

The fusiform face area is tuned for curvilinear patterns with more high-contrasted elements in the upper part

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The ability to identify conspecifics from the face is of primary interest for human social behavior. Newborns' visual preference for schematic face-like stimuli has been recently related to a sensitivity for visual patterns with a greater number of elements in the upper compared to the lower part. At the adult level, neuroimaging studies have identified a network of cortical areas devoted to the detection and identification of faces. However, whether and how low-level structural properties of face stimuli contribute to the preferential response to faces in these areas remain to be clarified. Using functional magnetic resonance imaging (fMRI), here we investigated whether the adults' face-sensitive cortical areas show a preference for top-heavy patterns, similarly to newborns' preference. Twelve participants were presented with head-shaped and square patterns with either more elements in the upper or the lower vertical part. In the right fusiform gyrus ('fusiform face area', FFA), an area showing a preference for faces over other visual object categories, there was a larger activation for curvilinear patterns with more high-contrast elements in the upper part, even though these patterns were not perceived as face stimuli. These findings provide direct evidence that the FFA is tuned for geometrical properties fitting best with the structure of faces, a computational mechanism that might drive the automatic detection of faces in the visual world.

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In human social and biological interactions, it is critical from birth to identify conspecifics for communication, and the face readily provides the required non-verbal information. This

particular visual object encapsulates structural rules (e.g., two horizontal eyes placed above a central nose and mouth). In humans, it is well established that this configuration spontaneously captures newborns' attention more than other complex visual objects (Fantz, 1963). Newborns' remarkable early visual preference for schematic face-like patterns has been found with both moving and static stimuli (Goren et al., 1975; Johnson and Morton, 1991), as well as realistic faces (e.g., Macchi Cassia et al., 2004), suggesting that humans have a specific and innate perceptual ability to process faces (Farah et al., 2000). Yet, recently, such newborns' visual preferences have been related to a larger sensitivity to visual patterns presenting a greater number of high-contrast elements in the upper compared to the lower vertical part of the stimulus, rather than to faceness per se (Macchi Cassia et al., 2004; Turati et al., 2002). This phenomenon has been observed for schematic head-shaped and square patterns (Turati et al., 2002), as well as realistic faces, presenting more scrambled high-contrasted elements in the upper part (Macchi Cassia et al., 2004). This non-specific perceptual bias may optimally satisfy the constraints of newborns' immature visual system and may originate from an upper-field advantage in visual sensitivity (Simion et al., 2002).

In human adults, neuroimaging studies have considerably increased our knowledge of the functional organization of the human visual cortex (for a review, see Grill-Spector and Malach, 2004). A network of areas highly responsive to faces has been identified within the ventral visual pathway (Haxby et al., 2000): the right middle fusiform gyrus (the so-called 'fusiform face area' (FFA)—Kanwisher et al., 1997) (e.g., Gauthier et al., 2000; Grill-Spector et al., 2004; Halgren et al., 1999; Rossion et al., 2000), and in the inferior occipital gyri, the so-called occipital face area (OFA) (e.g., Gauthier et al., 2000). However, little is known about the basic elements of face stimuli that trigger responses in these areas. Most importantly, it is unknown whether general properties shared

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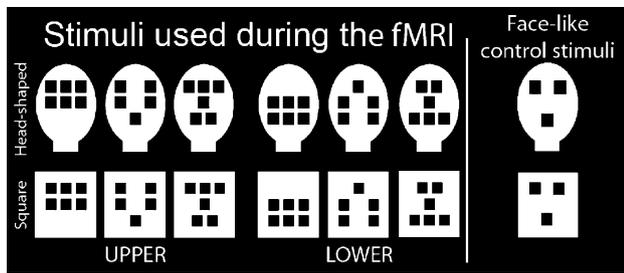


Fig. 1. Examples of stimuli used during and after (right—face-like control stimuli) fMRI scanning.

by face stimuli but also present in non-face patterns, such as a top-heavy structure, determine the response properties of these regions.

Here, we used functional magnetic resonance imaging (fMRI) to investigate whether the very same vertical asymmetry that determines newborns' preference is an important property that plays a role in shaping the response of adult face-sensitive areas in the occipito-temporal cortex. Since attention modulates activation in the face areas (Wojciulik et al., 1998), we used non-facial stimuli to prevent the attentional biases that could arise from the perception of artificial faces with misplaced features or a mixture of face features inserted in non-curvilinear shapes. Indeed, such attentional biases would be confounded in the brain activations, leading to a difficult interpretation of the results. This experimental procedure would also have had the disadvantage to explicitly reveal the nature of the question investigated in our study to the participants. Most importantly, the use of non-face stimuli permitted both to explore the development of the face system and to investigate whether and how low-level visual structural properties shape information processing at the level of high-order non-retinotopic visual areas (Levy et al., 2001; Halgren et al., 1999), such as those devoted to face (and object) processing. To this end, we first functionally identified the brain areas responding preferentially to faces by comparing the processing of faces and non-face objects. We then sampled the visual input space by presenting the participants with twenty high-contrasted curvilinear and square patterns with either more elements in the upper or in the lower part (see Fig. 1 and Methods). After the scanning session, participants evaluated the *faceness* of the presented stimuli, as well as two schematic face-like control stimuli. We expected that *at least* curvilinear patterns with more high-contrast elements in the upper part will enhance the responses of the human adult cortex coding for faces as their low-level structural properties fit best with those of human faces.

Methods

Stimuli

Faces and objects

Twenty full front photographs of unknown faces (<http://www.faces.kyb.tuebingen.mpg.de>) and 20 pictures of common objects (object databank at <http://www.cog.brown.edu/~tarr/stimuli.html>) were used.

Head-shaped and square patterns

Twenty symmetrical patterns were created for each condition. We created a set of configurations comprising a minimum of 4

elements and a maximum 7 elements (Fig. 1), in order to sample at the maximum the space covered by all the images (faces and objects) and consequently extract a general rule rather than an observation related to a sub-sample of possible patterns. The number of the elements was greater either in the upper or in the lower half of the stimulus, and the identical set of configurations was adapted for the use in the different conditions.

Control stimuli

We created two schematic face-like stimuli (Fig. 1), inscribed in head-shaped and square patterns, in order to control for the evaluation of the faceness of the stimuli used during the scanning sessions.

Participants

Twelve adult subjects (8 women) with normal vision voluntarily participated in the study. All the participants gave written informed consent, and the protocol was approved by the ethical committee of the University Hospital of Geneva.

Imaging methods

Experiments were performed on a 1.5 T whole-body system (Philips Medical Systems) using the standard head coil configuration. Acquired multi-slice volume was positioned on sagittal scout images. A first GRE (gradient-recalled-echo) T1-weighted sequence (TR (repetition time) = 162 ms; TE (echo time) = 4.47 ms; flip = 80°; FOV (field of view) = 250 mm; matrix = 256 × 256; slice thickness = 5 mm) was performed to acquire the same volume as in the functional session. Anatomical reference images consisted of a 3D-GRE T1-weighted sequence (TE = 15 ms; FOV = 250 mm; matrix = 256 × 256; slice thickness = 1.25 mm). For the localizer block paradigm and the experiment, functional imaging consisted of an echo planar imaging (EPI) GRE sequence (TR = 3000 ms; TE = 40 ms; flip = 80°; FOV = 250 mm; matrix = 128 × 128; 30 contiguous 5 mm axial slices). A vacuum cushion (PAR Scientific A/S, Denmark) was used to minimize head movement.

Tasks

Face and object epochs (18 s; 6 TR) were counterbalanced and separated by baseline epochs (fixation cross, 9 s; 3 TR). Two runs were performed, using a 'localizer' block design alternating periods of faces ($n = 20$) and objects ($n = 20$) (Kanwisher et al., 1997), with six epochs of each experimental condition (faces or objects) in each run. In each face and object epoch, 24 stimuli were presented for 750 ms, without any offset, but a small shift of position (20 pixels) between consecutive images. Four of the twenty four images were repeated twice consecutively, and subjects were required to detect the immediate repetitions by pressing a response key (one-back task). When perception of objects is contrasted to face perception (objects–faces), a robust activity has been identified in the bilateral parahippocampal gyri (PHG) (e.g., Epstein and Kanwisher, 1998; Rossion et al., 2003). We also took these brain regions as regions of interest in our experimental conditions.

Two counterbalanced runs of head-shaped ($n = 20$) and square patterns ($n = 20$) with either more elements in the upper or the lower vertical part (Fig. 1) followed the *localizer* scan. In each

epoch, 24 stimuli were presented (18 s; 6 TR) and separated by baseline epochs (fixation cross, 9 s; 3 TR). Participants had to detect the immediate repetition of the same stimulus (4 out of 24 images) and report their answers with a response key. All the images were displayed for 600 ms on a black background with an interleaved fixation cross (150 ms). Participants were required to fixate this cross during all the experiment.

After the scanning sessions, participants were debriefed. Firstly, we asked the participants for their general impressions and what they thought was the aim of the scanning sessions. No feedback on their answers was provided. Secondly, they were instructed to rate on a Likert scale of 1 (non face-like) to 8 (face-like) the faceness of the patterns and two schematic face-like control stimuli, which were not presented during the fMRI scanning sessions. All these stimuli were randomly presented in sequence on a computer monitor, and participants were required to express their faceness judgment by pressing the respective key (1 to 8) of a computer keyboard. Stimuli were presented without time constraints, and the following stimulus appeared after the response with an inter-stimulus interval of 2 s. After this final stage, according to our ethical policy, the real aim of the study was explained in detail to the participants.

Image and behavioral analyses

Collected data were processed with cross-correlation analysis (Bandettini et al., 1993) after motion correction (Woods et al., 1993) using MEDx software (Sensor Systems, Sterling, VA, USA) (Gold et al., 1998). Data were smoothed spatially by convolution with a Gaussian kernel (full width half maximum (FWHM) = $6 \times 6 \times 6 \text{ mm}^3$). The cross-correlation, expressed in terms of Z values, was calculated pixelwise between a delayed boxcar function and the set of measurements. Individual Z score maps were then normalized to the Talairach space by applying an affine transformation (Talairach and Tournoux, 1998). Afterwards, the statistical distribution of the Z values for each subject was calculated, and a probability value for each Z value was obtained (Moser et al., 1996). Clusters of size of $>0.08 \text{ cm}^3$ (>10 voxels; voxel size after normalization was $2 \times 2 \times 2 \text{ mm}^3$) showing a statistically significant Z score (typically Z threshold = 3.0, at $P < 0.002$, uncorrected) in the faces–objects comparison were considered (Forman et al., 1995). The choice of the cluster size threshold was based on the minimal detected size of FFA activation reported in the initial work of Kanwisher et al. (1997). We then computed additional post hoc analyses to reveal the influence of the perceived stimuli on the detected MRI signal. For this purpose, clusters activated during the localizer block paradigm were identified for each subject (size $>0.08 \text{ cm}^3$, at $P < 0.002$, uncorrected) and used as regions of interest (ROIs). Note that clusters with signal intensity $<50\%$ of the mean intensity of the

functional images were ruled out. Principally, six ROIs were identified, including the right FFA, the left FFA, the right OFA, the left OFA, the right PHG and the left PHG (e.g., Rossion et al., 2003). Furthermore, for each defined ROI, a mean timecourse (i.e. BOLD signal change in percent) was obtained by averaging the timecourses of individual voxels within the ROI. Then, the different experimental conditions were compared by using 2×2 repeated measure ANOVAs in each individual ROI separately, with Shape (head-shaped vs. square) and Greater element position (upper vs. lower) as factors. Only effects with a P value < 0.05 are considered significant, although they are not necessarily reported in the presence of a high-order interaction. Planned, pairwise, two-tailed t tests were applied at each level of the factors for analyzing interaction effects.

In order to investigate whether the subjective perceived faceness of the presented patterns modulated brain activations, when appropriate, we conducted Pearson correlation analyses across subjects between brain responses averaged across all the voxels of the ROI and the behavioral rating scores. Faceness ratings scores were normalized by rescaling raw rating score values between 0 (minimum) and 1 (maximum) for each individual. The normalization process neutralizes subjective differences in faceness rating across the participants, as all participants share values in the same range. Finally, in the appropriate ROIs, in order to further investigate whether brain activations and faceness rating scores were linked, we carried out a 2×2 repeated measure ANOVA with the BOLD signal for Shape (head-shaped vs. square) and Greater element position (upper vs. lower) as factors and the normalized faceness scores as a covariate (Winer et al., 1991).

Results

Behavioral results

No significant differences were observed for the behavioral performances during fMRI scanning sessions. As expected, the two schematic face-like control patterns obtained the highest score ($M = 0.96$ for the head-shaped; $M = 0.67$ for the square—Likert scale values normalized from 0 to 1) in the faceness evaluation performed after the fMRI scanning sessions. Faceness rating scores were larger for the schematic face-like control stimuli presented outside scanning as compared to the non-face visual patterns used for the experimental conditions during fMRI scanning (minimum significant value, $t(11)$, $P < 0.01$ —see Table 1).

Neuroimaging results

A significant activation for the comparison between faces and objects was found in all the subjects in two brain areas: the right

Table 1

Mean (\pm SE) of the normalized faceness ratings (Likert scale: 0 = non-face-like; 1 = face-like) and their respective P values when compared to the control stimuli

	Head-shaped		Square		Faceness ratings for the control stimuli
	Upper	Lower	Upper	Lower	
Faceness	0.25 (0.07)	0.13 (0.03)	0.14 (0.06)	0.01 (0.007)	0.96 (0.03)
$t(11)$, P	<0.001	<0.001	<0.001	<0.001	Head-shaped
$t(11)$, P	<0.01	<0.001	<0.001	<0.001	Square

FFA for faces (rFFA; $(x, y, z) = 40, -50, -17$) and the bilateral parahippocampal gyri (PHG) for objects (Fig. 2).

Because there was no interaction between the left and right activation in the PHG (Talairach coordinates respectively of $(x, y, z) = -21, -56, -10$; $(x, y, z) = 23, -52, -10$), their signal was averaged (Epstein and Kanwisher, 1998). Other brain regions were activated for faces, but not in all the subjects. The left FFA (IFFA; $(x, y, z) = -38, -52, -17$) was activated in ten participants, the right OFA (rOFA; $(x, y, z) = 33, -76, -8$) in seven and the left OFA (IOFA; $(x, y, z) = -36, -79, -14$) in six. In these regions, the only significant interaction between the Shape and Greater element position was found in the right FFA ($F(1,11) = 7.73$, $P = 0.0178$) (Fig. 3). Head-shaped patterns with a greater number of elements in the upper vertical part (mean percentage signal change = 0.35%) showed larger responses in the rFFA compared to all other conditions (post hoc t test comparisons, with: head-shaped lower, mean percentage signal change = 0.11%, $t(11)$, $P < 0.001$; square upper, mean percentage signal change = 0.12%, $t(11)$, $P < 0.01$ and lower, mean percentage signal change = 0.14%, $t(11)$, $P < 0.001$).

There was no correlation between normalized faceness scores of the head-shaped patterns with a greater number of elements in the upper vertical part and the rFFA activations (Pearson correlation; $r = -0.38$, $P = 0.22$). However, normalized faceness scores of the head-shaped patterns with a greater number of elements in the upper part positively correlated with IFFA activations (Pearson correlation; $r = 0.66$, $P < 0.03$).

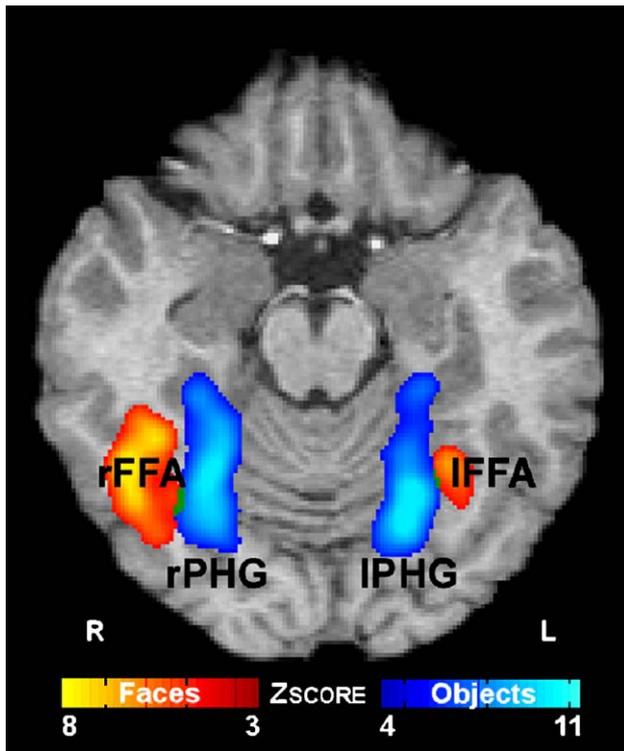


Fig. 2. Functional regions of interest for faces (FFAs—red) and objects (PHGs—blue) defined by the localizer paradigm. Note, because the group average is reported, the occipital face area activities are not illustrated since approximately only half of the subjects activated these brain regions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

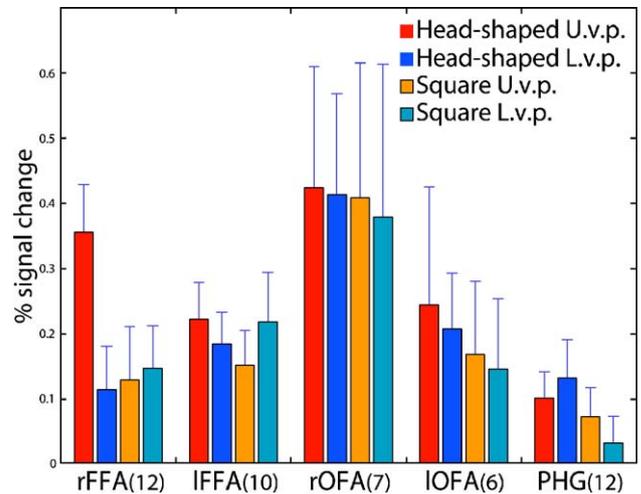


Fig. 3. Mean BOLD percentage signal change measures across participants, and their standard errors, related to the processing of the experimental visual patterns within the functionally defined brain areas. The number of participants that presented significant activations for faces and objects within their respective selective regions is reported in parenthesis.

In order to investigate whether normalized faceness scores and brain activations observed in the rFFA are linked, we performed a 2×2 repeated measure ANOVA with the BOLD signal for Shape (head-shaped vs. square) and Greater element position (upper vs. lower) as factors and the normalized faceness scores as a covariate. As observed for the previous statistical analysis, a significant interaction was observed between the Shape and Greater element positions ($F(1,11) = 6.356$, $P = 0.03$), head-shaped patterns with more elements in the upper part showed larger responses in this brain region (post hoc t test comparisons, with: head-shaped lower $t(11)$, $P < 0.01$; square upper $t(11)$, $P < 0.05$ and lower, $t(11)$, $P < 0.01$).

Discussion

The role of low-level structural properties in the responses of the mature neural adult face and object recognition system was investigated by presenting geometric visual patterns with either more elements in the upper or the lower visual part. Verbal reports pointed out that none of the participants noticed that the presented visual patterns aimed to study face processing, instead, some of the participants thought that this experiment was designed to explore counting mechanisms. More objectively, behavioral results reinforced this view by showing that the patterns used during the fMRI scanning sessions were not perceived as schematic face-like stimuli. Indeed, normalized faceness ratings scores for the experimental patterns were significantly lower than those attributed to schematic (head-shaped and square) face-like control stimuli not presented during the fMRI experiment. This observation demonstrates that the patterns used in the scanner were clearly dissimilar from noticeable face-like shapes.

In order to conceal the aim of our study, we did not measure the activations for schematic face-like control stimuli. Nevertheless, a previous study investigated the perception of schematic face-like stimuli by using an experimental design fully comparable with our procedure (localizer scan, one-back repetition task and localization of ROI for faces) and a scanner with a similar magnetic field strength (1.5 T). Tong et al. (2000) found in the rFFA larger

activations for human faces (1.6 mean percentage signal change) compared to schematic face-like patterns (0.9 mean percentage signal change). Given this observation, schematic patterns explained at least more than 50% of the mean percentage signal change elicited by real faces. In our study, head-shaped patterns with more elements in the upper part evoked relatively weak activations (0.35 mean percentage signal change) compared to those observed for real faces (1.9 mean percentage signal change), therefore explaining only about 18% of the mean percentage signal change evoked by the presentation of real faces. Although these are indirect observations, such important differences at the level of the rFFA activations strongly suggest that our patterns were not processed with the same strength than faces or schematic face-like stimuli. This result resonates with the significant differences observed behaviorally in terms of faceness rating scores between the control schematic face-like patterns and the experimental patterns. Despite these lines of evidence in favor of an explicit non-facial information processing of the presented patterns, a functionally defined region responding preferentially to faces, the rFFA (Kanwisher et al., 1997), showed enhanced activations for curvilinear patterns with more high-contrast elements in the upper part. Critically, the averaged responses of this brain region were not correlated with the normalized subjective larger faceness ratings observed for the head-shaped with more elements in the upper part. This finding eliminates the possibility of a straightforward miming between the similarity to faces and the activations observed in this area. However, averaged activations in its homologous region, the IFFA, significantly correlated with these rating scores. It is interesting to speculate on the nature of this result. IFFA activations have been found to be positively correlated with the magnitude of the recognition advantage for same- compared to other-race faces (Golby et al., 2001). Interestingly, despite the presence of this significant correlation with the behavior, IFFA responses did not discriminate between the experimental conditions tested in the Golby et al. (2001) study (same- vs. other-race faces), an observation that is in line with our findings (the IFFA did not show any sensitivity for the visual patterns). At the functional level, it has been suggested (Kosslyn et al., 1989) that pathways in the left hemisphere may drive categorical visual processes that maximize similarities among exemplars in a category, whereas right-hemisphere pathways may mediate coordinate visual processes that maximize individuation between exemplars in a category. This position is in line with previous findings showing face feature-based tuning for the IFFA and a whole-based tuning for the rFFA (Rosson et al., 2000). Thus, IFFA activations might be related to extract fine-grained processing necessary to detect invariant information for constructing visual categories (such as the patterns used in our study). rFFA activations might instead relate to processes permitting an optimal identification of the object of these categories at the individual level. Future studies are necessary to clarify the precise nature of such mechanisms in the IFFA and how the interaction of this region with its homologous part in the right hemisphere affects optimal high-order visual information processing.

The task performed by the participants outside the scanner was to explicitly rate the faceness of the presented stimuli. *By definition*, the curvilinear patterns with more elements in the upper part presented in the scanner are those that fit best with this criterion, and they accordingly received the highest faceness rating scores from the participants compared to the other experimental patterns. At the first sight, this finding could represent another possible explanation

of the increase of activation observed in the rFFA. However, if it was only faceness, rFFA activations would be parametrically and linearly related to the degree of faceness of the presented stimuli, but our findings do not support this view. Indeed, for instance, head-shaped patterns with more elements in the lower part obtained the second score in terms of faceness ratings but evoked the smallest activations in the rFFA. A comparison between faceness ratings for head-shaped patterns with more elements in the upper visual part with those in the lower is not significant, despite that the same comparison in terms of BOLD signal is highly significant. Critically, the repeated measure ANOVA with faceness rating scores as covariate still showed a significant interaction, larger activations in the rFFA for head-shaped pattern with more elements in the upper part, demonstrating that there are differences that can be observed at the level of the BOLD signal which are independent of the normalized faceness scores. Thus, our data support the view that BOLD activations are not linearly affected by the degree of faceness ratings of the stimuli used in our fMRI scanning sessions. Altogether, our observations favor instead an automatic stimulus-driven discrimination and reveal a precise geometrical tuning in the face recognition system for high-contrasted curvilinear patterns with more elements in the upper part. Such a visual property might be relevant for detecting geometrical shapes best fitting with the structure of faces within the visual world.

Our fMRI results resonate with recent developmental findings from newborns, which demonstrate a comparable visual preference for non-face-like (Turati et al., 2002) or face-like (Macchi Cassia et al., 2004) stimuli presenting more elements in the upper part. Interestingly, contrary to the behavioral observations made in newborns (Turati et al., 2002), the human adult rFFA was enhanced to top-heavy patterns only when a curvilinear contour was also present. This suggests that during the life span learning and experience with faces may have shaped brain responses for patterns which best fit with face geometry. The curvilinear contour plays a major role in normal face processing (Kosslyn et al., 1995), and concentric radial patterns activate the rFFA (Wilkinson et al., 2000). Our data provide direct evidence for the existence of a curvilinear vertical asymmetry bias within the mature fine-tuned functional face recognition system. The brain responses elicited by the perception of real faces in the localizer task were larger (1.9 mean percentage signal change) than those evoked by the visual patterns (0.35 mean percentage signal change), with identical task demands. Consequently, a *small* part of the signal encapsulated in the rFFA responses for faces can be attributed to mechanisms sensitive to the structural geometry properties of the visual input itself. It is worth noting, however, that despite our data show that participants did not process these stimuli as face patterns, it is difficult to unambiguously conclude on the non-specific nature of such effects. To put it concretely, is it because our curvilinear non-face patterns with more elements in the upper part were more similar to faces that we observed automatic enhanced activations in the rFFA or, conversely, is it because face geometry optimally satisfies the non-specific geometric tuning of this brain region that this area has developed a sensitivity for processing faces? Future studies are necessary to clarify the causal inferences of such effects.

Among the functionally defined regions for faces and objects, the rFFA is the unique region showing a modulation of its responses for the presented visual patterns. This observation converges with evidence coming with different approaches revealing a right hemisphere advantage for face processing. A unilateral lesion of the right hemisphere is sufficient for leading to

prosopagnosia, the inability to recognize familiar faces (e.g., Landis et al., 1986). Moreover, some prosopagnosic patients seem to be disrupted in the presence of the vertical asymmetry as they use only the lower part of the face (i.e., the mouth) for face identification (Caldara et al., 2005). Developmental studies have shown better face discrimination performances in infants in the left visual field (de Schonen and Mathivet, 1990) and the necessity of a normal stimulation of the right hemisphere during the early period of life for developing an efficient face recognition system (Le Grand et al., 2003). Moreover, larger responses for faces in the rFFA compared to the IFFA have been found in most fMRI studies (e.g., Grill-Spector et al., 2004; Kanwisher et al., 1997; McCarthy et al., 1997). We should acknowledge, however, that the procedure we have applied to identify the critical ROIs (FFAs and PHGs) diminished the detectability of the OFA regions (we identified the rOFA in 7 out of 12 participants and the IOFA in only 6 participants) and consequently decreased the statistical power of the performed analyses.

Most interestingly, when faces are presented upside-down, face recognition is disproportionately impaired compared to object recognition in similar viewing conditions, leading to the so-called face inversion effect (for a recent review see Rossion and Gauthier, 2002; Yin, 1969). Nevertheless, the vertical asymmetry encapsulated in the face structure is inverted when faces are presented upside-down, displaying a great number of high-contrasted elements in the lower part of the stimulus. fMRI studies that compared the processing of upright and inverted faces found a decrease in the activity of the rFFA when faces are inverted (e.g., Kanwisher et al., 1998; Yovel and Kanwisher, 2004). In line with these fMRI findings, we found a decrease of the activity in the rFFA when the subjects were presented with patterns with more elements in the lower visual part, even when those patterns were inscribed in a curvilinear contour. Thus, one of the factors explaining the face inversion effect could be related to the basic structural properties of the stimulus itself, namely, the difference in the greater number of elements present in the vertical axis, as suggested by recent behavioral findings (Sekuler et al., 2004). These low-level geometrical quantitative differences might modulate in turn the configural mechanisms involved in subsequent information processing.

Another consideration regarding the functional role of the rFFA lies in the increase of activation in this region for non-face visual objects for which subjects have developed expertise (Gauthier et al., 1999; Tarr and Gauthier, 2000). Our findings suggest that this process may have been facilitated by basic configural properties shared by the non-face objects used in these studies (e.g., greebles in Gauthier et al., 1999; cars and birds in Gauthier et al., 2000) since these visual objects have curvilinear shapes with more informative elements in the upper part.

Finally, it is interesting to report that a comparable computational rule has been and is still used for creating algorithms in artificial systems dedicated to the identification and recognition of faces among visual objects. To achieve this aim, these algorithms construct curvilinear boundary maps by using the particular spatial arrangement of eye and mouth positions (e.g., Hsu et al., 2002), capturing the vertical asymmetry intrinsically present in human faces. Here, we revealed the existence and optimality of a similar computational rule for face processing at the level of the adult human brain. Crucially, our data suggest that the neurons of this brain region could use this rule to rapidly detect a particular geometry in the visual world, the human face.

Several million years of natural selection have symmetrically shaped human faces (Gardner, 1964) with a curvilinear contour and larger proportion of high-contrasted features in the upper (e.g., eyes, eyebrows, forehead) compared to the lower part of the face (e.g., mouth, chin). These structural properties embedded in human faces fit well with the newborns' immature visual system and adults' mature face recognition system, which are both tuned to process patterns that have more elements in the upper part. Human adults required the curvilinear contour for exhibiting a neural preference for such asymmetrical vertical bias. Future studies are necessary to investigate whether this calibration occurs just following the specialization of newborns' neural pathways dedicated to face processing, from primitive subcortical circuits to elaborate cortical representations (de Schonen and Mathivet, 1989; Johnson and Morton, 1991) or occurs ultimately in a mature face recognition system, working as *computational* mechanism for automatic face detection.

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