered). This change in stimulus location was made so that specific elements of the non-scrambled face and car stimuli (e.g., the eyes or headlights) do not appear at the same location at each trial, as it would be the case for scrambled stimuli even without jittering position. Participants performed a one-back identity task (two or 3 targets per block; 30 targets for each condition in total).

### 2.2.3. Imaging acquisition parameters

Functional MR images of brain activity were collected using a 3T head scanner (Siemens Allegra, Siemens AG, Erlangen, Germany) at the University of Maastricht, with repeated single-shot echo-planar imaging: echo time (TE) = 30 ms, flip angle (FA) =  $90^\circ$ , matrix size =  $64 \times 64$ , field of view (FOV) =  $224 \times 224 \text{ mm}^2$ , slice order descending and interleaved, slice thickness = 3.5 mm. Repetition time (TR) was 2250 ms, 36 slices (the whole brain is scanned 293 times per run, 48 times per condition per run). A three-dimensional (3D) T1-weighted data set encompassing the whole brain was acquired to provide detailed anatomy ( $1 \text{ mm}^3$ ) thanks to a ADNI sequence (TR = 2250 ms, TE = 2.6 ms, FA =  $9^\circ$ , matrix size =  $256 \times 256$ , FOV =  $256 \times 256 \text{ mm}^2$ , 192 slices, slice thickness = 1 mm, no gap, total scan time = 8 min 5).

### 2.2.4. Data analysis of the imaging experiments

**2.2.4.1. Preprocessing.** The fMRI signal in the different conditions was compared using BrainVoyager QX (Version 1.9.10, Brain Innovation, Maastricht, The Netherlands). Prior to analysis, the functional data sets were subjected to a series of preprocessing operations. Preprocessing consisted of a linear trend removal for excluding scanner-related signal, a temporal high-pass filtering applied to remove temporal frequencies lower than three cycles per run, and a correction for small interscan head movements by a rigid body algorithm rotating and translating each functional volume in 3D space. The data were corrected for the difference between the scan times of the different slices. Data was not smoothed in the spatial domain. In order to be able to compare the locations of activated brain area across participants all anatomical as well as the functional volumes were spatially normalized (Talairach & Tournoux 1988) and the statistical maps computed were overlaid to the 3D T1-weighted scans in view to calculate Talairach coordinates for all relevant activation clusters. Subsequently, the functional data were analyzed using one multiple regression model (General Linear Model; GLM) consisting of predictors, which corresponded to the particular experimental conditions of each experiment. The predictor time courses used were computed on the basis of a linear model of the relation between neural activity and hemodynamic response, assuming a rectangular neural response during phases of visual stimulation (Boynton, Engel, Glover, & Heeger, 1996). All coregistrations were done manually and the corrections of the movement were optimized (sinc interpolation, only one run rejected out of 80, so that only one run was available for one of the participants).

**2.2.4.2. Statistical analyses and contrasts of interest.** We performed both a random effect group analysis, and a random effect analysis based on definition of areas in each individual participant. In the group analysis, we performed five contrasts of interests. The main contrasts of interests were the interaction  $\{(F-O) - (SF-SO)\}$  and conjunction  $\{(F-O) \text{ and } (F-SF)\}$  contrasts. Both of these contrasts were aimed at isolating the areas responding more to faces than non-faces objects, and for which this difference could not be accounted for by low-level visual cues. In addition, we used the single contrast (F-O) as performed in the large majority of face localizer studies (see Berman et al., 2010) and the contrast (F-FS), which is used in a number of studies also (e.g., Eger, Schyns, & Kleinschmidt, 2004; Ishai et al., 2005). Finally, we also identified areas that responded to shape (e.g., Lateral Occipital Complex, LOC, Malach et al., 1995) by the contrast O-SO. Given that the conjunction contrast proved to be the most interesting to reveal the set of areas involved in face perception in the group analysis, we performed the individual participant analysis with this contrast.

**2.2.4.3. Statistical threshold for definition of areas.** At the group level, a conservative identical statistical threshold was used for all areas, using the false discovery rate (FDR) method to correct for multiple comparisons (Storey, 2003). A threshold of  $q(\text{FDR}) < 0.001$ , which activated the whole visual cortex including the ventral and dorsal pathways when all the conditions were compared together to the fixation cross baseline (one large cluster of  $\pm 80,000$  voxels around V1) was selected. This common threshold was also lowered to reveal other clusters ( $q(\text{FDR}) < 0.01$ ,  $q(\text{FDR}) < 0.05$ ).

In the individual participant analysis, we used the conjunction contrast  $\{(F-FS) \text{ and } (F-O)\}$  and fixed the size of the FFA at  $200 \text{ mm}^3$ . This size-based threshold was used to identify the other face-preferential areas (see Fox et al. (2009) for a similar approach with  $50 \text{ mm}^3$  cluster size of FFA).

**2.2.4.4. BOLD latency mapping.** In a complementary analysis, to compare the time-course of activations across areas (Formisano & Goebel, 2003), we calculated for each of them the bold estimation of the onset time of the response to first face in each block of faces (432 trials in total) using a piece-wise linear trapezoidal model for the response without forcing a return to baseline (interpolation factor 2; Richter, Somorjai, Summers, & Jarmasz, 2000).

## 3. Results

### 3.1. Behavioral data

Behavioral data of 4 of the 40 participants in the one-back task was not recorded due to a technical error. Overall, participants performed the task quite well in all conditions (mean accuracy rates:  $96 \pm 1.84\%$ ; mean response times:  $545 \pm 63 \text{ ms}$ , see Table 1 for all data). A 2 (Category: Faces vs. Objects)  $\times$  2 (Shape: Intact vs. Scrambled) ANOVA with 36 participants was performed on accuracy rates. There was no effect of category ( $F_{1,35} = 1.08$ ;  $p = 0.305$ ), participants performing the one-back task equally well for pictures of faces or cars. However, there was a significant effect of shape ( $F_{1,35} = 35.21$ ;  $p < 0.0001$ ). This effect was qualified by a significant interaction between shape and category ( $F_{1,35} = 13.13$ ;  $p < 0.001$ ), due to the relatively lower performance for scrambled objects than the other three conditions ( $95.5 \pm 1.8\%$ ; Supplementary material, Fig. S1). Importantly, there were no significant differences between Faces and Scrambled Faces, or Faces and Objects ( $ps > 0.06$ ). With respect to response times (RT), there was a main effect of category ( $F_{1,35} = 19.35$ ;  $p < 0.0001$ ) and of shape ( $F_{1,35} = 4.34$ ;  $p = 0.04$ ). These main effects were qualified by a significant interaction between the two factors ( $F_{1,35} = 10.26$ ;  $p < 0.003$ ). There was no difference

between Faces and Scrambled Faces in terms of response speed ( $p = 0.87$ ) but participants were faster for Objects than Faces ( $p < 0.0001$ ) and Scrambled Faces ( $p < 0.0001$ ) (see Table 1 for all values, see also Supplementary Fig. 1B).

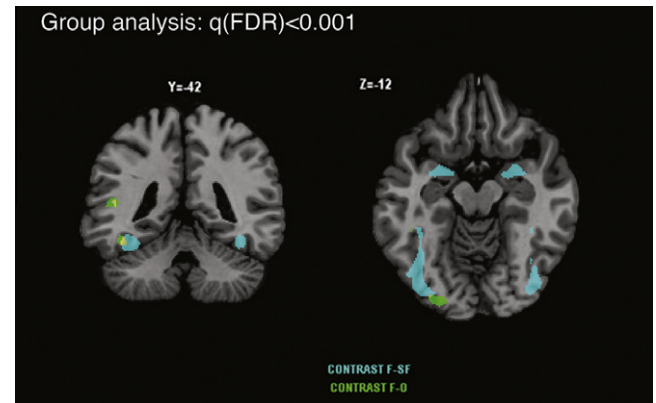
### 3.2. Neuroimaging results

#### 3.2.1. Group analysis [degrees of freedom (df) = 39]

3.2.1.1. *Single contrasts: Faces vs. Scrambledfaces/Faces vs. Objects.* At  $q(\text{FDR}) < 0.001$  ( $t = 5.22$ ), we report 12 clusters for the contrast F–SF (Table 2) and 17 clusters for F–O (Table 3).

We made the following observations:

- (1) Changing the procedure to define the statistical threshold affects the number and size of the clusters differently for the two contrasts. The contrast (F–SF) at  $q(\text{FDR}) < 0.001$  leads to a large set of clusters, including a very large right FFA, compared to the few clusters disclosed by the contrast (F–O).
- (2) When faces are compared to scrambled faces (F–SF) at  $q(\text{FDR}) < 0.001$ , there is a large cluster in the right ventral stream that encompasses the whole right fusiform gyrus (Fig. 2). There is no distinction between the OFA and FFA. Increasing the statistical threshold to  $p(\text{Bonferroni corrected}) < 0.05$  allows a separation between the anterior and posterior parts of the fusiform gyrus. However, other areas that are often found relevant for face processing (e.g., pSTS) are no longer significant at this conservative threshold.



**Fig. 2.** Comparison of the activation maps when performing faces vs. objects (F–O) and faces vs. scrambled faces (F–SF) (yellow = overlap). Note the large ventral occipito-temporal activations observed for faces vs. scrambled faces, a comparison that is used in several studies to define “face-selective” areas such as the FFA and OFA (e.g., Fairhall & Ishai, 2007). The overlap of the activation maps is relatively good at the level of the FFA but the right OFA as identified by the two contrasts does not correspond to the same area at all.

- (3) There is a right hemispheric dominance for both F–O (75% of voxels, without cerebellum) and F–SF (69%).
- (4) When the statistical maps obtained in the two contrasts are superimposed to each other, the right FFA as defined by (F–SF) overlaps with the FFA as defined by F–O (Fig. 2). There

**Table 2**

Talairach coordinates of all the areas found in the random analysis for the 40 participants. Contrast: F–SF.

Threshold: $q(\text{FDR}) < 0.001$	Talairach coordinates:			Cluster size mm <sup>3</sup>	Strength $t$ max
	x	y	z		
Right fusiform gyrus in temporal and occipital lobe (FFA and OFA mixed)	36	–57	–15	<b>3589</b>	<b>10.63</b>
Right superior temporal sulcus	47	–57	15	<b>66</b>	<b>5.83</b>
Right (middle) superior temporal sulcus	46	–40	10	<b>71</b>	<b>6.90</b>
Right amygdala	20	–6	–9	<b>1229</b>	<b>9.09</b>
Right perirhinal cortex (BA 38)	28	–4	–27	<b>22</b>	<b>5.30</b>
Right hippocampus	32	–23	–6	<b>35</b>	<b>6.39</b>
Right thalamus (pulvinar)	8	–28	1	<b>52</b>	<b>6.51</b>
Right gyrus rostral	0	41	–5	<b>19</b>	<b>5.63</b>
Left fusiform gyrus (BA 20 or 37) = left FFA	–37	–42	–17	<b>468</b>	<b>8.40</b>
Left fusiform gyrus or inferior occipital gyrus (BA 19) = left OFA	–38	–74	–12	<b>737</b>	<b>7.04</b>
Left amygdala	–23	–5	–9	<b>1022</b>	<b>9.49</b>
Left cuneus (BA 17)	–9	–73	7	<b>91</b>	<b>6.71</b>

**Table 3**

Talairach coordinates of all the areas found in the random analysis for the 40 participants. Contrast: F–O.

Threshold: $q(\text{FDR}) < 0.001$	Talairach coordinates			Cluster size mm <sup>3</sup>	Strength $t$ max
	x	y	z		
Right fusiform gyrus (BA 37) = right FFA	40	–44	–16	<b>331</b>	<b>7.34</b>
Right inferior occipital gyrus (BA 18) = right OFA	25	–88	–10	<b>571</b>	<b>7.71</b>
Right superior temporal sulcus	48	–48	8	<b>624</b>	<b>6.57</b>
Right amygdala	19	–6	–9	<b>630</b>	<b>9.30</b>
Right perirhinal cortex (BA 38)	25	0	–28	<b>32</b>	<b>5.27</b>
Right precentral gyrus (BA 6)	42	0	34	<b>1395</b>	<b>7.43</b>
Right superior frontal gyrus (BA 6)	3	4	52	<b>19</b>	<b>5.30</b>
Right thalamus (pulvinar)	5	–26	–1	<b>331</b>	<b>8.13</b>
Right thalamus (ventro-lateral part)	11	–13	13	<b>53</b>	<b>6.51</b>
Right thalamus (medial dorsal part)	1	–12	11	<b>61</b>	<b>5.70</b>
Right internal capsule	22	–23	–2	<b>20</b>	<b>5.34</b>
Left inferior occipital gyrus (BA 18) = left OFA	–20	–90	–12	<b>819</b>	<b>8.03</b>
Left amygdala	–21	–5	–9	<b>429</b>	<b>8.15</b>
Left lingual gyrus (BA 17)	–7	–95	–2	<b>17</b>	<b>5.27</b>
Left thalamus (pulvinar)	–8	–25	–5	<b>17</b>	<b>5.62</b>
Left cerebellum	–12	–64	–40	<b>26</b>	<b>5.52</b>
Cerebellum (oculomotor vermis)	–3	–60	–24	<b>1140</b>	<b>8.80</b>



is also a good overlap between the pSTS as defined in the two contrasts. However, the definition of the OFA differs completely in the two contrasts. That is, there is no overlap at all between the large right hemisphere cluster in the inferior occipital cortex defined by (F–SF) and the small cluster defined by (F–O).

- (5) To define the right OFA as a spatially independent cluster from the right FFA by means of the contrast F–SF, it is necessary to use a much more conservative threshold ( $t = 7.45$ ,  $p < 0.000$ ). This threshold corresponds to a right FFA of  $500 \text{ mm}^3$ . If, for a fair comparison, the same size of FFA is considered in the contrast F–O ( $t = 4.22$ ,  $p < 0.000$ ) then the OFA cluster defined by (F–SF) responds to shape, largely independently of the category (O–SO:  $p < 0.000001$ ; F–O:  $p = 0.17$ ) (Fig. 3). In contrast, the more posterior cluster identified by (F–O) (Fig. 3) responds highly to scrambled stimuli, and more to scrambled faces than scrambled objects (SF–SO,  $p < 0.007$ ). Therefore, using the contrast F–SF is inadequate to define the OFA, irrespective of the severity of the statistical threshold used.

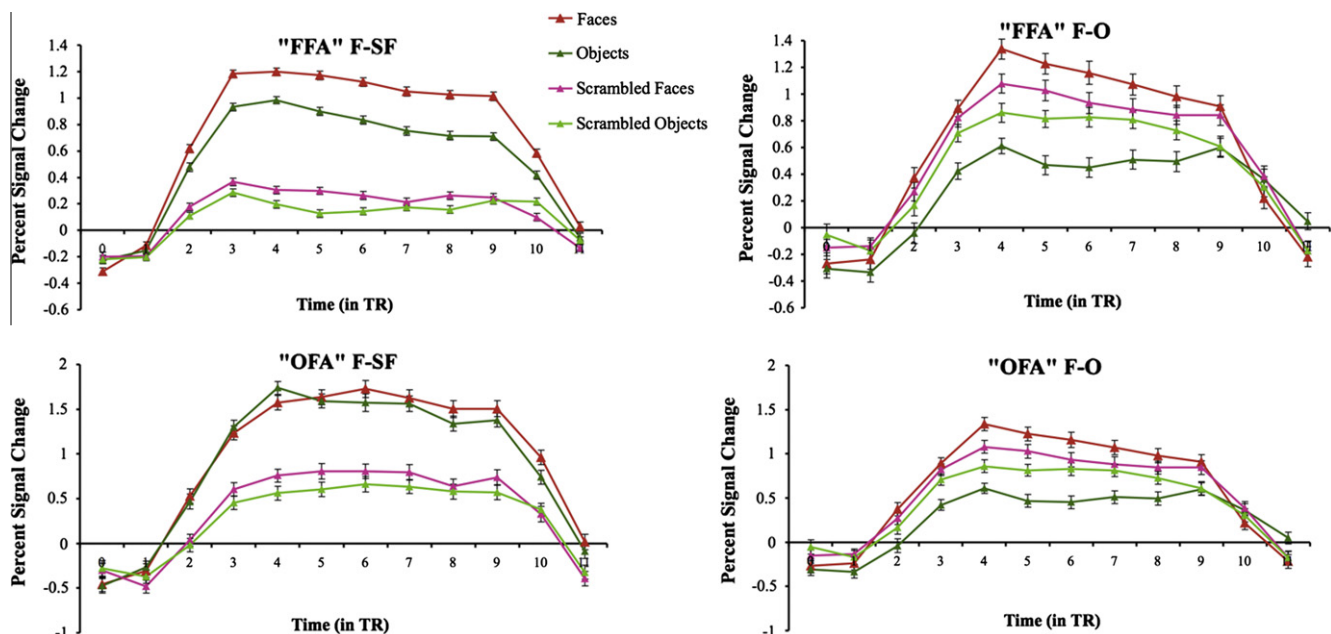
**3.2.1.2. Interaction {(F–SF) – (O–SO)}.** At  $q(\text{FDR}) < 0.001$  ( $t = 5.22$ ), there are only four clusters (Supplementary material Table S1): the right and left amygdalas, the left cuneus and an area of the right inferior occipital cortex. Notably, the FFA was not identified by this contrast. Moreover, the area of the right inferior occipital cortex does not respond more to intact than scrambled stimuli  $\{(O + F) = (SF + SO)$ ,  $p = 0.85\}$ .

**3.2.1.3. Conjunction {(F–SF) and (F–O)}.** The conjunction contrast identified eight face-preferential clusters at  $q(\text{FDR}) < 0.001$  ( $t = 5.09$ ), including the FFA and OFA. There was a strong right hemispheric dominance, with only the amygdala identified in the left hemisphere. Lowering the statistical threshold to  $q(\text{FDR}) < 0.01$  identified 16 face-preferential clusters at  $q(\text{FDR}) < 0.01$  ( $t = 4.29$ ), including the FFA and OFA (Fig. 4; Table 4A). Only three clusters

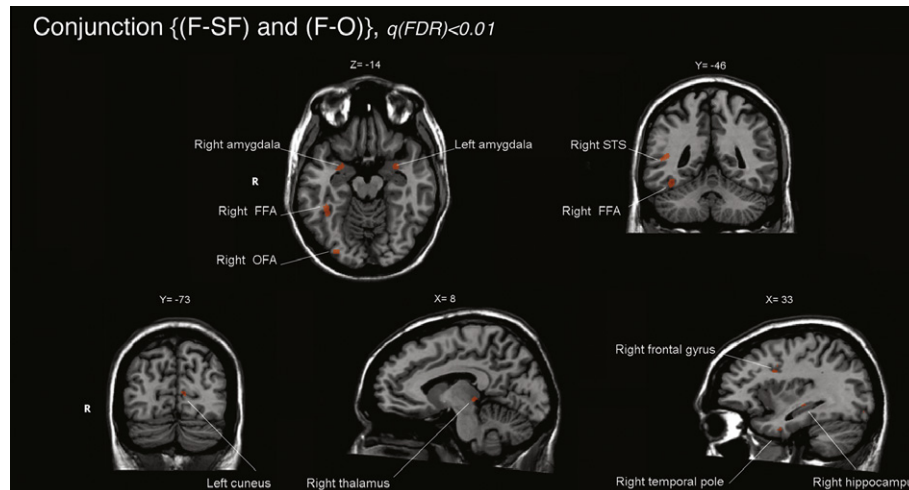
are found in the left hemisphere (cuneus, thalamus and amygdala). We made the following observations:

- (1) There is a strong right hemispheric dominance (79% of voxels, excluding cerebellum) and neither the FFA nor OFA were disclosed in the left hemisphere in this group analysis.
- (2) In the right hemisphere, the three clusters of the “core face perception system” (Haxby et al., 2000) are identified: the right middle fusiform gyrus (BA 37) or FFA, right inferior occipital gyrus (BA 18) or OFA, and pSTS. There are also three clusters of the extended face processing system: the right amygdala, left amygdala, and right AIT (right perirhinal and fusiform cortex, BA 38) (Fig. 4).
- (3) Among all the areas identified, the FFA is the least face-selective, in the sense that it responds strongly to nonface objects (O–SO,  $p < 0.000001$ ). Moreover, it responds also highly to low-level characteristics of faces (SF–SO,  $p < 0.00001$ ; with both conditions significantly above baseline) (Fig. 5). Note that these contrasts are not independent of the area's definition, which selects voxels where the response to O and SF is minimal (i.e., {(F–SF) and (F–O)}). This issue is taken into account below.
- (4) In contrast to the FFA, the identified OFA responds to all stimuli. Keeping in mind the non-independence of the contrasts, it is interesting to note that the OFA does not show any difference of activation for O vs. SO ( $p = 0.86$ ; Fig. 5). Moreover, its sensitivity to faces is not accounted for by low-level visual cues (SF–SO,  $p = 0.4$ ; Fig. 5). Among the other face-preferential areas identified, there were small but significant effects of O–SO in the right amygdala and AIT ( $ps < 0.05$ ), and in the right STS for SF–SO ( $p < 0.01$ ) (all other  $ps > 0.05$ ) (Supplementary material, Fig. S3).

The conjunction analysis also disclosed a number of other potentially interesting face-preferential clusters (Table 4A and Supplementary material Fig. S4) in the right prefrontal cortex (NS for SF–SO and O–SO) at the junction between the Precentral Gyrus



**Fig. 3.** BOLD response of the areas labeled as the right FFA and OFA when defined in the two contrasts (F–SF on the left; F–O on the right) (TR = 2250 ms). Note that the FFA, irrespective of the contrast used, responds highly to nonface objects, and also shows a larger response to scrambled faces than scrambled pictures of cars. The OFAs as defined in the two contrasts are different areas (see Fig. 2), showing completely different response properties. These graphs illustrate that comparing the behavior of this OFA across studies when it is defined by the different contrasts F–SF or F–O is misleading.



**Fig. 4.** Group analysis (random effect) revealing the set of face-preferential areas at a conservative statistical threshold ( $q(\text{FDR}) < 0.01$ ) in the conjunction contrast:  $\{(F-SF) \text{ and } (F-O)\}$ . Note the right hemispheric dominance, or exclusivity, for the areas usually disclosed (FFA, OFA, pSTS), but also for face-preferential activations observed in the anterior temporal lobe, prefrontal cortex and hippocampus.

**Table 4A**

Talairach locations of all the areas found in the random analysis for the 40 participants. Contrast: CONJUNCTION: (F-O) and (F-SF). Note that at this threshold, the large majority of clusters (13/16) are disclosed in the right hemisphere.

Threshold: $q(\text{FDR}) < 0.01$	Talairach coordinates			Cluster size mm <sup>3</sup>
	x	y	z	
Right fusiform gyrus (BA 37) = right "FFA"	38	-43	-17	<b>501</b>
Right inferior occipital gyrus (BA 18) = right "OFA"	29	-84	-12	<b>169</b>
Right superior temporal sulcus	48	-48	9	<b>1089</b>
Right superior temporal sulcus	40	-53	16	<b>19</b>
Right amygdala	20	-6	-9	<b>1144</b>
Right perirhinal cortex and fusiform gyrus (BA 38)	28	0	-28	<b>178</b>
Right precentral gyrus (BA 6)	34	2	34	<b>8</b>
Right precentral gyrus (BA 6)	34	5	28	<b>33</b>
Right hippocampus	31	-23	-5	<b>41</b>
Right thalamus (pulvinar)	6	-29	1	<b>149</b>
Right thalamus (lateral geniculate nucleus)	9	-23	-5	<b>12</b>
Right thalamus (medial dorsal part)	1	-16	7	<b>14</b>
Left amygdala	-21	-6	-10	<b>846</b>
Left cuneus (BA 17)	-8	-74	7	<b>58</b>
Left thalamus (medial dorsal part)	-1	-11	7	<b>12</b>
Cerebellum (oculomotor vermis)	-2	-56	-23	<b>102</b>

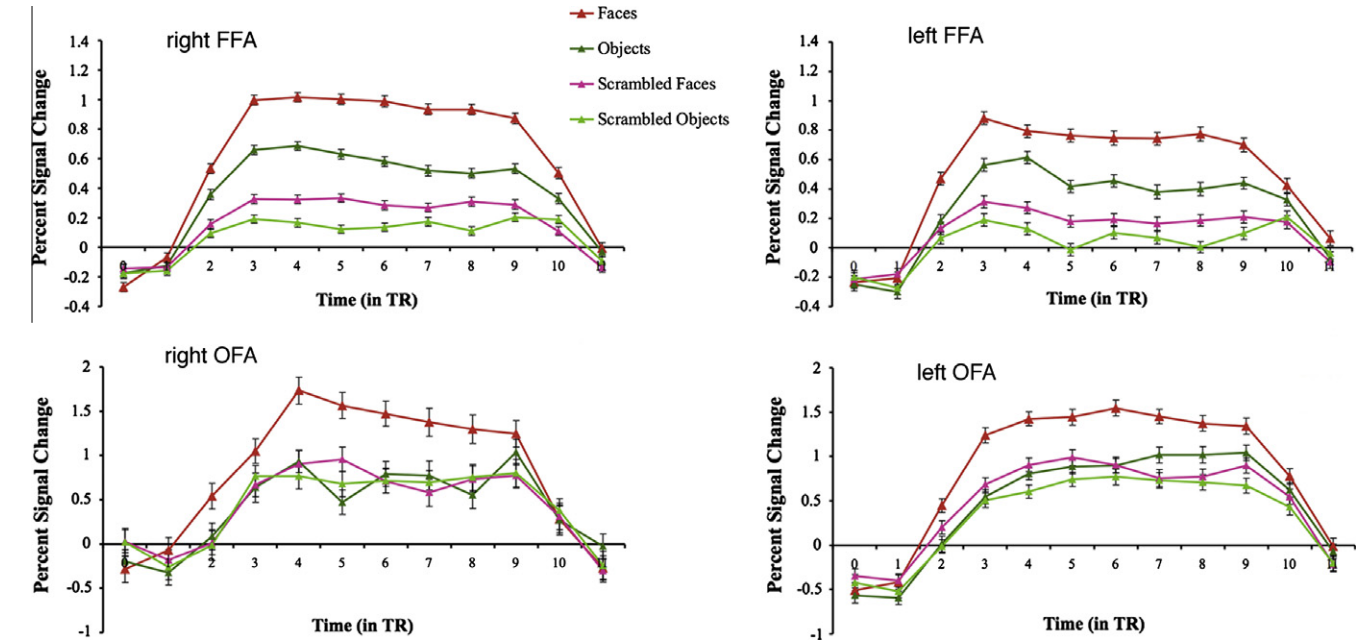
and Inferior frontal Gyrus (Operculum part), in the dorsal part of the right middle hippocampus, and in the pulvinar. There was also a small cluster close to the left primary visual cortex V1 (left cuneus, BA 17) where all conditions were deactivated compared to baseline, but the deactivation was less pronounced for faces, and one cluster in the cerebellum.

(6) Finally, in order to disclose face-preferential areas in the left hemisphere, the statistical threshold had to be reduced substantially. At  $q(\text{FDR}) < 0.05$  ( $t = 3.38$ ), there were 10 additional clusters, including seven clusters in the left hemisphere (Table 4B) (Fig. 6). These seven face-preferential areas all have homologous areas in the right hemisphere, activated at a more severe threshold. Among these clusters, there were two small significant clusters in the left fusiform gyrus (BA 37), which could both correspond to the left FFA [their global size being 2.3% of the right FFA' size at this statistical threshold], 1 cluster in the left inferior occipital gyrus (BA 18), corresponding to a left OFA [=15.1% of the right OFA size], and a small cluster in the STS [=0.4% of the right STS' size]. Other clusters were found in the left precentral gyrus, anterior inferior temporal cortex [BA 38 = 2.5% of the right homologous area' size], and left hippocampus [11.2% of the right equivalent area's size].

Areas of the left hemisphere activated by the conjunction contrast showed more or less the same response profile as their right homologous areas (Fig. 5 and Supplementary material Fig. S5). The left FFA responds significantly to non face objects (O-SO:  $p < 0.0008$ ) and its preferential response to faces is partly driven by low-level features (SF-SO:  $p < 0.000001$ ).

**3.2.1.4. Conjunction  $\{(F-SF) \text{ and } (F-O)\}$  on independent data sets: run 1 vs. run 2.** A major observation of the analysis reported above is that the FFA responds strongly to nonface objects independently of their low-level features (O-SO), but also strongly to low-level visual characteristics of faces (SF-SO). In contrast, other face-sensitive areas, in particular the OFA, present with a much more high-level face-selective profile of response. To strengthen these observations using an independent group analysis, we defined the areas using a single run per subject (the first or the second randomly) with the contrast  $\{(F-SF) \text{ and } (F-O)\}$ . The other run was then used to test the contrasts (O-SO and SF-SO). The face-selective areas identified at  $q(\text{FDR}) < 0.05$  ( $p$  uncorrected  $< 0.001$ ,  $t_{39} = 3.57$ ) were identical, although of smaller size than when two runs were used (Table S2). Even considering that the spatial overlap between

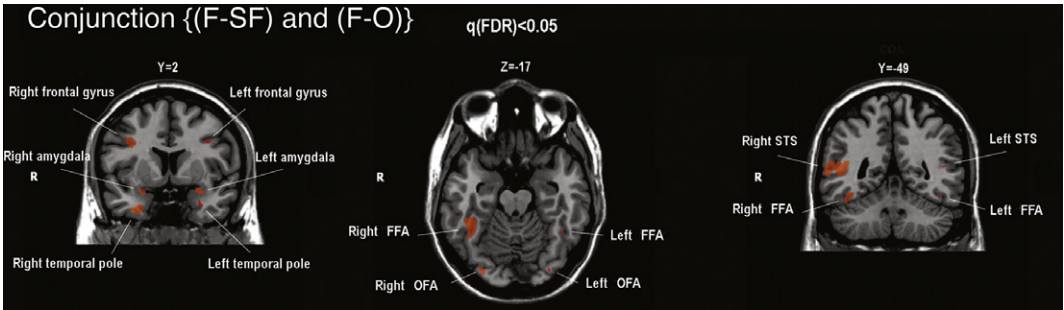




**Fig. 5.** Percent signal change in the areas FFA and OFA defined by the conjunction contrast  $\{(F-SF) \text{ and } (F-O)\}$  (error bars = standard error of the mean; TR = 2250 ms). Note that the FFA responds highly to nonface objects, and also shows a larger response to scrambled faces than scrambled objects. In contrast, the OFA identified in this contrast respond above baseline for all conditions, but it does not respond more to scrambled faces than scrambled objects, and to intact objects than scrambled objects. Thus, paradoxically, the OFA appears to show a more face-selective response to faces than the FFA. This observation is valid in the two hemispheres but more pronounced in the right hemisphere. Importantly, it also holds when these areas are defined using one run per subject, and the statistical tests are made using the other run (see supplementary material for time-courses, Fig. S2).

**Table 4B**  
Talairach coordinates of the additional clusters found in the random analysis for the 40 participants with a lower statistical threshold. Contrast: CONJUNCTION: (F-O) and (F-SF).

Threshold: $q(\text{FDR}) < 0.05$ : (right FFA = 1212 mm <sup>3</sup> )	Talairach Coordinates:			Cluster size mm <sup>3</sup>	Strength <i>t</i> max
	<i>x</i>	<i>y</i>	<i>z</i>		
Left fusiform gyrus (BA 37) = left FFA	-39	-40	-20	18	3.41
Left fusiform gyrus (BA 37) = left FFA	-42	-49	-17	10	3.54
Left inferior occipital gyrus (BA 18) = left OFA	-30	-84	-13	100	4.30
Left superior temporal sulcus	-44	-48	10	18	3.44
Left perirhinal cortex and fusiform gyrus (BA 38)	-28	2	-25	19	3.53
Left precentral gyrus (BA 6)	-35	4	31	62	3.94
Left hippocampus	-22	-22	-4	20	3.46
Right cuneus (BA 17)	10	-68	7	140	3.76
Precuneus	2	-58	37	148	4.82
Inferior rostral gyrus	2	41	-5	17	3.38



**Fig. 6.** Group analysis (random effect) disclosing the set of face-preferential areas at a more liberal statistical threshold ( $q(\text{FDR}) < 0.05$  ( $t = 3.38$ )) in the conjunction contrast:  $\{(F-SF) \text{ and } (F-O)\}$ . Note the right hemispheric dominance for all the areas usually disclosed (FFA, OFA, pSTS, anterior temporal lobe, prefrontal cortex), and the homology between these areas across hemispheres.

the voxels identified in one localizer run and the other may not always be high (Duncan et al., 2009), this independent analysis confirmed the observations reported above. Among all the areas identified, the right FFA is the least face-selective, in the sense that

it responds strongly to all the conditions but also more to nonface objects than scrambled objects (O-SO,  $p < 0.000001$ ). Moreover, it responds also highly to low-level characteristics of faces (SF-SO,  $p < 0.0008$ , with both conditions presenting a response signifi-

cantly above baseline) (Table S2 and Fig. S2). The right pSTS showed a similar behavior (see Table S3). In contrast, the right OFA does not show any difference of activation for O vs. SO ( $p = 0.62$ ). Moreover, its sensitivity to faces is not accounted for by low-level visual cues (SF–SO,  $p = 0.51$ ) (Table S3).

### 3.2.2. Individual subject analysis

Given the outcome of the group analysis, we used only the conjunction contrast {(F–FS) and (F–O)} in the individual participant analysis. Besides clarity, there are a few other reasons why this contrast was privileged. First, it is the only contrast that removes the low-level face cues and isolates what is specific about the face shape. Second, it identifies the FFA, unlike the interaction contrast. Finally, it is the conjunction contrast that was used to define the areas individually in all our previous studies using this localizer (Jiang et al., 2009, 2011; Rossion et al., 2011; Ramon et al., 2010a). We limited the size of the FFA (right middle fusiform gyrus, BA 37) at 200 mm<sup>3</sup> to identify the other face-preferential areas. At this threshold, only four participants out of 40 did not present a significant activation in the FFA and were not taken into consideration. We made the following observations:

- (1) There is a huge amount of variability between individual participants in terms of the level of activation of the right middle fusiform gyrus in response to faces. The average  $t$  value was at 4.33, with a standard deviation of 1.23.
- (2) The number of areas identified (Table 5) at that criterion, and their spatial distribution, also vary enormously across participants. Interestingly, the correlation between the  $t$  value at the fixed FFA size (200 mm<sup>3</sup>) for each participant and the number of voxels activated in the whole brain ( $r = -0.39$ ) explained only 15% of the variance between individuals. The remaining variance must thus be accounted for by the individual variability of the other areas.

**3.2.2.1. The right fusiform gyrus.** In addition to the FFA, 15 of the 36 participants had a second smaller area activated in the anterior fusiform gyrus (BA 20) (Fig. 7 and Table 5). This area has an average size of  $70 \pm 69$  mm<sup>3</sup>. For 6 of the 36 participants, there was also a

second spatially distinct face-preferential area in the middle fusiform gyrus ( $48 \pm 46$  mm<sup>3</sup>,  $t = 6.64$ ). In two participants, the three clusters could be identified and well separated spatially.

The anterior fusiform face-preferential area found in 15 participants has a higher degree of face-selectivity than the FFA: the contrast SF–SO is not significant ( $t_{14} = 1.63$ ,  $p = 0.13$ , random effect in ROI analysis) contrary to the right FFA ( $t_{14} = 2.64$ ,  $p < 0.019$ ). The contrast O–SO is significant in the two areas ( $t_{14} = 6.35$ ,  $p < 0.00002$  for the anterior area and  $t_{14} = 9.67$ ,  $p < 0.000001$  for the FFA, random effect in ROI analysis), but the difference is significantly higher in the FFA than in the anterior area ( $t_{14} = 2.97$ ,  $p < 0.005$ ).

**3.2.2.2. The left fusiform gyrus.** A left FFA (BA 37) is found in 31 participants (mean size:  $149 \pm 229$  mm<sup>3</sup>). There is also a second area in the anterior fusiform gyrus (BA 20) ( $102 \pm 164$  mm<sup>3</sup>) in 14 of these 31 participants and also a second area in the middle fusiform gyrus ( $31 \pm 7$  mm<sup>3</sup>) for 3 participants.

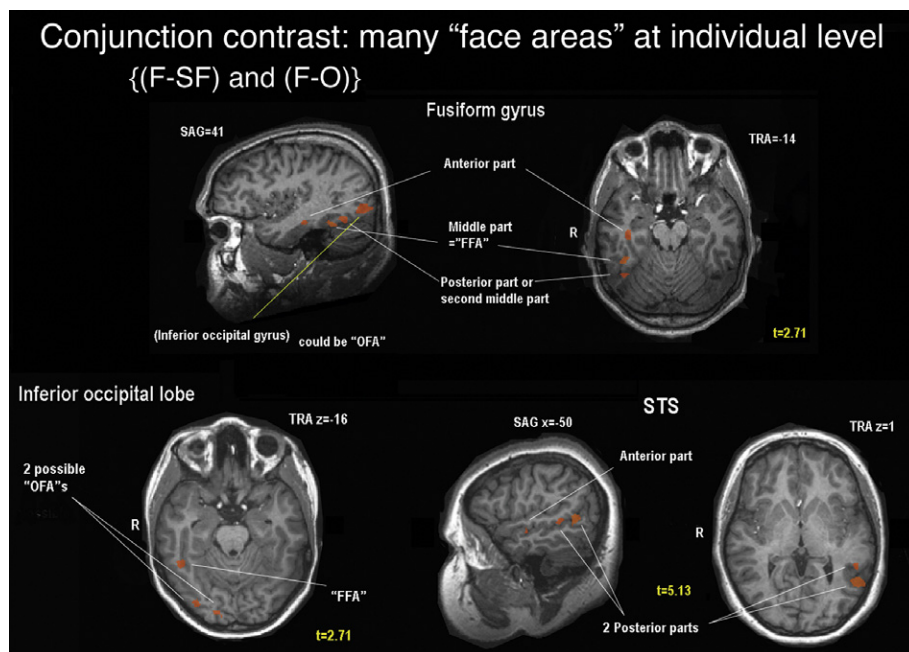
The left anterior fusiform face-preferential area found in 14 participants also has a higher degree of selectivity to faces than the left FFA. The contrast SF–SO is not significant ( $t_{13} = 0.91$ ,  $p = 0.381$ , random effect in ROI analysis) contrary to the left FFA ( $t_{13} = 2.18$ ,  $p < 0.048$ ). The contrast O–SO is significant for the two areas ( $t_{13} = 5.00$ ,  $p < 0.0002$  for the anterior area and  $t_{13} = 5.5$ ,  $p < 0.0001$  for the FFA) without any difference between the two ( $t_{13} = 1.28$ ,  $p = 0.12$ ).

**3.2.2.3. Comparison of the left and right hemispheres.** The left FFA is smaller in size than the right FFA ( $t_{35} = 1.740$ ,  $p < 0.045$ ). However, there is no difference for the anterior fusiform area ( $t_{35} = 0.52$ ,  $p = 0.3$ ). The lateralization of the FFA (number of voxels in the right middle fusiform/number of voxels in the left and right middle fusiform) is  $71 \pm 26\%$ , which is not different than the average value for all areas of the network ( $68 \pm 19\%$ ) ( $t_{35} = 1.02$ ,  $p = 0.16$ ). Interestingly, the disparity in spatial localization is greater in the left than the right FFA. That is, the distance from each single of the 36 right FFAs to the centre of all the 36 right FFAs is smaller than the distance from each of the 31 left FFAs to the centre of the 31 left FFAs ( $t_{51} = 1.67$ ,  $p < 0.050$ ; Fig. 8; Table 5 for the other areas).

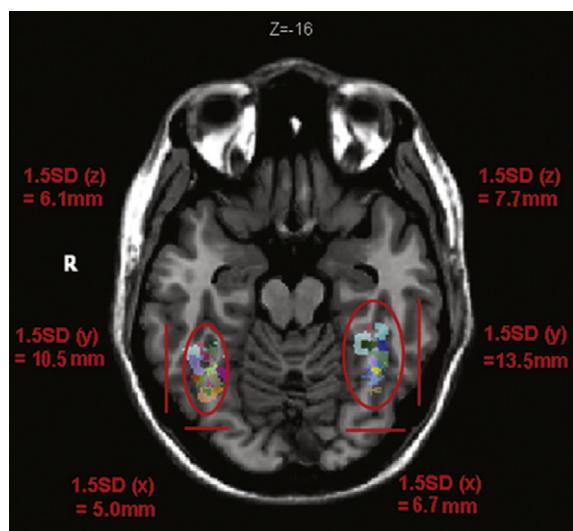
**Table 5**

Number of participants (out of 36) per localization of face areas identified with the conjunction contrast {(F–FS) and (F–O)} when a 'FFA' of 200 mm<sup>3</sup> is considered in the middle fusiform gyrus (BA 37). In italics, all the regions which could potentially be considered as right and left "OFA"s (9 participants on the right and 12 subjects on the left have no activations in all these regions).

Localisation	Talairach coordinates			Number of subjects (out of 36) when a right "FFA" of 200 mm <sup>3</sup> is considered		
	x	y	z	1 area	2 areas	3 or > areas
Right middle fusiform gyrus (BA 37)	36.9±3.4	−48.3±7.0	−15.4±4.1	30	6	0
Right anterior fusiform gyrus (BA 20)	37.8±4.0	−32.6±7.5	−17.2±4.0	15	0	0
Right posterior fusiform gyrus (BA 19)	36.2±4.2	−64.7±4.4	−13.0±6.1	8	0	0
Right inferior occipital gyrus (BA 19)	38.1±8.1	−72.2±8.5	−10.6±4.1	12	0	0
Right inferior occipital gyrus (BA 18)	32.2±7.1	−81.7±3.5	−10.2±6.0	20	0	0
Right posterior STS	48.7±6.0	−44.4±4	6.5±7.3	12	6	6
Right anterior STS	47.5±3.3	−12.3±11.9	−7.4±6.4	5	3	0
Right precentral gyrus (BA 6)	33.4±6.2	1.2±6.3	36±4.3	9	0	0
Right anterior inferotemporal cortex	31.8±3.3	−1.4±2.5	−25.3±2.7	8	0	0
Right amygdala	18	−7	−10	1	0	0
Left middle fusiform gyrus (BA 37)	−39.1±4.6	−46.9±9.0	−17.0±5.3	28	3	0
Left anterior fusiform gyrus (BA 20)	−35.7±3.1	−30.1±7.9	−17.3±5.5	14	0	0
Left posterior fusiform gyrus (BA 19)	−35.4±4.4	−67.5±6.2	−15.12±5.0	9	0	0
Left inferior occipital gyrus (BA 19)	−36.1±7.5	−72.2±5.9	−15.4±3.1	11	0	0
Left inferior occipital gyrus (BA 18)	−34.4±4.5	−81.2±2.9	−8.4±6.9	10	0	0
Left posterior STS	−50.1±5.3	−52.6±8.0	9.9±6.3	7	4	2
Left anterior STS	−	−	−	0	0	0
Left precentral gyrus (BA 6)	−42.7±6.3	9.3±2.3	23±1.7	2	0	0
Left anterior inferotemporal cortex	−31±2.8	−1.44±5.2	−25.8±5.4	4	0	0
Left amygdala	−18	−7	−7.5	1	0	0



**Fig. 7.** Illustration of the numerous face-preferential clusters that can be observed in individual brains. Top: One participant showing four significant clusters in the conjunction contrast  $\{(F-SF) \text{ and } (F-O)\}$  in the ventral stream, with one cluster in between the FFA and OFA and one cluster anterior around the usual localization of the FFA. Bottom, left: Another participant's brain in which two face-preferential clusters are observed in the occipital lobe and could potentially be defined as the OFA (the lateral cluster was defined based on similarity of coordinates with other participants). Bottom, right: Three significant clusters along the left STS in one participant.



**Fig. 8.** Disparity in spatial localization of the right and left FFAs. The distance from each single right FFA to the centre of all the 36 right FFAs is smaller than the distance from each of the 31 left FFAs to the centre of the 31 left FFAs ( $t_{51} = 1.67$ ,  $p < 0.050$ ).

**3.2.2.4. The inferior occipital cortex.** In the inferior occipital cortex, there is at least one face-preferential area for 27 participants in the right hemisphere, and one area for 24 participants in the left hemisphere (Table 6). This OFA can be found in both hemispheres for 20 participants out of 40. In 5 participants, neither the left or right OFA was disclosed. In the right hemisphere, 10 participants have two face-preferential clusters in the occipital lobe, and 2 participants have 3 clusters. In the left hemisphere, 4 participants have 2 clusters and one has 3 clusters. All these spatially distinct areas could be potentially considered as OFAs, and thus 30% of the participants could have more than one right OFA, and 8.33%

more than one left OFA (Fig. 7). The lateralization of the OFA (number of voxels in the right/number of voxels in the left and right) is  $62 \pm 39\%$ , which is not different than the average lateralization value, considering all areas identified in all participants presenting an OFA (31) ( $67 \pm 19\%$ ) ( $t_{31} = -0.914$ ,  $p = 0.18$ ). We note that the area found in the right BA 18 (20 participants) has a high degree of face-selectivity: the contrast SF-SO is not significant ( $t_{18} = 0.94$ ,  $p = 0.36$ , random effect in ROI analysis). The contrast O-SO is significant ( $t_{18} = 3.01$ ,  $p = 0.008$ , random effect in ROI analysis) but less so than in the right FFA of the 20 participants ( $t_{19} = 2.09$ ,  $p < 0.025$ ).

**3.2.2.5. The STS.** Activation was found in the right posterior STS for 24 participants out of 36 (mean of  $229 \pm 337 \text{ mm}^3$ ), and in the left posterior STS for 13 subjects ( $138 \pm 218 \text{ mm}^3$ ). However, there were different clusters in the superior temporal sulcus for individual participants. Ten participants present significant activations in both hemispheres. The left STS area is much smaller in size than the right STS ( $t_{35} = 2.83$ ,  $p < 0.004$ ). The lateralization of the STS (number of voxels in the right/number of voxels in the left and right) is  $77 \pm 36\%$ , which is more than the average value considering all areas identified in all participants presenting with a functional STS (27) ( $65 \pm 19\%$ ) ( $t_{26} = 1.90$ ,  $p = 0.034$ ). In 24 participants having activation in the right STS, 6 have two areas, 3 have 3, 2 have 4 and 1 has 5 in the right posterior STS (Talairach coordinates  $y < -35$ ). To complicate matters further, 8 of the 24 have also activations in a more anterior section of the STS (Talairach coordinates  $y > -35$ ) (3 of the 8 have 2 areas). From the 13 participants having activation in the left STS, 4 participants have 2 areas, one have 3 and one has 4 in the left posterior STS (Talairach coordinates  $y < -35$ ). None of them present significant activation in the anterior part (Talairach coordinates  $y > -35$ ) of the left STS.

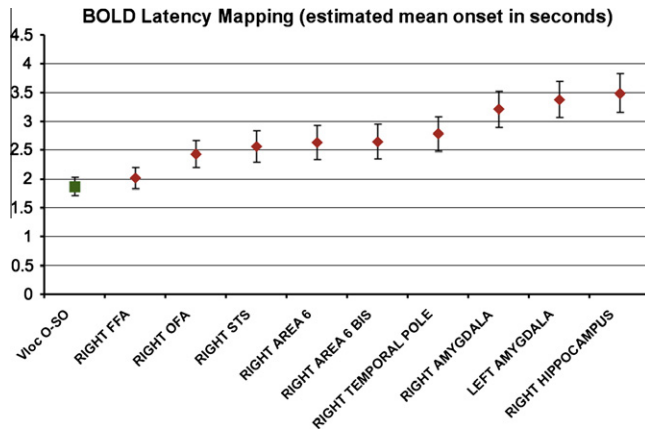
The right STS has a high degree of face-selectivity. The contrast SF-SO is not significant ( $t_{23} = 1.20$ ,  $p = 0.22$ , random effect in ROI analysis). The contrast O-SO is significant ( $t_{23} = 7.173$ ,  $p = 0.000001$ , random effect in ROI analysis) but much less than



**Table 6**

Individual subjects analysis. At fixed ( $200 \text{ mm}^3$ ) size of right FFA, all the clusters (potential OFAs) found in the posterior part of the fusiform gyrus (in the occipital lobe, BA 19) and in the inferior occipital gyrus (BA 18 or 19) for the 36 participants who presented with a FFA of at least  $200 \text{ mm}^3$ .

Right Hemisphere	Posterior fusiform gyrus	Inferior occipital gyrus, BA19	Inferior occipital gyrus, BA18	Total in right hemisphere
N of brains	8	12	20	27
Mean size ( $\text{mm}^3$ ) $\pm$ SD	$114 \pm 113$	$45 \pm 54$	$110 \pm 168$	$140 \pm 185$
Mean size ( $\text{mm}^3$ ) $\pm$ SD on the 36 brains	$23 \pm 66$	$15 \pm 38$	$66 \pm 140$	$104 \pm 170$
Left Hemisphere	Posterior fusiform gyrus	Inferior occipital gyrus, BA19	Inferior occipital gyrus, BA18	Total in left hemisphere
N of participants	9	11	10	24
Mean size ( $\text{mm}^3$ ) $\pm$ SD	$81 \pm 140$	$62 \pm 135$	$71 \pm 83$	$85 \pm 131$
Mean size ( $\text{mm}^3$ ) $\pm$ SD on 36 brains	$18 \pm 72$	$19.81 \pm 78$	$18.81 \pm 51$	$56 \pm 113$



**Fig. 9.** Results of the Bold Latency Mapping (BLM) analysis (mean onset in seconds and 0.05% confidence interval). Onset time of the response to first face in each block (432 trials in total) across the areas of the core and extended face network [conjunction contrast,  $t = 4.29$ ;  $q(\text{FDR}) < 0.01$ ] and in the posterior ventral part of LO (Grill-Spector et al., 1999), an area that does not respond more to faces than objects. Among all areas responding preferentially to faces, the right FFA shows the earliest onset response, significantly before the OFA ( $t_{18} = 4.00$ ,  $p < 0.0008$ ). It is activated as early as the ventral part of the LO complex ( $t_{18} = -1.880$ ,  $p = 0.076$ ).

in the right FFA of the same 24 participants ( $t_{23} = 7.30$ ,  $p < 9.84 \times 10^{-8}$ ). The left STS presents the same response profile. The contrast SF–SO is not significant ( $t_{12} = -1.22$ ,  $p = 0.25$ ), and the contrast O–SO is significant ( $t_{12} = 2.24$ ,  $p < 0.045$ ).

**3.2.2.6. Other areas.** With respect to the other face-preferential areas identified in the group analysis (conjunction contrast), there were very few clusters found at the individual level: bilateral amygdala in 1 out of 36 participants, right AIT (right perirhinal and fusiform cortex, BA 38) in 8 participants ( $98 \pm 160 \text{ mm}^3$ ) and left AIT in 4 participants (mean of  $53 \pm 64 \text{ mm}^3$ ). Two of these participants presented bilateral AIT activations. Face-sensitivity in the

precentral gyrus (BA 6) was found for 9 participants in the right hemisphere ( $24 \pm 39 \text{ mm}^3$ ) and 2 of these participants also presented a cluster in the left homologous area (mean of  $21 \pm 28 \text{ mm}^3$ ). For one participant only there was a significant activation in the right hippocampus, and for 3 participants an activation in the left cuneus (BA 17, mean of  $31 \pm 12 \text{ mm}^3$ ). The fact that these areas were found in the group analysis means that they are only slightly – and most of the time below threshold – activated by faces in individual participants, but consistently across participants.

### 3.2.3. BOLD latency mapping

When the onset time of the response to first face in each block (36 participants, 12 trials per participant, 432 trials in total) is compared across all face-preferential areas [conjunction contrast,  $t = 4.29$ ;  $q(\text{FDR}) < 0.01$ ], the right FFA appears to show the earliest onset response (Fig. 9 and Table 7). Its mean onset time precedes that of the right OFA ( $t_{18} = 4.00$ ,  $p < 0.0008$ ) and is as early ( $t_{18} = -1.880$ ,  $p = 0.08$ ) as the ventral posterior part of the LO complex (Grill-Spector et al., 1999), an area that does not respond more to faces than other objects. This early response of the FFA is associated with a lower variance across trials (see Table 7) because there are more participants in which a FFA could be identified than an OFA. In order to take this issue into account, the analysis was also performed only on the 20 subjects who presented also an OFA defined in the inferior occipital gyrus (BA 18). The BOLD response still rises earlier in the right FFA than the OFA ( $2.35 \pm 0.17 \text{ s}$  and  $2.53 \pm 0.15$  for the OFA) although the difference does not reach significance with this smaller amount of participants ( $p < 0.09$ ).

## 4. General discussion

In this large-scale fMRI face localizer analysis, we aimed at providing an overview of the whole set of areas responding more to

**Table 7**

Comparison of the bold estimation of the onset time of the response to first face in each block of faces (480 trials in total) for each area of the core and extended network found with the conjunction (F–O) and (F–SF).

Areas of the core and extended network (random analysis)	Onset (second) [Single-trial (mean and 0.050000% statistical confidence)]		Distance from the calcarine ( $\text{mm}^3$ ) ( $x = 0$ $y = -75$ $z = 5$ )
Right “FFA”	2.017	0.182	54
Right “OFA”	2.428	0.237	35
Right STS	2.561	0.273	55
Right area 6	2.632	0.297	89
Right area 6 BIS	2.649	0.299	90
Right temporal pole	2.786	0.303	86
Right amygdala	3.211	0.314	73
Left amygdala	3.384	0.310	74
Right hippocampus	3.487	0.335	61
v-LOC <sup>a</sup>	1.860 (faces)	0.162	42
	1.808 (objects)	0.158	

<sup>a</sup> Area found by the contrast O–SO. F–O nonsignificant.

faces than control visual stimuli in the human brain. We also aimed at describing not only the nature of the sensitivity to faces in these areas, but also their degree of lateralization, variability in localization and level of activation across a large set of participants. Concerning the nature of sensitivity to faces, we mean clarifying whether a larger response to faces in a given area reflects *face-specificity* (i.e., the area does not respond to nonface objects at all) or *face-preference* (the area responds more to faces than objects), and whether this larger response to faces can be accounted for even partially by low-level visual cues. We made a number of observations that have implications at both the methodological and theoretical levels. We discuss these implications in turn, in the context of a mini-review of the current status of the field regarding the neural basis of face perception as derived from neuroimaging.

#### 4.1. Methodological issues

##### 4.1.1. Interest of the face localizer and conjunction contrast

Functional localizers are widely used in neuroimaging studies of high level vision, and in face perception studies in particular, in order to define functional areas of interest that can be further tested for their response properties. The functional localizer used in the present study presents several interests.

First, by performing the conjunction of two contrasts (F–SF and F–O), it allows controlling *simultaneously* for high-level (i.e., shape-related) and low-level visual characteristics of faces. In line with previous observations (Berman et al., 2010) we found that using one of these two different procedures (F–SF or F–O) does not affect much the localization of the FFA's center of activation (Figs. 2 and 3), even though its size may change substantially. However, if one wants to define the OFA or other face-sensitive areas, the F–SF contrast is not appropriate at all because it identifies areas that may not be present with a larger response to faces than other categories (e.g., the LOC). Therefore, defining a significant cluster in the inferior occipital gyrus using this F–SF contrast as being “face-selective” (e.g., Eger et al., 2004; Fairhall & Ishai, 2007) can be misleading, an issue that will be addressed below. Moreover, using the interaction contrast of the factorial face localizer {(F–SF) – (O–SO)} is not recommended because the FFA is not disclosed by this contrast.

A second interest of the present localizer is that rather than contrasting faces to various object shapes, it relies only on a single nonface object category for comparison. This approach avoids the bias of having a much larger variability in shape, color and texture in the object condition compared to the face condition. Pictures of cars were chosen as the category of comparison to faces, for a number of reasons detailed in the methods section, and which make cars a very good control stimulus set in our opinion. Admittedly, there are also some limitations due to this particular choice of cars as a category. For instance, one cannot exclude that the voxels identified as responding preferentially to faces here also respond strongly to living things in general. Moreover, it would be preferable to ensure that participants of a given study are not experts in recognizing makes of cars, since their FFA might be smaller when contrasting faces to cars (Gauthier et al., 2000b; Xu, 2005).

Third, this localizer can be performed with an active one-back task, which allows monitoring participants' level of attention during the task. Given that accuracy rates were not significantly different between Faces and Scrambled Faces, or between Faces and Objects, the larger response to faces cannot be attributed to an increase of task difficulty for faces as compared to control stimuli, contrary to a functional localizer in which faces are compared to objects from various categories. Admittedly, there were significant behavioral differences between conditions when considering a large sample of participants. In terms of accuracy rates, the perfor-

mance was slightly slower for scrambled objects (95.5%) than the other three conditions, something that can be considered as reflecting a ceiling effect. Moreover, this condition is not included in the conjunction contrast, which considers only faces, scrambled faces and objects, three conditions for which there is no difference in accuracy rates. With respect to correct RTs, the only limitation is that participants were significantly slower for faces than cars. However, they were not slower for faces than scrambled faces and therefore, any confound in terms of task difficulty is removed if the conjunction contrast is used ((F–SF) and (F–O)).

Fourth, while quite well controlled, the present localizer, which provides 48 measures of the entire brain by condition, appears to also show robustness and sensitivity in terms of identifying the different areas of interest, across the whole brain. Obviously, it is certainly not as sensitive than a face localizer in which dynamic video clips of faces and objects are compared (Fox et al., 2009). However, in the present approach, we rather emphasized the tight control of object shape and low-level visual cues, ensuring that the groups of voxels activated truly reflect face-shape preferential response.

Finally, the same localizer can be used to define general object areas (LOC) by means of the contrast [(O + F) – (SO + SF)] (rather than O–F, which is sometimes used to define the LOC, e.g., Andrews & Schluppeck, 2004).

##### 4.1.2. Interindividual variance and ROI definition

At the group level, the set of areas responding preferentially to faces is easily identified by the conjunction contrast {(F–O) and (F–SF)}: one area in the lateral part of inferior occipital gyrus (OFA), one in the middle fusiform gyrus (FFA), one or possibly two in the superior temporal sulcus (pSTS), one in the medial part of the infero-temporal cortex, the amygdala, as well as activations in the hippocampus and the precentral sulcus (Figs. 4 and 6). In all these areas, the differential response to faces and control stimuli is larger in the right than the left hemisphere. However, when the statistical threshold is less conservative, all these areas are disclosed in both hemispheres at homologous locations (Fig. 6). These areas are identified in a group analysis because they show a strong preferential response to faces that cannot be accounted for by low-level visual cues, but also because they are activated in all, or at least a large subset, of the individual brains. Moreover, in order to disclose these activations at the group level there must be a sufficient spatial overlap between the localization of face-preferential activation in the different individual brains. For instance, face preferential activation in the amygdala can be difficult to disclose at the individual level (significant in only 1 participant out of 40 here), but since there is a relatively small degree of spatial variance across individual brains in the localization of this area, a highly significant face preferential response in the amygdalas is observed at the group level.

At the individual level, the analysis shows that there is a large amount of inter-individual variance in the number of areas, their level of activation and size. This variance cannot be merely accounted for by a general factor such as the sensitivity to faces of a given brain. Indeed, the *t*-value (mean  $4.24 \pm 1.24$  SD) of the right FFA (rFFA) when the size of the area is fixed at  $200 \text{ mm}^3$  for each participant accounts for 15% only of the variance across participants in terms of the total number of voxels activated by this contrast. In other words, if a participant presents a particularly highly significant rFFA, it does not necessarily mean that he/she will present a particularly large number of other face-preferential voxels: there are genuine differences across individuals in terms of relative sizes (i.e., significance) of the different face preferential areas in the brain. Consequently, using the exact same statistical criterion to identify a given area in each individual brain of a group of participants cannot be recommended. If the same conservative statistical threshold is used for all individual brains for instance, the FFA or other

areas might be identified only in a subset of participants. If a liberal statistical threshold is used, the areas might too large in size in some individual brains, so that they overlap with each other (e.g., OFA merged with FFA). Therefore, using a different statistical threshold for each individual brain in order to define the ROIs seems to be the correct way of dealing with this issue.

Another issue raised by the individual analysis is that a substantial number of participants present with face preferential responses in more than one area in the inferior occipital gyrus, in the fusiform gyrus, or in the posterior STS. Given this, how can one define an OFA, FFA, or pSTS objectively in an individual brain, and make sure that it is the same functionally-defined area that is grouped across individual brains in an analysis? Our data suggest that functional criteria can be used to label the areas correctly in individual brains. First, the level of activation for objects and scrambled faces is informative because it differs between the different areas. For instance, the FFA responds largely to objects and scrambled faces, while the other face-preferential area in the anterior fusiform gyrus (BA 20) does not respond to scrambled faces and only to a small extent to nonface objects. Second, anatomico-functional criteria, such as the spatial relations of the face areas to retinotopic visual areas, as well as to visual areas responding more to body parts than objects, could also be used (Weiner & Grill-Spector, 2010). However, relying on such criteria may not be possible from a practical point of view, if they require collecting so much data in each participant of a given study. In any case, there are certainly genuine differences in the number of face-sensitive clusters present in various human brains, so that attempting to label each of these clusters and make them correspond across individual brains may not be possible after all.

## 4.2. Neural basis of face perception

### 4.2.1. A large set of areas

The right hemisphere areas identified are well known and were all included in the “core” and “extended” neural face processing system defined by Haxby et al. (2000; see also Gobinni & Haxby, 2007): the inferior occipital gyrus (“OFA”), the middle fusiform gyrus (“FFA”), the infero-temporal cortex [AiT], the posterior part of the superior temporal sulcus (pSTS) and the amygdalas. These observations thus confirm the large distribution of face representations in the human brain (see also Fox et al., 2009; Ishai et al., 2005; Pinsk et al., 2009; Pitcher, Dilks, Saxe, Triantafyllou, & Kanwisher, 2011b; Rossion et al., 2003a; Sergent et al., 1992; Tovee, 1998; Tsao et al., 2008; as well as Ku, Tolia, Logothetis, and Goense (2011), Pinsk et al. (2009), Tsao et al. (2006, 2008) for imaging in the monkey brain, and Allison et al. (1994, 1999) and Barbeau et al. (2008) for intracranial recording studies in the human brain). All of these areas respond largely to faces and not, or to a very small extent, to objects or scrambled faces. The only notable exception is the FFA, which responds also largely to objects and scrambled faces.

In addition, we also found face preferential activation in the thalamus (pulvinar) bilaterally, the right hippocampus and the prefrontal cortex, and the left cuneus. Even though their function may be quite general, these additional areas appear to play a greater role for faces than the objects used in the present localizer. Increase of activation in the pulvinar nucleus of the right thalamus has been found for expressive and salient faces in several studies (e.g., Morris, Friston, & Dolan, 1997; Vuilleumier, Armony, Driver, & Dolan, 2003) and is thought to play a modulatory role in selective visual processing. Alternatively, this region has also been disclosed during the encoding of novel faces and face-name associations, a process that involves the bilateral hippocampus with a right hemispheric predominance (Kirwan & Stark, 2004; Schwarze et al., 2009; Sperling et al., 2001). The hippocampus has also been associated with active maintenance of novel faces across a short delay

period (Ranganath & D'Esposito, 2001), and has been disclosed as being part of the cortical face network identified when comparing faces to scrambled faces (Ishai et al., 2005). However, whether part of the hippocampus is specifically or preferentially involved for faces, as the results of the present study would suggest, has so far not been investigated. The area activated in the prefrontal cortex is located between the precentral gyrus and the inferior frontal gyrus (operculum), and has also been found to be involved during one-back tasks, particularly when object representations need to be updated (Bar et al., 2001; Derrfuss, Brass, Neumann, & von Cramon, 2005) or when the difficulty related to a face task increases (Schiltz, Dricot, Goebel, & Rossion, 2010). As for the left cuneus, BOLD signal in this area indicates a smaller deactivation for faces than the other conditions of the study, suggesting that this area is part of a face network pre-activated in “resting state” (Zhang, Tian, Liu, Li, & Lee, 2009).

### 4.2.2. The right hemispheric dominance for face perception across the whole set of areas

The results of our large-scale analysis emphasize the right hemispheric dominance for unfamiliar face perception. This RH dominance is well-established, but its extent has not been well characterized before. Acquired prosopagnosia follow either bilateral or right unilateral occipito-temporal lesions (Bouvier & Engel, 2006; Hecaen & Angelergues, 1962; Landis, Regard, Blietle, & Kleihues, 1988). Left unilateral lesions are found in only a handful of cases of prosopagnosia, all left-handed (Mattson, Levin, & Grafman, 2000; Barton, 2008b) but for one case with an epileptic seizure-related damage to the left fusiform gyrus possibly extending to the contralateral area (Wright, Wardlaw, Young, & Zeman, 2006). Multiple sources of evidence ranging from divided visual field studies (Hillger & Koenig, 1991; Parkin & Williamson, 1987), event-related potentials [ERPs, e.g. (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Rossion, Joyce, Cottrell, & Tarr, 2003b)] or single-cell recordings in the nonhuman primate brain (Perrett et al., 1988) have supported the dominant role of the right posterior visual areas in processing face stimuli [see also (Zangenehpour & Chaudhuri, 2005)]. Neuroimaging studies have also largely supported the right hemispheric dominance for face perception [e.g., (Kanwisher et al., 1997; McCarthy, Puce, Gore, & Allison, 1997; Sergent et al., 1992)]. Yet, strangely enough, current models of the neural basis of face processing based on neuroimaging (Haxby et al., 2000; Ishai, 2008) do not even consider this RH bias. Moreover, the extent of the RH bias has not been specified by neuroimaging studies, which have either focused on the right FFA only (Kanwisher et al., 1997; McCarthy et al., 1997) or on the whole ventro-temporal cortex without distinguishing different areas (Sergent et al., 1992).

As our individual analysis indicates, the right lateralization does not only concern the FFA (lateralization index: 71%), but also the OFA (61%) and the pSTS (77%), the latter showing the strongest lateralization index of all the areas of the network (average, 68%). Two factors appear to contribute to the group level massive right lateralization. First, there is a larger preferential response to faces in the right than the left hemisphere for all, or at least a large subset, of the participants. Second, the spatial disparity between the ROI localization of different individual brains appears to be larger in the left than the right hemisphere, at least as far as the FFA and AiT are concerned. Considering these two factors, when one performs a group analysis, the areas that survive a conservative statistical threshold are all localized in the right hemisphere. The only exception is the amygdala, which is found bilaterally (with a right hemisphere advantage also) and for which the spatial disparity factor is not really an issue.

The functional reason(s) behind this lateralization of face perception remains somewhat unclear. The classical view holds that



the right hemisphere is specialized in holistic processing and the left in analytic processing, with the faces considered as a typical example of a visual stimulus requiring global/holistic/configural perception (Bradshaw, Nettleton, & Taylor, 1981; Levy, 1969; Nebes, 1971; for a review see Sergent, 1988). Divided visual field studies have supported this view, whether the face stimuli have to be merely categorized as faces (Parkin & Williamson, 1987; see also Crouzet, Kirchner, & Thorpe, 2010) or individualized (Hillger & Koenig, 1991; Levy & Nagylaki, 1972; although see Sergent, 1984). Further studies have shown that the RH specialization for faces is related to the processing of low-spatial frequency information (de Schonen & Mathivet, 1989; Sergent, 1985), which supports holistic processing (Goffaux & Rossion, 2006; Sergent, 1986). Studies of cases of prosopagnosia have also supported this view, since the syndrome is often associated with the inability to process individual faces holistically (e.g., Barton, Press, Keenan, O'Connor, 2002; Levine & Calvanio, 1989; Ramon, Busigny, & Rossion, 2010b; Sergent & Signoret, 1992; Sergent & Villemure, 1989). More recently, neuroimaging studies have shown that when holistic processing of faces is required or enhanced, the right hemisphere dominance over the left hemisphere increases significantly, in particular at the level of the FFA (Goffaux et al., 2011; Harris and Aguirre, 2010; Rossion et al., 2000; Schiltz & Rossion, 2006; Schiltz et al., 2010).

Note that all areas showing a preferential response to faces do not have to be involved in holistic face processing to show a RH bias. It may be that there is a right hemispheric bias in the first area of the network that shows face-preferential response (i.e., the FFA, see Goffaux et al., 2011; Rossion, 2008, and below), and that this bias is then carried over in the remaining part of the network. Finally, with respect to this issue, there is recent evidence that the right hemispheric lateralization for face perception might be smaller in left-handed individuals (Badzakova-Trajkov, Haberling, Roberts, & Corballis, 2010; Willems, Peelen, & Hagoort, 2009), but whether this holds for the whole set of areas as identified here remains unknown.

#### 4.2.3. The FFA as the least face-selective area of the whole set

**4.2.3.1. The FFA is not a face-selective area.** The BOLD responses in the different areas revealed a surprising observation: among all areas showing a preferential response to pictures of faces, the area showing the least *specific* response to faces was the (bilateral) FFA. This was true both for the group analysis and the individual participants' data. Indeed, the FFA responded to a large extent to pictures of cars (above baseline and significantly above the response to scrambled cars). This is not a novel observation, as the FFA is known to respond to familiar stimuli such as cars from many previous studies (e.g., Dricot et al., 2008; Gauthier et al., 2000b; Grill-Spector, Henson, & Martin, 2006a; Grill-Spector, Sayres, & Ress, 2006b; Harel, Gilaie-Dotan, Malach, & Bentin, 2010; Peelen, Fei-Fei, & Kastner, 2009; Xu, 2005), and to all kinds of object shapes in fact (e.g., Ishai et al., 2005; Kanwisher et al., 1997; Tsao et al., 2008). Moreover, object-related activation in the FFA appears to be functional, since large repetition suppression, or adaptation, effects are also found for nonface objects in the FFA (Avidan, Hasson, Hendler, Zohary, & Malach, 2002; Dricot et al., 2008; Grill-Spector & Malach, 2001).

The larger response to faces may be due to all voxels in the FFA responding more but not exclusively to faces than objects, or to the FFA being composed of a subpopulation of voxels responding selectively to faces interspersed with other clusters responding equally strongly to all object categories (Grill-Spector, Sayres, & Ress, 2007; Grill-Spector et al., 2006a; Grill-Spector et al., 2006b; Hanson & Schmidt, 2011). Since electrophysiological recordings in a putative homologous area in the monkey brain reveals neurons that respond exclusively to faces (Tsao et al., 2006), it is the latter interpretation that is probably correct. High-resolution fMRI and

multivoxel pattern analysis also support this view (Grill-Spector et al., 2006a; Grill-Spector et al., 2006b; Grill-Spector et al., 2007; Hanson & Schmidt, 2011). However, a new observation of the present study is that the other areas identified in the face localizer do not present, or to a much smaller extent, a significant response to pictures of cars. While a BOLD response above baseline was found for cars also in the OFA and perhaps in the pSTS, it did not differ between cars and their scrambled counterparts. Thus, contrary to the FFA, there is a general response to visual stimuli in these areas with a particular increase for stimuli perceived as faces. Moreover, in the pSTS, amygdala and AiT, the response to all other conditions than faces was not even above baseline (Supplementary material Fig. S3). As acknowledged above, it may be that these areas would show a significant response to other object shapes, for instance pictures of birds or mammals, as used in some studies (Gauthier et al., 2000a; Xu, 2005). A significant response to body parts, which is found in the FFA (Chao, Martin, & Haxby, 1999; Pinsk et al., 2009; Tsao et al., 2008; Weiner & Grill-Spector, 2010), may also be observed in these other areas. Nevertheless, by using cars, we presented a highly familiar and complex control visual stimulus, and yet we did not find much evidence for a significant response to these nonface shapes in these other areas.

Considering that the FFA is the face-preferential area that shows the least degree of specificity, it is difficult to understand, and somehow regrettable, that so many studies in this field focused almost exclusively on the FFA to address important issues about the nature of face representation (e.g., Kanwisher, Tong, & Nakayama, 1998; Kanwisher et al., 1997; Loffler, Yourganov, Wilkinson, & Wilson, 2005; Wilkinson et al., 2000; Yue, Cassidy, Devaney, Holt, & Tootell, 2011). Most importantly, the issue of whether the larger response to faces in areas of the human brain reflects domain-specific processes or rather reflects flexible processes that can be modulated by visual expertise has often focused exclusively on the FFA (Kanwisher, 2000; Kanwisher & Yovel, 2006; Tarr & Gauthier, 2000), which is in fact the area showing evidently the least degree of specialization for faces to start with. To be honest, this focus on a single area has often been advocated by proponents of the domain-specificity view (e.g., Yovel & Kanwisher, 2004), while effects of visual expertise have also been tested in some other areas such as the OFA or the anterior fusiform gyrus (e.g., Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999). In any case, we believe that the important and yet unresolved question of whether faces are supported by domain-specific neural representations or representations that can accommodate nonface geometries following visual expertise should be considered at the level of the entire set of areas rather than a single area. The present observations in fact suggest that this question might even be more relevant in other areas— who show little or no response to nonface objects in novice observers – than in the FFA.

**4.2.3.2. Sensitivity to low-level visual cues of faces in the FFA.** Another interesting observation is that the FFA, contrary to, or much more than, other face-preferential areas, responds significantly more to low-level visual cues of faces, i.e. phase-scrambled faces, than low-level cues of objects, i.e. phase-scrambled cars (see also Andrews et al., 2010). This observation holds when using independent contrasts to define and test the FFA. In the present study, these low-level features could be of two kinds. First, differences in amplitude spectrum for face and car images (i.e., amplitude at the different frequencies). It has been shown that faces have natural specific characteristics in the frequency domain (Bosworth, Bartlett, & Dobkins, 2006; Keil, 2008; Keil, 2009; Keil, Lapedriza, Masip, & Vitria, 2008), and amplitude spectrum (AS) has been claimed to account for face-specific effects, such as the face pop-out effect in visual search (VanRullen, 2006, but see Hershler & Hochstein, 2006). AS also appears to contribute to fast saccadic

responses towards faces (Crouzet & Thorpe, 2010; Honey, Kirchner, & VanRullen, 2008), even though phase information (i.e., the structure of a face) accounts for the largest part of such effects (Crouzet & Thorpe, 2010; Morand, Grosbras, Caldara, & Harvey, 2010).

Color is a second low-level cue that may contribute to the differences observed in the FFA signal between scrambled faces and scrambled cars. It is widely acknowledged that color contribute to object categorization at multiples levels (see Price & Humphreys, 1989; Rossion & Pourtois, 2004; Tanaka, 2001). With respect to faces, there is evidence that face-selective neurons in the monkey infero-temporal cortex are sensitive to the diagnostic color of faces as a category. If faces are presented in gray-level, or in non-diagnostic color (e.g., a blue face), the cells' response is attenuated and delayed compared to the response to normally colorized faces (Edwards, Xiao, Keyser, Földiák, & Perrett, 2003). Here, the scrambled stimuli preserved the overall color that characterize faces, and which was clearly different than the cars' colors. In fact, if participants were asked to categorize the scrambled images used in the present experiment according to their category, they would probably rely heavily on color to do the task. Another aspect worth mentioning is that color is certainly more uniform for a car picture compared to a face picture, but the variations of colors *between* items presented in a block were certainly smaller for faces than cars. Unless all stimuli would be presented in grayscale, this parameter is particularly difficult to control, and may also have played a role in the differences observed. An event-related fMRI experiment with the same stimuli in grayscale would help clarifying and controlling better the contribution of this factor to the effects observed.

Usually, the contribution of low-level cues to behavioral face categorization is interpreted as evidence for a contribution of low-level visual areas, or pathways, rather than the dominant classical ventral visual stream (Honey et al., 2008; VanRullen, 2006). However, the present observations question this interpretation: a high-level visual area such as the FFA, whose response is driven largely by phase information of the images and which has been associated with the phenomenological perception of a face (e.g., Jiang & He, 2006; Tong, Nakayama, Vaughan, & Kanwisher, 1998), is also particularly sensitive to the low-level visual cues that characterize face stimuli.

Overall, these observations are in agreement with the findings that the FFA does not only respond preferentially to the perception of a face *per se*, but is sensitive to low-level visual features in general, such as spatial frequency power spectrum (Andrews et al., 2010), size, contrast and position of the (face) stimuli (Yue et al., 2011), as well as to simple characteristics of visual stimuli that are shared by faces (e.g., concentric form, higher number of elements in the top part of the stimulus, see Caldara et al., 2006; Wilkinson et al., 2000, respectively). Unfortunately, most of these previous studies concentrated on the FFA only, but did not investigate the response to such manipulations in other face-preferential areas. Here, we found that while the FFA was tuned to low-level cues of faces, other areas identified responded preferentially to high-level features of faces only: the difference between scrambled faces and scrambled cars was small and even non-significant in many of these areas: OFA, amygdala, pSTS. Interestingly, and somewhat paradoxically, the OFA, which is located much more posteriorly than the FFA, was less sensitive to low-level cues of faces than the FFA. Given that low-level visual differences between faces and objects are likely to generate the earliest differences in time between the processing of these categories (see Rossion and Caharel (2011) in particular), this observation is compatible with the view that the FFA may be the earliest area of the network to show a preferential response to faces, an issue that we address next.

#### 4.2.4. The OFA and the timing precedence of the FFA

Even at a conservative statistical threshold, the group analysis identified an area in the lateral inferior occipital cortex of the right

hemisphere that responded preferentially to faces, and which corresponded well to the so-called OFA (also called the inferior occipital gyrus, IOG, in some studies, e.g., Schiltz & Rossion, 2006; Weiner & Grill-Spector, 2010). Face-preferential clusters in the inferior occipital gyrus are still largely neglected by the community of neuroimagers interested in the neural basis of face processing (although see Pitcher et al., 2011a), for several reasons. First, the influential study of Kanwisher et al. (1997) focused exclusively on the FFA, which was considered by the authors as being the only area carrying out face perception. As a result, a large number of subsequent studies interested in understanding the nature of face representation also focused exclusively on the FFA (Kanwisher et al., 1998; Loffler et al., 2005, with reviews devoted specifically to this area: Berman et al., 2010; Kanwisher & Yovel, 2006), neglecting the OFA. Moreover, a number of neuroimaging studies using face localizers are not interested in face processing *per se*, but use the response properties of the most well-known and easily identifiable FFA to address other theoretical issues, which is reasonable. Second, the FFA is the largest area in size among the areas showing a preferential response to faces (e.g., Tsao et al., 2008). In comparison, the OFA is smaller in size and is less consistently disclosed in individual brains (e.g., Gilaie-Dotan & Malach, 2007; Rossion et al., 2003a; Rossion et al., 2003b). Here, in the right hemisphere, we found an area that could be labeled an FFA in 36 participants, and an OFA in 27 participants of our individual analysis. The OFA is also an area that is less consistent across studies in terms of its average coordinates (see Pitcher et al., 2011a) or even across participants within the same study (see Rossion et al., 2003a). However, even with the less powerful and spatially crude PET method, an OFA could already be identified and clearly separated from the FFA in the right hemisphere (Rossion et al., 2000). Currently, with more powerful magnets and analysis methods, face preferential responses in the inferior occipital cortex are now found consistently, and should no longer be ignored. Moreover, lesion studies suggest a critical role of face-preferential clusters such as the OFA in face processing, with some studies reporting that the largest overlap of lesions causing prosopagnosia falls in the territory of the right OFA rather than the right FFA (Bouvier & Engel, 2006; Rossion et al., 2003a). Also, transcranial magnetic stimulation (TMS) applied to the territory of the rOFA affects various aspects of face processing (e.g., Pitcher, Walsh, Yovel, & Duchaine, 2007; Pitcher et al., 2011a). FMRI studies have also identified areas responding preferentially to faces in the occipital cortex of the monkey, which have been related to the OFA (Pinsk et al., 2009; Tsao et al., 2008).

Here, interestingly, the OFA disclosed at the group level showed a higher degree of specificity to face perception than the FFA, since there was no sensitivity to object shape in this area (scrambled cars not different than cars), and no evidence of a preferential response for scrambled faces over scrambled cars. Hence, the OFA appears to present a higher degree of face specificity than the FFA, with the caveat that we compared faces to only one category (cars). This observation strengthens the claim that face-preferential responses in the inferior occipital cortex need to be taken into account when addressing issues concerning the domain-specificity and nature of face representation in the human brain (Rossion et al., 2003a; Rossion et al., 2003b; Tovee, 1998).<sup>1</sup>

<sup>1</sup> Our findings may appear to contradict the statement that the OFA is the least face-selective area of the whole set (Tsao et al., 2008, Fig. S8; Weiner & Grill-Spector, 2010). However, in the latter studies, the authors defined the areas and measured face-preference indexes without considering low-level responses to scrambled stimuli. Given the low-level parameters enhance the preferential response to faces of the FFA but not the OFA, it is not surprising that Tsao et al. (2008) reached this conclusion, which is technically correct but does not concern the preferential response to face presentations *per se*. Note also that the labeling of this area as an OFA in Tsao et al. (2008) study is subject to caution (see Weiner & Grill-Spector, 2010).

The contribution of face-specific clusters in the inferior occipital gyrus to face perception is unclear. According to the classical view of the flow of information in visual cortex, an OFA could be the first relay of a hierarchy of face processing stages taking place in the ventral stream and beyond (amygdala, prefrontal cortex) (Haxby et al., 2000; Ishai, 2008; Pitcher et al., 2011a). In line with this view, some authors have suggested that the OFA would play a rather low-level role in face processing (Eger et al., 2004; Rotshtein, Henson, Treves, Driver, & Dolan, 2005; Pitcher et al., 2011a). Supporting evidence come from the modelization of effective connectivity by means of DCM, revealing exclusive feedforward outputs from the OFA to the FFA and pSTS within the core aspect of the face perception model (Fairhall & Ishai, 2007). TMS to the OFA also impairs processing of facial parts in faces if it is applied early on (dual pulses, 60–100 ms, Pitcher et al., 2007). However, the interpretation of these findings is problematic, in particular because of the OFA definition in these studies. Critically, Fairhall and Ishai (2007) as well as Eger et al. (2004) defined the rOFA as a large area of the occipital cortex responding more to faces than scrambled faces (F–SF). As illustrated here in Fig. 3, such a definition encompasses the whole LOC at least and thus its relevance for face perception is unclear. Consequently, it is not surprising that other fMRI studies using DCM have found opposite results than Fairhall and Ishai (2007) with stronger outputs from FFA to OFA than the opposite during face processing (Rotshtein, Vuilleumier, Winston, Driver, & Dolan, 2007 who has defined the “OFA” in contrasting high and low spatial-frequency components in faces). Similarly, Pitcher et al. (2007) defined an OFA based on an average coordinate of previous studies, ignoring the large amount of interindividual variance in terms of OFA localization. More recent TMS evidence collected after individual definition of the OFAs rather suggests that the early contribution of the OFA to face perception is general, with a later response carrying specific information about faces (Pitcher, Walsh, Duchaine, & Kanwisher, 2010).

However, there is perhaps much stronger evidence against the view that preferential responses to faces in the inferior occipital gyrus (OFA) would necessarily precede and lead to face-preferential responses in the fusiform gyrus (FFA). Most importantly, brain damage to the right inferior occipital cortex, wiping out any face preferential response in this area, does not prevent right FFA activation (Rossion et al., 2003a). Bilateral FFA activation has also been reported in a patient with bilateral inferior occipital lesion and no OFAs (Steeves et al., 2006). In the normal brain, brief presentation of low-spatially filtered face stimuli activates the rFFA, while longer durations are necessary to activate the rOFA (and other areas) for both low- and high-spatial frequency faces (Goffaux et al., 2011). In the same vein, slowing down face detection by gradual rephasing of information in visual scenes (Sadr & Sinha, 2004) leads to face preferential responses emerging first in the rFFA and then in the rOFA (Jiang et al., 2011). Overall, these studies point to a contribution of a face cluster in the inferior occipital gyrus (OFA) in face perception that would generally follow rather than precede the face-preferential response in the middle fusiform gyrus (FFA). This view is compatible with a non-hierarchical view of face perception (Rossion, 2008; Rossion et al., 2003a; Rossion et al., 2003b) and suggests a direct functional pathway from early visual cortices to the middle fusiform gyrus. We would like to argue that the present findings strengthen this view, by showing first that the area that is the most sensitive to low-level visual information, paradoxically, is the most anterior area of the two, the FFA, and second that the FFA onset latency – as estimated by the BOLD latency mapping analysis – precedes significantly the latency of activation of the OFA. Admittedly, this latter source of evidence should be taken with great care, considering that general differences between areas in terms of vasculature could account for such differences. However, interestingly, the BOLD Latency Mapping

analysis reported a significant delay in the BOLD response of the left FFA compared to the right FFA, two areas that are anatomically analogous, suggesting that such a general factor does not merely accounts for the effects observed.

#### 4.2.5. The multiple face-preferential clusters in fusiform, inferior occipital gyrus and superior temporal sulcus

Although this area was not evinced in the group analysis, many participants (60%) presented with another significant cluster in the fusiform gyrus (BA 20), slightly anterior but clearly spatially different than the area identified as the FFA (BA 37) (Fig. 7 and Table 5). This anterior fusiform face area was bilateral and also showed a more specific response to faces than the FFA. An anterior face-preferential response has been described in recent studies (Tsao et al., 2008) in many individual human brains and labeled the AFP1 (anterior face patch 1). This area is clearly distinguishable from the AiT cluster identified also here and in other studies (e.g., Rajimehr et al., 2009). For a substantial amount of participants, we also found two significant clusters in the STS, as also reported in recent studies (Fox et al., 2009; Pinsk et al., 2009), as well as two clusters in the inferior occipital cortex (OFA). The second cluster in the inferior occipital cortex, located in between the FFA (middle occipital gyrus, BA 37) and OFA (inferior occipital gyrus, BA 18), in the posterior fusiform gyrus (pFus) or in the inferior occipital gyrus (BA 19), has also been described previously. However, it has either been combined with the anterior cluster to form the FFA (e.g., Grill-Spector & Malach, 2004), or considered as the OFA (e.g., Rotshtein et al., 2005: 42, –69, –18 –Talairach coordinates). Recently, two studies defined these areas specifically in the human brain, as FFA-1 (Pinsk et al., 2009) or pFus (Weiner & Grill-Spector, 2010).

Hence, a simple localizer as used here may already be sufficient to reveal a quite large set of areas showing a preferential (or exclusive) response to faces. The small number of participants showing many additional areas than the ones identified in the group analysis may just be due to a lack of power with only two face localizer runs. If many runs of the same experiment were performed in every single subject, then it is likely that in each individual brain, a set of six or more areas responding preferentially to faces would be found in the ventral visual stream only, as in the monkey brain (Pinsk et al., 2009; Tsao et al., 2006; Tsao et al., 2008). This observation complicates seriously the definition of the areas of interest in individual participants of a given study (which area “really” corresponds to the FFA or the OFA?). Unless additional criteria can be defined, such as the location of the face-preferential clusters with respect to functionally defined retinotopic visual areas (Weiner & Grill-Spector, 2010), these observations point to single participant analyses in which the functional areas need not necessarily be defined as corresponding across many participants. From a theoretical point of view, while the presence of many face clusters or areas all along the ventral stream is in agreement with early PET and intracranial recording studies of face processing (Allison et al., 1994; Allison et al., 1999; Sergent et al., 1992), it raises a number of outstanding questions: what are the respective function(s) of these areas?; why are there so many areas showing a preferential response to faces?; and why are they spatially separated all along the ventral stream?

## 5. Conclusions

We performed a large-scale analysis of whole-brain factorial face localizer that provides a good control for low-level visual cues characterizing faces. It corresponds to two runs of about 10 min each and it allows localizing areas sensitive to object shape also. Both at the group and individual participants levels, we report a



massive right hemispheric dominance of the whole set of areas, which was maximal in the pSTS. The group-level FFA showed the least selective response to the perception of a face *per se* in the sense that it responded also more to objects than scrambled objects, and, importantly more to scrambled faces than scrambled objects. In comparison, the face-preferential responses in the inferior occipital cortex, identified as the OFA showed a more selective response. This sensitivity of the FFA to low-level facial features, coupled with its early onset latency in the BOLD response, reinforce the view that it might actually be the earliest area of a very large network of areas to present face-preferential responses following visual stimulation. Finally, the large number of areas showing a preferential response to faces even in the same gyri, as well as the variability in terms of their localization suggest that there is a need to develop additional criteria to define and compare these areas across multiple brains. Alternatively, such observations encourage in-depth single participant studies and analyses in which the functional areas need not necessarily to be defined precisely and corresponded across many participants, rather considering the set of areas as a whole in each individual brain.

## Acknowledgments

We thank Corentin Jacques for making the stimuli, Christine Schiltz for helpful comments on a previous version of this paper, and Rainer Goebel for allowing us to use the fMRI facilities at the University of Maastricht. The authors are supported by the Belgian National Fund for Scientific Research (FNRS).

## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.bandc.2012.01.001](https://doi.org/10.1016/j.bandc.2012.01.001).

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