Distinct and Convergent Visual Processing of High and Low Spatial Frequency Information in Faces

Pia Rotshtein[1,2], Patrik Vuilleumier[3], Joel Winston[2], Jon Driver[2,4] and Ray Dolan[2]

[1]Behavioural Brain Science Centre, School of Psychology, University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK, [2]Wellcome Centre for Neuroimaging at University College London, UK, [3]Laboratory for Neurology and Imaging of Cognition, Department of Neuroscience and Clinic of Neurology, University Medical Centre, Geneva, Switzerland and [4]UCL Institute of Cognitive Neuroscience and Department of Psychology, University College London, UK

We tested for differential brain response to distinct spatial frequency (SF) components in faces. During a functional magnetic resonance imaging 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 occipitotemporal 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 occipitotemporal 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, occipitotemporal cortex, repetition

Introduction

Faces provide complex visual information at multiple spatial frequencies (SFs), 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, magnocellular (MC) and parvocellular (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., Livingstone and Hubel 1988; Bullier 2001; Lamme 2001). 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/V5 (middle temporal complex) (Shipp 2001), whereas inputs from PC and MC pathways that reach V1 separately remain partly separated up to V3 and V4 (Shipp and Zeki 1995).

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., Blakemore and Campbell 1969; Fiorentini et al. 1983; Parker and Costen 1999; Schyns and Oliva 1999;

Ojanpää and Näsänen 2003), single-cell recordings in monkeys (Rolls and Baylis 1986), electroencephalographic recording in humans (e.g., McCarthy et al. 1999; Goffaux, Gauthier, and Rossion 2003; Goffaux, Jemel, et al. 2003; Pourtois et al. 2005), and functional magnetic resonance imaging (fMRI) (Winston et al. 2003; Eger, Schyns, and Kleinschmidt 2004; Iidaka et al. 2004; Gauthier et al. 2005). However, these studies have yielded some apparently conflicting conclusions. Some researchers have suggested that low SF are particularly important for face processing (Harmon 1973; Dailey and Cottrell 1999), 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 (Schyns and Oliva 1994, 1997, 1999; Oliva and Schyns 1997; Morrison and Schyns 2001; Goffaux, Jemel, et al. 2003; Peyrin et al. 2005). 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 (Blakemore and Campbell 1969; Marr 1982; Schyns and Oliva 1994; Oliva and Schyns 1997; McCarthy et al. 1999; Parker and Costen 1999; Bullier et al. 2001; Lamme 2001; Bar 2003).

Studies manipulating the SF bands of faces while measuring brain responses using fMRI (Vuilleumier et al. 2003; Eger, Schyns, and Kleinschmidt 2004; Iidaka et al. 2004; Gauthier et al. 2005) 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 occipitotemporal network involved in processing different SF ranges while delineating functional connections between the various regions involved. Results of previous studies (Vuilleumier et al. 2003; Eger, Schyns, and Kleinschmidt 2004; 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, Schyns, and Kleinschmidt 2004), whereas high SF information is reported to be processed in bilateral inferior occipital gyrus (IOG), right FFG (Vuilleumier et al. 2003; Eger, Schyns, and Kleinschmidt 2004), 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, Schyns, and Kleinschmidt 2004; Gauthier et al. 2005).

However, one caveat for the above studies (Vuilleumier et al. 2003; Eger, Schyns, and Kleinschmidt 2004; 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 nonspecific 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 the high SF ranges conjointly, using "hybrid" stimuli that superimpose different low and high SF faces together, as originally introduced by Schyns et al. (Schyns and Oliva 1994, 1997, 1999; Oliva and Schyns 1997; 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 a priori by 2 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, 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, 1999; see Fig. 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 2 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
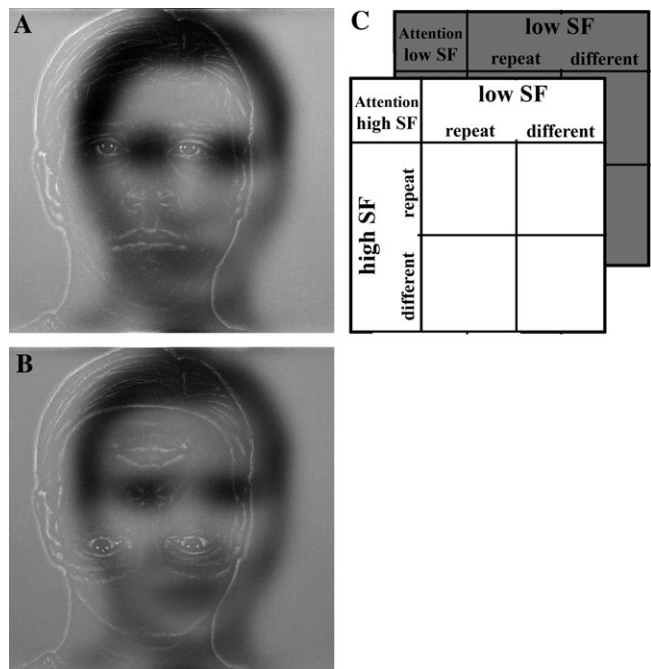
Figure 1. Stimuli and experimental design. (A) Example of a hybrid stimulus used in the experiment. Each hybrid contained 2 partly overlapping filtered faces. In this example, the face offset to the right is the low SF face, and the face on the left is the high SF face. The offset direction for each 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, whereas 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.

(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 precued 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 1 of 2 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 with when it is ignored (O'Craven et al. 1997, 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 2 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 nonface stimuli (Eger, Henson, et al. 2004; 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 occipitotemporal 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, Harrison, and Penny 2003), 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 occipitotemporal cortex converge in the right FFG.

Materials and Methods

Subjects
Fifteen healthy volunteers were recruited (8 females, mean age 29.5 years, range 22–43 years, all right handed). All reported normal vision, no past neurological or psychiatric history, and no structural brain abnormalities. Unfortunately, 2 months after the experiment, one female subject was diagnosed as having multiple sclerosis 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 and Institute of Neurology, London.

Stimuli
Fifty-six faces (28 females) with neutral expressions were chosen from the Karolinska Directed Emotional Faces set (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 because 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 cutoff frequency corresponds to 50% of the magnitude of the filter. Therefore, to minimize overlap between frequencies, the distance between the cutoff frequencies was 1.5 octaves. These cutoffs were chosen to fit previous psychophysical findings suggesting that MC visual pathways are preferentially sensitive to SF below 1.5 cycles per degree, whereas 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), whereas the original contrast gradient was kept for the other half, counterbalanced across subjects. Importantly, the 2 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 nonspecific visual cues with our SF manipulation. Each hybrid face was created by overlapping 2 filtered faces, one with high and one with low SF, each depicting a different identity. These 2 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 2 different scaling procedures (i.e., maximal contrast for low SF or its original contrast; Figs. 1A,B, 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 × 2 × 2 factorial design (Fig. 1C). The 3 critical factors were low SF faces (repeat vs. differ), high SF faces (repeat vs. differ), and selective attention (low vs. high SF). There were 30 events in each condition, distributed in a mixed blocked design. Each hybrid stimulus was shown for 500 ms with an interstimulus interval (ISI) of 750 ms. 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 (1-6) 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 6–9 s. 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 4 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 blood oxygen level–dependent contrast weighted echo-planar images (EPIs) for the functional scans. Images were reconstructed using trajectory-based reconstruction (Josephs et al. 2000). Twenty-six oblique slices, 3 mm thickness, with 1.5 mm gap were acquired, resulting in an in-plane resolution of $3 \times 3 \times 4.5$ mm, with 90° flip angle, 50 ms echo time, and 2340 ms slice repetition time. To minimize susceptibility artefacts, slices were tilted at 30° along the frontal-temporal cortex (Deichmann et al. 2003). Subsequent to the functional scans, a T1-weighted structural image ($1 \times 1 \times 1$ mm resolution) was acquired for coregistration and display of the functional data.

Data Analysis

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

Voxel-Based Analysis

Voxel-based analysis was performed across subjects using random-effects analysis (Penny et al. 2003). We first tested whether the different scaling procedures affected occipitotemporal 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 hemodynamic response function (Friston, Glaser, et al. 2003). 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 1/128 Hz. For each subject, we calculated a contrast that tested for any main effect of scaling (i.e., type of low SF image) and additional set of contrasts for each simple effect of interest under the 2 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 relatively unconservative 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 8 experimental conditions (resulting from our $2 \times 2 \times 2$ design, Fig. 1C) with further regressors of no interests for the fillers, targets, the movement parameters, and the harmonics depicting the frequencies up to 1/128 Hz. The regressors were convolved with the canonical hemodynamic response function (Friston, Glaser, et al. 2003). 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 voxelwise. Consistent effects across subjects (random-effects second-level analysis; Penny et al. 2003) were then tested for using 1-sample t-tests on the resultant first-level contrast images. Comparisons across main effects (high vs. 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 both the repetition and attention manipulations and for regions that showed sensitivity to both 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. 1999, 2005). Here we tested for voxels showing independent significant responses to both 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 modeling (DCM; Friston, Glaser, et al. 2003) as implemented in SPM2 to estimate the effective connectivity (or functional coupling) between putative occipitotemporal regions (activated by our basic contrasts) 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 occipitotemporal 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 interindividual 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 2 types of connection: The first is the effect of the stimulus input that perturbs the network. Here, these inputs were defined as the 8 experimental conditions (reflecting the $2 \times 2 \times 2$ design). We anticipated that the effects of stimulus inputs would mirror the effects observed in the voxel-based analysis for the stimulus-driven manipulation, that is, 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 5 (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 1-sample t-tests against the null hypothesis that the connection strength equaled zero.

Functional Localizer Analysis

Although many researchers, particularly in the field of face processing, have advocated a functional ROIs (fROIs) 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, although we initially conducted a conventional SPM analysis, we subsequently implemented fROI approach to our data, focusing on the right FFA. The method for localizing FFA within each individual subject was as followed:

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

Stimuli. Ten 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 gray) but with the outline of the face kept intact. Ten 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 gray 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 11-s duration were separated with a 6.3-s fixation point presented on a gray background. Each stimulus was presented for 250 ms, with an stimulus onset asynchrony of 850 ms. 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 preprocessing. The data were acquired using an identical magnetic resonance sequence and protocol as above and were preprocessed using an identical procedure as above.

ROI analysis. ROI analysis was performed using the MarsBar toolbox (Brett et al. 2002) that is implemented in SPM2. In each subject, the right 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 2 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 occipitotemporal 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. Because no effects were found for the different scaling procedure (i.e., maximal or original low SF contrast, see Materials and Methods) and no significant interactions were found in occipitotemporal cortices between this factor and the others, here we report and discuss SPM results for the main effects or conjunction of the 3 factors (high SF repetition, low SF repetition and attention) only.

Functional Sensitivity of Occipitotemporal Cortex to Distinct SF Information

Preferential processing of low 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 and Fig. 2*A*). To confirm the selectivity of these effects for low SF, we further compared the effects of low versus high

Table 1
LSF effects

Region	H	Z-statistics	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 att: 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 and LSF att					
MOG	L	3.27	−36	−87	6
	R	2.94	33	−90	12

Note: LSF, low SF; HSF, high SF; rep, repeat; diff, different; att, attention; H, hemisphere; PCS, precentral sulcus; IPS, intrapriatal sulcus; IFG, inferior forntal gyrus; L, left; and R, right hemispheres.

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 (Table 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 2 effects did not significantly interact (for 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 high 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 and Fig. 2*B*). 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 because 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. 2*A*). 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 arises 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
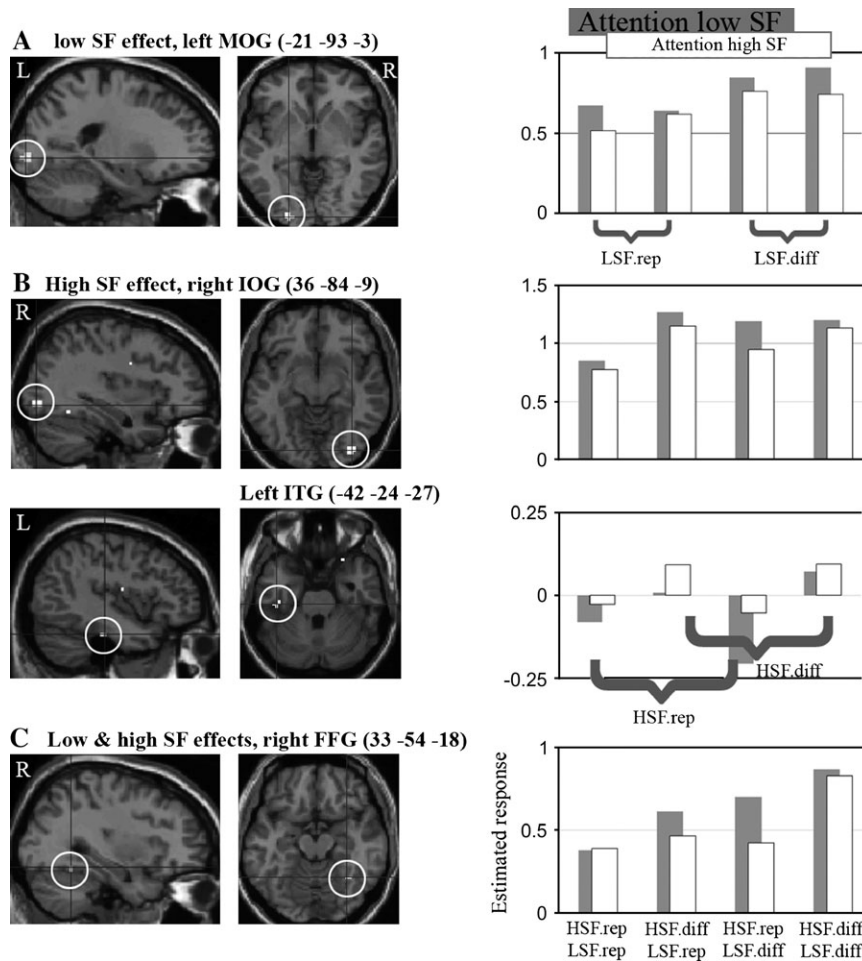
Figure 2. Voxel-based SPM analysis results. On the left, statistical parametric maps (SPMs) depicting regions sensitive to (*A*) low SF changes versus repetition (LSF diff minus LSF rep), (*B*) high SF change versus repetition (HSF diff minus HSF rep), and (*C*) both high and low SF information in faces (conjunction of the 2 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 within the circle (exact coordinates are given above each axial slice, in MNI space); *x* axis depicts the 8 experimental conditions, gray 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 standard error mean for all plots was 0.11, ranging from 0.06 to 0.17. LSF/HSF, low/high SF; rep, repeat; diff, different.

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. 2*C*) 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 2 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 FFA responses. We also implemented an fROI analysis for the right FFA. As described in the Materials and Methods, 12 of our 14 original subjects took part in a separate functional localizer scan that 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 (±standard deviation): 43(±9) –45(±6) –20(±7), cluster size: 304(±229) × 3 mm³). 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

Table 2
HSF effects

Region	H	Z-statistics	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 of high SF att: HSF att − LSF att					
ITG	L	1.8[a]	−42	−24	−27
aCG	L	3.55	−15	42	3
OFC	L	3.14	−24	48	−6
D. Conjunction of HSF repetition and HSF att effects					
ITG	L	1.8[a]	−42	−24	−27

Note: HSF, high SF; LSF, low SF; rep, repeat; diff, different; att, attention; H, hemisphere; SFG, superior frontal sulcus; aCG, anterior cingulate gyrus; OFC, orbital frontal cortex; M, middle; L, left; and R, right hemispheres.
[a]P = 0.03.

Table 3
Regions used in the 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] and [HSF diff − HSF rep])	34.2 (7.9)	−47.7(9.1)	−17.7 (6.4)	3.2 (0.5)

Note: The 5 ROIs were identified reliably in 10 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 standard deviation [SD] in parentheses). The Z column shows the average Z-statistics across subjects in the first-level analysis (and the SD in parentheses). The conjunction analysis used to identify the right FFG in each subject was based on the global null hypothesis. HSF, high SF; LSF, low SF; rep, repeat; diff, different; att, attention.

left and right MOG was affected by repetitions of low SF faces and by attention to those faces but was 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, whereas 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, Schyns, and Kleinschmidt 2004), but this effect was significantly stronger with repetitions of high SF faces than with low SF faces (see above and Fig. 2*B*). We then tested the effective connectivity between all the above regions using DCM.

Effective Connectivity Analysis

The DCM we designed was based on the results of the voxel-based analysis (see above). Focusing on occipitotemporal cortices, the model included 5 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. 3). 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 5 ROIs (P < 0.005, uncorrected) were reliably delineated in 10 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 2 types of connections, as implemented in SPM2 (see Friston, Harrison, and Penny 2003 and our Materials and 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 8 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 effects of visual input on left and right

MOG were 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 3 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 than from a bottom-up modulation of the stimulus input (Friston and Buchel 2000).

We next tested the intrinsic connections between regions, without any constraints on the model for the 5 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 2 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 3 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), whereas its projections to the left MOG were not significant (ITG-to-lMOG: $t_9 = 1.8$, P = 0.1).
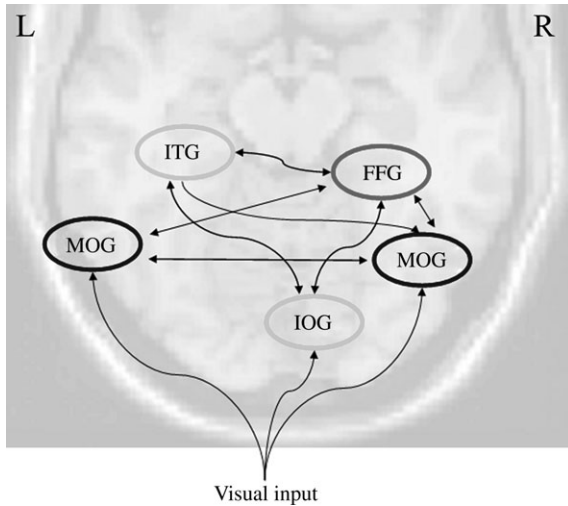
Figure 3. DCM results. The 5 ROIs that were used in the DCM are schematically overlaid on an axial slice of occipital cortex. ROIs primarily sensitive to low SF face repetitions are marked in black, those sensitive to high SF face repetitions are marked in light grey, and those processing both high and low SF are marked in grey. 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, that is, positive.

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, 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 nonspecific visual cues on our SF manipulations (i.e., by always stimulating both high and low SF ranges together here) while using orthogonal manipulations (repetition and attention) to assess regional sensitivity to high or low SF information in the faces. We demonstrated that high and low SF information from faces may undergo both dissociable and convergent processing in different regions of occipitotemporal 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 2 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 converge to generate 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 3 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 with when they were repeated across successive trials and when low SF faces were attended as compared with when they were ignored (Table 1 and Fig. 2A). 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 MC 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 with when they were repeated (Table 2 and Fig. 2B). 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 with when they were not (Table 2C,D). 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, Schyns, and Kleinschmidt 2004).

It is worth noting that our findings appear to be in good agreement with the above studies (Vuilleumier et al. 2003; Eger, Schyns, and Kleinschmidt 2004) 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 vs. 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, 1999) and event related potentials (Goffaux, Jemel, et al. 2003) work.

Low and high SF 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 occipitotemporal 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), whereas 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 nonface 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, whereas local processing (i.e., high SF) was associated with IOG responses. On the other hand, the IOG was reported to process local information mostly from low SF stimuli, whereas 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 challenge any simple one-to-one correspondence (Boutet et al. 2003). Thus, further research is needed to tease apart the relations 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 because 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 2 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 and 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 (Winston et al. 2004; Rotshtein et al. 2005), generalizing over high and low SF information (Vuilleumier et al. 2003; Eger, Schyns, and Kleinschmidt 2004). The right IOG also showed some sensitivity to repetition of both high and low SF faces here (see also Eger, Schyns, and Kleinschmidt 2004), 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., Blakemore 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 Occipitotemporal Cortex

Our effective connectivity analysis focused on 5 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 stimulus 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 interhemispheric connections are not surprising because it is known that such homologous brain regions are heavily interconnected (Innocenti 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 where these converge. 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, 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 suggests 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 backward 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 backward projections might therefore support a flexible role for feedback based on a coarse-to-fine processing stream (Bullier 2001; Bar 2003) as well as 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 2 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, 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 2 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, 2006; Schacter et al. 2004). Our data suggest that these 2 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 and 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 occipitotemporal 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, Henson, et al. 2004; 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 preattentively (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 most previous studies (Eger, Henson, et al. 2004; 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 occipitotemporal cortices observed here does not preclude that such interactions cannot arise else where in the brain.

Finally, it is worth noting that independent low and high SF repetition effects arose even though the 2 stimuli spatially overlapped. This further strengthens our observations, underlining the selective sensitivity of different regions in ventral and

dorsal occipitotemporal cortices to a specific SF range regardless of the visual stimuli presented at the same time in a different range.

Conclusions

Our study demonstrated dissociable processing in occipitotemporal 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).

Notes

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