Recovery from adaptation to facial identity is larger for upright than inverted faces in the human occipito-temporal cortex

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Abstract

Human faces look more similar to each other when they are presented upside-down, leading to an increase of error rates and response times during individual face discrimination tasks. Here we used functional magnetic resonance imaging (fMRI) to test the hypothesis that this perceived similarity leads to a lower recovery from identity adaptation for inverted faces than for upright faces in face-sensitive areas of the occipito-temporal cortex. Ten subjects were presented with blocks of upright and inverted faces, with the same face identity repeated consecutively in half of the blocks, and different facial identities repeated in the other blocks. When face stimuli were presented upright, the percent signal change in the bilateral middle fusiform gyrus (MFG) was larger for different faces as compared to same faces, replicating previous observations of a recovery from facial identity adaptation in this region. However, there was no significant recovery from adaptation when different inverted faces were presented. Most interestingly, the difference in activation between upright and inverted faces increased progressively during a block when different facial identities were presented. A similar pattern of activation was found in the left middle fusiform gyrus, but was less clear-cut in bilateral face-sensitive areas of the inferior occipital cortex. These findings show that the differential level of activation to upright and inverted faces in the fusiform gyrus is mainly due to a difference in recovery from adaptation, and they explain the discrepancies in the results reported in previous fMRI studies which compared the processing of upright and inverted faces. The lack of recovery from adaptation for inverted faces in the fusiform gyrus may underlie the face inversion effect (FIE), which takes place during perceptual encoding of individual face representations.
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1. Introduction

For almost four decades, behavioral studies have revealed that picture–plane inversion dramatically impairs face recognition (e.g. Hochberg & Galper, 1967). A landmark paper on this topic is that of Yin (1969), in which face recognition was found to be more affected by inversion than the recognition of other object categories, an observation called the face inversion effect (FIE; for a recent review, see Rossion & Gauthier, 2002). Since then, strong decreases of performances and/or increases in response times for inverted faces have been obtained in old–new recognition paradigms (e.g. Carey, Diamond, & Woods, 1980) and two-alternative-forced choice paradigms with or without delay (e.g. Freire, Lee, & Symons, 2000; Leder & Bruce, 2000;

Valentine & Bruce, 1986; Yin, 1969). Behaviorally, the effects of orientation reversal are virtually identical for unfamiliar and familiar faces (e.g. Collishaw & Hole, 2000), and they are observed when orientation is manipulated in separate blocks—or in between subjects designs—(e.g. Valentine and Bruce, 1986) as well as in randomized presentation of upright and inverted faces (e.g. Carey & Diamond, 1977; Diamond & Carey, 1986; Yin, 1969).

It was originally suggested that the decrease of performance for inverted faces was related to memory encoding (Valentine, 1988), but this view has been challenged by subsequent work, showing massive effects of inversion during simultaneous presentation of unfamiliar faces (e.g. Farah, Wilson, Drain, & Tanaka, 1998; Moscovitch, Berhmann, & Winocur, 1997; Phelps & Roberts, 1994; Searcy & Bartlett, 1996). Furthermore, there is no interaction between the decrease of performance for inverted faces and having a delay or not, or its length (1, 5 or 10 s), in sequential matching tasks (Freire et al., 2000). This supports the view that the effect of face inversion occurs primarily

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during perceptual encoding, in agreement with the findings that effects of face inversion in event-related potentials are observed on the latency and amplitude of the early face-sensitive N170 component (e.g. Bentin, Allison, Puce, Perez, & McCarthy, 1996; Rossion et al., 2000), or perhaps even earlier (Itier & Taylor, 2002; Linkenkaer-Hansen et al., 1998). It is also generally acknowledged that inverting faces impairs the perceptual coding of several sources of information, including face parts and their spatial relationships (for a review, see Maurer, Le Grand, & Mondloch, 2002). Yet, the perception of relationships between face parts, or configural information, seems to suffer most from inversion, while at the other extreme, local variations of surface information (e.g. brightness or color changes) seem relatively unaffected (e.g. Leder, Candrian, Huber, & Bruce, 2001; Rhodes, Brake, & et Atkinson, 1993; Searcy and Bartlett, 1996).

Comparing the processing of faces presented upright and inverted is one of the most widely used paradigm in the behavioural and neuropsychological literature, generally for the purpose of investigating face-specific mechanisms and/or the configural processing of faces (e.g. Farah et al., 1998; Moscovitch et al., 1997). However, little is known about whether and how upright and inverted faces are processed differently in the human brain. Recently, neuroimaging studies have investigated the neural correlates of face inversion. Since the source of the decrease of performance for inverted faces is thought to be located at the stage of perceptual encoding, one would expect to observe significant differences between upright and inverted faces in some or all of the cortical visual areas responding preferentially to faces, namely in the *inferior occipital gyrus* (IOG), the *lateral part of the middle fusiform gyrus* (MFG) and the *superior temporal sulcus* (STS; e.g. Kanwisher, McDermott, & Chun, 1997; Puce, Allison, Gore, & McCarthy, 1995; Sergent, Ohta, & MacDonald, 1992; for a review, see Haxby, Hoffman, & Gobbini, 2000). Two functional magnetic resonance imaging (fMRI) studies found a small but significant decrease following face inversion bilaterally in the MFG (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Haxby et al., 1999), whereas sizeable effects of inversion (between 0.3 and 0.5% signal change—PSC—difference between upright and inverted conditions) were found in two other studies in the right MFG (Kanwisher, Tong, & Nakayama, 1998; Yovel & Kanwisher, 2004). However, there was no significant decrease observed in the MFG for inverted faces relative to upright faces in the only study that used an event-related paradigm (Aguirre, Singh, & D'Esposito, 1999). The effect of face inversion on other face-sensitive areas was reported by two of these studies, showing larger activity upright than inverted faces in the IOG and the posterior part of the STS (Gauthier et al., 1999; Haxby et al., 1999).

Considering the large decrease of performance that is generally found for inverted faces in behavioral studies, it is somewhat surprising that inverting a face stimulus does not affect the level of activation in face-sensitive cortical areas more dramatically (Aguirre et al., 1999; Haxby et al., 1999). Furthermore, one needs to clarify why some studies reported only small effects of inversion in the MFG (Gauthier et al., 1999; Haxby et al., 1999)

or even failed to find effects of inversion (Aguirre et al., 1999), while others disclosed relatively strong inversion effects in the same area (Kanwisher et al., 1998; Yovel and Kanwisher, 2004).

The present study was designed to clarify these discrepancies, and more generally to improve our understanding of the neural mechanisms underlying the reduction of hemodynamic activity in response to inverted faces in face-sensitive areas of the occipito-temporal cortex. Our working hypothesis is based on two observations. First, behaviorally, the effects of face inversion are measured when at least *two* faces have to be discriminated at the individual level (either two percepts in a matching task for instance, or a stored representation or a percept in an old/new recognition task), not when the perception of a *single* face in upright and inverted orientation is compared. In other words, the massive decrease of accuracy and increase in RT found in matching individual faces upside-down is related to the reduced ability to perceive *differences* between individual faces ('they all look alike upside-down'). Second, a large number of fMRI studies have shown that repeating the same face stimulus leads to a decrease of activation in face-sensitive occipito-temporal areas, as compared to the presentation of different face stimuli (e.g. Gauthier et al., 2000; Grill-Spector & Malach, 2001; Schiltz et al., 2005; Winston, Henson, Fine-Goulden, & Dolan, 2004). This reduced brain activation after repeated exposure to a stimulus reflects a general phenomenon known as repetition–suppression (Henson, 2003), or fMR-adaptation (Grill-Spector and Malach, 2001). The neurophysiological mechanisms underlying the fMR-adaptation effect are not clear at this stage, but a straightforward interpretation of the phenomenon observed at a large scale is a reduction in the spiking rate of the adapted neurons (Grill-Spector and Malach, 2001). At the population level, magnetoencephalographic (MEG) recordings suggest that neural adaptation to shape causes a significant reduction in both activation strength and peak latency of the visual responses (Noguchi, Inui, & Kakigi, 2004).

In general, brain regions that show suppression are those that are involved in processing the stimulus of interest, which means that suppression does not simply reflect a general decrease of attentional level. Repetition–suppression, or fMR-adaptation, can thus be used as a tool to measure the sensitivity of a given brain area to certain stimulus properties (see Grill-Spector and Malach, 2001). For instance, the reduction of the BOLD response to the repetition of the same facial identity in the MFG and IOG is taken as evidence that these regions are not simply involved in detecting a facial pattern, but also play a role in individual face discrimination (Gauthier et al., 2000; Grill-Spector and Malach, 2001; Schiltz et al., 2005; Winston et al., 2004).

Given these observations, it is conceivable that when different individual faces are presented consecutively during a block of trials, inverted faces, looking more similar to each other, may yield less recovery from adaptation (Grill-Spector and Malach, 2001) than upright faces. Here we aimed at testing precisely this hypothesis: that recovery from adaptation is weaker during a block of trials when different face stimuli are presented upside-down than when they are presented upright, leading to an overall decrease of activation for inverted faces as measured

during the entire block of trials. If this hypothesis is correct, it may account, at least in part, for discrepancies between previous fMRI studies comparing the processing of upright and inverted faces, and clarify the stages at which the effects of face inversion takes place in the human brain.

To test whether a reduced recovery from adaptation to facial identity may account for the lower signal generally found for inverted faces, we ran an fMRI experiment in which we compared the BOLD response to upright and inverted faces in a 2×2 factorial design, crossing the factors *orientation* (upright and inverted) and *adaptation* (identical versus different faces). We predicted a significant interaction between the two factors in the areas of the occipito-temporal cortex that respond preferentially to faces, due to a larger recovery from adaptation to upright faces.

2. Materials and methods

2.1. Subjects

A total of 12 subjects participated in the imaging experiments. However, the data of two subjects had to be discarded because they did not present a significantly larger response to faces than objects in the localizer scans, preventing to test the hypotheses of this experiment. The subjects gave their informed written consent prior to the fMRI experiments. The study was conformed to the Declaration of Helsinki and was approved by the Ethics Committee of the Medical Department of the University of Louvain. All subjects proved to be strongly right-handed according to the Edinburgh Inventory (Oldfield, 1971).

2.2. Stimuli and procedures

Three categories of stimuli were used: pictures of upright faces, upside-down faces, objects for both the localizer and the inversion–adaptation experiments. For the inversion–adaptation scans, 60 pictures of faces (half male) were used for each category, minimizing the number of repetition for each picture across epochs and runs. Stimuli were images subtending, on average, $\pm 3°$ of the visual field, they were matched for mean luminosity and varied location by 20 pixels in X (10%) and 40 pixels in Y (13%). Since facial identity is known to be processed automatically in the neuronal populations tested (Gauthier et al., 2000; Rolls, 1992), we used an independent detection task in both of our fMRI experiments, as done previously (e.g. Gauthier et al., 2000; Rotshtein, Henson, Treves, Driver, & Dolan, 2005; Schiltz et al., 2005; Winston et al., 2004). More precisely, the subject's task was to detect the occurrence of rare face stimulus that appeared in red color, in a block of grayscale stimuli (color detection task). There were one or two target trials by epoch, the same number of targets for all conditions on average. Using an independent detection task ensured that subjects were paying attention during the whole experiment, while performing at the same level for all conditions. Thus, differences between conditions were independent of performance during scanning and could not be attributed to different level of arousal (e.g. higher attention level when performing a harder discrimination on inverted faces). 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 (Fig. 1).

2.3. Stimuli and procedures of the imaging experiments

Subjects were scanned with a 1.5T Philips Gyroscan Intera scanner at the University of Louvain, St.-Luc Clinic, Brussels provided with standard
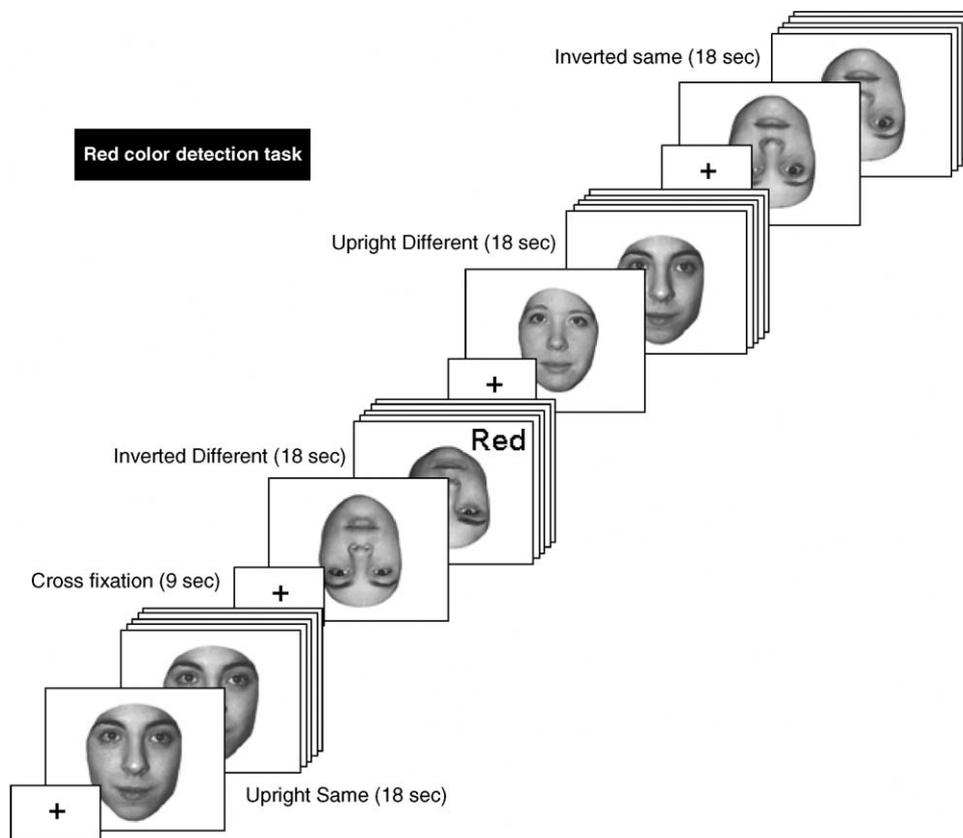

Fig. 1. Example of the inversion–adaptation experiment. Each scanning session consisted of alternating blocks of different and same six faces presented upright or upside-down (inverted) and of a cross fixation task. The subject's task was to detect a face stimulus that appeared in red color. Note that a mask, not represented here for sake of clarity was inserted in between each face picture.

quadrature birdcage head coils. In each session, a 3D T1-weighted data set encompassing the whole brain was acquired for every subject (110 slices, 1.5 mm slice thickness, matrix size $= 256 \times 256$). Single shot gradient-echo-planar imaging (EPI) was performed using the BOLD contrast effect as an indirect marker of local neuronal activity (Ogawa, Lee, Kay, & Tank, 1990). For both the localizer and the inversion–adaptation experiments, 30 5 mm axial slices (TR $= 3000$ ms, TE $= 40$ ms, FA $= 90°$, matrix size $= 64 \times 64$, FOV $= 250$) were acquired. To localize the face-sensitive regions, two or three independent 'localizer' scans were run in which subjects viewed alternating blocks of faces, blocks of objects (18 s blocks, 24 items presented for 750 ms per block) and a cross fixation screen (9 s blocks). During the blocks of faces and objects stimulation, subjects performed a one-back within-category discrimination task, as in previous studies (e.g. Kanwisher et al., 1997). Each localizer run lasted 5 min 33 s (111 TRs). Following the localizer scans, three scanning sessions were acquired using an fMR-adaptation design, which consisted of alternating blocks of different faces and same faces presented upright or upside-down (18 s blocks) and a cross fixation screen (9 s blocks). Each face block consisted of six stimulus presentations of 1500 ms followed by 500 ms of mask and 1000 ms blank. Each inversion–adaptation scanning session lasted 7 min 21 s (147 TRs).

2.4. Data analysis of the imaging experiments

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

We analyzed separately the face-localizer and inversion–adaptation experiments, on the normalized brain scans for each subject. First, the contrast (faces minus objects) was computed using the 'localizer' scans and the face-sensitive regions were localized in each individual subject. The regions of interest (ROI) were located in the right middle fusiform gyrus (rMFG), left middle fusiform gyrus (lMFG), right inferior occipital gyrus (rIOG), left inferior occipital gyrus (lIOG) and the right superior temporal sulcus (rSTS). We also computed the contrast (objects minus faces), and the regions responding more to objects than faces (right and left parahippocampal gyrus (rPG and lPG); Kanwisher et al., 1997) were localized in each individual subject. All of these ROI of contiguous voxels were considered significant at $p < 0.05$ (false discovery rate) or $p < 0.05$ (one-tailed, Bonferroni-corrected for multiple comparisons). At this threshold, the minimum cluster size found was of 12 voxels for the IOG, 25 for the MFG and 127 for the PG. The mean cluster size of each ROI is described in Section 3. Second, the above-defined ROIs were used to test for fMR-adaptation to facial identity in a repeated-measure ANOVA with two factors: *orientation* (upright versus inverted) and *adaptation* (same versus different). Four regressors for the face inversion–adaptation experiment were included in the model: upright different (UD), upright same (US), inverted different (ID) and inverted same (IS). Finally, to further test our hypothesis that a larger response to upright than inverted faces occurs as a result of adaptation, ANOVA analyses were also performed in these regions separately for each third (6 s, two faces) of the stimulation blocks. To account for the hemodynamic response delay, the data points were shifted of one TR for the analyses, starting at second data point. Note that because of the sluggishness of the hemodynamic response, the data points of the different windows are not independent (see Formisano & Goebel, 2003). This complementary analysis was thus not aimed at identifying a specific time-point at which a difference between conditions would start or end, but to test further the hypothesis that any difference between upright and inverted faces would increase over time and repetition of identities.

3. Results

3.1. Behavioral data

In the inversion–adaptation experiment, subjects performed the color detection task at ceiling in all condition (mean accuracy: 100%), but were significantly slower during the upright conditions (543.5 ± 27.5 ms) than during the inverted conditions (502.7 ± 18.6 ms; $F_{(1,27)} = 7.89$, $p = 0.02$) with no interaction between orientation and adaptation factors ($F_{(1,27)} = 0.53$, $p = 0.48$).

3.2. Neuroimaging results

3.2.1. Whole time-course analyses

In the 'localizer' paradigm, there was a significantly larger response to faces compared to objects for nine subjects in the right middle fusiform gyrus (37 ± 3, -48 ± 7, -20 ± 4; mean cluster size: 975 voxels), nine subjects in the left fusiform gyrus (-37 ± 3, -47 ± 8, -19 ± 6; mean cluster size: 701 voxels), nine in the right inferior occipital gyrus (34 ± 5, -74 ± 10, -18 ± 6; mean cluster size: 773 voxels), nine in the left inferior occipital gyrus (-32 ± 4, -67 ± 7, -19 ± 14; mean cluster size: 446 voxels) and eight in the right superior temporal sulcus (49 ± 7, -53 ± 10, -8 ± 5; mean cluster size: 963 voxels). In the 'localizer' paradigm, we also found a significantly larger response to objects as compared to faces for 10 subjects in the right parahippocampal gyrus (25 ± 3, -48 ± 7, -16 ± 4; mean cluster size: 693 voxels) and in the left parahippocampal gyrus (-26 ± 3, -52 ± 6, -16 ± 3; mean cluster size: 627 voxels). In the ROI–GLM analysis, each of these ROIs was tested for fMR-adaptation to facial identity.

The ROI located in the *rMFG* showed higher BOLD signal for upright faces than for inverted faces ($p = 0.008$) and for different than for same faces ($p = 0.04$). Most importantly, there was a significant interaction between orientation and adaptation ($p = 0.03$). This was due to a higher activity during upright different than during upright same faces stimulation ($p = 0.01$; Figs. 2 and 3), whereas there was no significant difference between different and same faces when the pictures were presented upside-down ($p = 0.29$). In the *lMFG*, there was also a higher activation level in response to upright faces than to inverted faces ($p = 0.002$) and for different than for same faces ($p = 0.007$). There was no significant interaction between the two factors ($p = 0.38$). Although simple effects are not conventionally inspected in the absence of a significant interaction, it is interesting to note that there was a higher signal during blocks of upright different faces than during upright same faces stimulation ($p = 0.001$; Figs. 2 and 3), but no significant difference between different and same faces when the pictures were presented upside-down ($p = 0.11$). A significant difference was found between the different and same faces visual stimulations in both the *rIOG* and the *lIOG* ($p = 0.06$ and 0.01, respectively), but there was no effect of orientation ($p = 0.81$ and 0.11, respectively) and no significant interaction between the two factors ($p = 0.37$ and 0.91, respectively). There was no significant effect of orientation or adaptation in the *rSTS*, where the signal was
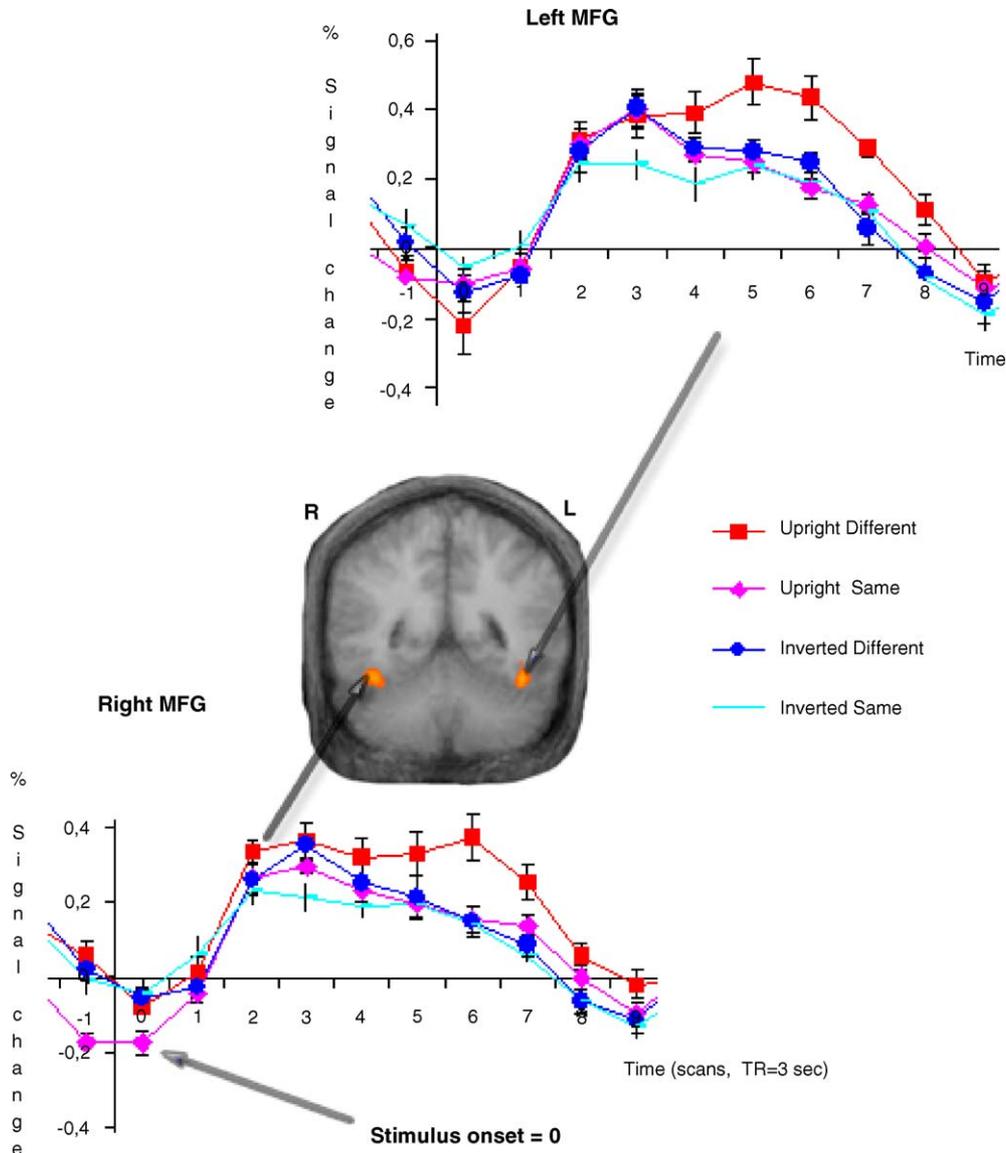
Fig. 2. Coronal slice passing through the rMFG and lMFG activated when participants viewed faces as compared to objects, projected onto the averaged high-resolution MRI of the 10 participants normalized into the Talairach space (L: left; R: right). Averaged time courses of the rMFG and lMFG during the four conditions of the inversion–adaptation experiment: upright different, upright same, inverted different and inverted same.

extremely low (<0.1 PSC) and variable across subjects. Finally, the ROIs located in the *rPG* and in the *lPG* showed neither significant effect of orientation ($p = 0.5$ and 0.5, respectively) nor adaptation ($p = 0.2$ and 0.3, respectively). Moreover, there was no significant interaction between the two factors ($p = 0.6$ and 0.3, respectively).

3.3. Analysis of the stimulation blocks in separate time windows

During the initial epoch of face stimulation (6 s, two faces, see Section 2), there was no difference between BOLD signal for upright faces compared to inverted faces ($F_{(1,27)} = 2.58$, $p = 0.12$) in the *rMFG*, but there was already a higher signal for different than for same pairs of faces ($F_{(1,27)} = 10.26$, $p = 0.005$). However, there was no interaction between the two

factors ($F_{(1,27)} = 0.12$, $p = 0.73$). In the second epoch of face stimulation, there were main effects of orientation ($F_{(1,27)} = 4.84$, $p = 0.04$) and adaptation ($F_{(1,27)} = 5.49$, $p = 0.03$). The interaction did not reach significance ($F_{(1,27)} = 1.98$, $p = 0.17$), even though there was a significant effect of adaptation for upright faces only ($p < 0.01$; inverted faces: $p = 0.35$, see Fig. 4). In the third epoch of face stimulation, there was a main effect of orientation ($F_{(1,27)} = 48.08$, $p < 0.0001$) and of adaptation ($F_{(1,27)} = 9.02$, $p = 0.008$). There was an interaction between the orientation and adaptation factors ($F_{(1,27)} = 7.21$, $p = 0.01$) highlighting the differential adaptation for upright and inverted faces in the rMFG ($p = 0.002$ and 0.62, respectively; see Figs. 3 and 4).

In the *lMFG*, the results were quite similar as in the rFMG (see Fig. 4). In the first time-course's window, the activation level of the lMFG was not significantly different for upright faces and for inverted faces ($F_{(1,27)} = 3.81$, $p = 0.07$), but was
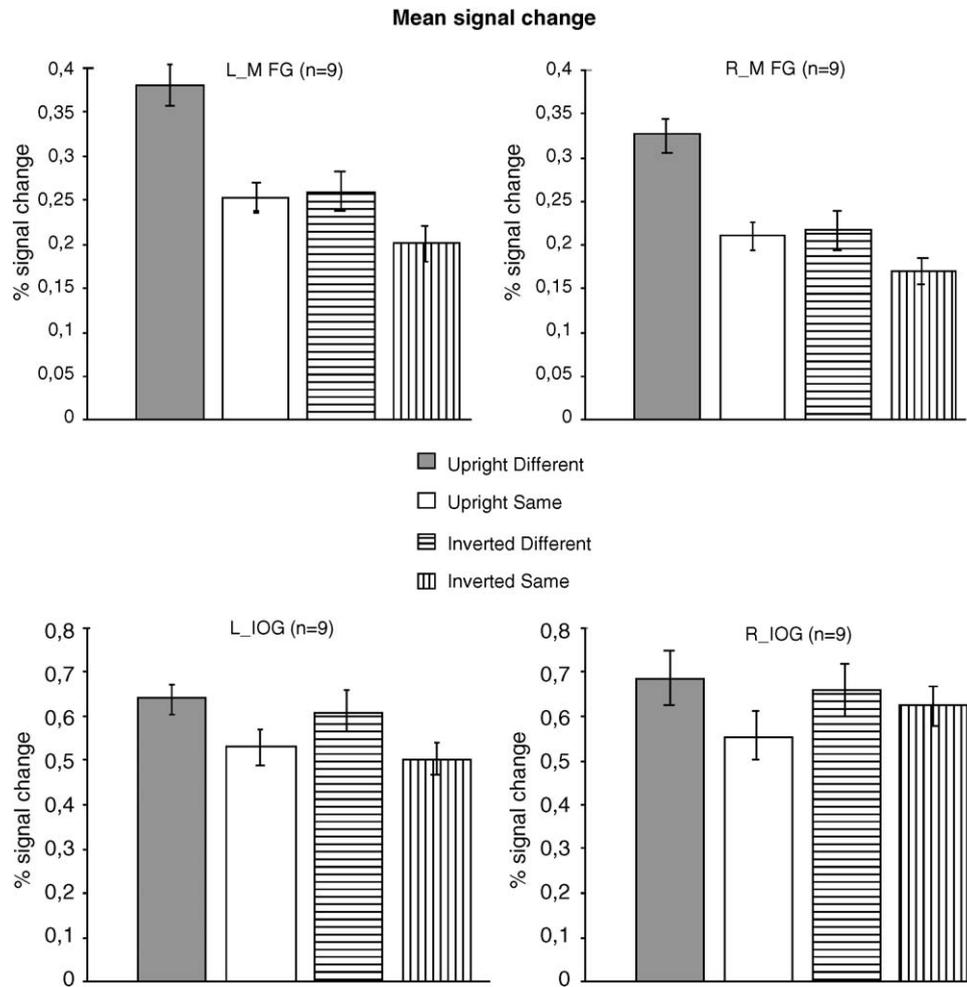
Mean signal change

Fig. 3. Plots of the mean BOLD signal change during the four conditions of the inversion–adaptation experiment: upright different, upright same, inverted different and inverted same. The percentage of signal change is observed in four ROIs: rMFG, lMFG, rIOG and lIOG, defined functionally in an independent face-localizer experiment.

larger for different than for same faces ($F_{(1,27)} = 5.24$, $p = 0.03$), without any interaction between the two factors ($F_{(1,27)} = 2.73$, $p = 0.11$). In the second time-course's window, there was a larger BOLD signal for upright faces than for inverted faces ($F_{(1,27)} = 14.54$, $p = 0.001$). We also observed a higher signal for different than for same faces ($F_{(1,27)} = 45.79$, $p < 0.0001$). The interaction between the two factors did not reach significance ($F_{(1,27)} = 3.61$, $p = 0.07$), even though the difference between different and same stimuli was larger for upright faces ($p < 0.0001$) than for inverted faces ($p = 0.038$; Fig. 4). In the third 6 s epoch, there was a larger BOLD signal for upright faces than for inverted faces ($F_{(1,27)} = 38.52$, $p < 0.0001$), and a larger response for different than for same faces ($F_{(1,27)} = 12.89$, $p = 0.002$). As illustrated in Figs. 3 and 4, there was an interaction between the two factors ($F_{(1,27)} = 9.95$, $p = 0.006$), reflecting the recovery from adaptation for upright faces ($p < 0.001$) but not for inverted faces ($p = 0.92$).

In the right IOG, there was no significant effect during the first time window. In the second time window, there was only a significant difference same and different faces when presented upright ($p = 0.01$) but not upside-down ($p = 0.9$). The interaction between adaptation and orientation was not significant in the

third window either ($p = 0.19$), although there was also a clear difference between different and same faces in upright orientation ($p < 0.001$) but not upside-down ($p = 0.4$). Similar results were found in the left IOG, with main effects of adaptation found during the three time windows ($p = 0.04$, 0.02 and $p < 0.001$, respectively) and an interaction between adaptation and orientation which became significant only in the last epoch ($p = 0.034$), reflecting the significant effect of adaptation for upright faces ($p < 0.001$) but not for inverted faces ($p = 0.59$).

4. Discussion

In line with previous observations, there was a significant decrease of fMRI signal in the lateral part of the middle fusiform gyrus for inverted as compared to upright face stimuli (Gauthier et al., 1999; Haxby et al., 1999; Kanwisher et al., 1998; Yovel and Kanwisher, 2004). This difference was qualified by a significant interaction between orientation and face identity repetition in these areas. When different face stimuli were presented during a block, there was a larger response to upright as compared to inverted faces. However, when the same face identity was repeated, the response was almost identical for upright and
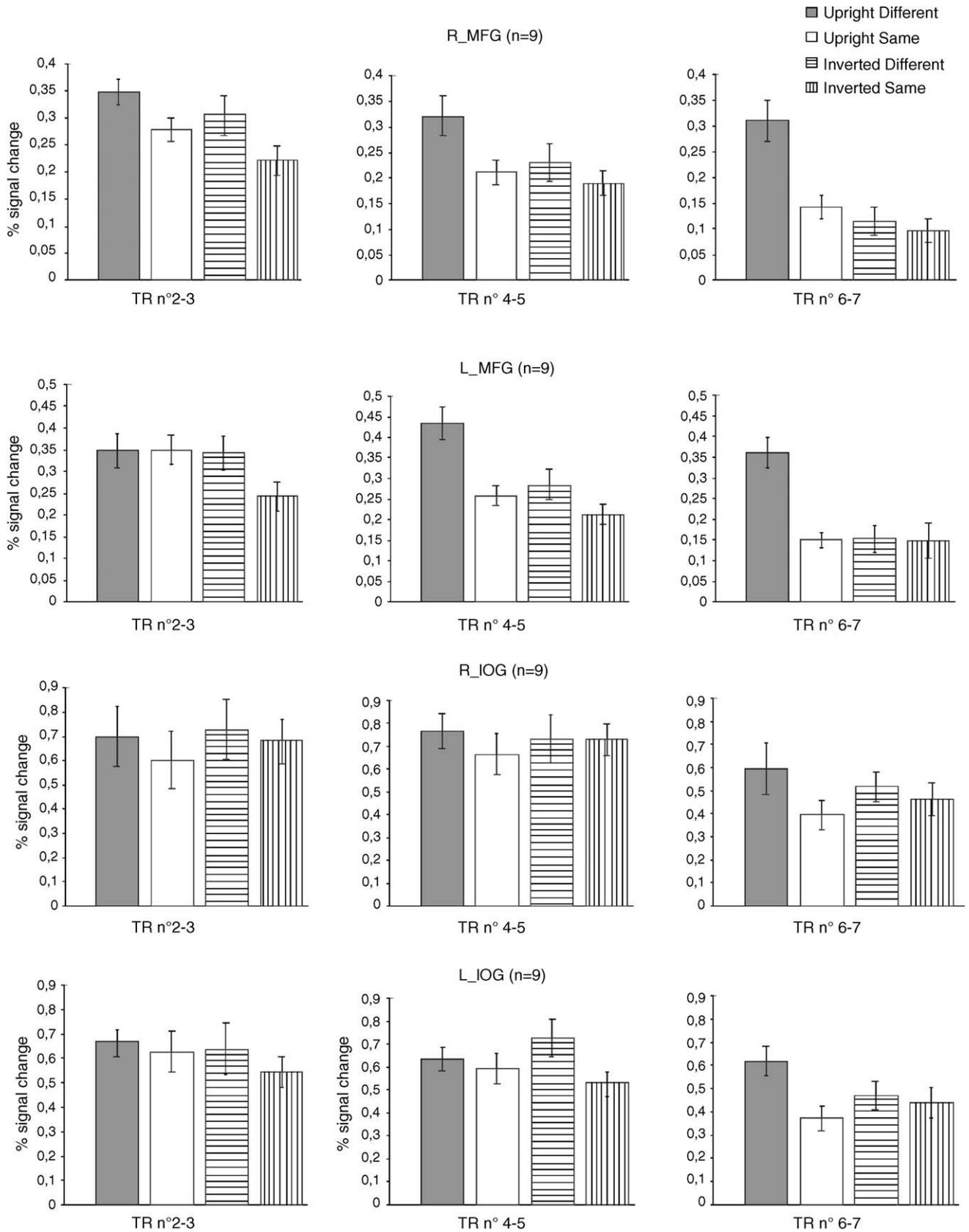
Fig. 4. Plots of the mean BOLD signal change during the four conditions of the inversion–adaptation experiment: upright different, upright same, inverted different and inverted same. The percentage of signal change is observed, during three time windows of 6 s, in four ROIs: rMFG, lMFG, rIOG and lIOG, defined functionally in an independent face-object-localizer experiment.

inverted orientations. Most interestingly, the difference between upright and inverted faces emerged significantly in later parts of the block stimulation, clearly reflecting a difference between upright and inverted faces in the amount of recovery from adaptation to facial identity.

In previous block design fMRI studies comparing the processing of upright and inverted faces in the lateral part of the middle fusiform gyrus, the decrease associated with face inversion was characterized as being of small magnitude, in comparison to the much larger difference observed when comparing faces and non-face objects in this area (e.g. Kanwisher et al., 1998). However, the effects of face inversion were significant in all block design studies, including the study by Haxby et al. (1999), and were substantial in the right MFG in at least two studies (Kanwisher et al., 1998: 0.4 and 0.5% signal change difference for one-back matching and passive viewing, respectively; Yovel and Kanwisher, 2004: 0.3 PSC in a matching task). In all of these studies, the effect of face inversion was assessed by comparing the overall PSC for upright and inverted faces during blocks of stimulation with different identities. Considering the blocks with different faces only, the results of the present study largely confirm these findings of a larger response to upright than inverted face orientation. Here, critically, there was a condition where the same face stimulus was repeated throughout a block, allowing comparison of the effect of adaptation for upright and inverted faces. This comparison suggests that the lower level of activation for inverted faces that was found previously was mainly due to a weaker recovery from adaptation for these stimuli. It is an important result because it suggests that the population of neurons in the middle fusiform gyrus responds almost equally well to upright and inverted faces initially. However, when distinct facial identities are presented consecutively in an inverted orientation, there is a suppression of the population's response, leading to an overall decrease of activation during a block of stimulation. A weaker recovery from adaptation for inverted faces correlates with the large amount of behavioral studies cited in Section 1 showing that faces presented upside-down are much harder to discriminate than upright faces (for reviews, see Maurer et al., 2002; Rossion and Gauthier, 2002). In sum, the present observations indicate that there is orientation selectivity for faces in the fusiform gyrus that emerges with the presentation of multiple facial identities.

In this context, it is interesting to note that the strongest effects of face inversion described previously were found in the experiments that used the longest epoch durations, i.e. 30 s in Kanwisher et al. (1998), which is exactly what is expected if the effect of inversion are mainly due to neural adaptation. Other factors such as the number of different faces presented during a block, the rate of stimulation and the similarity between individual faces may play a role in the magnitude of the PSC difference between upright and inverted faces in these areas, such that it is difficult to compare the results observed by studies that differ according to all these parameters. For instance, the present results suggest that the difference between upright and inverted faces in the MFG will increase with the number of different facial identities presented during a block. Interestingly, these findings may also account for the absence of significant inversion effects

in the MFG reported by the only study using event-related stimulation (Aguirre et al., 1999). In that study, upright and inverted face stimuli were presented briefly (200 ms), one-by-one, interleaved with other pictures (cars upright and inverted, faces and cars scrambled). Because the signal was averaged over single events rather than over a block of stimulation, it was not, or much less, subject to differential adaptation effects for upright and inverted orientations.

It should also be noted that most of the neuroimaging studies comparing upright and inverted faces have used active discrimination tasks, mixing trials with identical faces and different faces during a block and reporting lower performance rates during blocks of inverted faces (Gauthier et al., 1999; Haxby et al., 1999; Kanwisher et al., 1998; one-back task; Yovel and Kanwisher, 2004, matching task). Because inverted faces are harder to match, subjects may attend more strongly to the visual stimuli during this condition, leading to an attentionally driven increase of activation in the MFG (Wojciulik, Kanwisher, & Driver, 1998), compensating in part for the lower recovery from adaptation found for inverted faces. Here, to avoid any such potential confounds: (1) either the faces in a block were all different, or the same face stimulus was repeated[1], while (2) subjects performed an orthogonal color detection task at the same level of performance for all conditions. It is interesting to note that subjects were slightly slower at detecting the colorized face items for upright faces than inverted faces. This slowing down may be possibly related to a mandatory processing of face identity in the upright condition, which might have diverted attention from the color detection task. However, most importantly, there was no significant interaction between repetition of identity and orientation in RTs, whereas the critical fMRI findings reflect precisely such an interaction. That is, subjects were slowed down for upright faces, but not more during blocks presenting different identities than the same facial identity. This behavioral effect does not appear to be directly related with our fMRI findings.

4.1. Neurophysiological mechanisms

A lack of intrinsic amplitude difference (i.e. without considering differential adaptation rates) between upright and inverted faces is not as surprising as it may appear at first glance. Face-selective cells in the monkey infero-temporal cortex (see Desimone, 1991; Rolls, 1992) respond equally strongly to

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[1] It may be argued that the exact same image was repeated, not different pictures of the same facial identity, and thus that adaptation found in face-sensitive areas may be image-based rather than identity-based. However, the same methodology was used in previous fMRI face-adaptation experiments, except in two event-related studies (Eger, Schyns, & Kleinschmidt, 2004; Winston et al., 2004) that reported the same results as the other studies. In a block design, six photographs of each face, without large change in viewpoint or facial expression, would have been needed. In any case, the effects reported here are unlikely to be due to low-level adaptation since they take place in high level visual areas, and a mask was inserted between each face picture. Most importantly, the conditions of stimulation were identical for upright and inverted conditions except for orientation (i.e. any effect of repeating the exact same picture was the same for upright and inverted orientations), and the effects of interest concern the conditions during which different pictures were presented.

upright and inverted faces (Perrett, Oram, & Ashbridge, 1998; Perrett, Rolls, & Caan, 1982) and the occipito-temporal N170 scalp potential in humans is also equally large or most often larger in amplitude to faces presented upside-down than upright faces (e.g. Bentin et al., 1996; Rossion et al., 2000).

The neuronal mechanisms underlying the differential fMRI-repetition effect for upright and inverted faces in are not clear at this stage. At the behavioural level, different adaptation patterns for upright and inverted faces have been interpreted as reflecting the process of distinct neuronal populations coding for upright and inverted faces in the fusiform gyrus (Rhodes et al., 2004). However, single-cell recording studies show that the same neurons in the monkey inferior temporal cortex respond to upright and inverted faces (e.g. Perrett et al., 1982, 1998). The neurons generally discharge with a different spike rate to distinct facial identities, allowing encoding information useful for identifying individual faces in a sparse distributed network (Rolls & Tovee, 1995; Young & Yamane, 1992). The patterns of discharge to different facial identities in a network of cells may overlap more when the faces are presented upside-down, reflecting the difficulty to discriminate individual faces. Accordingly, when different faces are presented in succession, a suppression of the population response is observed for the inverted orientation because of this large overlap of the population response between trials. To our knowledge, the effect of repetition on upright and inverted faces has not been investigated in single-cell recording studies. ERP studies have shown a reduction of both response amplitude and peak latency of the N170 when the same facial identity is repeated immediately (e.g. Itier and Taylor, 2002); see also the MEG study of Noguchi et al. (2004), but no interaction with stimulus orientation has been reported. The decrease observed for the repetition of the same face identity, or for different identities when the faces are presented upside-down, may thus reflect both a suppression of response and a faster rate of accumulation of activity in these conditions (see James & Gauthier, 2005; Noguchi et al., 2004).

4.2. Sensitivity to perceived differences between faces and the role of configuration

It is generally stated that faces form a visually homogenous category (e.g. Damasio, Damasio, & Van Hoesen, 1982); all exemplars of the category sharing a common first-order configuration, i.e. two symmetrically placed eyes above a central nose and mouth (Diamond and Carey, 1986). Despite this visual homogeneity, the perceptual system is tuned to discriminate individual faces readily, based on both variations of local individual features and idiosyncratic relationships between these features (the so-called second-order configuration, Diamond and Carey, 1986). When faces are presented upside-down, these variations, in particular the metric relationships between features, are much harder to extract (see Le Grand, Mondloch, Maurer, & Brent, 2001; Rhodes et al., 1993; Searcy and Bartlett, 1996). Even though the physical difference between two upright faces and between two inverted faces is strictly identical, the perceptual system has been tuned to discriminate more efficiently between individual faces presented in their canonical orientation. Our

observations show that neurons in the middle fusiform gyrus respond to a perceived difference rather than to an actual physical difference between stimuli. This is in agreement with recent findings showing that the right MFG shows no sensitivity to a physical difference between two face stimuli as long as they are perceived as similar faces, but shows release from adaptation when stimuli are perceived as different identities (Rotshtein et al., 2005; see also Eger et al., 2004).

In the present study, the faces differed both by local features and by their configuration. Future studies will have to clarify whether the reduced recovery from adaptation found for inverted faces is mainly to a lack of discrimination of configural relationships than to featural differences for inverted faces. In a recent fMRI study, the response to upright and inverted faces differing either by local features or by configural changes was measured in the lateral fusiform gyrus (Yovel and Kanwisher, 2004). It was found that inversion reduced the activation in the MFG, equally largely for configural and local manipulation. However, unfortunately, the authors could not replicate previous behavioural evidence that face inversion affects more the configuration than the local features (e.g. Freire et al., 2000; Leder and Bruce, 2000; Le Grand et al., 2001; Rhodes et al., 1993; Searcy and Bartlett, 1996), preventing to draw strong conclusions about the sensitivity of these 'face areas' in processing face configuration[2].Sensitivity to face inversion across identity repetition is larger in the fusiform gyrusIn the present study we found a bilateral effect of face inversion in the fusiform gyrus, equally large in the right and left hemisphere. The right hemisphere is notoriously dominant in face processing, as supported by neuropsychological data (e.g. Sergent & Signoret, 1992), neuroimaging (e.g. Rossion et al., 2000; Sergent et al., 1992), event-related potential (e.g. Rossion, Joyce, Cottrell, & Tarr, 2003), and behavioural studies using lateralized visual field presentations (e.g. Hillger & Koenig, 1991). However, with the exception of a recent neuroimaging study (Yovel and Kanwisher, 2004), the effects of face inversion are usually bilateral (e.g. Bentin et al., 1996; Gauthier et al., 1999; Haxby et al., 1999; Rossion et al., 2003a), consistent with the present observations.

More importantly, whereas adaptation to facial identity was also observed here in bilateral face-sensitive areas of the inferior occipital cortex, as previously reported (e.g. Gauthier et al., 2000; Schiltz et al., 2005), the effects of orientation were not significant when considering the whole epochs of stimulation in these posterior areas. It is yet unclear how these two areas differ in terms of face processing functions. Face-related activation in the right fusiform gyrus can be observed despite a lesion to the ipsilateral inferior occipital cortex (Rossion & Caldara et al., 2003), but the two areas appear to be necessary for normal individual face processing (Schiltz et al., 2005). As a matter of fact, the lesions causing prosopagnosia—the inability to recognize faces (see Behrmann & Moscovitch, 2001; Sergent and Signoret,

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[2] Note that this absence of behavioural effect may be due to several methodological differences in this experiment (Yovel and Kanwisher, 2004) compared to previous studies (e.g. one basic face used and repeated, subjects told where the critical changes to discriminate faces were located, etc.).

1992)—encompass more often the inferior occipital cortex than the middle fusiform gyrus (Bouvier & Engel, 2005). Haxby et al. (2000) have suggested that the inferior occipital gyrus is involved more in the processing of individual face features than on whole face representations, the latter being extracted at the level of the fusiform gyrus. As mentioned above, it is widely acknowledged that inverting faces impairs the perceptual coding of both the face parts and their configural relationships (Maurer et al., 2002), but that the encoding of configural information suffers most from inversion (e.g. Freire et al., 2000; Leder and Bruce, 2000; Le Grand et al., 2001; Rhodes et al., 1993; Searcy and Bartlett, 1996). The stronger effects of face inversion found here in the fusiform gyri may thus reflect the larger receptive field of neurons in this area, which would be sensitive to both global (i.e. configural) and local (featural) information, whereas neurons in the inferior occipital gyrus may be more sensitive to local, fine-grained, differences between individual faces (see Eger et al., 2004; Schiltz et al., 2005).

5. Conclusion

Inverted faces are not discriminated efficiently by the face processing system, leading to a weaker recovery from adaptation in the fusiform face-sensitive area when different faces are presented upside-down. These observations may account for discrepancies in the results found in previous fMRI studies comparing the processing of upright and inverted faces, and are in agreement with neurophysiological recordings of face-related activity in monkeys and humans. The reduced recovery from adaptation for inverted faces in the human occipito-temporal cortex may underlie the face inversion effect, taking place during perceptual encoding of individual face representations.

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