

Faces are represented holistically in the human occipito-temporal cortex

Christine Schiltz^{a,b,*} and Bruno Rossion^{a,c}

^aLaboratoire de Neurophysiologie, Université catholique de Louvain, Belgium

^bEducational Measurements and Applied Cognitive Science Unit, University of Luxembourg, Luxembourg

^cUnité Cognition et Développement, Université catholique de Louvain, Belgium

Received 22 March 2006; revised 4 May 2006; accepted 6 May 2006

Available online 25 July 2006

Two identical top parts of a face photograph look different if their bottom parts differ. This perceptual illusion, the ‘face composite effect’, is taken as strong evidence that faces are processed as a whole rather than as a collection of independent features. To test the hypothesis that areas responding preferentially to faces in the human brain represent faces holistically, we recorded functional magnetic resonance imaging (fMRI) during an adaptation paradigm with the composite face illusion. In both the middle fusiform gyrus (MFG) and the inferior occipital gyrus (IOG), we observed a significantly larger response to the same top face when it was aligned with different bottom parts than with the same bottom part, with a most robust effect in the right middle fusiform gyrus. This difference was not found when the top and the bottom face parts were spatially misaligned or when the faces were presented upside-down. These findings indicate that facial features are integrated into holistic face representations in areas of the human visual cortex responding preferentially to faces.

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Keywords: Face perception; Visual system; Fusiform gyrus; Holistic processing; Composite illusion; fMRI

Introduction

It has long been noted that a human face is perceived as an undecomposed whole rather than as collection of individual features (Galton, 1883). Holistic face processing has been empirically demonstrated in behavioral studies, showing that the identification of a facial feature is highly dependent on the whole face context (e.g. Sergent, 1984a; Young et al., 1987; Tanaka and Farah, 1993). However, it remains unknown how individual features are integrated into holistic face representations in the

human brain. Neuroimaging studies identified several occipito-temporal cortical areas responding preferentially to faces in humans, with a right hemispheric dominance (e.g. Sergent et al., 1992; Puce et al., 1995; Kanwisher et al., 1997; Rossion et al., 2000). Two of these areas are located in the ventral pathway, in the lateral middle fusiform gyrus (MFG), also known as the “fusiform face area” (‘FFA’, Kanwisher et al., 1997), and posterior to it, in a region of the inferior occipital cortex (IOG), also known as the “occipital face area” (‘OFA’, Gauthier et al., 2000).¹ These areas play a critical role in the extraction of individual face representations (Gauthier et al., 2000; Rossion et al., 2003; Grill-Spector et al., 2004; Schiltz et al., 2006). In line with the hierarchical nature of the primate visual system (Felleman and Van Essen, 1991), it has been proposed that the face-sensitive neurons of the inferior occipital gyrus (IOG) represent facial features, whereas whole facial identities would be represented in the middle fusiform gyrus (MFG) (Haxby et al., 2000).

To identify the cortical areas in the human brain which represent faces holistically, we designed an fMR-adaptation paradigm (Grill-Spector and Malach, 2001; Henson, 2003; Grill-Spector et al., 2006) using the most compelling demonstration of holistic face processing reported in the behavioral literature, namely the ‘composite face effect’ (Young et al., 1987). In the ‘composite face effect’, two identical top parts of a face are perceived as being different if their respective bottom parts belong to different identities. However, this perceptual illusion vanishes if the top and the bottoms parts of the faces are laterally offset (i.e. misaligned) or inverted (Fig. 1) (Young et al., 1987). The composite face effect has been observed for familiar and unfamiliar faces, in recognition or face matching experiments

* Corresponding author. Laboratoire de Neurophysiologie (NEFY), Université catholique de Louvain, Avenue Hippocrate 54-49, 1200 Brussels, Belgium. Fax: +32 27645465.

E-mail address: schiltz@nefy.ucl.ac.be (C. Schiltz).

Available online on ScienceDirect (www.sciencedirect.com).

¹ Even though this terminology (‘FFA’, ‘OFA’) is largely used, it is also somewhat misleading as these regions do respond to other stimuli than faces and to a different level to distinct objects (e.g. Ishai et al., 2000; Grill-Spector et al., 2004). Therefore, we will use the more neutral labels MFG and IOG referring to the anatomical localization of the functionally defined regions which respond to a larger extent to faces.

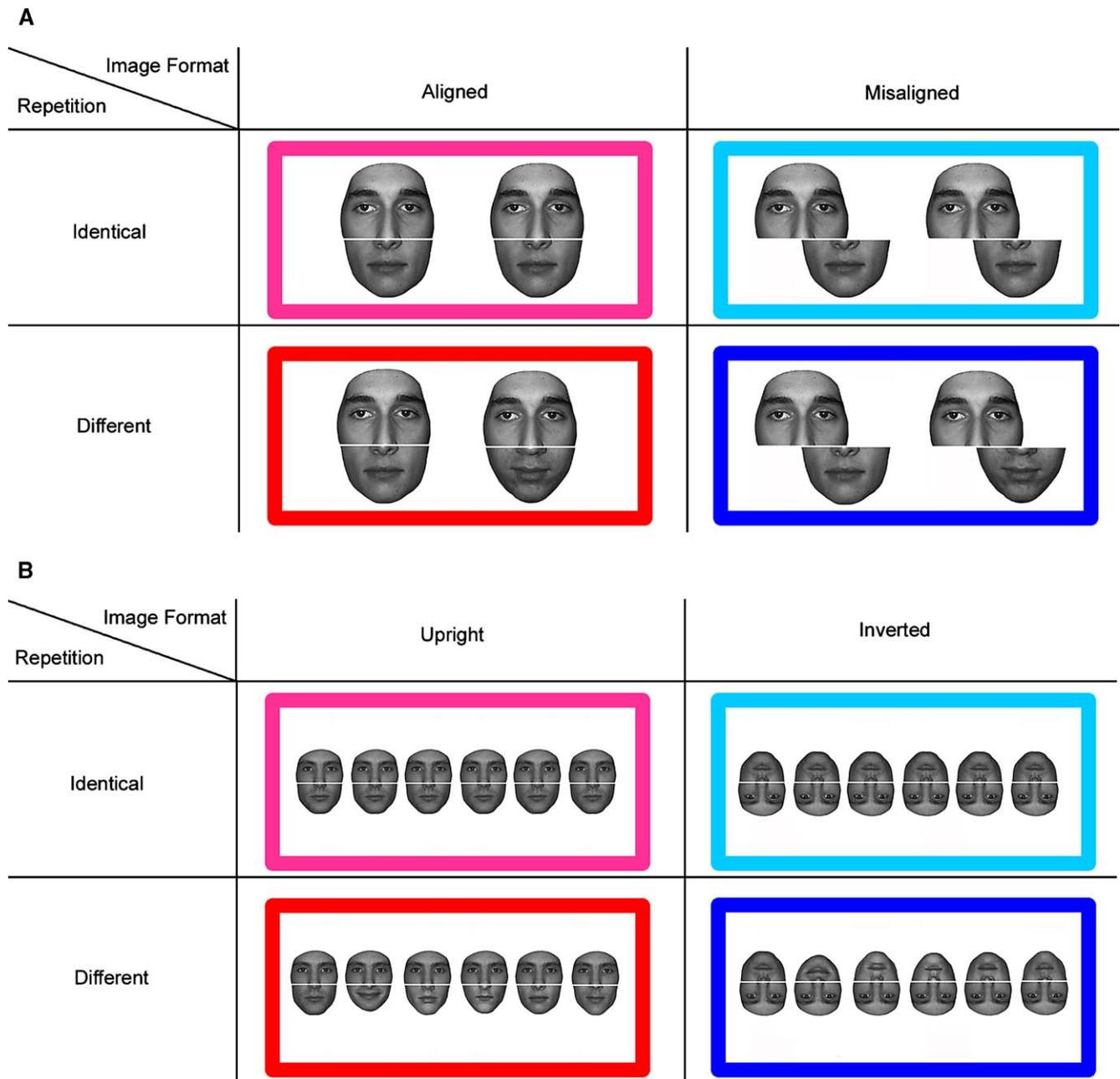


Fig. 1. 2×2 factorial design of the two fMRI adaptation experiments. (A) In experiment 1 ($n = 16$), the factors ‘repetition’ (identical or different bottom parts) and ‘alignment’ (aligned or misaligned top and bottom parts) were crossed in a factorial design to obtain four conditions: (1) aligned different (ali_dif), (2) aligned identical (ali_id), (3) misaligned different (misali_dif), (4) misaligned identical (misali_id). The two top parts of the faces are perceived as different when they are aligned with different bottom parts (composite face illusion). (B) In experiment 2 ($n = 12$), the aligned top and bottom face parts were presented either upright or upside-down. The composite face illusion is illustrated here by presenting six face identities. Note that the composite illusion vanishes for face stimuli presented upside-down.

(e.g. Young et al., 1987; Le Grand et al., 2004; Goffaux and Rossion, in press). Here, we used a 2×2 block design with the factors ‘image format’ and ‘repetition’ to test for a neuronal composite effect. In areas coding faces holistically, we hypothesized to find a larger response in the ‘different’ compared to the ‘identical’ face condition (fMR-adaptation), but only when the top and the bottom parts were spatially aligned and the faces were presented upright. That is, when subjects have the subjective impression of viewing different top parts of faces during a block of trials (Fig. 1).

Materials and methods

Stimuli and imaging procedures

Twenty-nine (17 for experiment 1 and 12 for experiment 2) adult subjects (ages 19 to 31, 17 male) were scanned in a 1.5 T Philips Gyroscan Intera scanner at the University of Louvain provided with standard quadrature birdcage head coils. Single shot gradient echo-planar imaging (EPI) was performed using the BOLD contrast effect as an indirect marker of local neuronal

activity (Ogawa et al., 1990). In both experiments 1 and 2, we acquired thirty 5 mm axial slices (TR = 3000 ms, TE = 40 ms, FA = 90°, matrix size = 64 × 64, FOV = 250, in-plane resolution 3 × 3 mm²) over four runs, each run lasting 8 min 15 s (165 TRs) and 9 min 36 s (192 TRs) respectively. A 3D T1-weighted data set encompassing the whole brain was acquired for every subject (110 slices, 1.5 mm slice thickness, matrix size = 256 × 256 × 256).

While being scanned, subjects viewed blocks ($n = 12$ stimuli/block) of grayscale images with faces, objects or scrambled faces. All images were separated into two parts by a white gap of 4 pixels width on average and subjects had to focus on the top part of the stimuli to detect the rare occurrence of tops colorized in red (2 ± 1 target per block). Stimuli were presented for 500 ms followed by a 1000 ms blank screen and subtended 3° on average. 18 s stimulus blocks were interleaved with 9 s fixation block. A set of 6 different top halves of faces (3 males) and 24 different bottom halves of faces (12 males) were combined to create 72 different composite faces (3 female/male top halves with the 12 female/male bottom halves). Thus, we minimized the number of repetitions for each picture across epochs and runs (4 repetitions). For the non-face conditions, sets of 72 different objects ($n = 9$ subjects in experiment 1) or houses ($n = 8$ subjects in experiment 1 and $n = 12$ subjects in experiment 2) and 72 phase-scrambled composite faces were used. In the first fMRI experiment ($n = 16$), we crossed ‘repetition’ (identical/different bottom parts) and ‘alignment’ (aligned/misaligned top and bottom parts) in a factorial design to obtain four conditions: aligned different (ali_dif), aligned identical (ali_id), misaligned different (misali_dif), misaligned identical (misali_id) (Fig. 1). In experiment 2 ($n = 12$), ‘repetition’ (identical/different bottom parts) was crossed with ‘orientation’ (upright/inverted stimuli) obtaining the conditions: upright different (up_dif), upright identical (up_id), inverted different (inv_dif), inverted identical (inv_id) (Fig. 1). Thus, in both experiments, the ‘different’ blocks contained 12 distinct face bottoms, whereas in ‘identical’ blocks the same bottom part was presented 12 times. In all four conditions, the task was to concentrate on the top face parts, which were identical throughout a block. To ensure that subjects concentrated on the top parts and performed at the same level for all conditions, they had to press a key when the top parts appeared colorized in red. In the second experiment, an independent face condition consisting of a set of 72 different new faces (faces) was also included. Stimuli and blocks were displayed in a pseudo-random order with a PC running E-prime 1.1 (PST, Inc.) through a projector surface located over the head of the subject and viewed with an angled mirror.

Supplementary behavioral experiment

To directly test the face composite illusion in our paradigm, we also collected supplementary behavioral data in an independent group of subjects, using a block design and an orthogonal color detection task. Seventeen (8 for experiment 1 and 9 for experiment 2) adult subjects (7 male) were tested with the same experiments used for fMRI, with only one run of trials. Subjects performed the same task as during scanning, i.e. having to concentrate on the top face parts and ignoring the bottom parts and they had to press a key when the top parts appeared colorized in red. After each block of 12 faces, they had to indicate how many different identities they had seen during the block, with the hypothesis that, on average, subjects would report more different facial identities when the

bottom parts were different and aligned with the top parts than in the other conditions.

Data analysis

The fMRI signal in the different conditions was compared using BrainVoyager QX (Version 1.3, BrainInnovation, Maastricht, The Netherlands) applying a regression analysis. Prior to analysis, preprocessing consisted of linear trend removal, temporal high-pass filtering (removing frequencies lower than 3 cycles/run) and correction of small interscan head movements (Friston et al., 1995). Data were spatially smoothed using a Gaussian filter of 2.8 mm full width at half-maximum (FWHM) and transformed into Talairach space (Talairach and Tournoux, 1988). For anatomical reference, the statistical maps computed were overlaid to the 3D T1-weighted scans. The predictor time courses of the regression model 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 et al., 1996).

First, the areas responding preferentially to faces were defined independently for each individual subject, in experiment 1 by the contrast [(ali_dif + ali_id + misali_dif + misali_id) – 2 (objects + scrambled)] and in experiment 2 by the contrast [2 (faces) – (houses + scrambled)]. All contiguous voxels in the middle fusiform gyrus and the inferior/middle occipital gyrus significant at $P < 0.05$ (one-tailed, corrected for multiple comparisons) were considered for further analysis. Second, the above-defined individual regions of interest (ROIs) were tested for an interaction between the factors ‘repetition’ and ‘image format’. In experiment 1, we applied a repeated-measure ANOVA and calculated the contrast [(ali_dif – ali_id) – (misali_dif – misali_id)] and in experiment 2 we used the contrast [(up_dif – up_id) – (inv_dif – inv_id)] to test for the interaction.

Third, we performed a whole brain analysis for each study to highlight the regions showing a larger BOLD signal in response to objects than faces. In experiment 1, we applied the contrast [4 (objects) – (ali_dif + ali_id + misali_dif + misali_id)] and in experiment 2 we calculated the contrast [(houses) – (faces)]. Given that the activated regions responding preferentially to objects in the parahippocampal gyri were exceedingly large, only voxels with $Z > 16$ were considered for the interaction analysis.

Results

fMRI experiment 1

For each subject, we first identified the areas responding preferentially to faces in the IOG and MFG as regions of interest (ROIs) (Fig. 2) (see Materials and methods). In the MFG, there was a significant interaction between alignment and repetition, in both the right (Talairach coordinates, mean ± SD, 38 ± 4, –48 ± 8, –18 ± 7, 1127 voxel size, $n = 13/16$) and the left (–39 ± 4, –47 ± 5, –17 ± 4, 491 voxel size, $n = 12/16$) hemisphere (right: $t = 3.54$, $P < 0.01$; left: $t = 3.62$, $P < 0.01$). The interaction reflected the significant difference between blocks of different and identical bottom parts for aligned face stimuli (right: $t = 4.41$, $P < 0.01$; left: $t = 3.81$, $P < 0.01$), combined with the absence of difference for misaligned face stimuli (right: $t = 0.64$, $P = 0.4$; left: $t = -0.74$, $P = 0.5$). In short, we observed a larger response in the ‘different’ compared to the ‘identical’ face condition, but only when the top

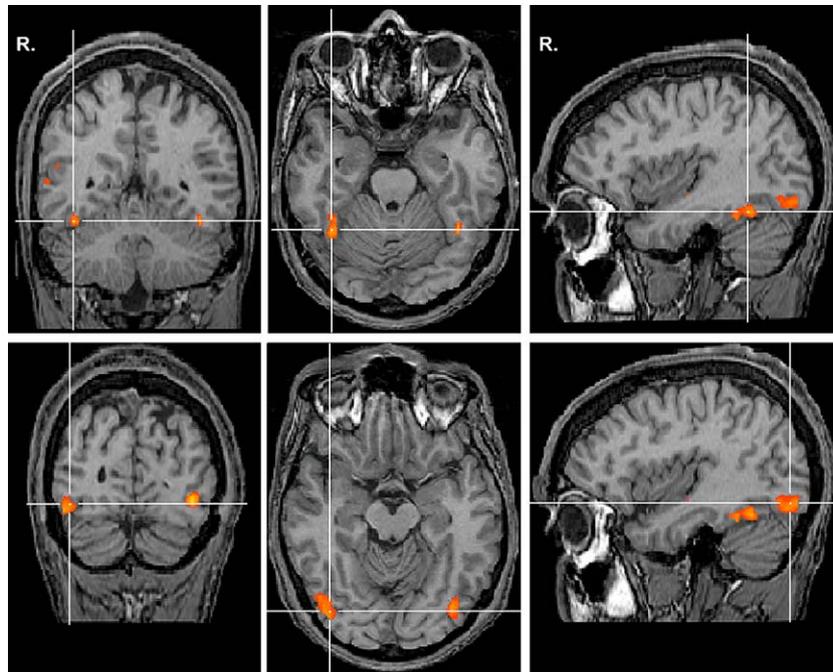


Fig. 2. Face-sensitive areas in the IOG and MFG. Coronal, transversal and sagittal views of the bilateral MFG (top row) and IOG (bottom row) regions responding more to faces than to non-face stimuli (objects and scrambled faces) in the group analysis of experiment 1 ($P < 0.05$ corrected for multiple comparisons).

and the bottom parts were aligned (Figs. 3A and 6A). This neural response pattern is consistent with the subjective impression of viewing different faces, which occurs in the ‘different’ blocks consisting of aligned face parts (see complementary behavioral results below). Note that the amount of physical image differences between ‘different’ and ‘identical’ conditions was perfectly matched between the aligned and the misaligned conditions. A similar, albeit less clear-cut, response pattern was observed in the IOG (Figs. 3A and 6A). The interaction between alignment and repetition was significant in the right (37 ± 4 , -75 ± 6 , -12 ± 6 , 1009 voxel size, $n = 10/16$) and left (-36 ± 6 , -73 ± 6 , -11 ± 6 , 763 voxel size, $n = 13/16$) hemisphere (right: $t = 2.27$, $P = 0.049$ and left: $t = 5.34$, $P = 0.001$), reflecting a larger difference between the BOLD response to ‘different’ and ‘identical’ blocks for aligned than misaligned face stimuli (aligned – right: $t = 3.28$, $P = 0.01$ and left: $t = 6.55$, $P = 0.001$, misaligned – right: $t = 1.71$, $P = 0.12$ and left: $t = 0.11$, $P = 0.92$). Even though offsetting the bottom of a face disrupts holistic perception (Fig. 1A), it appears clearly that neurons in the rMFG initially respond equally strong to misaligned than to aligned faces (Fig. 4). However, whereas the level of activation remains sustained when the bottom parts of the faces differ in the aligned format, it drops in the presence of the same physical changes in the misaligned image format (Fig. 4), similarly to the conditions where the faces are identical on all trials (aligned or misaligned). These results indicate that faces are processed holistically in the two regions of the human occipito-temporal cortex (MFG and IOG) showing a preference for faces.

fMRI experiment 2

The results of experiment 2 largely corroborated the observations of the first experiment. In the MFG, there was a strongly significant interaction between orientation and repetition in the

right hemisphere (38 ± 4 , -47 ± 7 , -19 ± 4 , 498 voxel size, $n = 12/12$, $t = 5.47$, $P < 0.001$) (Figs. 3b and 6b), but we observed only a trend in the left hemisphere (-38 ± 3 , -44 ± 6 , -16 ± 4 , 379 voxel size, $n = 10/12$) ($t = 1.96$, $p = 0.09$). The interaction reflected a significantly higher BOLD response level for ‘different’ compared to ‘identical’ upright face stimuli (right: $t = 5.43$, $P < 0.001$; left: $t = 2.33$, $P < 0.05$), combined with the absence of such a difference for inverted face stimuli ($t = -1$, $P = 0.4$ and $t = -0.47$, $P = 0.7$ respectively). In the IOG, the interaction between inversion and repetition was significant, but weaker than in the rMFG (rIOG: 39 ± 4 , -77 ± 7 , -11 ± 7 , 542 voxel size, $n = 11/12$, $t = 2.91$, $P < 0.05$) (lIOG: -38 ± 6 , -77 ± 7 , -9 ± 3 , 312 voxel size, $n = 8/12$, $t = 3.37$, $P < 0.01$) (Figs. 5 and 6B). Thus, in experiment 2, despite the fact that subjects concentrated on the top part (i.e. eyes and forehead) of the face in both the upright and the inverted conditions, the level of activation in the MFG and IOG was significantly higher when the bottom part changed (vs. identical) only for upright, but not for inverted faces. This again suggests that the higher BOLD response observed in the upright different condition is induced by the perceived differences in the top face parts, resulting from holistic face perception in the latter case only. This observation matches with two recent studies showing that the differential level of activation to upright and inverted faces in the fusiform gyrus is mainly due to a higher susceptibility to adaptation of inverted faces (Mazard et al., 2006; Yovel and Kanwisher, 2004), which was attributed to the lack of holistic processing of facial identity in this image format, in line with behavioral evidence (e.g. Tanaka and Farah, 1993; Young et al., 1987).

To test directly whether the magnitude of the composite face illusion was larger in the MFG than in the IOG, we considered the two experiments together in an ANOVA with the levels ‘region’ (MFG vs. IOG), ‘format’ (aligned/upright vs. misaligned/inverted),

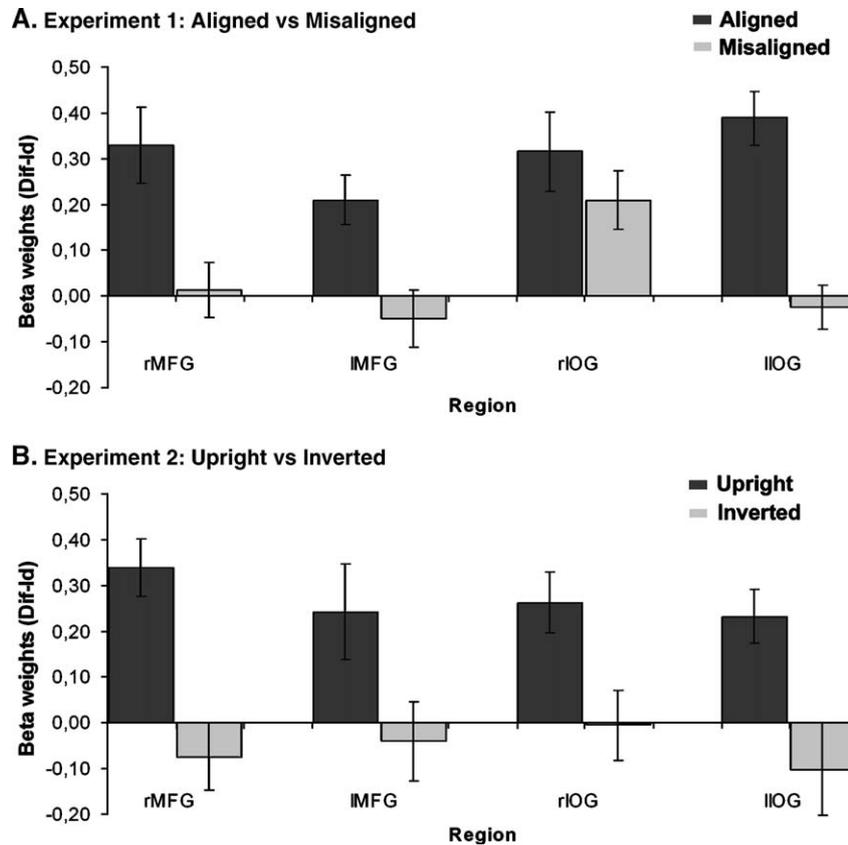


Fig. 3. Reduced susceptibility to fMR-adaptation in the aligned/upright compared to the misaligned/inverted conditions in the MFG and the IOG. To illustrate the magnitude of the neuronal composite effect, fMR-adaptation (computed by subtracting the beta weights of ‘same’ from ‘different’ conditions) is plotted in the four regions responding preferentially to faces in the occipito-temporal cortex. Beta weights refer to the scaling of regressors in a GLM, in which the BOLD response is modeled by the linear convolution of boxcars of neural activity by an assumed BOLD impulse response function.

‘repetition’ (different vs. identical) and ‘hemisphere’. The 4-way interaction between these factors was significant ($F_{1,37} = 5.12$; $P = 0.03$). This was due to the interaction between ‘adaptation’, ‘format’ and ‘region’ being significant in the right hemisphere, ($F_{1,20} = 3.75$; $P = 0.06$), but not in the left hemisphere ($F_{1,17} = 1.85$; $P = 0.19$). Thus, only in the right hemisphere there was a larger difference in the amount of adaptation between image formats in the MFG than in the IOG (Figs. 3 and 6). Besides the highly significant interaction between ‘format’ and ‘repetition’ described in the analyses above, there was another 2-way interaction, between ‘format’ and ‘region’, such that in the MFG, upright/aligned stimuli gave rise to a larger signal than inverted/misaligned stimuli ($P = 0.01$) overall, whereas there was an opposite trend in the IOG (inverted/misaligned > upright/aligned, $P = 0.08$; see Fig. 6).

Finally, we tested the interaction between alignment and repetition in an area responding more to scenes, houses and objects than to faces (Epstein and Kanwisher, 1998), located bilaterally in the parahippocampal gyrus (GPH). Contrary to the strong neuronal composite effect observed in the neighboring face-sensitive fusiform gyrus, no significant interactions were obtained in this object-preferring region in neither of the two experiments (experiment 1: rGPH (26, -48, -13; 997 voxel size) $P = 0.3$ and lGPH (-27, -49, -13; 1451 voxel size) $P = 0.3$, experiment 2: rGPH (26, -48, -12; 2442 voxel size) $P = 0.3$, lGPH (-26, -48, -12; 1000 voxel size) $P = 0.07$).

Behavioral results during fMRI experiments

In the four composite face conditions, the performance in the color detection task was at ceiling in experiment 1 (all conditions: 99%) and in experiment 2 (between 97% and 98% accuracy). Mean correct response times were virtually identical for all conditions in experiment 1 (ali_dif: 450 ± 88 ms, misali_dif: 459 ± 87 ms, ali_id: 465 ± 86 ms, misali_id: 458 ± 90 ms) and experiment 2 (up_dif: 437 ± 53 ms, inv_dif: 434 ± 46 ms, up_id: 457 ± 56 ms, inv_id: 435 ± 40 ms).

Face composite illusion outside of the scanner

In both experiments, when asked how many different persons they had seen during a block (and despite concentrating exclusively on the identical top parts of the faces), subjects perceived significantly more identities in the ‘different’ conditions when the faces were aligned/upright (ali_dif: 3.4 ± 2.8 , up_dif: 2.4 ± 1.3) compared to the misaligned/inverted format (misali_dif: 1.5 ± 1.1 , $t = 3.4$, $P < 0.01$; inv_dif: 1.8 ± 1.0 , $t = 2.7$, $P < 0.03$). In the ‘identical’ condition, image format did not affect the number of identities (ali_id: 1.3 ± 0.7 , misali_id: 1.2 ± 0.7 , $t = 0.45$, $P < 0.7$; up_id: 1.1 ± 0.3 , inv_id: 1.5 ± 0.7 , $t = -2$, $P < 0.09$). The interaction between the number of different identities perceived and the format of the faces was

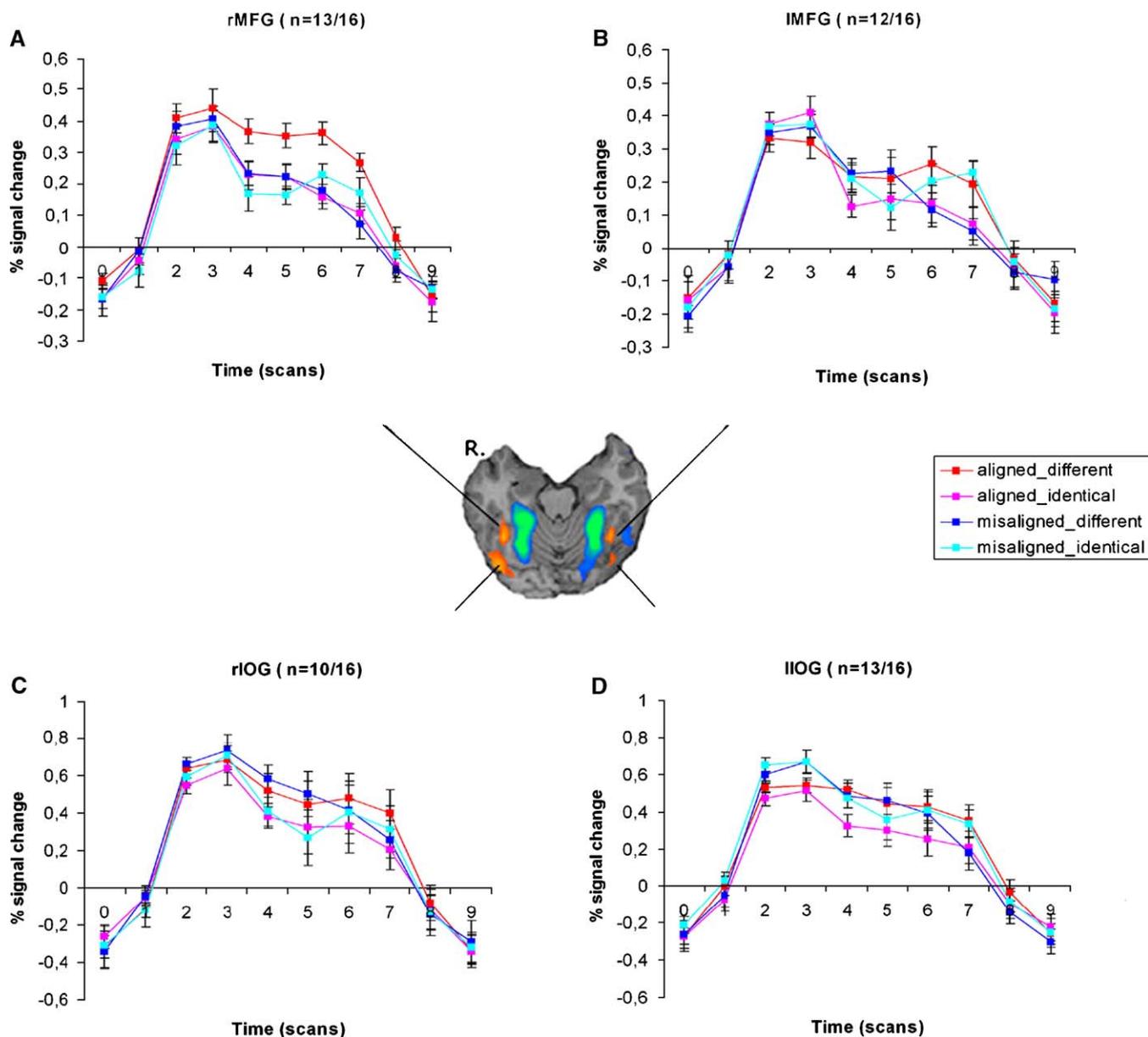


Fig. 4. Time course of the neuronal composite effect in the MFG and IOG measured in experiment 1 (aligned vs. misaligned faces). The average percent signal change (\pm SE) from baseline fixation is plotted for the identical and the different composite face conditions in the four regions responding preferentially to faces: (A) right MFG, (B) left MFG, (C) right IOG and (D) left IOG. A block of trials lasted for 18 s during which 12 face stimuli were presented in succession. There was a significantly larger BOLD response to different (as compared to identical) bottom parts of faces when the two face halves were aligned than when they were misaligned. This neural response pattern is in line with the subjective impression of viewing different faces, which occurs exclusively in the ‘different’ blocks consisting of aligned face parts. A transversal slice through the brain of subject 1 illustrates the four regions responding more to faces than to non-face stimuli (objects and scrambled faces) in the MFG and the IOG (yellow-orange) and the regions responding more to non-face stimuli compared to faces (blue-green) in the group analysis ($P < 0.05$ corrected for multiple comparisons). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

highly significant in both experiments (experiment 1: $F_{1,8} = 13.6$ $P < 0.006$; experiment 2: $F_{1,7} = 10$ $P < 0.01$).

Discussion

In the two areas of the fusiform and inferior occipital gyri responding preferentially to faces, we observed less susceptibility to fMR-adaptation to facial identity when the two halves of a face stimulus are perfectly aligned with each other than when the

same parts are spatially misaligned. This suggests that neurons in these areas integrate information from the two face parts into a representation of the whole face. Moreover, the integration of face parts in these regions breaks down when faces are presented upside-down, in agreement with behavioral evidence (Young et al., 1987; Maurer et al., 2002; Le Grand et al., 2004). From the results of the two experiments, we conclude that faces are represented holistically in the two functional areas responding preferentially to faces in the human ventral visual pathway.

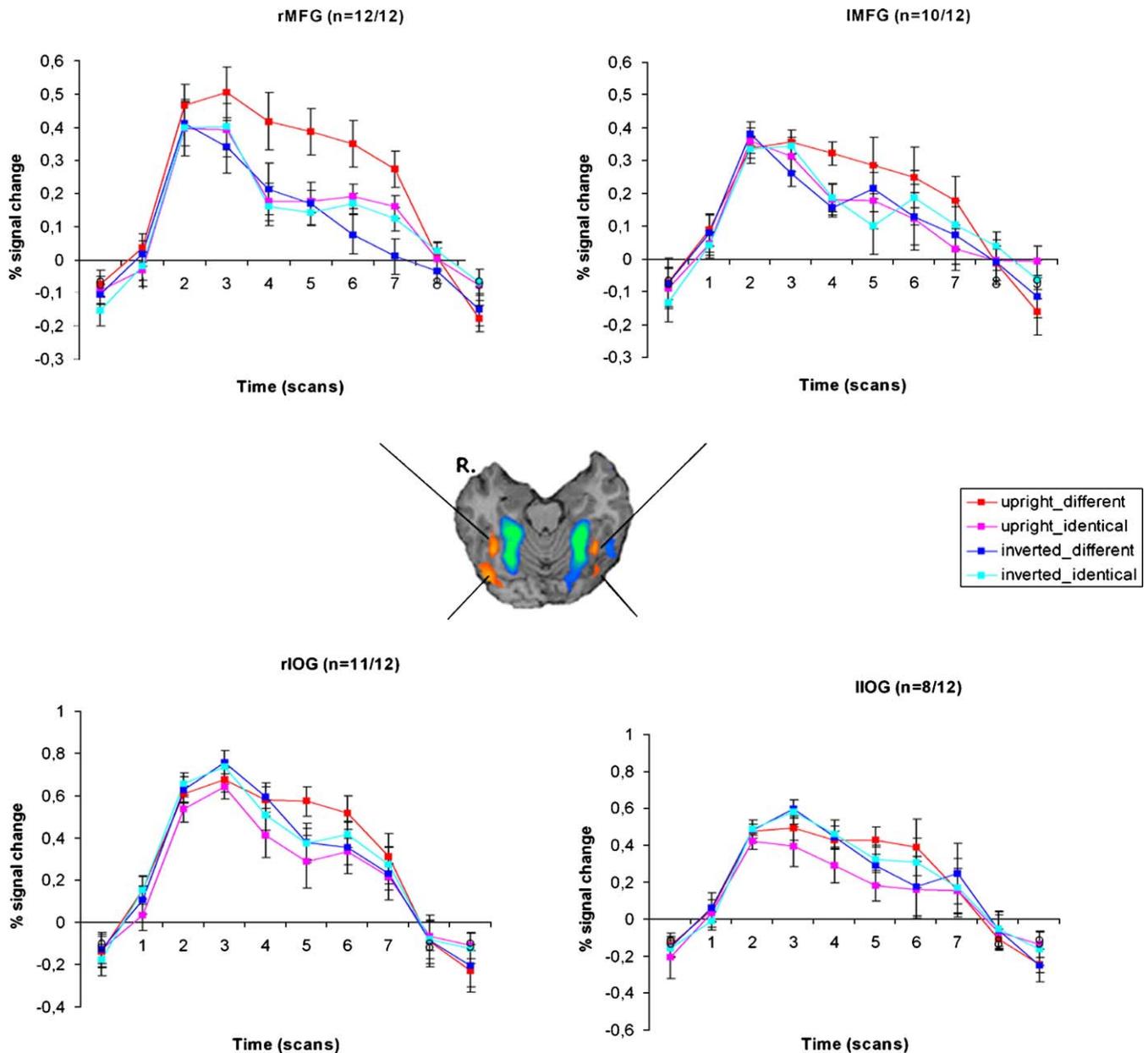


Fig. 5. Time course of the neuronal composite effect in the MFG and IOG measured in experiment 2 (upright vs. inverted faces). The average percent signal change (\pm SE) from baseline fixation is plotted for the identical and the different composite face conditions in the four regions responding preferentially to faces: (A) right MFG, (B) left MFG, (C) right IOG and (D) left IOG. The differential fMR-adaptation (different vs. identical bottom parts) was significantly larger for upright than for inverted faces in all four regions, again in line with the observation that holistic processing takes place in the upright condition, but is disrupted by face inversion. A transversal slide through the brain of subject 1 illustrates the four regions responding more to faces than to non-face stimuli (objects and scrambled faces) in the MFG and the IOG (yellow-orange) and the regions responding more to non-face stimuli compared to faces (blue-green) in the group analysis ($P < 0.05$ corrected for multiple comparisons). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Attention and differences in low-level visual image attributes are unlikely to explain our results. The 2×2 design used in the present experiments offers a control for low-level visual image attribute differences since the result of interest is expressed as an interaction between alignment (experiment 1) or orientation (experiment 2) and a change of facial identity. If the results were simply due to spatial alignment (or to orientation), we should have observed a larger activation when face parts were aligned (or upright), irrespective of a change in the identity of the composite faces. It has been shown that increased attention to faces modulates activation of the MFG

(Wojciulik et al., 1998). However, for attention to account for our findings, subjects would have had to be more attentive to upright and aligned faces, but only when the bottom part of the face differed from trial to trial. This is very unlikely, given that the task – detecting a rare color changes occurring on the top part of the face stimulus – was identical in all conditions and thus orthogonal to the manipulation of interest and that there was no indication in behavioral results that subjects were differentially attentive in some conditions. Finally, even though attention to faces may increase activity only in regions coding faces (Wojciulik et al., 1998), the

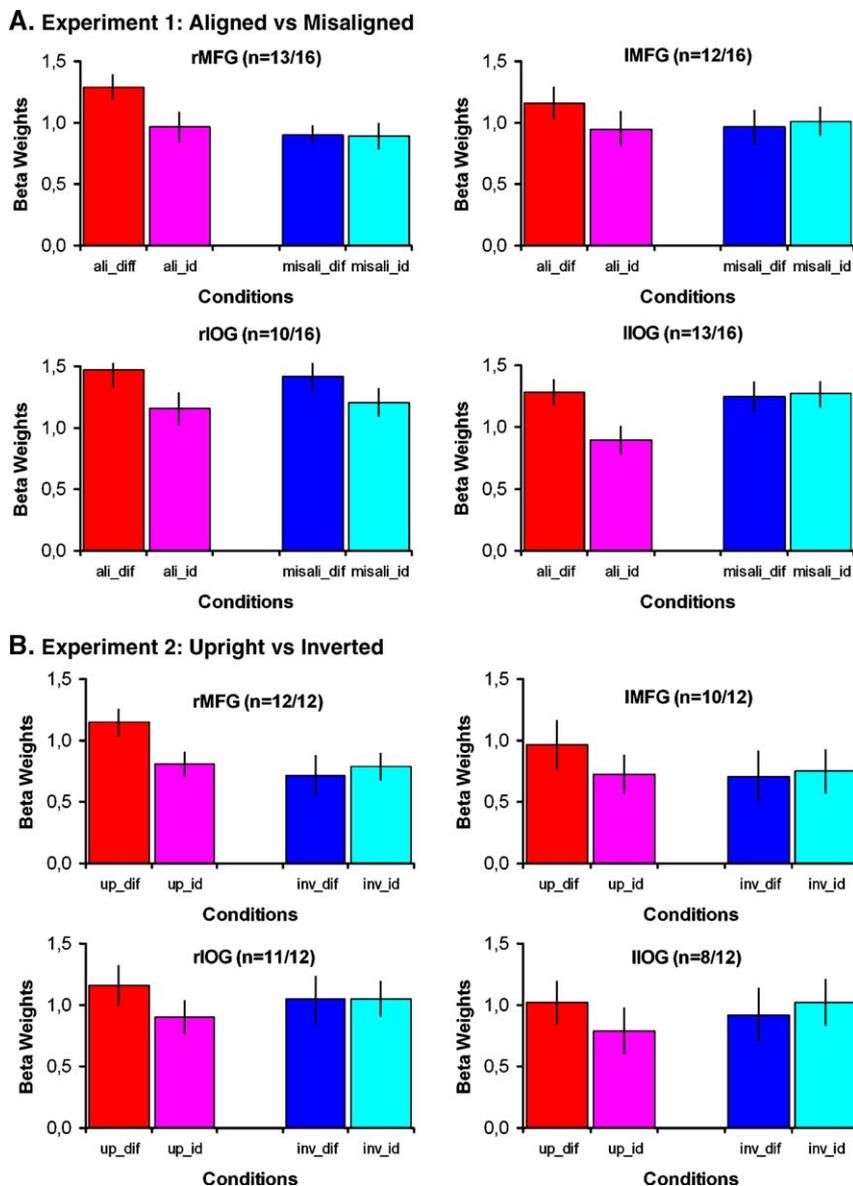


Fig. 6. Magnitude of the neural face composite effect in the four regions of interest responding preferentially to faces: right/left MFG, right/left IOG. The beta weights in the four experimental conditions are plotted for each region. Beta weights refer to the scaling of regressors in a GLM, in which the BOLD response is modeled by the linear convolution of boxcars of neural activity by an assumed BOLD impulse response function (A). In experiment 1, differential fMRI-adaptation (different vs. identical bottom parts) was significantly larger for aligned than for misaligned faces in the four regions. (B) In experiment 2, the same neuronal composite effect occurred with upright compared to inverted composite faces. In the four regions, a significantly higher BOLD response level for 'different' compared to 'identical' upright face stimuli was found in combination with the absence of such a difference for inverted face stimuli.

increases of activation observed when different whole facial identities were perceived in a block of trials were not found in the parahippocampal gyrus responding more to house stimuli and were not equally large in the two functional face areas in the two hemispheres (Figs. 3–6), as could be expected if the effect was due to a general attentional modulation.

The finding that faces are represented holistically in the fusiform and inferior occipital areas responding preferentially to faces is without precedent. It is consistent with neurophysiological experiments showing that a large proportion of face-selective cells in the monkey infero-temporal cortex (IT) are sensitive to the whole facial organization: removal of a part of the face (Tsunoda et al., 2001) or scrambling the parts (Desimone et al., 1984) causes a

marked reduction in neuronal response strength. It is also consistent with the observation in positron emission tomography (PET) of a reduced right fusiform activation when human subjects have to discriminate faces on specific facial features (Rossion et al., 2000). In addition, there is evidence that face recognition deficits in brain-damaged patients (prosopagnosia; Bodamer, 1947) following lesions of the bilateral or right occipito-temporal cortex concern the ability to process faces holistically (Sergent and Signoret, 1992; Farah et al., 1998; Barton et al., 2002; Boutsen and Humphreys, 2002).

The reduced susceptibility to adaptation that we observed in response to upright aligned face stimuli in high-level visual areas supports the view that holistic processing of faces takes place at

a perceptual stage (Farah et al., 1998) rather than being related to post-perceptual processes (Wenger and Ingvalson, 2003). This is consistent with behavioral evidence of the composite face illusion observed in old/new recognition and in face matching experiments (Young et al., 1987; Maurer et al., 2002; Le Grand et al., 2004), both for familiar and unfamiliar faces. Recent behavioral experiments with unfamiliar faces also support this view, showing that the face composite effect is mainly supported by the low spatial frequencies of the stimulus (Goffaux and Rossion, in press).

The right hemispheric dominance for face processing is largely supported by neuropsychological evidence: prosopagnosia or other face recognition impairments follow bilateral or unilateral right-sided occipito-temporal lesions (e.g. Sergent and Signoret, 1992; Landis et al., 1988; Michel et al., 1989; Bouvier and Engel, 2006; see also Le Grand et al., 2003). Neuroimaging studies (e.g. Sergent et al., 1992; Kanwisher et al., 1997; Gauthier et al., 2000; Rossion et al., 2000, 2003; Grill-Spector et al., 2004; Schiltz et al., 2006; Zangenehpour and Chaudhuri, 2005) as well as behavioral measures during lateralized visual field stimulation (Hillger and Koenig, 1991) also support a right hemispheric dominance for face processing. Here, even though we also found evidence for holistic processing in the left hemisphere, there was a larger composite face illusion in the right hemisphere, consistent with the long-standing hypothesis that the right hemisphere superiority for face processing is related to privileged holistic encoding for face stimuli (Sergent, 1984b; Hillger and Koenig, 1991; Rossion et al., 2000).

As hypothesized, the integration of face parts into a holistic representation was more robust in the most anterior region responding preferentially to faces, namely in the lateral part of the middle fusiform gyrus. The differential fMR-adaptation to identity was less specific in the inferior occipital gyrus for aligned as compared to misaligned face stimuli, suggesting that facial features are treated somewhat more independently in this posterior region. This pattern of fMRI results is consistent with the hierarchical organization of information processing in the visual cortex, according to which local features are extracted in posterior areas and integrated into larger representations at higher stages in the occipito-temporal junction (Felleman and Van Essen, 1991; Riesenhuber and Poggio, 1999). However, the weak temporal resolution of fMRI does not allow clarifying whether the analysis of individual facial features temporally precedes the extraction of a holistic face representation. Behavioral studies suggest that the extraction of a holistic face representation perceptually dominates the analysis of detailed features (Tanaka and Farah, 1993) and may have a temporal precedence during the microgenesis of face perception (Sergent, 1986; Goffaux and Rossion, in press). Moreover, recent fMRI studies indicate that responses to faces can be observed in the middle fusiform gyrus despite a lesion of the inferior occipital cortex (Rossion et al., 2003; Schiltz et al., 2006; Steeves et al., 2006). In normal viewers, holistic representations of faces might thus be initially extracted in the middle fusiform gyrus and call upon processes in a lower-level face visual area to extract detailed information about facial features and build robust individual representations of faces (see discussion in Rossion et al., 2003; Schiltz et al., 2006; and recent electrophysiological evidence by Herrmann et al., 2005).

In conclusion, combining fMR-adaptation with the composite face illusion has enabled us to show that neurons responding preferentially to faces in the human occipito-temporal cortex represent the whole pictures of faces. These findings provide

strong evidence that holistic processing of faces takes place at the perceptual level (Farah et al., 1998; Goffaux and Rossion, in press). Because we found larger holistic effects in the MFG than in the IOG, they also partly support the view that face-sensitive neurons of the IOG represent facial features more independently, whereas the MFG extract representations of whole facial identities (Haxby et al., 2000).

Acknowledgments

We would like to thank M. Behrmann and the two reviewers for their insightful comments and V. Goffaux for help with the stimuli. This study was supported by a research grant (ARC 01/06-267, Communauté Française de Belgique-Actions de Recherche Concertées). Bruno Rossion is Research Associate at the National Foundation for Scientific Research (FNRS).

References

- Barton, J.J., Press, D.Z., Keenan, J.P., O'Connor, M., 2002. Lesions of the fusiform face area impair perception of facial configuration in prosopagnosia. *Neurology* 58, 71–78.
- Bodamer, J., 1947. Die-Prosop-agnosie. *Arch. Psychiatr. Nervenkr.* 179, 6–54.
- Boutsen, L., Humphreys, G.W., 2002. Face context interferes with local part processing in a prosopagnosic patient. *Neuropsychologia* 40, 2305–2313.
- Bouvier, S.E., Engel, S.A., 2006. Behavioral deficits and cortical damage loci in cerebral achromatopsia. *Cereb. Cortex* 2, 183–191.
- Boynton, G.M., Engel, S.A., Glover, G.H., Heeger, D.J., 1996. Linear systems analysis of functional magnetic resonance imaging in human V1. *J. Neurosci.* 16, 4207–4221.
- Desimone, R., Albright, T.D., Gross, C.G., Bruce, C., 1984. Stimulus-selective properties of inferior temporal neurons in the macaque. *J. Neurosci.* 4, 2051–2062.
- Epstein, R., Kanwisher, N., 1998. A cortical representation of the local visual environment. *Nature* 392, 598–601.
- Farah, M.J., Wilson, K.D., Drain, M., Tanaka, J.N., 1998. What is “special” about face perception? *Psychol. Rev.* 105, 482–498.
- Felleman, D.J., Van Essen, D.C., 1991. Distributed hierarchical processing in the primate cerebral cortex. *Cereb. Cortex* 1, 1–47.
- Friston, K.J., Frith, C.D., Turner, R., Frackowiak, R.S., 1995. Characterizing evoked hemodynamics with fMRI. *NeuroImage* 2, 157–165.
- Galton, F., 1883. *Inquiries into Human Faculty and Its Development*. Macmillan, London.
- Gauthier, I., Tarr, M.J., Moylan, J., Skudlarski, P., Gore, J.C., Anderson, A.W., 2000. The fusiform “face area” is part of a network that processes faces at the individual level. *J. Cogn. Neurosci.* 12, 495–504.
- Goffaux, V., Rossion, B., in press. Faces are “spatial”: holistic face perception is supported by low spatial frequencies. *Journal of Experimental Psychology: Human Perception and Performance*.
- Grill-Spector, K., Malach, R., 2001. fMR-adaptation: a tool for studying the functional properties of human cortical neurons. *Acta Psychol. Amst.* 107, 293–321.
- Grill-Spector, K., Knouf, N., Kanwisher, N., 2004. The fusiform face area subserves face perception, not generic within-category identification. *Nat. Neurosci.* 7, 555–562.
- Grill-Spector, K., Henson, R., Martin, A., 2006. Repetition and the brain: neural models of stimulus-specific effects. *Trends Cogn. Sci.* 1, 14–23.
- Haxby, J.V., Hoffman, E.A., Gobbini, M.I., 2000. The distributed human neural system for face perception. *Trends Cogn. Sci.* 4, 223–233.
- Henson, R.N., 2003. Neuroimaging studies of priming. *Prog. Neurobiol.* 70, 53–81.

- Herrmann, M.J., Ehli, A.C., Muehlberger, A., Fallgatter, A.J., 2005. Source localization of early stages of face processing. *Brain Topogr.* 18, 77–85.
- Hillger, L.A., Koenig, O., 1991. Separable mechanisms in face processing: evidence from hemispheric specialization. *J. Cogn. Neurosci.* 3, 42–58.
- Ishai, A., Ungerleider, L.G., Martin, A., Haxby, J.V., 2000. The representation of objects in the human occipital and temporal cortex. *J. Cogn. Neurosci.* 12 (Suppl. 2), 35–51.
- Kanwisher, N., McDermott, J., Chun, M.M., 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J. Neurosci.* 17, 4302–4311.
- Landis, T., Regard, M., Bliestle, A., Kleihues, P., 1988. Prosopagnosia and agnosia for noncanonical views. An autopsied case. *Brain* 111 (Pt 6), 1287–1297.
- Le Grand, R., Mondloch, C.J., Maurer, D., Brent, H.P., 2003. Expert face processing requires visual input to the right hemisphere during infancy. *Nat. Neurosci.* 6, 1108–1112.
- Le Grand, R., Mondloch, C.J., Maurer, D., Brent, H.P., 2004. Impairment in holistic face processing following early visual deprivation. *Psychol. Sci.* 15, 762–768.
- Maurer, D., Grand, R.L., Mondloch, C.J., 2002. The many faces of configural processing. *Trends Cogn. Sci.* 6, 255–260.
- Mazard, A., Schiltz, C., Rossion, B., 2006. Recovery from adaptation to facial identity is larger for upright than inverted faces in the human occipito-temporal cortex. *Neuropsychologia* 6, 912–922.
- Michel, F., Poncet, M., Signoret, J.L., 1989. Are the lesions responsible for prosopagnosia always bilateral? *Rev. Neurol. (Paris)* 145 (11), 764–770.
- Ogawa, S., Lee, T.M., Kay, A.R., Tank, D.W., 1990. Brain magnetic resonance imaging with contrast dependent on blood oxygenation. *Proc. Natl. Acad. Sci. U. S. A.* 87, 9868–9872.
- Puce, A., Allison, T., Gore, J.C., McCarthy, G., 1995. Face-sensitive regions in human extrastriate cortex studied by functional MRI. *J. Neurophysiol.* 74, 1192–1199.
- Riesenhuber, M., Poggio, T., 1999. Hierarchical models of object recognition in cortex. *Nat. Neurosci.* 2, 1019–1025.
- Rossion, B., Dricot, L., Devolder, A., Bodart, J.M., Crommelinck, M., De Gelder, B., Zoontjes, R., 2000. Hemispheric asymmetries for whole-based and part-based face processing in the human fusiform gyrus. *J. Cogn. Neurosci.* 12, 793–802.
- Rossion, B., Caldara, R., Seghier, M., Schuller, A.M., Lazeyras, F., Mayer, E., 2003. A network of occipito-temporal face-sensitive areas besides the right middle fusiform gyrus is necessary for normal face processing. *Brain* 126, 2381–2395.
- Schiltz, C., Sorger, B., Caldara, R., Ahmed, F., Mayer, E., Goebel, R., Rossion, B., 2006. Impaired face discrimination in acquired prosopagnosia is associated with abnormal response to individual faces in the right middle fusiform gyrus. *Cereb. Cortex* 4, 574–586.
- Sergent, J., 1984a. An investigation into component and configural processes underlying face perception. *Bra. J. Psychol.* 75, 221–242.
- Sergent, J., 1984b. Configural processing of faces in the left and the right cerebral hemispheres. *J. Exp. Psychol. Hum. Percept. Perform.* 10, 554–572.
- Sergent, J., 1986. Microgenesis of face perception. In: Ellis, H., Jeeves, M.A., Newcombe, F., Young, A.W. (Eds.), *Aspects of Face Processing*. In Dordrecht, Dordrecht.
- Sergent, J., Signoret, J.L., 1992. Varieties of functional deficits in prosopagnosia. *Cereb. Cortex* 2, 375–388.
- Sergent, J., Ohta, S., MacDonald, B., 1992. Functional neuroanatomy of face and object processing. A positron emission tomography study. *Brain* 115 (Pt 1), 15–36.
- Steeves, J.K., Culham, J.C., Duchaine, B.C., Pratesi, C.C., Valyear, K.F., Schindler, I., Humphrey, G.K., Milner, A.D., Goodale, M.A., 2006. The fusiform face area is not sufficient for face recognition: evidence from a patient with dense prosopagnosia and no occipital face area. *Neuropsychologia* 4, 594–609.
- Talairach, G., Tournoux, P., 1988. *Co-Planar Stereotaxic Atlas of the Human Brain*. Thieme Verlag, New York.
- Tanaka, J.W., Farah, M.J., 1993. Parts and wholes in face recognition. *Q. J. Exp. Psychol.* A 46, 225–245.
- Tsunoda, K., Yamane, Y., Nishizaki, M., Tanifuji, M., 2001. Complex objects are represented in macaque inferotemporal cortex by the combination of feature columns. *Nat. Neurosci.* 4, 832–838.
- Wenger, M.J., Ingvalson, E.M., 2003. Preserving informational separability and violating decisional separability in facial perception and recognition. *J. Exper. Psychol., Learn., Mem., Cogn.* 29, 1106–1118.
- Wojciulik, E., Kanwisher, N., Driver, J., 1998. Covert visual attention modulates face-specific activity in the human fusiform gyrus: fMRI study. *J. Neurophysiol.* 79, 1574–1578.
- Young, A.W., Hellowell, D., Hay, D.C., 1987. Configurational information in face perception. *Perception* 16, 747–759.
- Yovel, G., Kanwisher, N., 2004. Face perception: domain specific, not process specific. *Neuron* 44, 889–898.
- Zangenehpour, S., Chaudhuri, A., 2005. Patchy organization and asymmetric distribution of the neural correlates of face processing in monkey inferotemporal cortex. *Curr. Biol.* 15, 993–1005.