Article

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Reference

Distinct and convergent visual processing of high and low spatial-frequency information in faces

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Abstract

We tested for differential brain response to distinct spatial-frequency (SF) components in faces. During an fMRI experiment, participants were presented with 'hybrid' faces containing superimposed low and high SF information from different identities. We used a repetition paradigm where faces at either SF range were independently repeated or changed across consecutive trials. In addition, we manipulated which SF band was attended. Our results suggest that repetition and attention affected partly overlapping occipito-temporal regions but did not interact. Changes of high SF faces increased responses of the right inferior occipital gyrus (IOG) and left inferior temporal gyrus (ITG), with the latter response being also modulated additively by attention. In contrast, the bilateral middle occipital gyrus (MOG) responded to repetition and attention manipulations of low SF. A common effect of high and low SF repetition was observed in the right fusiform gyrus (FFG). Follow-up connectivity analyses suggested direct influence of the MOG (low SF), IOG and ITG (high SF) on the FFG responses. Our results reveal that different regions within occipito-temporal cortex extract distinct visual cues at different SF ranges in faces, and that the outputs from these separate processes project forward to the right FFG, where the different visual cues may converge.

Keywords

attention; DCM; fMRI; human; occipito-temporal cortex; repetition

Faces provide complex visual information at multiple spatial frequencies (SF), potentially ranging from global configuration properties to fine grained features, all simultaneously presented within the same visual image. Early processing stages in the visual system are known to dissociate in terms of the SF range of information they preferentially extract. In particular, magno-cellular (MC) and parvo-cellular (PC) visual pathways have different SF preferences, with the former being more sensitive to low SF ranges and the latter more sensitive to high SF ranges (e.g. Bullier, 2001; Lamme, 2001; Livingstone and Hubel, 1988). It has also been shown that these pathways project to distinct cortical regions, with the MC pathway projecting mostly to dorsal visual areas, including V2 and MT (Shipp, 2001); while inputs from PC and MC pathways that reach V1 separately, remain partly separated up to V3 and V4 (Shipp and Zeki, 1995).

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This neurophysiological evidence for dissociable SF processing routes has triggered abundant research on the role of high and low SF information in the visual recognition of faces, using psychophysics (e.g.Blackmore and Campbell, 1969; Fiorentini et al., 1983; Ojanpää and Näsänen, 2003; Parker and Costen, 1999; Schyns and Oliva, 1999); single cell recordings in monkeys (Rolls and Baylis, 1986); EEG recording in humans (e.g. Goffaux et al., 2003a; Goffaux et al., 2003b; McCarthy et al., 1999; Pourtois et al., 2005); and fMRI (Eger et al., 2004a; Gauthier et al., 2005; Iidaka et al., 2004; Winston et al., 2003). However, these studies have yielded some apparently conflicting conclusions. Some researchers have suggested that low SF are particularly important for face processing (Dailey and Cottrell, 1999; Harmon, 1973), but others argued that high SF might be more important for encoding facial identity (Fiorentini et al., 1983; Vuilleumier et al., 2003). Still another hypothesis maintains that SF information might be used flexibly depending on the task demands or the observer's strategy (Goffaux et al., 2003b; Morrison and Schyns, 2001; Oliva and Schyns, 1997; Peyrin et al., 2005; Schyns and Oliva, 1999; Schyns and Oliva, 1994; Schyns and Oliva, 1997). Finally, according to a 'coarse-to-fine' hypothesis, low SF information arriving faster to the cortex may generate an initial coarse representation of faces that is used to guide the processing of more detailed information conveyed by high SF (Blackmore and Campbell, 1969; Marr, 1982; Schyns and Oliva, 1994; Oliva and Schyns, 1997; Parker and Costen, 1999; McCarthy et al., 1999;Bullier et al., 2001; Lamme, 2001; Bar, 2003).

Studies manipulating the SF bands of faces while measuring the brain responses using fMRI (Eger et al., 2004a; Gauthier et al., 2005; Iidaka et al., 2004; Vuilleumier et al., 2003) have focused mostly on the responses of the fusiform gyrus (FFG) or the fusiform face area (FFA). One aim of the current study was to test explicitly the entire occipito-temporal network involved in processing different SF ranges while delineating connections between the various regions involved. Results of previous studies (Vuilleumier et al., 2003; Eger et al., 2004a; Iidaka et al., 2004; Gauthier et al., 2005) hint that both high and low SF information from faces are processed but using different pathways; although, to date, the anatomical localizations of these processes appear somewhat inconsistent across previous studies. Low SF faces are reported to be processed in bilateral parietal-occipital regions (Vuilleumier et al., 2003) or the calcarine sulcus (Eger et al., 2004a), while high SF information is reported to be processed in bilaterally inferior occipital gyrus (IOG), right FFG (Vuilleumier et al., 2003; Eger et al., 2004a), left inferior temporal gyrus (ITG; Vuilleumier et al., 2003), or just in the left occipital-temporal regions (Iidaka et al., 2004). Some integration of high and low SF has been tentatively suggested to occur in higher visual areas, such as the FFG and the functionally defined FFA (Vuilleumier et al., 2003; Eger et al., 2004a; Gauthier et al., 2005).

However, one caveat for the above studies (Vuilleumier et al., 2003; Eger et al., 2004a; Iidaka et al., 2004) is that they used stimuli containing only limited SF range (either high or low SF). As a result, the stimuli used differ markedly in their visual appearance and in their energy, contrast, luminance and so on. Thus the findings reported in those studies may reflect the non-specific visual dissimilarities between such images and not necessarily relate directly to any face- or identity-specific information within one or another SF range. Furthermore, presenting only one restricted SF range may potentially result in changes in the processing strategy that aims to compensate for the limited information available (Oliva and Schyns, 1997; Schyns and Oliva, 1997; Morrison and Schyns, 2001). Therefore, in the present study, we avoided effects that are merely due to stimulation of one or another SF range, by always stimulating both the low and high SF ranges conjointly, using 'hybrid' stimuli that superimpose different low and high SF faces together, as originally introduced by Schyns and colleagues (Schyns and Oliva, 1994; Schyns and Oliva, 1997; Oliva and Schyns, 1997; Schyns and Oliva, 1999; Morrison and Schyns, 2001) see Figure 1.

We thus revisited the potential roles of high versus low SF information in face processing using fMRI. Our aim was to determine any functional anatomical dissociation in occipito-temporal cortices for processing distinct SF information from faces. In addition we sought to assess the connectivity structure between the different areas implicated. This latter analysis was motivated apriori by two alternative connectivity schemes. The first is based on the traditional 'coarse-to-fine' hypothesis; low and high SF processes are hypothesized to be processed separately but in hierarchical order, such that the output from low SF processes is projected directly to regions processing high SF information (Bullier, 2001; Lamme, 2001; Bar, 2003) prior to further processing in higher-level regions. Alternative perspectives suggest that outputs from high and low SF processes project separately to a third higher region where they converge (e.g. in FFA Gauthier et al., 2005). The latter may be compatible with a 'flexible-usage' of SF information (Schyns and Oliva, 1994; Schyns and Oliva, 1997; Oliva and Schyns, 1997; Morrison and Schyns, 2001) and with a 'simple-to-complex' model (Riesenhuber et al., 2004; Jiang et al., 2006) according to which simple properties of faces are initially processed separately and the outputs of those processes are then combined possibly in the right FFG .

Our stimuli consisted of 'hybrid' face stimuli in which both high (SF > 24 cycle/image) and low (SF < 8 cycle/image) SF components were always presented conjointly, with different face identities being shown in each SF range and superimposed within a single stimulus (e.g. Schyns and Oliva, 1997; Schyns and Oliva, 1999; see Figs. 1). As mentioned above, this allowed us to avoid any low-level visual differences (such as contrast, energy, luminance, etc.) that might arise otherwise when presenting a single SF-filtered image for just one range or another (Schyns and Oliva, 1994). To determine the distinctive role of low and high SF cues in hybrid stimuli during face processing, we manipulated two orthogonal factors, with a bottom-up factor involving stimulus repetition (for each SF range) and a top-down factor involving selective attention, resulting in a 2×2×2 experimental design (Fig. 1c).

For our manipulation of stimulus-driven effects, the low and high SF-filtered face contained in each hybrid stimulus was either repeated or changed across successive trials, for each SF independently. Following the rationale of fMRI-adaptation (Grill-Spector et al., 1999), any regional sensitivity to a particular SF range should lead to greater neural activity when visual information in that SF range is changed, relative to when it is repeated. But the same region should not be influenced by repetitions in the other SF range if it does not process visual information in that range. Conversely, any brain region mediating processing of both low and high SF content should be modulated when the same face identity is changed versus repeated in either the low or the high SF component of hybrid stimuli.

For manipulation of our top-down factor, participants were required to pay attention to one or the other SF range across different trials for the same type of hybrid stimuli. Their task was to detect infrequent target stimuli (a face with inverted features; see Fig. 1b) appearing in the pre-cued SF range, while 'ignoring' the other SF range. Previous behavioral studies have shown that attention can modulate processing of different SF information in a stimulus (Sowden et al., 2003;Ozgen et al., 2005) and that it is possible to dissociate brain responses due to selective attention to one of two overlapping images (O'Craven, et al., 1999). We predicted that if a region is involved in processing visual information in a particular SF range (e.g. low SF), its activity should increase when that range is selectively attended (e.g. when concentrating on low SF components of hybrids) as compared to when it is ignored (O'Craven et al., 1997;O'Craven et al., 1999;Vuilleumier et al., 2001;Bentley et al., 2003). This attention manipulation also allowed us to distinguish purely stimulus-driven effects, due to the repetition of different SF cues from any uncontrolled spontaneous allocation of attention to just one particular SF range that might otherwise have arisen had we not explicitly directed attention to one or other SF range. Furthermore, by manipulating both repetition and attention, we could test whether these two factors provide comparable measures to assess the function of regions.

We were also interested in testing whether repetition effects on SF processes of faces interact with attention as observed in some other studies that use non-face stimuli (Eger et al., 2004b;Vuilleumier et al., 2005;Yi and Chun, 2005); or instead might be independent and additive here.

To anticipate our results, we found that distinct regions within occipito-temporal cortex are responsive to different SF ranges in faces, with stimulus repetition and selective attention producing independent and complementary effects on brain responses. We show a differential role for the bilateral middle occipital gyrus (MOG) in processing low SF information; for the right IOG and left ITG in processing high SF information; and for the right FFG in responding to both high and low SF. Using effective connectivity analysis (Friston et al., 2003a), we demonstrate that the outputs of low and high SF processing in MOG and IOG, respectively, are projected forward to the right FFG with no evidence for direct projections between the MOG and IOG. Similarly, the MOG (low SF) did not project to the left ITG (high SF), though the latter was found to have reciprocal functional connections with the right IOG (high SF) and right FFG (high *and* low SF). Thus, by delineating the neural substrates of fundamental visual processes involved in face processing for different SF ranges, our study provides new insights on the functional architecture and functional connectivity of the human visual recognition system, where the output of dissociated processes in posterior occipito-temporal cortex converge in the right FFG.

Materials and Methods

Subjects

15 healthy volunteers were recruited (8 females, mean age 29.5y, range 22-43y, all right handed). All reported normal vision, no past neurological or psychiatric history, and no structural brain abnormalities. Unfortunately, two months after the experiment, one female subject was diagnosed as having MS and therefore was excluded from the analysis. Written informed consent was obtained according to procedures approved by the Joint Ethics Committee of the National Hospital for neurology and Neurosurgery (NHNN) and Institute of Neurology (ION), London.

Stimuli

56 faces (28 females) with neutral expressions were chosen from the Karolinska Directed Emotional Faces set (KDEF, Lundqvist and Litton, 1998). An additional 74 faces from the same face set, with various expressions served as fillers. The fillers were introduced with the aim of disguising the repetition manipulation and minimizing strategic factors. All faces were achromatic and edited to place different 'inner' face features within an identical unisex outline (i.e. hair style, ears, chin contour, neck and shoulders, Fig. 1a,b). The latter manipulation was implemented to avoid possible confounds due to different SF information predominantly in the 'outer' and 'inner' features of a face, since it appears likely that 'outer' features vary primarily in low rather than in high SF range. Moreover, we wanted to constrain the effect of our manipulation to 'inner' face features, as it is known that these features are visually more important for face processing than the 'outer' contour features (Haig, 1986). In addition, 30 different 'oddball' target stimuli (Fig. 1b) were created for each SF range by inverting the inner face features within the upright outline. The required task was to detect such inverted oddballs, for just one SF range or the other as required by our attention manipulation.

Faces were filtered in Fourier space, using a Butterworth filter (Winston et al., 2003), set to filter either high frequencies (SF > 24 cycle/image; viewed as SF > 3.52 cycle/degree) or low frequencies (SF < 8 cycle/image; viewed as SF < 1.17 cycle/degree). Note that with a Butterworth filter, the cut off frequency corresponds to 50% of the magnitude of the filter.

Therefore, to minimize overlap between frequencies, the distance between the cut off frequencies was 1.5 octaves. These cut-offs were chosen to fit previous psychophysical findings suggesting that MC visual pathways are preferentially sensitive to SF below 1.5 cycles per degree, while PC pathways are sensitive to SF above this value (Skottun, 2000).

To optimize our repetition decrease measurements (see below) we scaled the high-pass SF images (that typically have rather low contrast) to have the maximum contrast possible with intensity values ranging from 0 to 255. This was done because prior work has shown that fMRI repetition-decrease may be affected by the contrast of the images, and is reduced or abolished for lower contrast images (Avidan et al., 2002). The contrast of half of the low SF images were equated to match the high SF images (i.e. 0-255), while the original contrast gradient was kept for the other half, counter balanced across subjects. Importantly, the two different scalings of the low SF images had no differential effects on the observed brain activity (see below).

We used hybrid faces as our stimuli to ensure that both SF ranges were presented conjointly and to avoid confounding non-specific visual cues with our SF manipulation. Each 'hybrid' face was created by overlapping two filtered faces, one with high and one with low SF, each depicting a different identity. These two overlapping faces were offset horizontally by 30 pixels (Fig. 1a) as pilot testing showed that this facilitated selective attention to one or the other SF range, as required by our task. The offset direction was random across mini epochs, but kept constant for all trials within a mini-epoch of the same condition (see below). The two different scaling procedures (i.e. maximal contrast for low SF, or its original contrast; Figs. 1a, 1b respectively) were counterbalanced between the repetition and attention conditions and across subjects. Importantly, the different scaling procedures did not affect the spectral power ratio of the hybrid stimuli as they had the same spectral power ratio as the original stimuli for the low and high SF range (disregarding the frequency range that was filtered out between 8-24 cycles/image). This suggests that our results should generalize to natural images. However, overall the power of the hybrid stimuli was less than the original images, with slightly less power for the hybrids for which the contrast of the low SF faces had been maximized. The hybrid combinations of particular faces and the type of scaling that was applied to particular stimuli were randomized across subjects, such that each subject was presented with an entirely different set of stimuli. This procedure should insure that any differences in fMRI responses to high and low SF could not be attributed to differences in the scaling procedure or to specific hybrid pairs. Finally, the resolution of the images was 512*512 pixels and they were presented with a 6.8° viewing angle.

Procedure

The experiment had a $2 \times 2 \times 2$ factorial design (Fig. 1c). The three critical factors were: low SF faces (repeat versus differ), high SF faces (repeat versus differ), and selective attention (low versus high SF). There were 30 events in each condition, distributed in a mixed blocked design. Each hybrid stimulus was shown for 500ms with an inter-stimulus-interval (ISI) of 750ms. An additional factor of no a-priori interest was the different scaling procedure applied (low SF: maximum contrast or original).

Repetition was manipulated by presenting hybrid stimuli in mini-epochs that contained a varying number of events (1 to 6) of the appropriate type (i.e., low SF-repeats only, high SF-repeats only, both low and high SF-repeats, or no repeats). The number of events per mini-epoch was varied in order to disguise the experimental structure and hence to minimize possible strategic effects that might otherwise have arisen due to systematic and conspicuous repetitions. These mini-epochs were presented successively, without any interruption between them. All events within a mini-epoch had the same offset direction (e.g. low SF on the right and high SF on the left) and the same scaling procedure (e.g. low SF with maximized contrast).

Attention to the low or high SF face within hybrid stimuli was manipulated over longer blocks (approximately 80 events each: experimental trials plus targets plus fillers). These blocks were separated by a fixation point presented for 6-9s. An explicit attention cue was presented to the subjects during the ISI period, both at the beginning and throughout each block, which instructed the subjects to attend only to a given SF range (by using the letter 'L' for attention to high SF, described to subjects as "Line-drawing faces", and the letter 'B' for attention to low SF, described as "Blurred faces"). Subjects had to report (by button press) any targets with inverted inner facial features that could occasionally appear in that particular SF range (15% of trials). There were four blocks in each attention condition. Each block started with 5 filler stimuli. A short practice run was administered prior to scanning.

After the fMRI experiment, subjects were debriefed and asked whether they had noticed any structure in the order of stimuli appearance. None reported any awareness of our manipulation of stimulus repetition, confirming the effectiveness of using fillers and varying the number of events per mini-epoch.

Imaging

We used a Siemens 1.5T Sonata system (Siemens, Erlangen, Germany) to acquire BOLD contrast weighted echo-planar images (EPI) for the functional scans. Images were reconstructed using TBR (Josephs et al., 2000). 26 oblique slices, 3 mm thickness, with 1.5mm gap were acquired, resulting in an in-plane resolution of 3*3*4.5mm, with 90° flip angle, 50ms echo time and 2340ms slice repetition time. To minimize susceptibility artefacts, slices were tilted at 30 degrees along the frontal-temporal cortex (Deichmann et al., 2003). Subsequent to the functional scans, a T1-weighted structural image (1*1*1 mm resolution) was acquired for co-registration and display of the functional data.

Data Analysis

Data were analysed using SPM2 (Wellcome Department of Imaging Neuroscience, London; www.fil.ion.ucl.ac.uk/spm). EPI volumes were spatially realigned to correct for movement artefacts, transformed to the MNI standard space (Ashburner and Friston, 2003a; Ashburner and Friston, 2003b), and smoothed using a 9mm Gaussian kernel.

Voxel-based analysis was performed across subjects using random effects analysis (Penny et al., 2003). We first tested whether the different scaling procedures affected occipito-temporal responses. For each subject, we computed a model with 16 regressors for each condition, following the factorial design: 2 (scaling, i.e. type of low SF image) by 2 (attention) by 2 (high SF repetition) by 2 (low SF repetition). Regressors of no interest included the fillers and inverted targets. All regressors were convolved with the canonical haemodynamic response function (Friston et al., 2003b). To correct for signal changes due to head movement, the 6 realignment parameters were included in the design matrix. To control for scanner and physiological noise additional regressors were added that depicted harmonic changes up to 1/128Hz. For each subject we calculated a contrast that tested for any main effect of scaling (i.e. type of low SF image) and an additional set of contrasts for each simple effects of interest under the two different scaling procedures (i.e. attention, high SF repetition and low SF repetition, see below). Consistency of effects across subjects was then tested using random effect models. We did not have any a-priori predictions regarding effects of the scaling (i.e. type of low SF image) and assessed this for completeness with a relative un-conservative threshold of P < 0.005 (uncorrected). The different scaling applied to the hybrid stimuli was found not to affect brain responses and also did not interact with any of the effects of interest. Therefore for simplicity we have collapsed across the scaling factor for the results reported here.

The model for each subject included the onset of each event in the eight experimental conditions (resulting from our 2×2×2 design, Fig. 1c) with farther regressors of no interests for the fillers, targets, the movement parameters and the harmonics depicting the frequencies up to 1/128Hz. The regressors were convolved with the canonical haemodynamic response function (Friston et al., 2003b). For each subject, the main effects of SF repetition were computed by subtracting the conditions where a face in a given SF range was repeated from those where a face in that SF range differed. The main effects of attention were computed by comparing the conditions where attention was directed to one SF range versus the other. Interactions between repetition and attention factors were also computed voxel-wise. Consistent effects across subjects (random-effects second-level analysis; Penny et al., 2003) were then tested for using one-sample t-tests on the resultant first-level contrast images. Comparisons across main effects (high versus low SF) and conjunction analyses were tested using paired t-tests, corrected for violation of the sphericity assumption. We used conjunction analyses (Nichols et al., 2005) to test for any cortical regions that were conjointly affected by <u>both</u> the repetition and attention manipulations, and for regions that showed sensitivity to <u>both</u> the high and low SF face-repetitions. Note that the conjunction test used here (Nichols et al., 2005) is more conservative than other conjunction methods that are based on the global null hypothesis (Friston et al., 2005;Friston et al., 1999). Here we tested for voxels showing independent significant responses to <u>both</u> effects. Importantly, this conjunction analysis also enabled us to test overlapping responses between contrasts that were not orthogonal (Nichols et al., 2005), as is the case with low and high SF repetition effects.

Effective connectivity analysis—We used dynamic causal modelling (DCM; Friston et al., 2003b) as implemented in SPM2 to estimate the effective connectivity (or functional coupling) between putative occipito-temporal regions (activated by our basis contrast) across our different experimental conditions. The aim of DCM is to assess and make inferences about the possible influence of one region on another in a given experimental context. Here we were interested in characterizing the functional connections between regions within occipito-temporal cortex that process different ranges of SF information in hybrid stimuli. The definition of these regions was based on the results obtained from the conventional voxel-based analysis of the group data (see below). To allow for inter-individual differences in peak activation, time series were extracted from the maxima voxel in each individual T-map using the appropriate contrasts (Ethofer et al., 2006).

We used DCM to explore two types of connection: The first is the effect of the stimulus input that perturbs the network. Here, these inputs were defined as the eight experimental conditions (reflecting the 2×2×2 design). We anticipated that the effects of stimulus inputs would mirror the effects observed in the voxel-based analysis for the stimulus-driven manipulation, i.e. repetition of SF. Of most interest to the current study is the second type of connections that we assessed with DCM. These describe intrinsic connections between putative regions in the context of the experiment. These intrinsic connections depict the effect that activity in one region can produce on another throughout the experiment. Here, we specified a fully connected model with all possible connections between our five (see below) regions of interest (ROIs). The main questions we wanted to explore were whether areas processing low SF might directly modulate areas processing high SF; and also whether initially separate processes of high and low SF information might then 'converge' via forward projection to a common area (see **Results** for more details).

The DCM model was initially estimated separately for each subject. In order to generalize our results to the population level, the estimated connection strengths from that analysis were then subjected to a second-level analysis using SPSS, where the significance of inferred connections was tested using one-sample t-tests against the null hypothesis that the connection strength equaled zero.

Functional localizer analysis—While many researchers, particularly in the field of face processing, have advocated a functional regions-of-interest (fROI) approach (Saxe et al., 2006), others have advocated a less constrained whole-brain voxel-based approach (Friston et al., 2006), as we have implemented above. For completeness, while we initially conducted a conventional SPM analysis, we subsequently implemented fROI approach to our data, focusing on the right fusiform face area (FFA). The method for localizing FFA within each individual subject was as followed:

Subjects: 12 subjects (7 females, mean age 30, range 22-43y) who also participated in the previous fMRI experiment (see above) underwent a functional localizer scan after the main experiment.

Stimuli: 10 achromatic photos of neutral faces taken from the Ekman's series were cropped to remove hair. To generate the scrambled faces, these faces were scrambled in a 15×10 grid (i.e. resulting in a pattern that resembled a checkerboard with various levels of grey), but with the outline of the face kept intact. 10 achromatic photos of houses were cropped to produce a similar elliptical shape and size as the intact and scrambled faces. All these stimuli were presented on a grey background.

Procedure: Stimuli for the functional localizer were presented in a block-design fashion, with 10 stimuli from the same category in each block (either faces, houses, or scrambled faces). The blocks of 11sec duration were separated with a 6.3sec fixation point presented on a grey background. Each stimulus was presented for 250ms, with an SOA of 850ms. The subjects' task was to detect an immediate repetition, by a button press, which occurred ~15% of the times equally distributed across all conditions. Each block was repeated 4-5 times.

Imaging and data pre-processing: The data were acquired using an identical MR sequences and protocol as above and were pre-processed using an identical procedure as above.

Region of interest analysis was performed using the MarsBar toolbox (Brett et al., 2002) that is implemented in SPM2. In each subject the right fusiform face area (FFA) was delineated using the contrast: [faces - (houses + scrambles)] at P < 0.005 threshold (uncorrected). The response of the FFA during the main 2×2×2 experiment was averaged across all the voxels within that functionally defined cluster. Consistencies across subjects of the main experimental factors (attention, high SF-repetition, low SF repetition) were tested using t-statistics in SPSS.

Results

During the main imaging experiment, subjects were asked to detect oddball targets with inverted inner features in the relevant (high or low) SF range. Performance accuracy (high SF 91.5±9.4% correct; low SF: 92.41±2.0%) and response times (high SF: 632 ± 67.1 ms; low SF: 637 ± 71.3 ms) were comparable for the two SF ranges. This behavioral pattern ensured that any effects observed in fMRI responses could not be attributed to trivial differences in task performance. It also argues indirectly against strategy differences for the high or low SF inversion detection task.

Our fMRI analysis primarily focused on activations in occipito-temporal regions, but for completeness we also report in the tables all regions showing significant effects above a conventional threshold of *P* < 0.001 uncorrected and involving more than 5 contiguous voxels. Since no effects were found for the different scaling procedure (i.e. maximal or original low SF contrast, see Methods) and no significant interactions were found in occipito-temporal cortices between this factor and the others, here we report and discuss SPM results for the main

effects or conjunction of the three factors (high SF repetition, low SF repetition and attention) only.

Functional sensitivity of occipito-temporal cortex to distinct SF information

Preferential processing of <u>low</u> SF in faces was determined by examining both repetition and attention effects for the corresponding stimulus conditions. Dorsal occipital regions, namely bilateral MOG and parietal areas, as well as the right FFG showed greater responses to different versus repeated low SF components in hybrid faces, regardless of the high SF components (Table 1a, Fig. 2a). To confirm the selectivity of these effects for low SF, we further compared the effects of low versus high SF face repetitions using a paired t-test. Only in the left MOG was the repetition effect for low SF faces significantly greater than that for high SF faces (Table 1b).

The attention manipulation showed results consistent with the above repetition effects: attending to low SF faces in hybrids produced greater responses in bilateral MOG, as compared with attending to high SF faces (Tables 1c). Moreover, a conjunction analysis showed that these attention effects overlapped with the low SF repetition effects in the same regions (Table 1d). In sum, bilateral MOG showed increased responses both when the low SF faces changed across successive hybrid stimuli and also when the low SF faces were selectively attended; but these two effects did not significantly interact (Post comparison of parameter estimates taken from the peak, left [-21 -93 -3]: $F_{1,13} = 0.11$, $P = 0.7$; right [30 -87 12]: $F_{1,13} = 0.76$, $P = 0.39$). Thus, repetition decreases for low SF faces in bilateral MOG were independent of whether attention was directed to low or to high SF.

Regional preference to <u>high</u> SF faces was similarly tested using main effects of repetition and attention. The right IOG, left ITG, and right FFG showed greater responses when high SF faces were changed rather than repeated across successive trials (Table 2a, Fig. 2b). But only in the right IOG and the left ITG were these repetition effects significantly greater for high than low SF faces (Table 1b), confirming a particular sensitivity of these regions to high SF information. By contrast, the effects of attention were less evident in these regions, since only the left ITG showed a trend for greater responses when attending to high versus low SF faces (post-hoc comparison of parameters estimates: $F_{1,13} = 3.79$, $P = 0.07$, see Fig. 2a). Consequently, only a trend was observed for overlapping effects in ITG when we examined the conjunction of repetition and attention for high SF faces (Table 1d), but here again attention did not interact with high SF repetition effects ($F_{1,13} = 0.39$, $P = 0.54$). These data indicate that the reduced response in left ITG due to repeating high SF faces across successive hybrid stimuli arise independently of the attended SF range. Moreover, attention did not affect the right IOG (54 -63 -9) response and did not interact with repetition effects in this region ($F_{1,13} = 2.8$, $P = 0.116$; $F_{1,13} = 1.95$, $P = 0.66$, respectively).

Finally, we performed a conjunction analysis between the low and high SF repetition effects that revealed importantly that both the right FFG ($Z = 3.27$, *MNI*: 33 -54 -15; Fig. 2c) and the right IOG ($Z = 3.11$, *MNI*: 36 -81 -6) were affected by these manipulations. Thus, changing a face in either SF range (or in both SF ranges) elicited an increased signal in these two regions. Attending to a specific SF range did not affect nor interact with SF repetitions in the right FFG (post-hoc comparison of the parameters estimates of the peak: attention manipulation: $F_{1,13} = 1.7$, $P = 0.2$; interaction of attention by low SF repetition: $F_{1,13} = 2.56$, $P = 0.13$; interaction of attention by high SF repetition: $F_{1,13} = 0.03$, $P = 0.86$) nor in the right IOG as reported above.

In order to allow some relation of our results to previous studies that focused on the functionally localized right fusiform face area (FFA) responses. We also implemented an fROI analysis for the right FFA. As described in the methods, 12 out of our 14 original subjects took part in a

separate functional localizer scan which aimed to localize their FFA. The FFA was identified in each subject as the cluster of voxels within the right FFG that show larger response to faces than houses plus scrambled faces. A reliable right FFA (at P < 0.005, uncorrected) was identified in 9 of the 12 subjects (location of peak response in MNI space, average (±s.d): 43 (±9) -45(±6) -20(±7), cluster size: 304(±229)*3mm^3). The size of the high and low SF repetition effects from the main experiment were then calculated on the averaged response of the separately defined right FFA cluster. Consistent effects across subjects were compared using t-tests in random effects models (in SPSS13.00). In accordance with the preceding voxel-based analysis, right FFA showed significantly larger responses when low SF faces differed than when they were repeated ($t_8 = 2.76$, P = 0.025, percent signal difference = 0.13) and also significantly larger responses when high SF faces differed than when they were repeated ($t_8 = 3.1$, P = 0.015, percent signal difference = 0.15). There was no significant effect for the attention manipulation ($t_8 = -1.48$, P = 0.17, percent signal difference [attending-low *minus* attending-high] = 0.09). These results for a separately defined right FFA thus confirm those found for the right FFG in the voxel-based analysis.

To summarize, using hybrid faces we observed different patterns of processing of SF information as a function of repetition and attention manipulations. Activity in both the left and right MOG was affected by repetitions of low SF faces and by attention to those faces, but were not influenced by the concomitant high SF components. Conversely, both the right IOG and left ITG responses were affected by repetitions of high SF faces, while attention to high SF produced only marginal increases in the left ITG. Right FFG was equally modulated by repetition of faces in either the high or low SF range. The right IOG also tended to respond to changes versus repetitions of faces in either SF range (as observed by others Eger et al., 2004a), but this effect was significantly stronger with repetitions of high SF faces than with low SF faces (see above and Fig. 2b). We then tested the effective connectivity between all the above regions using DCM (Dynamic Causal Modelling).

Effective connectivity analysis

The DCM we designed was based on the results of the voxel-based analysis (see above). Focusing on occipito-temporal cortices, the model included five regions of interest (ROIs): the left and right MOG (that we had found to be sensitive to low SF), right IOG and left ITG (that were sensitive to high SF) and right FFG (that was sensitive to both high and low SF see **Fig. 4a**). These ROIs were identified for each individual subject (see Table 3 for details) as the peak response that was anatomically located in the vicinity of the maxima obtained by the group analyses (i.e., in the second-level analysis across subjects, described above). All five ROIs (P < 0.005, uncorrected) were reliably delineated in 10 out of the 14 subjects (Table 3). The model was estimated separately for each of the 10 subjects. Significantly inferred connections across all subjects were then tested using one-sample t-tests.

We used DCM to explore two types of connections, as implemented in SPM2 (see Friston et al., 2003a and our Methods). First, the effect of stimulus input on posterior occipital regions (bilateral MOG and right IOG) was specified by the onset vectors corresponding to the eight experimental conditions, allowing us to model the impact of our bottom-up factors (i.e. SF repetition) on neural activity in each of these ROIs. In agreement with the results from the voxel-based analysis (see above), the effect of visual input on left and right MOG was found to depend on the repetition of low SF faces (left: $F_{1,9} = 103$, P < 0.001; right: $F_{1,9} = 171$, P < 0.001) and were larger than the effects of high SF repetition (left: $t_9 = 3.1$, P < 0.05; right: $t_9 = 3.1$, P < 0.05). In contrast, the effect of visual input on IOG depended on the repetition of high SF faces ($F_{1,9} = 47$, P < 0.001) and was larger than the effect of low SF repetition ($t_9 = -5.7$, P < 0.05). In both cases, the inferred input connections into these regions were positive when one SF range of information changed across successive trials and negative when SF

information was repeated. It is worth noting that the attention manipulation did not modulate the inferred input connections for any of these three ROIs (not even for the MOG that was shown above to be affected by attention). This latter result is not surprising as attention effects would be expected to arise from a top down modulation on connection rather then from a bottom up modulation of the stimuli input (Friston and Buchel, 2000).

We next tested the intrinsic connections between regions, without any constraints on the model for the five ROIs, allowing each region to affect any other region throughout the experiment. All significant and marginally significant inferred connections are depicted by black arrows in Figure 3. Robust reciprocal connections were observed between the right (r) and left (l) MOG (lMOG-to-rMOG: $t_9 = 3.2$, $P < 0.01$; rMOG-to-lMOG: $t_9 = 5.4$, $P < 0.01$). There was also a trend of these two ROIs to project to the right FFG (lMOG-to-FFG: $t_9 = 1.94$, $P = 0.083$; rMOG-to-FFG: $t_9 = 1.9$, $P = 0.088$). In contrast, there was no evidence that projections from the right or left MOG influenced the right IOG (lMOG-to-IOG: $t_9 = 0.4$, $P = 0.6$; rMOG-to-IOG: $t_9 = 0.11$, $P = 0.9$) or left ITG (lMOG-to-ITG: $t_9 = 1.6$, $P = 0.14$; rMOG-to-ITG: $t_9 = 1.5$, $P = 0.15$) responses. Neither was there any evidence that the right IOG affected the response of left or right MOG (IOG-to-lMOG: $t_9 = 1.02$, $P = 0.33$; IOG-to-rMOG: $t_9 = 1.3$, $P = 0.2$). However, activity in right IOG influenced the right FFG (IOG-to-FFG: $t_9 = 2.8$, $P < 0.05$) and also influenced left ITG responses (IOG-to-ITG: $t_9 = 3.7$, $P < 0.01$).

We also observed robust inferred backward projections from the right FFG to all three posterior occipital regions (FFG-to-lMOG: $t_9 = 6.9$, $P < 0.01$; FFG-to-rMOG: $t_9 = 3.23$, $P < 0.01$; FFG-to-rIOG: $t_9 = 6.1$, $P < 0.01$), as well as reciprocal connections with the left ITG (FFG-to-ITG: $t_9 = 6.35$, $P < 0.01$; ITG-to-FFG: $t_9 = 4.1$, $P < 0.01$). Similarly, the left ITG also projected backward to both the right IOG and right MOG (ITG-to-IOG: $t_9 = 11$, $P < 0.01$; ITG-to-rMOG: $t_9 = 3.1$, $P < 0.05$), while its projections to the left MOG were not significant (ITG-to-lMOG: $t_9 = 1.8$, $P = 0.1$).

Taken together, these results suggest that, in the context of the present experiment, there were reliable functional connections between the bilateral MOG and right FFG; as well as reliable connections of the right IOG and left ITG with right FFG. However, there were no direct functional connections between MOG and IOG and only partial backward projections from ITG to right (not left) MOG.

In summary, our connectivity results suggest that the outputs from distinct SF processing pathways (in bilateral MOG, right IOG and left ITG) were commonly projected to the right FFG, which in turn projected back to each of these posterior visual regions. But again there was no evidence that outputs from low SF processing in MOG might directly affect high SF processing in the right IOG and left ITG; nor vice versa. However, it is important to note that using hybrid stimuli may have compromised any direct coarse-to-fine processes, as the information in the low SF never predicted the information in the high SF (Schyns and Oliva, 1994; Schyns and Oliva, 1997). Therefore our connectivity results should be taken within the unique context of the stimuli.

Discussion

In this study, we used hybrid SF face stimuli in an effort to avoid effects of non-specific visual cues on our SF manipulations (i.e. by always stimulating both high and low SF ranges together here) while using orthogonal measurements (repetition and attention) to assess regional sensitivity to high or low SF information if the faces. We demonstrated that high and low SF information from faces may undergo both dissociable and convergent processing in different regions of occipito-temporal cortex. Further, we showed that the outputs of these different SF processes in posterior visual areas are apparently projected (as inferred form the DCM

'connections') to a common region in the right fusiform cortex, which responded to both types of SF information.

Specifically, differential processing of distinct SF features in faces was observed in the bilateral MOG, right IOG and left ITG, with the two former areas preferentially responding to visual changes in low SF faces, and the later responding preferentially to changes in high SF faces. Thus, neural responses in these visual regions were distinctively modulated by repetition of the low or high SF components in hybrid faces, as well as additively by selective attention to the low or high SF components of these faces. Intriguingly, however, outputs from MOG, IOG and left ITG were all found to project separately (as inferred from the observed DCM connections) to the right FFG, where low and high SF information could presumably be converge generating face representations independent of SF content.

Dissociable processing of low and high SF information in faces

We investigated processing of low and high SF information from faces using hybrid stimuli, in which low and high SF components were simultaneously presented in a single stimulus but independently manipulated. Preferential responses to low or high SF information in different brain regions were demonstrated by systematically varying the repetition of one or the other SF ranges in faces across successive hybrid stimuli, and by varying attention to one or the other SF range. This design allowed us to manipulate three factors independently, and to test for any interactions between them.

We found that selective processing of low SF information in faces arose in MOG in both hemispheres. These bilateral regions showed increased responses when low SF faces were changed as compared to when they were repeated across successive trials, and when low SF faces were attended as compared to when they were ignored (Table 2, Fig 3b). These findings may accord with a previous fMRI study that report greater responses to low than high SF faces (when presenting these separately) in bilateral dorsal occipital cortices (Vuilleumier et al., 2003) and with neurophysiological data showing that the main projections of the magnocellular pathway, conveying low SF, terminate in the dorsal occipital cortex (Shipp and Zeki, 1995).

In contrast, we found that processing of high SF information in faces primarily involved the right IOG and left ITG. Both regions showed increased responses when high SF faces were changed as compared to when they were repeated (Table 1a, Fig. 2a). But only the left ITG also showed some evidence for effects of attention, with a marginal increase in response when high SF faces were attended as compared to when they were not (Table 1). These results may also accord with some previous fMRI findings showing that right IOG and left ITG are activated by high SF more than by low SF aspects in faces, when these are presented separately (Vuilleumier et al., 2003;Eger et al., 2004a).

It is worth noting that our findings appear to be in good agreement with the above studies (Vuilleumier et al., 2003; Eger et al., 2004a) even though we have used a completely different task (i.e. gender decision task in those studies; detecting an inverted face here), different stimuli (i.e. a single SF range at a time in those studies; hybrid stimuli here) and different measurement for sensitivity to a particular SF range (i.e. subtraction of high versus low SF or vice-versa in those studies; repetition and attention manipulations here). This suggests that our results cannot solely be explained by the task, the stimuli or the particular manipulations used to measure SF sensitivity, instead reflecting a more general pattern. Nevertheless, future research still may be needed to further explore possible effects of different tasks on brain responses to different SF information, as potentially implied by some behavioral (Oliva and Schyns, 1997; Schyns and Oliva, 1997; Schyns and Oliva, 1999) and ERP (Goffaux et al., 2003b) work.

Low and high spatial frequency information is often thought to be related to global and local processing, respectively (e.g. Farah et al., 1998), although in our view this must be considered with caution. A few previous neuroimaging studies have suggested that global and local processing dissociated in the occipito-temporal cortices in a similar vein to the dissociation we have reported for low and high SF. For faces, only one study tested differential effects for local and global processing directly, by manipulating attention (Rossion et al., 2000). Focusing on FFA responses with an fROI approach, they reported an increased response in left FFA for attending the local versus the global aspects of faces. This might conceivably relate to our observation of increased responses in the left ITG for high versus low SF attention. They also found an increased response in the right FFA for attending global versus local elements of faces (Rossion et al., 2000), while we did not observe such differences for attending to one or other SF range here (though note that the response of the right FFA tended to be larger here when attending low SF than high SF, but this trend was not significant). Apparent discrepancies between the previous study and our own SF study on points of details may be hard to interpret as they might relate to differences in the task used, or potential differences between global processing and processing of low SF information per se (see below).

Other studies that investigated global and local processing in the context of high and low SF information, but for non-face stimuli, have reported some similar posterior dissociations to the one we have observed (Fink et al., 1999; Han et al., 2002). Global processing (i.e. low SF) was associated with MOG responses, while local processing (i.e. high SF) was associated with IOG responses. On the other hand, the IOG reported to process mostly local information from low SF stimuli, while the MOG was reported to process global information mostly from high SF stimuli (Fink et al., 1999). Such interactions between global/local and high/low SF processing suggest that the relationship between global/local and high/low SF has to be considered very carefully rather than naively equated. For instance, some high SF information can still allow some global or configural processing (e.g. see Altmann et al., 2003). Furthermore, systematic behavioral tests for any associations of particular SF ranges with global or local processing challenges any simple one-to-one correspondence (Boutet et al., 2003). Thus further research is needed to tease apart the relation between low/high SF and global/local processing of faces, as these seem to be not trivial. Our present results should perhaps be interpreted in terms of SF ranges per se, since this is what we manipulated.

Importantly, our current study tested not only for dissociations between low and high SF processing, but also for possible convergence of these two types of information. Right FFG (and also the functionally defined right FFA) showed robust effects of repetition for faces in either the high or low SF components of hybrids (Tables 1a, 2a). Thus, right FFG responses were increased by changes in either SF ranges (low and high SF) across successive hybrids, but decreased when the same face was repeated in one or the other (or both) SF ranges (Fig. 2c). This finding provides a new type of evidence that accords with other recent studies suggesting that face representation in right fusiform cortex might be relatively independent of low-level visual features (Rotshtein et al., 2005; Winston et al., 2004), generalizing over high and low SF information (Vuilleumier et al., 2003; Eger et al., 2004a). The right IOG also showed some sensitivity to repetition of both high and low SF faces here (see also Eger et al., 2004a), though its sensitivity to repetition of high SF faces was larger (Table 2b).

This complex pattern of regional sensitivities for distinct SF features raises the new question of whether reciprocal interactions might exist between these different regions, such as whether the processing of low SF has a top-down influence on regions that process high SF, as might be envisaged on some 'coarse-to-fine' accounts (e.g. Blackmore and Campbell, 1969); and of whether these separate regions specializing in low or high SF processing may send forward 'convergent' projections to an area such as the right FFG. We directly assessed such issues by

conducting an effective connectivity analysis using the DCM approach, which allowed us to infer functional connections between the implicated regions.

A connectivity model of SF processing of faces in the human occipito-temporal cortex

Our effective connectivity analysis focused on 5 regions of interest (ROIs) identified by our initial standard SPM analysis: the left and right MOG, right IOG, left ITG and right FFG (Fig. 3). The validity of the DCM was supported by its convergence with the results of the conventional voxel-based analysis, as shown by the differential effects of stimuli inputs on the posterior occipital ROIs. The inferred input connections into the bilateral MOG were strengthened with changes of low SF faces (relative to low SF repetitions), and into the right IOG with changes of high SF faces (relative to high SF repetitions). Furthermore, as expected the input connections were only affected by the bottom-up stimulus-driven manipulation of repetition and not by the top-down manipulation of attention. Our DCM analysis also revealed robust reciprocal connections between the homologous left and right MOG throughout the experiment. These strong inter-hemispheric connections are not surprising since it is known that such homologous brain regions are heavily interconnected (Innocenti G.M., 1984;Stephan et al., 2005).

One goal of our connectivity analysis was to test whether outputs of low SF processing (MOG) and high SF processing (IOG and left ITG) might directly project to the right FFG were it converges. Alternatively outputs from low SF processing may project to regions that process high SF information or vice-versa. Our connectivity results suggest that outputs from bilateral MOG projected onto the right FFG but not to the right IOG or left ITG. Similarly, outputs from the right IOG projected onto the right FFG and left ITG, but not to the right or left MOG. These results therefore suggest that, in the context of the current experiment and stimulus types, cortical visual pathways processing low and high SF information were separately fed forward into a third higher-level region, namely the right FFG, where they could presumably be combined. Such a connection structure may be compatible with the 'flexible-usage' hypothesis proposing that low and high SF components in faces can be used flexibly depending on task demands, and hence independently influence perception because they are initially coded separately (Schyns and Oliva, 1994; Schyns and Oliva, 1997; Oliva and Schyns, 1997; Morrison and Schyns, 2001; Peyrin et al., 2005). It may also be compatible with a recent proposed 'simple-to-complex' model that suggest that different aspects of a face are initially processed separately in posterior occipital regions and then are combined in the FFG (Riesenhuber et al., 2004; Jiang et al., 2006).

Our connectivity analysis provide no direct support for the idea that outputs from low SF processing are projected directly to regions preferentially processing high SF information, as might be predicted from the traditional 'coarse-to-fine' hypothesis (although note that the high and low SF faces always differed for the hybrid stimuli here, see below). However, the DCM proposed here might accommodate a modified version of the 'coarse-to-fine' idea in which facilitation of high SF processing by low SF information may arise in the right FFG (see Peyrin et al., 2005; Bar et al., 2006). Intriguingly, we observed robust backwards projections from the right FFG to both the MOG (bilaterally) and right IOG; and from the left ITG to right IOG and right MOG (Fig. 3). These backwards projections might therefore support a flexible role for feedback based on a 'coarse-to-fine' processing stream (Bullier, 2001; Bar, 2003) as well as a distinct 'fine-to-coarse' processing (Peyrin et al., 2005). In this way, information derived from low SF cues and encoded in right FFG might still influence and guide the high SF processing in more posterior cortical regions; this connection structure might similarly allow for a reverse influence of high on low SF processes (Peyrin et al., 2005). It should be emphasized that in the context of the current study, any such influences were apparently not mediated by direct

connections between, for example, low to high SF processes, but only through indirect feedback connections via the right FFG.

It is however important to note that in this experiment, the low and high SF information in one hybrid stimuli never matched because each filtered face (with high or low SF information) always had a different identity and the two faces in each hybrid were misaligned spatially. Therefore, it is possible that this mismatch between low and high SF information precluded efficient influences of the low SF on the high SF processing and vice-versa, because each SF range actually represented a different stimulus (Schyns and Oliva, 1994; Schyns and Oliva, 1997). Future studies could therefore adapt the methodological approach and connectivity analysis introduced here, to assess whether a direct 'coarse-to-fine' connection structure might emerge in a situation where outputs from the low SF face processing pathways might relate naturally to high SF processing.

Relations between repetition and attention effects on visual responses

Our study allowed us to compare two types of experimental manipulations that have commonly been used to test the response selectivity profile of particular cortical regions - namely, stimulus repetition (e.g. Grill-Spector and Malach, 2001) and selective attention (e.g. Vuilleumier et al., 2001; Bentley et al., 2003). Repetition and attention can act on sensory processing through distinct mechanisms, usually thought to involve bottom-up versus top-down factors, respectively. This was supported by the results of the DCM analysis, where the input connections were affected only by SF repetition and not by the attention manipulation. However, note that repetition may implicate a mixture of both bottom-up/stimulus-driven processes and top-down/strategic processes (in some other cases Kristjansson et al., 2002; Schacter et al., 2004; Kristjansson et al., 2006). Our data suggest that these two approaches can provide compatible measures of regional selectivity in some cases, as shown here for the bilateral MOG and left ITG responses, with the former regions being influenced similarly by both repetitions of low SF and attention to low SF; and the latter region being influenced by repetition of high SF and to some extent by attention to high SF. Moreover, we found that the effects of SF repetition and attention overlapped uniquely in a few specific regions within the visual cortex (Tables 1, 2), but not elsewhere across the whole brain.

However, in our experiment, the SF repetition manipulation was generally more informative than the attention manipulation for detecting regional differences in SF sensitivity in occipito-temporal cortices. In particular, repetition effects revealed reliable responses to high SF faces in the right IOG and left ITG, whereas attention to high SF faces only marginally affected the left ITG responses but not the right IOG. This apparent discrepancy between attending low *versus* high SF faces, might relate to the different susceptibility of low and high SF information to selective attention in the ventral occipito-temporal cortex. Accordingly, some previous studies have shown that responses associated with the PC pathway, conveying high SF, are not modulated by selective attention (Di Russo et al., 2001), whereas responses associated with the MC pathway, conveying low SF information, are modulated by attention (Di Russo et al., 2001) though see (Ozgen et al., 2006).

Intriguingly, attention and repetition effects did not interact, in our experiment, suggesting that SF repetition effects could arise in these regions independent of attention control. This finding contrasts with some previously reported results showing that attention can modulate the magnitude and nature of repetition effects in visual cortex (Eger et al., 2004b; Murray and Wojciulik, 2004; Vuilleumier et al., 2005; Yi and Chun, 2005). This apparent discrepancy may result from the different impact of attention mechanisms on object processing, as examined in previous studies, relative to the impact on face processing as examined in our study. There is growing evidence that faces are processed to some extent pre-attentively (Lavie et al., 2003; Palermo and Rhodes, 2006), possibly more so than for other classes of visual objects, which

may be sufficient for the effects of repetition to emerge as here. In addition, in the most previous studies (Eger et al., 2004b; Murray and Wojciulik, 2004; Vuilleumier et al., 2005), repeated stimuli were always attended and followed an initial stimulus that could be either attended or not, whereas in our experiment the initial and repeated stimuli were always both either in the focus of attention, or outside attention. One recent study (Yi and Chun, 2005) that manipulated attention and repetition orthogonally used scenes rather than faces and observed significant interaction only within the parahippocampal gyrus. The parahippocampal gyrus has been implicated in mnemonic processes by numerous studies (Brown and Xiang, 1998; Henson et al., 2003) and hence may react differently to repetition than sensory cortices. Therefore it is important to stress that the lack of interaction in posterior occipito-temporal cortices observed here does not preclude that such interactions can not arise else where in the brain.

Finally, it is worth noting that independent low and high SF repetition effects arose even though the two stimuli spatially overlapped. This further strengthens our observations, underlining the selective sensitivity of different regions in ventral and dorsal occipito-temporal cortices to a specific SF range regardless of the visual stimuli presented at the same time in different range.

Conclusions

Our study demonstrated dissociable processing in occipito-temporal cortex, with distinct regions specialized in processing low or high SF components from faces. The outputs from these posterior cortical regions converge separately onto the right FFG, where this information can presumably be combined to generate a visual representation of a face relatively independent of its SF range. This functional architecture may accord with a 'flexible usage' hypothesis for processing low and high SF depending on task demands (Schyns and Oliva, 1997; Morrison and Schyns, 2001) and with a recent 'simple-to-complex' model for face processing (Riesenhuber et al., 2004; Jiang et al., 2006). It remains to be determined whether similar patterns of selectivity and connectivity are found under different stimulus conditions, such as when high and low SF information in hybrid faces are congruent (Bar et al., 2006), or when different stimulus categories are used, such as common objects or scenes (Peyrin et al., 2005).

Acknowledgments

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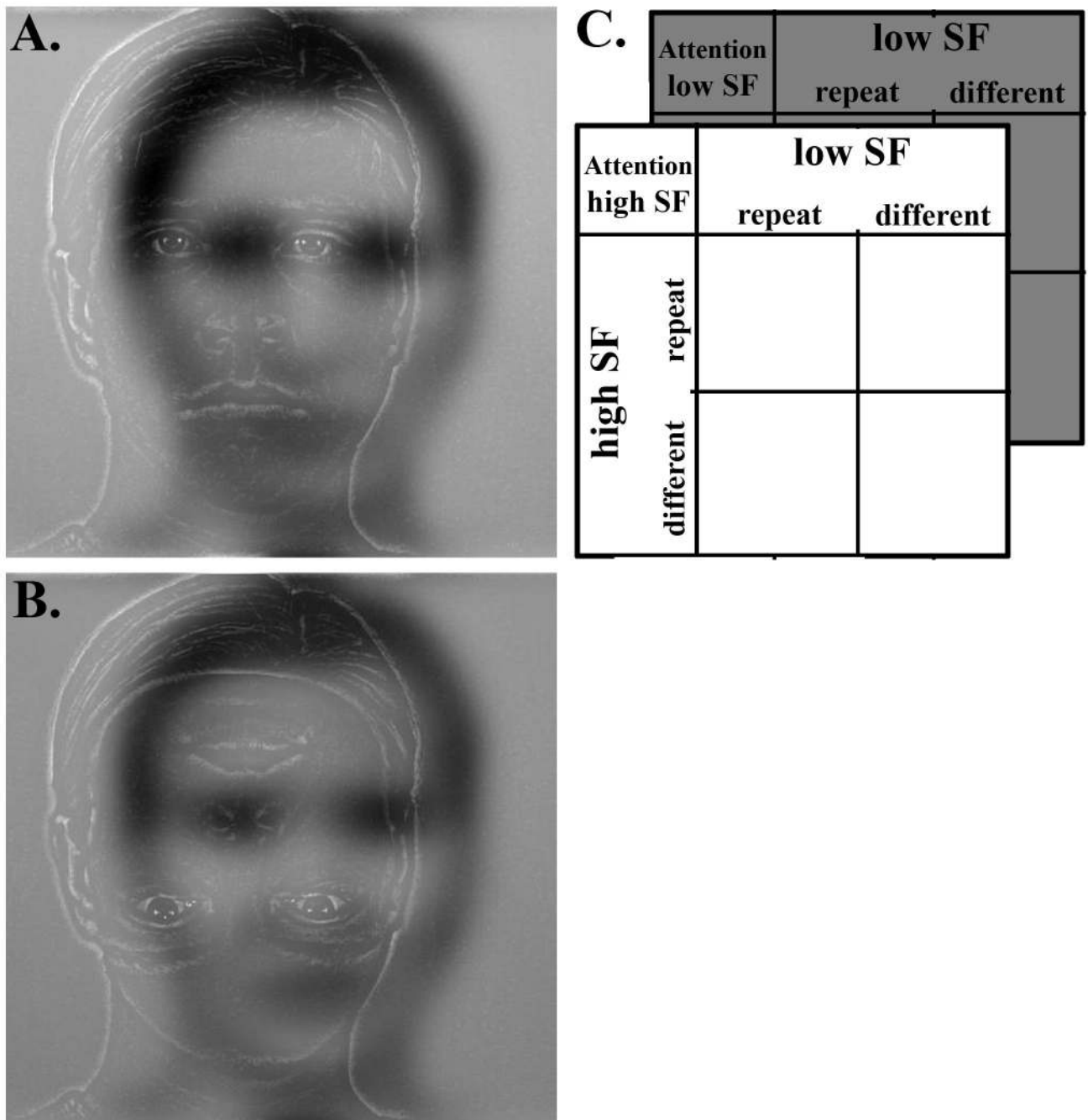
Figure 1. stimuli and experimental design
a) Example of a hybrid stimulus used in the experiment. Each hybrid contained two partly overlapping filtered faces. In this example, the face offset to the right is the low SF face, and the face on the left is the high SF face. The offset direction for each SF filtered face was randomized and counterbalanced across conditions. In this example, the high and low SF faces were scaled to match in contrast. **b)** Example for 'oddball' inverted target stimulus in the high SF attention condition. Note that only the inner features are inverted. In this example, the contrast of the high SF face was maximized while the contrast of the low SF had its original values **c)** Experimental design. There were 2 (attention: to Low SF or high SF) × 2 (low SF: repeat or differ) × 2 (high SF: repeat or differ) factors.
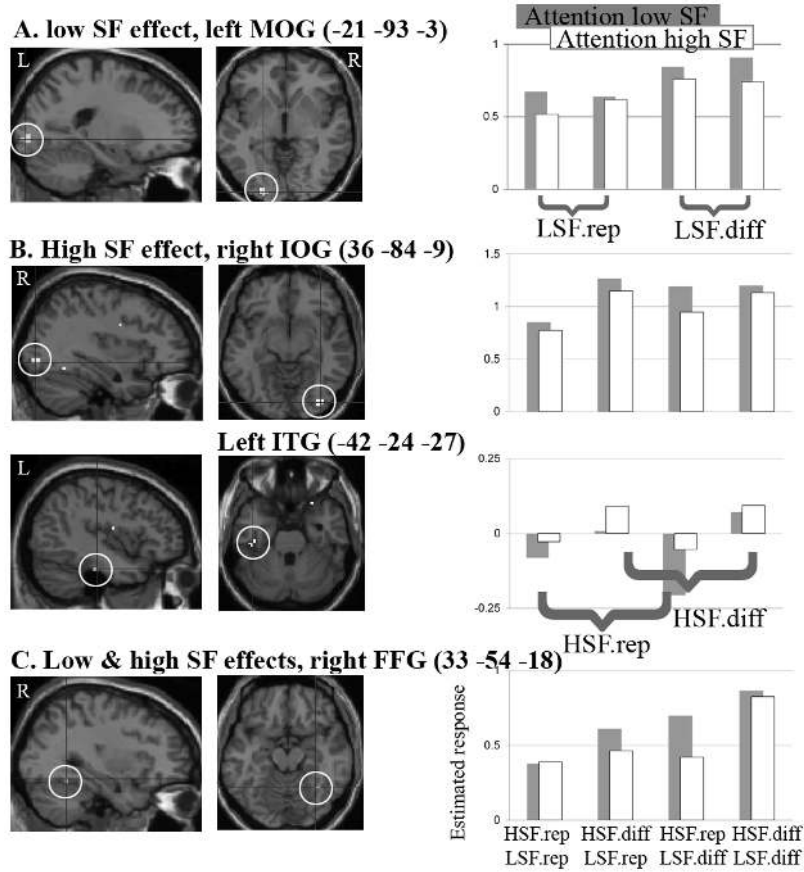
Figure 2. Voxel-based SPM analysis results
On the left, statistical parametric maps (SPMs) depicting regions sensitive to (**a**) low SF changes versus repetition (*lsf.diff* minus *lsf.rep*), (**b**) high SF change versus repetition (*hsf.diff* minus *hsf.rep*), and (**c**) both high and low SF information in faces (conjunction of the two former contrasts). The SPMs are shown at a conventional threshold of P < 0.001, uncorrected, and overlaid on sagital and axial T1 images of one of our participants. The histograms show the parameter estimates for the different experimental conditions, taken from the maxima voxel marked with a circle (exact coordinates are given above each histogram, in MNI space); x-axis depicts the 8 experimental conditions, grey bars for attending low SF and white bars for attending high SF, the full condition labeling can be found at the bottom of the last plot; y-axis depicts the estimated response size (SPM 'beta values'), averaged SEM for all plots was 0.11, ranging from 0.06 to 0.17. Acronyms: LSF/HSF: low/high SF; rep: repeat; diff: different.
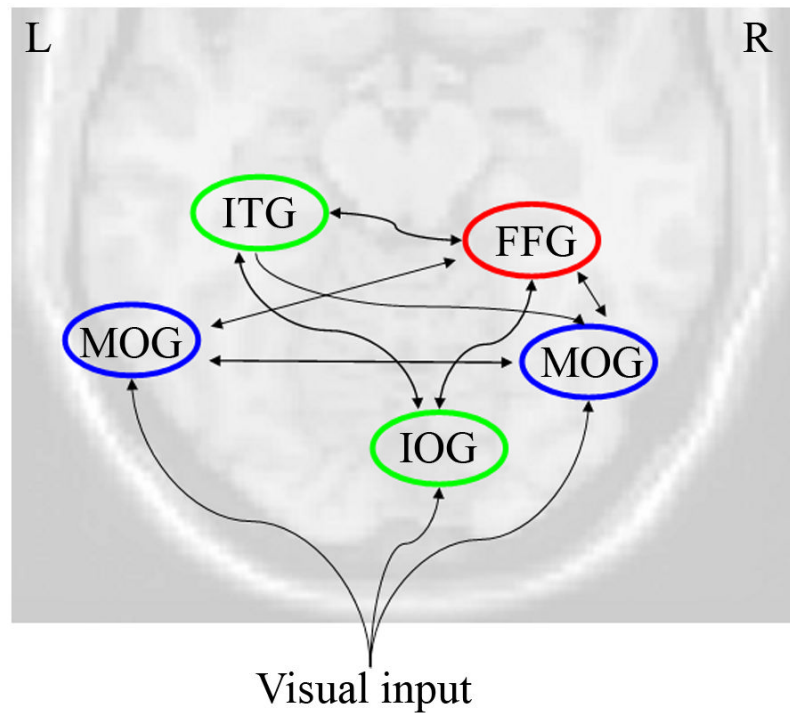
Figure 3. Dynamic causal model results
The five ROIs that were used in the DCM are schematically overlaid on an axial slice of occipital cortex. ROIs primarily sensitive to low SF face repetitions are marked in blue, those sensitive to high SF face repetitions marked in green, and those processing both high and low SF are marked in red. Black arrows describe intrinsic connections that were observed throughout the experiment (independent of repetition and attention manipulations; see text for statistical values). All these connections were excitatory, i.e., positive.

Table 1

low SF effect

Region	H	Z-stats	MNI(x,y,z)		
A. Main effect of low SF repetition: LSF.diff - LSF.rep					
MOG	L	4.05	-21	-93	-3
		3.64	-33	-87	3
		3.29	-39	-75	12
	R	3.40	30	-87	12
		3.25	45	-84	12
FFG	R	3.59	42	-51	-12
IPS	R	3.49	27	-72	33
PCS	R	4.36	24	-12	60
	L	3.34	-24	-12	54
B. Comparison of SF repetition effects: LSF repetition - HSF repetition (masked by LSF.diff - LSH.rep, P < 0.01)					
MOG	L	3.24	-39	-75	9
C. Main effect of low SF attention: LSF.att - HSF.att					
MOG	L	3.20	-39	-93	12
	R	3.11	39	-93	9
IPS	R	3.94	27	-90	33
IFG	R	4.15	60	-6	12
D. Conjunction of LSF repetition & LSF attention					
MOG	L	3.27	-36	-87	6
	R	2.94	33	-90	12

Acronyms: LSF, low SF; HSF, high SF; rep, repeat; diff, different; att, attention; H, hemisphere; MOG, middle occipital gyrus; FFG, fusiform gyrus; PCS, pre-central sulcus; IPS, intrapriatal sulcus; IFG, inferior fomtal gyrus; L, left and R, right hemispheres.

Table 2

High SF effects

Region	H	Z-stats	MNI(x,y,z)		
A. Main effect high SF repetition: *HSF.diff - HSF.rep*					
IOG	R	3.64	36	-84	-9
		3.28	48	-66	-12
ITG	L	3.45	-42	-24	-27
FFG	R	3.20	36	-57	-15
Insula	R	3.40	42	0	15
	L	3.3	-36	-3	18
B. Comparison of SF effects: *HSF repetition -LSF repetition (masked by HSF.diff - HSF.rep, P < 0.01)*					
IOG	R	2.61	54	-63	-9
ITG	L	3.52	-45	-24	-27
SFG	M	3.48	3	6	69
C. Main effect high SF attention: *HSF.att - LSF.att*					
ITG	L	1.8$^£$	-42	-24	-27
aCG	L	3.55	-15	42	3
OFC	L	3.14	-24	48	-6
D. Conjunction of HSF repetition & HSF attention effects					
ITG	L	1.8$^£$	-42	-24	-27

HSF, high SF; LSF, low SF; rep, repeat; diff, different; att, attention; H, hemisphere; IOG: inferior occipital gyrus; ITG: Inferior temporal gyrus; SFG: superior frontal sulcus; aCG: anterior cingulate gyrus; M: middle; L: left and R: right hemispheres

$^£$$P = 0.03$.

Table 3

Regions used in the dynamic casual model (DCM)

	Contrast	*MNI(x,y,z)*	*Z*
Left MOG	*LSF.diff - LSF.rep*	-28(7.5) -85.5(6.8) -2.4(10.6)	3.2(0.6)
Right MOG	*LSF.diff - LSF.rep*	31(13.7) -82.8(11.5) 5.1(12.5)	2.93(0.4)
Right IOG	*HSF.diff - HSF.diff*	37.2(10.8) -83(10.5) -5.7(8)	3.6(0.46)
Left ITG	*HSF.diff - HSF.diff*	-37.8(8.2) -27.6(10) -23.4(13)	3.107(0.38)
Right FFG	Conj ([*LSF.diff - LSF.rep*] & [*HSF.diff - HSF.rep*])	34.2(7.9) -47.7(9.1) -17.7(6.4)	3.2(0.5)

The five regions of interests were identified reliably in 10 out of the 14 subjects who participated in the experiment. The contrast column specifies the statistical tests used to identify each region in each subject. The MNI column gives the average coordinates across all subjects for the location of each region (with the STDEV in parentheses). The Z column shows the average Z statistics across subjects in the first level analysis (and the STDEV in parentheses). The conjunction analysis used to identify the right FFG in each subject was based on the global null hypothesis.