Electrophysiological and Haemodynamic Correlates of Face Perception, Recognition and Priming

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Face perception, recognition and priming were examined with event-related functional magnetic resonance imaging (fMRI) and scalp event-related potentials (ERPs). Face perception was associated with haemodynamic increases in regions including bilateral fusiform and right superior temporal cortices, and a right posterior negativity (N170), most likely generated in the superior temporal region. Face recognition was associated with haemodynamic increases in fusiform, medial frontal and orbitofrontal cortices, and with a frontocentral positivity from 550 ms poststimulus. Face repetition was associated with a positivity from 400 to 600 ms and behavioural priming. Repetition of familiar faces was also associated with earlier onset of the ERP familiarity effect, and haemodynamic decreases in fusiform cortex. These data support a multi-component model of face-processing, with priming arising from more than one stage.

Introduction

There is considerable evidence that the brain possesses systems that are important for processing faces. Moreover, these systems appear specialized for different aspects of face-processing. Face-responsive neurons in the inferior temporal gyrus (ITG) of the macaque brain, for example, are sensitive to face identity, whereas neurons in the superior temporal sulcus (STS) are relatively more sensitive to facial expression (Hasselmo *et al*., 1989). Evidence for specialization of face processes in humans comes from prosopagnosia, a face-processing deficit following inferior occipitotemporal lesions (Damasio *et al*., 1990). Some patients appear impaired in their perception of faces ('apperceptive prosopagnosia'), whereas others appear able to perceive faces, but unable to recognize familiar ones ('associative prosopagnosia') (De Renzi *et al*., 1991); though see Davidoff and Landis (Davidoff and Landis, 1990), Farah *et al*. (Farah *et al*., 1995) and Gauthier *et al*. (Gauthier *et al*., 1999).

An influential model of face processing was proposed by Bruce and Young (Bruce and Young, 1986). This model includes an initial stage of 'structural encoding', after which at least two processing routes diverge, one for face recognition and others for detection of facial attributes such as sex, expression and gaze. The recognition route contains 'face recognition units' (FRUs), which contain perceptual representations of familiar faces, and 'personal identity nodes' (PINs), which are required for subsequent retrieval of semantic information about the corresponding person. Apperceptive prosopagnosia can be explained by damage to the structural encoding stage; associative prosopagnosia is most simply explained by damage to FRUs, or a disconnection between FRUs and PINs, given that semantic information is normally accessible via other means (such as a person's voice).

The Bruce and Young (Bruce and Young, 1986) model has also been used to account for the behavioural phenomenon of repetition priming. Repetition priming refers to faster (or more accurate) processing of repeated versus initial presentations of a stimulus. For example, people's reaction times (RTs) to recognize a face are generally faster if it was seen recently. According to the model, repetition priming reflects the strengthening of FRU–PIN connections (Burton *et al*., 1999). This locus for priming is based mainly on two findings from Ellis *et al.* (Ellis *et al*., 1990). Firstly, priming was found for familiar faces using a familiarity-judgement task, but not for unfamiliar faces (explicable if no FRUs exist for unfamiliar faces). Secondly, priming was not found for familiar or unfamiliar faces using expression- or sex-judgement tasks (explicable if such tasks do not utilize the recognition route). A recent study by Goshen-Gottstein and Ganel (Goshen-Gottstein and Ganel, 2000), however, found priming of sex-decisions for both familiar and unfamiliar faces, provided that obvious sex-predictive features, particularly the hair, were removed. They argued that participants' use of simple heuristics such as hair-style when judging the sex of faces like those of Ellis *et al*. (Ellis *et al*., 1990) obscured any priming effects. Their data suggest alternative loci for priming, perhaps within a single- route in which both sex and identity are processed (Ganel and Goshen-Gottstein, 2002), or at earlier stages in the Bruce and Young (Bruce and Young, 1986) model, prior to recognition, such as structural encoding. Importantly for present purposes, the use of sex-decisions on hair-deleted faces allows the study of repetition priming with and without face recognition (i.e. for both familiar and unfamiliar faces).

Haemodynamic techniques such as fMRI have identified brain regions associated with face-processing, most notably in fusiform, ventral occipital and superior temporal cortex. Haxby *et al*. (Haxby *et al*., 2000) associated the lateral midfusiform (LMF) with processing the invariant aspects of faces, corresponding to the recognition route of Bruce and Young (Bruce and Young, 1986) and possibly the ITG in the Macaque. The precise role of the LMF is contentious however. Some argue that its function is not specific to faces (Gauthier *et al*., 2000; Haxby *et al*., 2001; Malach *et al*., 2002). Furthermore, though it is generally activated during face perception, when comparing face versus non-face stimuli for example (Kanwisher *et al*., 1997), it is not always activated during face recognition, when comparing familiar versus unfamiliar faces for example (Gorno-Tempini *et al*., 1998; Nakamura *et al*., 2000). For reasons not fully understood however, other studies have found effects of both face recognition and priming in the LMF (George *et al*., 1999; Henson *et al*., 2000, 2002).

The temporal characteristics of face-processing have been elucidated by electrophysiological techniques. Intracranial ERPs reveal a negative potential peaking ~200 ms post-stimulus, in both ventral and lateral temporal regions, which is greater to faces than scrambled faces or non-face objects (Allison *et al*., 1999). A similar negativity has been recorded extracranially, which typically peaks around 170 ms over posterior scalp sites

(the 'N170') (Bentin *et al.*, 1996). Interestingly, these 'early' potentials do not appear sensitive to the familiarity or repetition of faces. Such effects only arise in later ERP components (Puce *et al.*, 1999; Bentin and Deouell, 2000; Eimer, 2000; Schweinberger *et al.*, 2002a). These data suggest that haemodynamic correlates of recognition and priming in the fusiform reflect later, possibly re-entrant, neural effects (Henson and Rugg, 2002).

The studies reviewed above have not directly compared the processes of face perception, recognition and priming. Therefore, in the present study, we used scalp ERPs and event-related fMRI (efMRI) within a common paradigm (see Fig. 1), in which priming was indexed by RTs for sex-decisions to hair-deleted faces. This allowed us to compare these processes in terms of both their temporal evolution (in the ERP data) and their cerebral localization (in the efMRI data). We operationalized face perception by comparing unfamiliar faces versus scrambled faces; face recognition by comparing familiar with unfamiliar faces; and face priming by comparing repeated with initial presentations of both familiar and unfamiliar faces.

Materials and Methods

Participants

Forty-four British volunteers gave written consent to participate in the study: 21 for the efMRI experiment and 23 for the ERP experiment. The data from three participants in the efMRI experiment, and from five in the ERP experiment, were not analysed: four because of technical problems and four because of a failure to recognize enough famous faces. The 18 remaining participants in the ERP experiment contained 10 men and eight women, aged 19–35 (median 23), and the 18 participants in the efMRI experiment contained 10 men and eight women, aged 23–32 (median 28). All volunteers reported themselves to be right-handed and in good health, with no history of neurological illness. The study was of the type approved by university ethics committees (references: UCL/UCLH 99/0048, NH/ION 00/N031).

Materials

The familiar faces were of 32 famous men and 32 famous women; the unfamiliar faces were of 32 men and 32 women previously unseen by participants. The faces were derived from sets used by Goshen-Gottstein and Ganel (Goshen-Gottstein and Ganel, 2000) and Gorno-Tempini *et al.* (Gorno-Tempini *et al.*, 1998). All faces were greyscale images of frontal or three-quarter views of Caucasian adults, with a neutral or smiling expression. No face had obvious sex-predictive features such as facial hair, jewellery, glasses or excessive cosmetics. All faces were edited to remove scalp hair. The contrast between face and background was matched subjectively. A 'scrambled' version of each face was created by permuting the phase of each spatial frequency in the image while maintaining a constant power density spectrum (see Fig. 1). These scrambled images were subsequently cropped by the outline of the original face to equate retinal size (resulting in a small potential change in spectral power). For the efMRI experiment, stimuli were presented on a mirror 30 cm above the participant; for the ERP experiment, stimuli were presented on a monitor ~90 cm in front of the participant. In both cases, the stimulus was scaled so as to subtend horizontal and vertical visual angles of ~4 and 5°, respectively.

Procedure

The experiment was run in two phases, with a short rest period of ~1 min in-between. During Phase 1, participants rated the left–right symmetry, relative to an imaginary vertical line through the centre of each image, of 64 faces intermixed with 64 scrambled versions of those faces. This task can be performed on both faces and scrambled faces, and encourages configural processing of faces, with no requirement for semantic elaboration (minimizing explicit memory encoding). The faces comprised 16 from each of the four categories of male/female and familiar/unfamiliar. Participants indicated one of four symmetry ratings using the index and middle fingers of each hand (ordered left-to-right or right-to-left from 1 = least to 4 = most symmetrical). An idea of the range of different symmetries was provided by a prior practice phase with eight surplus stimuli. Participants were informed that they may recognize some faces as famous people, but that this was irrelevant to their task. They were not informed about Phase 2 until finishing Phase 1.

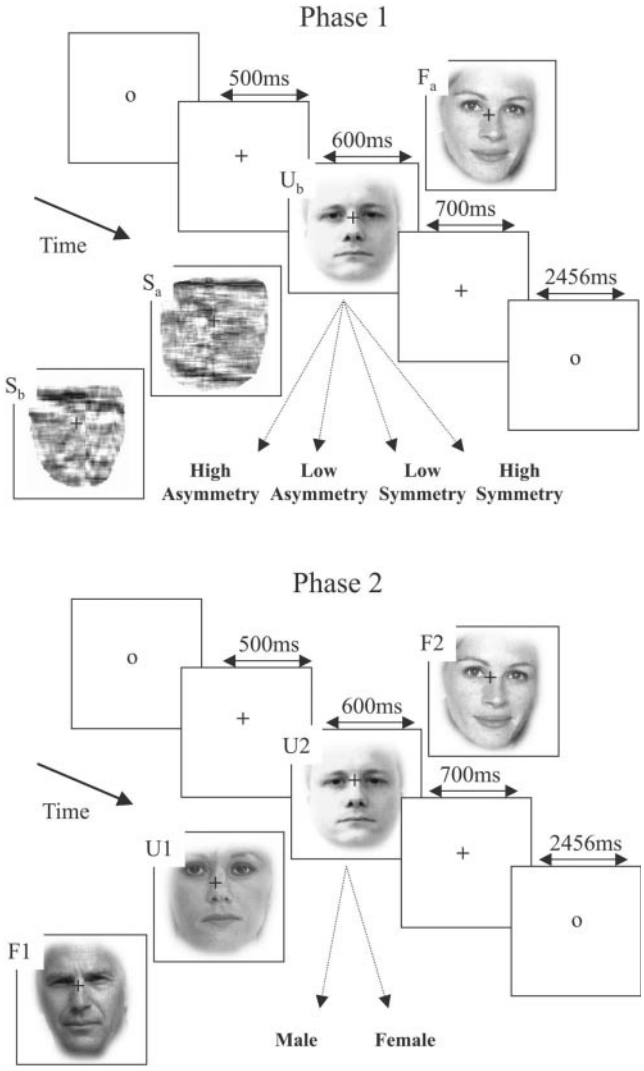

Figure 1. Trial format in Phase 1 and Phase 2, together with examples of Unfamiliar (U), Familiar (F) and Scrambled (S) faces in Phase 1, and first (F1 and U1) and second (F2 and U2) presentations of familiar/unfamiliar faces in Phase 2. Each face in Phase 1 (e.g. Fa and Ub) had a corresponding scrambled version (i.e. Sa and Sb).

During Phase 2, participants were presented with 128 non-scrambled faces, half of which were seen in Phase 1, and indicated whether each face was male or female using their index fingers. They were asked to respond as accurately and as quickly as possible. Again, a practice session of eight extra faces was provided. Participants were informed that they may notice some faces repeated from Phase 1, but that this was irrelevant to their task. The mean time between presentations of a face repeated from Phase 1 to Phase 2 was ~12 min, with a maximal possible range of 8–263 intervening faces. A final debriefing followed Phase 2, in which participants were shown all the faces and indicated whether or not they recognized each face as famous. They did not have to name the person, but did have to be sure they had seen the person somewhere before starting the experiment (hence use of the term 'recognition' rather than 'identification', though most of the recognized faces were likely to be identified as particular persons).

The timing of stimulus events was identical during both phases and is shown in Figure 1. Participants were instructed to fixate on a symbol in the centre the screen at all times. A trial was initiated when the fixation

symbol changed from a circle to a cross, 500 ms after which the stimulus was presented, for 600 ms. The fixation cross remained during the stimulus and for 700 ms afterwards. The face was displayed such that the fixation cross occurred between and slightly below the eyes. Participants in the ERP experiment were instructed not to blink while the cross was on the screen. Participants could respond at any time from the appearance of the stimulus until the next trial. The stimulus onset asynchrony (SOA) was 4256 ms. The order of stimuli and assignment of faces to conditions was randomized for each participant within an experiment. The assignment of responses to fingers was counter-balanced across participants. Four surplus stimuli comprised a 'run-in' at the start of each phase, but were not analysed.

EEG Acquisition

The electroencephalogram (EEG) was recorded from 29 silver/silver chloride electrodes using an elasticated cap (Falk Minow Easycap 'montage 10', http://www.easycap.de./easycap/; montage inset in Fig. 2), plus an electrode on each mastoid process. Recordings were made with reference to a mid-frontal electrode and subsequently algebraically re-referenced (see below). Impedances were nearly always less than 5 K Ohms. Vertical and horizontal electro-oculograms (EOG) were recorded from electrode pairs situated above and below the right eye and on the outer canthi. EEG and EOG were amplified with a bandwidth of 0.03–30 Hz (3 dB points) and digitized (12 bit) at a rate of one point/5 ms. The recording epochs began 100 ms prior to stimulus onset (baseline) and lasted 1280 ms.

fMRI Scanning

A 2 T Vision system (Siemens, Erlangen, Germany) was used to acquire 32 T_2*-weighted transverse echoplanar images (EPI) (64 × 64 3 × 3 mm^2 pixels, T_E = 40 ms) per volume, with blood oxygenation level dependent (BOLD) contrast. EPIs comprised 2 mm thick axial slices taken every 3.5 mm, acquired sequentially in a descending direction. Each phase comprised 240 volumes collected continuously with a repetition time (T_R) of 2432 ms. The first five volumes of each session were discarded to allow for equilibration effects. The ratio of SOA to T_R ensured that the impulse response was sampled every 610 ms (over trials).

Basic Analysis Strategy

There were three conditions of interest for Phase 1 — familiar faces (F), unfamiliar faces (U) and scrambled faces (S) — and four conditions for Phase 2 — initial and repeated presentations of familiar and unfamiliar faces (F1, F2, U1 and U2, respectively). The same basic analyses — repeated-measures analyses of variance (ANOVAs) — were performed on the behavioural, ERP and efMRI data. These ANOVAs were based on a number of planned contrasts. Two contrasts were tested for Phase 1 data: (i) unfamiliar versus scrambled faces ('face perception', in the absence of recognition), and (ii) familiar versus unfamiliar faces ('face recognition'). Four contrasts were tested for Phase 2 data: first versus second presentations for (i) familiar and (ii) unfamiliar faces ('face priming'), (iii) the interaction between familiarity and repetition, and (iv) familiar versus unfamiliar faces for first presentations only (face recognition in Phase 2, unconfounded by repetition). A final contrast across phases was tested to see whether the effects of face familiarity depended on the task (namely, the interaction between first presentations of familiar versus unfamiliar faces and Phase 1 versus 2).

In the behavioural analyses, these contrasts were supplemented by a factor of participant group (ERP/efMRI). In the ERP analyses, the contrasts were supplemented by two factors characterizing electrode position (see below), and repeated for time windows of interest. In the efMRI analyses, the contrasts were supplemented by a factor of response function (see below), and repeated across voxels. The main difference between the ERP and efMRI analyses was thus, in keeping with conventional methods, whether ANOVAs were performed separately according to time (ERP time-window), or according to space (MRI voxel).

Behavioural Analyses

Reaction times less than 200 ms or greater than 3500 ms were excluded, following Goshen-Gottstein and Ganel (Goshen-Gottstein and Ganel, 2000). All trials were restricted to faces that were correctly judged as familiar or unfamiliar during debriefing. Trials in Phase 2 were further restricted to correct sex decisions. Six participants in the efMRI group were excluded from Phase 1 analyses because of technical problems recording key presses. Symmetry ratings in Phase 1 were collapsed into a univariate variable by linear weighting (–3, –1, 1, 3) of the four response categories, scaled to a minimum of –100% (asymmetric) and maximum of +100% (symmetric). ANOVAs were performed on this symmetry scale and on median RTs. Phase 2 ANOVAs were performed on error proportions and on RTs. Owing to their skewed nature across participants, RTs were analysed after a log transform, and error proportions after a square-root transform. Only effects surviving $P < 0.05$, in the absence of higher-order interactions, are reported.

ERP Analysis

Trials that contained blinks, horizontal or non-blink eye movements, A/D saturation, or EEG drifts were rejected on the basis of visual inspection at an individual participant level without knowledge of conditions. Trials were averaged according to condition and behaviour as described above. For four participants, recordings were lost for right occipital (site 42), left temporal (site 47) and right mastoid (RM) sites due to technical problems. These sites were not used in the amplitude or topographic analyses (see below). The RM problem however meant that the data were re-referenced to the left mastoid rather than linked mastoids. (When recordings from the 14 remaining participants were referenced to linked mastoids, the results were very similar to those from all 18 participants with a left mastoid reference, including the right-lateralization of the N170; see Results.) All ERP waveforms were based on a minimum of 60% artefact-free trials per condition (~25 on average). The average waveforms were low-pass smoothed to 20.7 Hz using a zero phase-shift filter.

ERPs were quantified by measurement of the mean amplitude (with respect to mean pre-stimulus baseline) of specific latency regions. ANOVAs included data from Easycap sites 49, 8, 37, 45, 14, 41 (corresponding approximately to F7, FZ, F8, PO7, PZ, PO8 in the extended 10–20 system; see Fig. 2 inset), factorized by laterality (left–central–right) and rostrality (anterior–posterior). These sites were selected on the basis of related effects in previous studies. Differences in scalp topographies were tested by ANOVAs of amplitude differences over all valid sites (n = 27), after normalizing to the range over sites (McCarthy and Wood, 1985). All ANOVAs used a Greenhouse–Geisser correction for non-sphericity. Scalp potential and current source density (CSD) maps were created by spline interpolation (Perrin *et al.*, 1987).

efMRI Analysis

Analysis of the fMRI data was performed with Statistical Parametric Mapping (SPM99, Wellcome Department of Cognitive Neurology, London, UK). All volumes were coregistered to the first volume, and then unwarped to allow for EPI distortions (Andersson *et al.*, 2001). The time-series for each voxel was realigned temporally to acquisition of the middle slice. Images were normalized to a standard EPI template based in Talairach space (Ashburner and Friston, 1999) and resampled to 3 × 3 × 3 mm^3 voxels. The normalized images were smoothed with an isotropic 8 mm full-width-at-half-maximum (FWHM) Gaussian kernel (final estimated smoothness was 10 × 10 × 10 mm^3 FWHM). The time-series in each voxel was highpass-filtered to 1/120 Hz and scaled to a grand mean of 100, averaged over all voxels and scans within a session.

Statistical analysis was performed in two stages of a Mixed Effects model. In the first stage, neural activity was modelled by a delta function at stimulus onset. The ensuing BOLD response was modelled by convolving these delta functions with a set of haemodynamic response functions (HRFs) consisting of a canonical HRF and its partial derivatives with respect to latency and dispersion (Friston *et al.*, 1998). Previous work suggests that these functions are sufficient to capture the majority of variability in the BOLD impulse response with such stimuli and tasks (Henson *et al.*, 2001). The resulting time-courses were down-sampled at the midpoint of each scan to form covariates in a General Linear Model. Separate covariates were modelled for each condition of interest (see above), together with one for incorrect responses and another for missed responses. Also included for each session were six covariates to capture residual movement-related artefacts (the three rigid-body translations and three rotations determined from initial coregistration), and a single covariate representing the mean (constant) over scans. Parameters for each covariate were estimated by an ordinary least squares fit to the data.

Table 1
Symmetry ratings (max. = +100, min. = –100) and median correct reaction times (RTs) for scrambled (S), unfamiliar (U) and familiar (F) faces in Phase 1

	S	U	F
Rating (%)	–29.2 (5.5)	36.1 (5.6)	22.0 (5.4)
RT (ms)	1544 (66)	1472 (82)	1619 (86)

Standard errors in parentheses ($n = 30$).

Contrasts of the parameter estimates comprised the data for the second-stage analyses, which treated participants as a random effect (Holmes and Friston, 1998). Separate ANOVAs were performed for each contrast of interest (see Basic analysis strategy), with the three HRFs comprising a factor. In other words, each analysis tested for a specific effect on the shape of the BOLD impulse response. Statistical Parametric Maps (SPMs) of the *F*-statistic were constructed, using the nonsphericity correction described in Friston *et al*. (Friston *et al*., 2002). We concentrate on regions that survived $P < 0.05$ volume-corrected for regions of interest (Worsley *et al*., 1995), but also tabulate for completeness all regions of at least 10 contiguous voxels that survived $P < 0.001$ uncorrected. The regions of interest were defined by the perception, recognition and priming contrasts (see Tables 3–5), in order to detect brain regions common to the three processes. The regions were localized on coregistered structural T_1 images. Stereotactic coordinates correspond to the standard Montreal Neurological Institute (MNI) brain. These coordinates bear a close, but not exact, match to the atlas of Talairach and Tournoux (Talairach and Tournoux, 1988).

Results

Behavioural Results

The classification of faces as familiar/unfamiliar during debriefing is shown in Table 2 (upper row). Over 85% of famous faces were recognized as familiar, and less than 10% of unfamiliar faces were misclassified as familiar. There was a main effect of participant group, $F(1,34) = 6.61$, $P < 0.05$, reflecting better classification by the ERP group than efMRI group, but this effect did not interact with familiarity or repetition. The tendency to classify a famous face as familiar increased following repetition, as confirmed by the planned contrast on repetition effects, collapsed across participant group, $F(1,35) = 18.7$, $P < 0.001$ [any increase in false recognition of unfamiliar faces did not reach significance, $F(1,35) = 2.76$, $P = 0.10$]. Subsequent analyses are restricted to correct classifications.

Phase 1

The symmetry ratings in Phase 1 are shown in Table 1. Unfamiliar faces were rated more symmetrical than scrambled faces, $F(1,28) = 36.8$, $P < 0.001$, and more symmetrical than familiar faces, $F(1,28) = 14.6$, $P < 0.001$. RTs were longer for familiar than unfamiliar faces, $F(1,28) = 42.7$, $P < 0.001$, and marginally so for scrambled versus unfamiliar faces, $F(1,28) = 3.93$, $P = 0.06$. No effects of participant group approached significance.

Phase 2

The RTs and errors for the sex decisions in Phase 2 are shown in Table 2 (bottom two rows). More errors were made in judging the sex of unfamiliar than familiar faces, though the numbers were too small to analyse. RTs were shorter for second than first presentations, and for familiar than unfamiliar faces, as confirmed by main effects of repetition, $F(1,34) = 15.9$, $P < 0.001$, and familiarity, $F(1,34) = 76.1$, $P < 0.001$. There was no familiarity-by-repetition interaction, $F(1,34) < 1$, nor any effects of participant group. Planned one-tailed tests, collapsing across participant group, confirmed that repetition priming occurred for both unfamiliar (24 ms), $t_{35} = 2.58$, $P < 0.01$, and familiar (31 ms), $t_{35} = 3.07$, $P < 0.005$, faces.

Table 2
Correct familiar/unfamiliar classifications during debriefing, together with median correct RTs and errors for sex decisions to first and second presentations of correctly classified unfamiliar (U1 and U2) and familiar (F1 and F2) faces in Phase 2

	U1	U2	F1	F2
Classification (%)	92.4 (1.2)	90.9 (1.2)	85.2 (1.6)	90.7 (1.2)
RT (ms)	738 (30)	715 (26)	676 (28)	645 (25)
Errors (%)	8.7	11.0	4.3	3.1

Standard errors in parentheses ($n = 36$).

ERP Results

ERPs during Phase 1 showed an early and sustained vertex-maximal positivity, together with a pronounced posterior N170, for faces versus scrambled faces, followed by a later frontal positivity for familiar versus unfamiliar faces (Fig. 2). Phase 2 ERPs showed a similar frontal positivity for familiar faces, which appeared to onset earlier for repeated faces, together with a transient centroparietal positivity associated with face repetition (Fig. 3). Analyses focused on three time windows encompassing these effects: 150–190 ms (N170), 400–600 ms (repetition effect) and 600–800 ms (familiarity effect).

Phase 1

The comparison of unfamiliar versus scrambled faces revealed an enhanced N170 at right posterior sites, as confirmed by an interaction between stimulus, laterality and rostrality in the 150–190 ms window, $F(1.2,20.6) = 19.9$, $P < 0.001$. The scalp potential and current source density maps (Fig. 4*A*) showed a maximal N170 at site 41 (over right occipitotemporal cortex). The concurrent vertex positivity for scrambled faces was sustained throughout the 400–600 ms and 600–800 ms windows, with a stimulus by laterality by rostrality interaction in each case, Fs > 9.1, $P < 0.005$.

No significant differences between unfamiliar and familiar faces were found in the 150–190 ms or 400–600 ms windows. Only in the 600–800 ms window was an effect of familiarity detected, as an interaction between familiarity, laterality and rostrality, $F(1.9,32.6) = 3.59$, $P < 0.05$. This interaction reflected a sustained frontocentral positivity for familiar faces that onset approximately 550 ms, and was maximal over frontopolar electrodes (Fig. 4*B*).

The question arises whether any of the aforementioned ERP effects can be attributed to differential EOG artefact across the experimental conditions. As can be seen in Figure 2, whereas the vertical EOG appears to differ for scrambled versus intact faces, in all cases the condition effects are greater in magnitude over the scalp. Thus, although statistical analysis of the EOG channels revealed reliable effects in all latency regions for the contrast between scrambled and unfamiliar faces, the greater size of these effects over the scalp means that they cannot be exclusively ocular in origin. Indeed, it is possible that the differential effects evident in the vertical EOG channel reflect 'contamination' with EEG activity, rather than vice versa, especially in the case of the small, transient effect evident in the N170 latency range. In keeping with the impression given in Figure 2, the contrast between familiar and unfamiliar faces was not significant in the EOG channels in any time region.

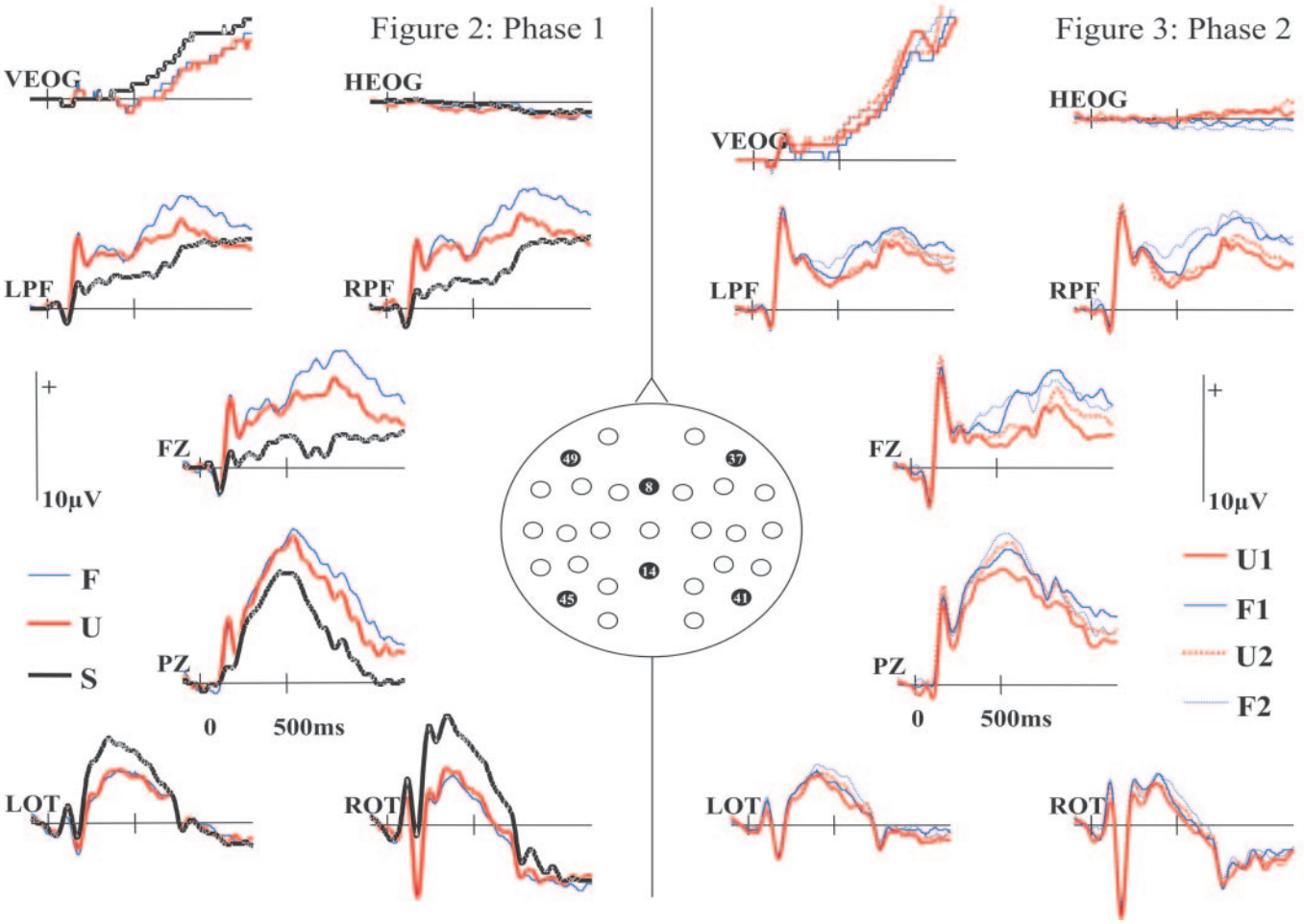

Figure 2. ERPs in Phase 1 at selected electrodes from the montage (inset): vertical (VEOG) and horizontal (HEOG) electro-occulograms, left and right prefrontal (LPF/RPF, Easycap sites 49/37), frontocentral (Fz), parietocentral (Pz) and left and right occipitotemporal (LOT/ROT, Easycap sites 45/41). Note that the relatively poor resolution of VEOG amplitude reflects the lower gain at which this channel was amplified, to avoid blink-related saturation.

Figure 3. ERPs in Phase 2. See Figure 2 legend for more details.

Phase 2

The planned comparisons of repetition effects in the 150–190 ms window revealed a repetition-by-laterality interaction for unfamiliar faces, $F(1.5,25.3) = 4.5$, $P < 0.05$, but not familiar faces. This reflected an apparent reduced vertex positivity/enhanced N170 for first (U1) versus second (U2) presentations of unfamiliar faces. However, there was some suggestion of a residual baseline effect in the averaged ERP for the U1 condition (a negative shift at trial onset; Fig. 3), so this effect is not discussed further.

In the 400–600 ms window, there was a greater positivity for repeated faces, both familiar, $F(1,17) = 8.7$, $P < 0.01$, and unfamiliar, $F(1,17) = 9.6$, $P < 0.01$. The topography of the unfamiliar repetition effect had a midline maximum (Fig. 4*C*), consistent with a repetition-by-laterality interaction, $F(1.8,31.4) = 3.3$, $P < 0.05$. The fact that this effect was clearly seen in participants whose individual data did not show baseline shifts suggest that it is unlikely to reflect the possible U1 baseline artefact mentioned above. The topography of the familiar repetition effect had maxima over parietal and right frontal sites (Fig. 4*D*), with no interactions with laterality or rostrality. A topographic analysis directly comparing repetition effects for familiar and unfamiliar faces failed to find a significant difference however (though see below).

In the 600–800 ms window, the planned comparison for familiarity effects on first presentations alone (F1 versus U1) revealed interactions between familiarity and laterality, $F(1.9,32.7) = 6.3$, $P < 0.005$, and between familiarity and rostrality, $F(1,17) = 7.2$, $P < 0.05$. As expected, the topography of this familiarity effect, a frontocentral positivity (Fig. 4*E*), resembled that during Phase 1 (cf. Fig. 4*B*). Indeed, no interactions were found with task (when Phase 1/Phase 2 was added as a factor); nor were differences found in a topographic analysis. However, a topographic analysis directly comparing this familiarity effect against the above repetition effect for unfamiliar faces, revealed an interaction between effect (F1–U1, 600–800 ms, versus U2–U1, 400–600 ms) and electrode, $F(3.4,58.6) = 4.10$, $P < 0.01$. This suggests that different generators underlie the familiarity and repetition effects.

The factorial analysis in the 600–800 ms window revealed an interaction between repetition, familiarity and laterality, $F(1.9,33.0) = 3.5$, $P < 0.05$, though no effects reached significance in separate comparisons of the repetition effects for familiar and unfamiliar faces. Closer inspection of the frontal

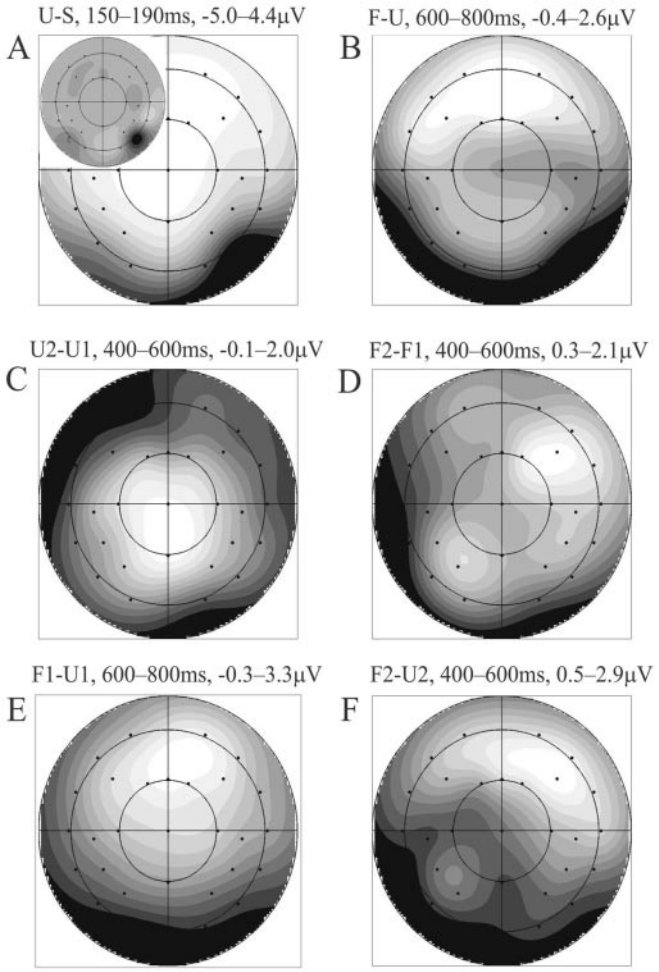

Figure 4. Scalp potential difference maps for (*A*) unfamiliar versus scrambled faces 150–190ms, with Current Source Density (CSD) map inset, (*B*) familiar versus unfamiliar faces in Phase 1, 600–800ms, (*C*) second versus first presentations of unfamiliar faces in Phase 2, 400–600ms, (*D*) second versus first presentations of familiar faces in Phase 2, 400–600ms, (*E*) first presentations of familiar versus unfamiliar faces in Phase 2, 600–800ms, (*F*) second presentations of familiar versus unfamiliar faces in Phase 2, 400–600ms. Greys scaled to max/min of differences, light = positive, dark = negative. Note that CSDs for the effects in (*B*)–(*F*) did not add any information, and are therefore not shown.

electrodes in Figure 3 suggested that one reason for the familiarity-by-repetition interaction was that the familiarity effect onset earlier for repeated presentations of faces (in that the red and blue broken lines diverge earlier, at ~350 ms, than the red and blue solid lines, which diverge at ~550 ms).

To explore this further, a *post hoc* ANOVA was performed in a 350–550 s window on the subset of frontal electrodes over which the familiarity effect was largest (Fig. 4*B*), organized by left versus right frontal electrodes (sites 50-49-19 and 36-37-9). This confirmed an interaction between familiarity and repetition, $F(1,17) = 5.2$, $P < 0.05$, with more positive-going waveforms for repeated familiar faces (F2) than for the other three conditions. The presence of an earlier-onsetting frontal familiarity effect, additional to the centroparietal repetition effect, may explain the apparent (though nonsignificant) difference between the topographies of the 400–600 ms repetition effects for familiar versus unfamiliar faces (i.e. the repetition effect in Fig. 4*D* may reflect a combination of the effects in Fig. 4*C*,*F*).

The above ANOVAs were repeated on the data from the EOG channels; none revealed any significant condition effects, making it unlikely that the ERP findings reflected artefact due to differential eye-movements.

efMRI Results

The efMRI data revealed multiple regions showing effects of face perception, face recognition and face repetition, as shown in Tables 3–5 and Figures 5–7. We concentrate on regions that are of interest based on previous studies.

Phase 1

Bilateral fusiform and lateral ventral occipital regions were more active to unfamiliar than scrambled faces, whereas more medial and posterior bilateral occipital regions were more active to scrambled faces (Fig. 5*A*). Other notable regions more active to faces were the posterior horizontal segment of the right STS, and, at an uncorrected level, bilateral hippocampi, bilateral inferior frontal gyri, and medial and orbital frontal gyri (Table 3).

The right and left LMF regions showed similar response profiles (Figs 5*B* and 6D, respectively), with greatest response to familiar faces, and least response to scrambled faces. The face activations in lateral occipital (Fig. 5*C*) and right STS (Fig. 5*D*) regions did not appear sensitive to familiarity. The right-lateralization of the STS region was confirmed by a significant interaction between face activation (U–S) and hemisphere (using homologous coordinates for the left STS, –51 –66 +12) in a *post hoc* ANOVA on the canonical HRF parameter estimate, $F(1,17) = 8.7$, $P < 0.01$. No such interaction was found using homologous coordinates for the LMF region, or for the occipital region, Fs < 1.

Regions showing differential responses to familiar and unfamiliar faces are shown in Figure 6*A* and Table 4. The most extensive region was in medial superior frontal gyrus, which was more active for familiar than either unfamiliar or scrambled faces (Fig. 6B). A medial orbitofrontal region showed a more graded pattern (Fig. 6*C*), as did the left LMF (Figure 6D, and right LMF at a lower threshold; see Fig. 5*B*). A region in left superior temporal gyrus showed greatest responses to familiar faces at an uncorrected level, but was superior to the right STS region in Figure 5*D*.

Phase 2

Regions showing effects of the various planned comparisons in Phase 2 are shown in Table 5. Several regions showed greater responses to first presentations of familiar than unfamiliar faces (no region showed relatively greater responses to unfamiliar faces). The most notable region was in the left LMF, overlapping that found in the analogous contrast for Phase 1. This region also showed a significant repetition-related decrease for familiar faces. The homologous right LMF region showed a similar pattern (Fig. 7*A*), as confirmed by an interaction between familiarity and repetition, $F(1,17) = 5.28$, $P < 0.05$, but no interactions with hemisphere, Fs < 2.7, Ps > 0.12, in a *post hoc* ANOVA.

A familiarity effect was also seen in the right posterior STS region that showed an effect of face perception, though not face recognition, in Phase 1 (Fig. 7*B*). Another region showing a familiarity effect was found in right prefrontal cortex, which was difficult to localize, but most probably lay deep within either the inferior frontal or medial frontal sulci. A nearby region in Phase 1 showed the opposite pattern however – a greater response to unfamiliar than familiar faces – as confirmed by an interaction between task (phase) and familiarity. At an

Table 3

Face perception: regions showing differential responses to unfamiliar (U) and scrambled (S) faces in Phase 1, $F(2.7,45.3)>6.9$, $P<0.001$

Region	L/R	Size (cm^3)	BA	Coordinates		
				x	*y*	*z*
U>S						
Medial superior frontal gyrus	B	0.54	9	–3	+54	+30
Medial orbitofrontal gyrus	B	0.51	10/11	0	+39	–24
Inferior frontal sulcus	L	0.34	44/45	–42	+18	+21
	R	0.65	44/45	+42	+15	+24
Anterior medial temporal	R	0.49	20	+30	–9	–33
Hippocampus	L	0.65	–	–21	–12	–24
	R	0.54	–	+24	–12	–18
Posterior cingulate	B	2.43	23/31	–6	–51	+24
Precuneus	B	0.35	7	+3	–75	+36
Fusiform gyrus	L	4.67	37	–39	–51	–24**
Inferior occipital gyrus			19	–39	–81	–15
Fusiform gyrus	R	3.40	37	+42	–45	–27**
Inferior occipital gyrus	R	0.92	17/19	+42	–81	–15**
Superior temporal sulcus	R	3.67	39	+51	–66	+12**
S>U						
Anterior cingulate gyrus	B	0.35	24/32	–6	+36	+18
Posterior medial frontal gyrus	B	0.46	6	+6	+3	+60
Anterior superior temporal sulcus	L	0.54	21/22	–54	–18	–3
Collateral sulcus	L	1.76	18	–24	–60	–15**
Cuneus	R	1.02	17	+15	–63	+9
Posterior intraparietal sulcus	L	1.97	7	–18	–69	+51
	R	2.97	7	+27	–72	+45
Posterior occipital	L	6.29	18	–27	–96	+6**
Posterior calcarine			17	–12	–96	–6**
Lingual gyrus	R	11.61	18	+27	–75	–12**
Collateral sulcus			18	+30	–57	–12**
Posterior occipital			18	+33	–93	+12**
Posterior calcarine			17	+12	–102	+6**

L = left, R = right, B = bilateral, BA = Brodmann Area. Direction of effect determined by *post hoc t*-tests on canonical HRF.

**$P < 0.05$ whole-brain corrected.

Table 4

Face recognition: regions showing differential responses to familiar (F) and unfamiliar (U) faces in Phase 1, $F(2.8,48.1)>6.58$, $P<0.001$

Region	L/R	Size (cm^3)	BA	Coordinates		
				x	*y*	*z*
F>U						
Medial superior frontal gyrus	L	3.32	9	–6	+54	+39**
			9	–15	+39	+48
Medial orbitofrontal gyrus	B	0.94	10/11	–3	+45	–24*
Lateral orbitofrontal gyrus	L	0.86	11	–48	+27	–12
Middle frontal gyrus	L	0.57	8/9	–48	+15	+42
Fusiform gyrus	L	0.27	37	–39	–45	–24*
Cuneus/anterior calcarine	B	0.97	30/31	–3	–57	+12
Superior temporal gyrus	L	1.13	39	–48	–69	+27
U>F						
Anterior inferior frontal sulcus	R	0.51	9/46	+27	+45	+30
Anterior Sylvian fissure	L	0.54	6/22	–57	+3	+3
Posterior occipital	L	0.32	19	–24	–87	+18

See Table 3 legend for more details.

**$P<0.05$ whole-brain corrected. *$P<0.05$ corrected for set of all regions showing unfamiliar/scrambled differences in Table 3.

Table 5

Face priming: regions showing differential responses to initial and repeated presentations of familiar (F1 and F2) and unfamiliar (U1 and U2) faces in Phase 2, $F(2.9,48.2)>14.6$, $P<0.001$

Region	L/R	Size (cm^3)	BA	Coordinates		
				x	*y*	*z*
F1>U1						
Inferior/medial frontal sulcus	R	0.27	9/46	+21	+39	+12†
Middle frontal gyrus	L	0.40	8/9	–48	+18	+39
Temporal pole	L	0.24	38	–42	+9	–33
Fusiform gyrus	L	0.73	37	–39	–48	–24*[1]
Superior temporal sulcus	R	0.30	19	+48	–66	+9*[2]
Superior occipital gyrus	R	0.54	17	+24	–90	+24†
Posterior calcalrine sulcus	R	0.32	19	+24	–96	+3†
F1–F2>U1–U2						
Medial superior frontal gyrus	R	0.54	9	+6	+60	+24
Lateral calcarine sulcus	L	0.27	17	–12	–87	+9
U1–U2>F1–F2						
Superior parieto-occipital fissure	R	0.43	7/19	+12	–75	+39
F1>F2						
Inferior/medial frontal sulcus	R	0.78	9/46	+24	+39	+12
Fusiform gyrus	L	0.27	37	–36	–48	–27*[1]
Posterior fusiform gyrus	L	0.43	18	–21	–75	–18
Middle occipital gyrus	L	0.35	18	–30	–87	+15
Inferior occipital gyrus	R	0.62	17/19	+30	–96	–9**

See Table 3 legend for more details.

**$P<0.05$ whole-brain corrected in *F*-tests; *[1]$P<0.05$ corrected for set of all regions showing familiar/unfamiliar differences in Table 4. *[2]$P<0.05$ corrected for set of all regions showing unfamiliar/scrambled differences in Table 3. †Region shows interaction between phase and familiarity, $F(2.9,49.7)>6.4$, $P<0.001$.

uncorrected threshold, a greater response to familiar than unfamiliar faces was also seen in the left temporal pole (Fig. 7*C*). This is noteworthy because similar temporal pole regions showed the same effect in Phase 1, but did not exceed the extent threshold (three voxels around –33 +15 –36, and five voxels around +36 +18 –36), possibly because of fMRI susceptibility effects in anterior temporal regions.

Tests of repetition effects for familiar faces alone confirmed repetition-related decreases in left LMF (Fig. 7*A*), and also in a right posterior inferior occipital region (Fig. 7*D*), which appeared to reflect a more sustained response in the F1 condition. Tests of the interaction between repetition and familiarity revealed a region in the medial superior frontal gyrus, which was close to, but not overlapping with, the medial frontal region showing a familiarity effect in Phase 1. This region showed a greater decrease following repetition of familiar than unfamiliar faces. No regions evidenced repetition effects for unfamiliar faces alone, and no regions evidenced reliable repetition-related increases.

Discussion

The present study produced a number of important findings regarding the spatial and temporal relations between face perception, face recognition and face priming. The main findings can be summarized as follows. Face perception, as operationalized by unfamiliar versus scrambled faces, was associated with (i) an enhanced right posterior N170 and a sustained vertex positivity from ~150 ms onwards; (ii) increased haemodynamic responses in mainly bilateral LMF and right STS (together with decreased haemodynamic responses in medial occipital regions). Face recognition, as operationalized by familiar versus unfamiliar faces, was associated with (i) a sustained frontocentral positivity from approximately 550 ms; (ii) increased haemodynamic responses in mainly medial superior frontal, orbitofrontal, bilateral LMF and temporal pole regions. Face priming, as operationalized by initial versus repeated presentations of faces, was associated with (i) a centroparietal positivity maximal between 400 and 600 ms, plus

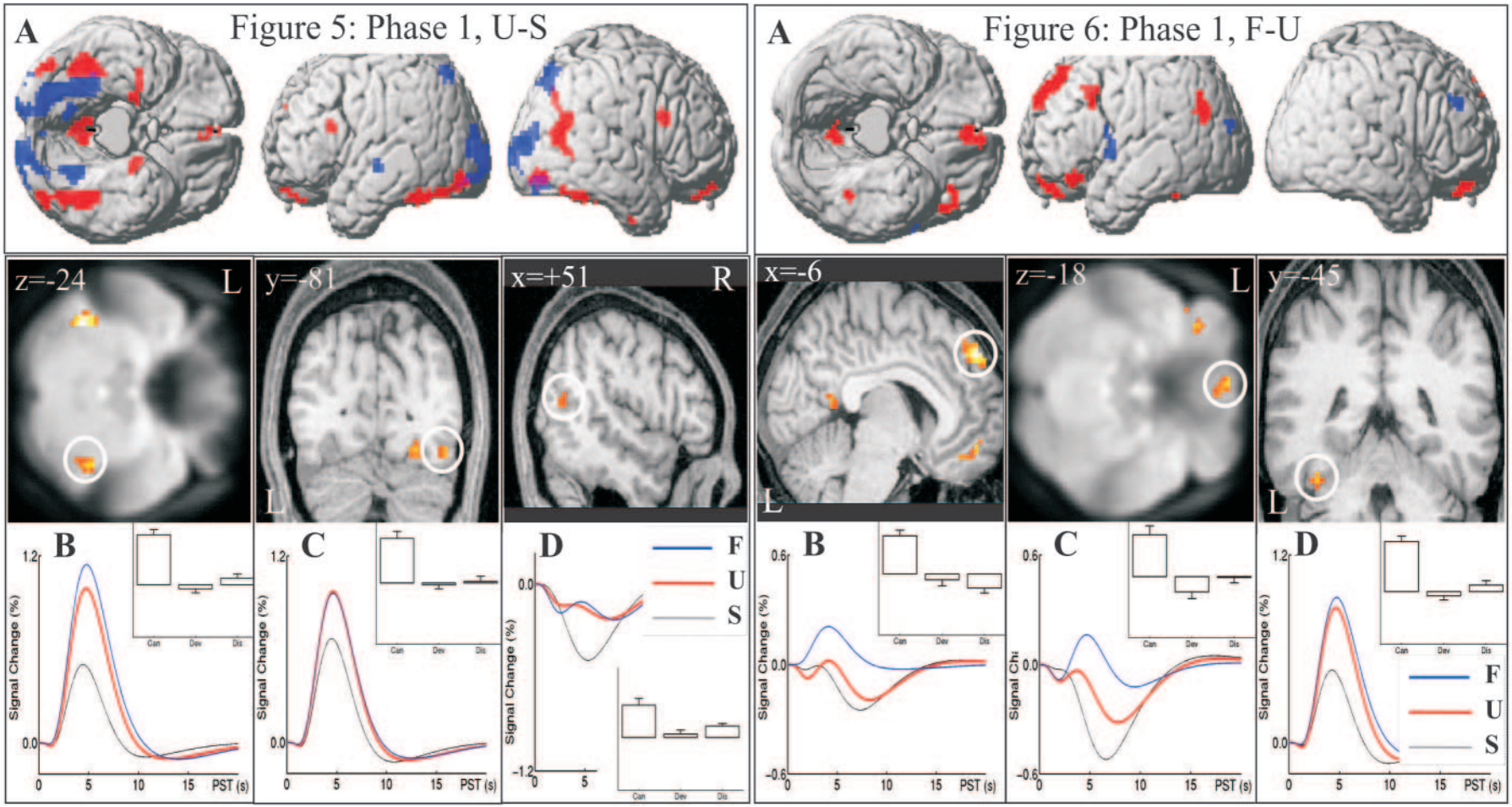

Figure 5. Face perception: regions showing differential responses to unfamiliar (U) and scrambled (S) faces. (*A*) Regions of at least 10 voxels surviving $P<0.001$ uncorrected in *F*-tests are rendered on a canonical normalized brain (with cerebellum artificially removed). Red indicates greater responses to unfamiliar faces; blue indicates greater responses to scrambled faces. (*B*) Regions showing significant differences at $P<0.05$ whole-brain corrected displayed in orange on a transverse section at $z=-24$mm through the mean normalized EPI across participants, together with plots from the maximum in the right LMF region circled (+42 –45 –27). The best-fitting event-related responses show % signal change, relative to grand mean over voxels, against post-stimulus time (PST) for familiar (blue), unfamiliar (red) and scrambled (black) faces. Inset are the U–S differences in parameter estimates, with standard error, for the canonical HRF (Can), its temporal derivative (Dev) and dispersion derivative (Dis) that parameterise the shape of the difference (which loads mainly on the canonical HRF parameter, indicating a difference in peak height). (*C*) The same group differences as in *B*, now displayed in coronal section at $y=-81$mm through a randomly selected normalized T_1 image of one participant, with plots from the circled lateral occipital region (+42 –81 –15). Note that the more medial occipital region showed greater responses to scrambled faces (not shown). (*D*) Sagittal section at $x=+51$mm through the normalized T_1 image in *B*, with plots from the right STS region (+51 –66 +12). Note that the main effect versus interstimulus baseline (i.e. offsets relative to zero in the event-related responses) cannot be estimated reliably in this short SOA design (Josephs and Henson, 1999).

Figure 6. Face recognition: regions showing differential responses to familiar (F) and unfamiliar (U) faces in Phase 1. (*A*) Regions of at least 10 voxels surviving $P<0.001$ uncorrected in *F*-tests are rendered on a canonical normalized brain. (*B*) Sagittal section at $x=-6$mm through a T_1 normalized structural showing medial superior frontal, orbitofrontal and posterior cingulate regions, with event-related responses and F–U differences in parameter estimates from the superior frontal region (–6 +54 +39). (*C*) Transverse section at $z=-18$mm through the mean normalized EPI, showing medial and lateral orbitofrontal regions, with plots from medial region (–3 +45 –24). (*D*) Coronal section at $y=-45$mm through the normalized T_1 image, with plots from left LMF region (–39 –45 –24). See Figure 5 legend for more details.

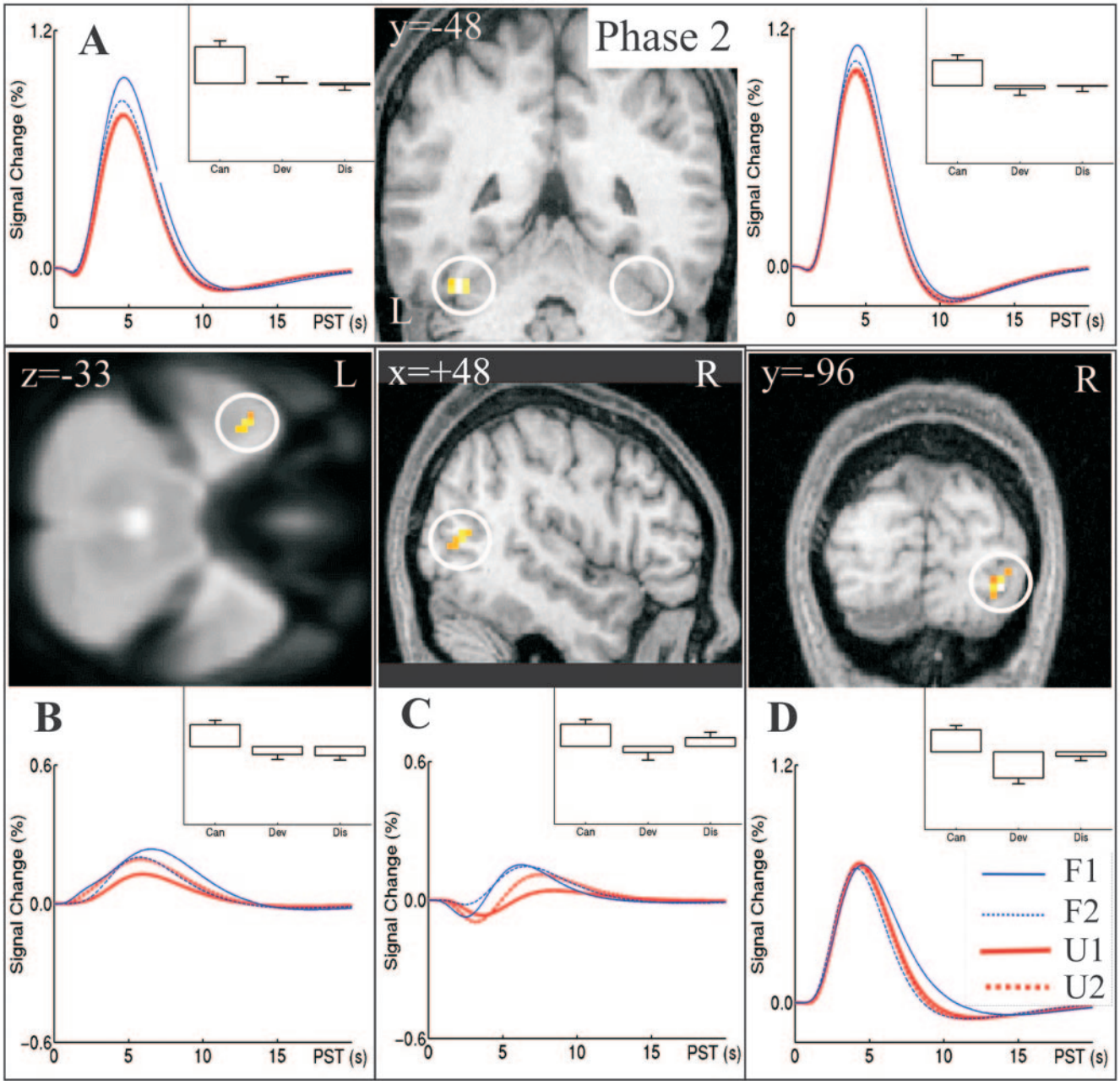

Figure 7. Face recognition and priming: regions showing differential responses to first and second presentations of familiar (F1 and F2) and unfamiliar (U1 and U2) faces in Phase 2. (*A*) Coronal section at $y=-48$mm through a T_1 normalized structural showing left and right LMF regions (±39 –48 –24), with event-related responses and F1–F2 parameter estimate differences. (*B*) Transverse section at $z=-33$mm through the mean normalized EPI, showing event-related responses and F1–U1 parameter estimate differences from a left temporal pole region (–42 +9 –33). (*C*) Sagittal section at $x=+48$ through a T_1 normalized image showing event-related responses and F1–U1 parameter estimate differences from a right STS region (+48 –66 +9). (*D*) Coronal section at $y=-96$ through the T_1 normalized image showing the event-related responses and F1–F2 parameter estimate differences in a right posterior inferior occipital region (+30 –96 –9). See Figure 5 legend for more details.

an earlier-onsetting familiarity effect for repeated familiar faces (onsetting ~350 ms); (ii) haemodynamic response decreases in bilateral LMF, right posterior occipital and possibly medial frontal regions, but only for familiar faces. Though several of these effects have been reported in previous studies, this is the first study to compare directly the effects of face perception, recognition and priming within the same paradigm, in both their spatial and temporal properties.

Face Perception

The present N170 deflection to faces resembles that found previously with a nose reference (Bentin *et al*., 1996; George *et al*., 1996; Eimer, 1998). It was maximal over posterior temporo-occipital electrodes, and clearly right-lateralized. Though this right-lateralization was not seen in all previous studies, it does not appear to be an artefact of the present mastoid reference, and is clearly seen in the reference-independent CSD (Fig. 4*A*). The N170 was not affected by face familiarity in Phase 1 or by repetition in Phase 2, consistent with previous studies (Bentin and Deouell, 2000; Eimer, 2000; Schweinberger *et al*., 2002). It has been attributed to structural encoding of face components (Eimer, 1998), a specialized eye-processor (Bentin *et al*., 1996),

or a combination of whole-face and face-part processes (Sagiv and Bentin, 2001), all of which may contribute to the present data.

Regions showing haemodynamic correlates of face perception are also in good agreement with previous studies. Activations were evident in bilateral LMF regions close to the central tendency of the functionally defined 'fusiform face area' (Kanwisher *et al.*, 1997), and extending posteriorly into occipital cortex, close to the 'occipital face area' (Gauthier *et al.*, 2000) and 'lateral occipital complex' (LOC) (Malach *et al.*, 2002). The location of the LMF regions relative to the Macaque ITG is unclear, though they may represent the human analogue of areas TF, CITv (Halgren *et al.*, 1999) or TE (Gauthier and Logothetis, 2000). Their location is consistent with the (typically extensive) occipitotemporal lesions associated with prosopagnosia (Damasio *et al.*, 1990). Given that the LMF, but not lateral occipital region, was further activated during face recognition (see below), the degree to which prosopagnosia is of an associative rather than apperceptive type (De Renzi *et al.*, 1991) may depend on the posterior extent of the lesion, with associative prosopagnosia arising when the lesion is restricted to regions within or anterior to the LMF.

In addition, faces activated a lateral temporal region in the posterior STS. Unlike the fusiform activation, this activation was strongly right-lateralized, consistent with previous studies (Puce *et al.*, 1996). Nearby sites in the human middle temporal gyrus show face-specific intracranial N200 ERPs (Halgren *et al.*, 1994; Allison *et al.*, 1999). Indeed, the concordance in the coordinates of the present region, +51 –66 +12, and those estimated by Allison *et al.* (Allison *et al.*, 1999), +51 –64 +9, is remarkable. The region is posterior to the typical sites of face-responsive neurons in monkey STS, though the anterior–posterior extent of these sites is considerable (Rolls, 1992). It has been argued that neurons within the monkey STS are involved in 'social attention' (Perrett *et al.*, 1992), using cues such as eye gaze, head direction and expression to determine the attention of others. This is consistent with the greater haemodynamic response in this region to faces with moving eyes or moving mouths (Puce *et al.*, 1998), and when people are attending to gaze direction (Hoffman and Haxby, 2000). The presence of eyes in the intact but not scrambled faces of the present study may automatically engage the same region, in the processing of gaze direction for example.

Other activations in the frontal cortex are also consistent with the face-responsive cells in inferior prefrontal cortex of the macaque (Scalaidhe *et al.*, 1999), while the medial temporal activations are consistent with face-responsive cells in human hippocampus (Heit *et al.*, 1988; Kreiman *et al.*, 2000), though interestingly, there was no evidence that the present hippocampal activations were sensitive to face familiarity or repetition. The face-related 'deactivations' in lingual and early visual regions may reflect low-level visual differences between the intact and scrambled faces (e.g. perceived symmetry differences), rather than face perception *per se*, though see Halgren *et al.* (Halgren *et al.*, 2000).

One might expect the fusiform 'face area', or nearby occipitotemporal sulcus (Bentin *et al.*, 1996; Halgren *et al.*, 2000), to be the generator of the scalp N170. We were unable to conduct a formal source localization in the present study, given the relatively low density of electrode coverage and lack of co-registration of electrode locations with cortical anatomy. However, several considerations suggest that fusiform cortex is unlikely to be the principal source of the present N170 (though it may of course contribute). Firstly, the focal nature of the CSD (Fig. 4*A*) suggests a superficial source, close to the scalp. Secondly, the N170 was markedly right-lateralized, whereas the fusiform face activation was bilateral. Thirdly, the fusiform activation showed effects of familiarity and repetition, whereas the electrode exhibiting the maximal N170 did not show such effects, at either the N170 peak, or at any other subsequent time during the recording epoch. Fourthly, the efMRI data suggest a more likely generator is the posterior STS, which is close to the scalp, showed a right-lateralized face effect, no sensitivity to face repetition, and only limited sensitivity to face familiarity. Given the above arguments concerning the Macaque STS, one possibility is that the present N170 was driven by rapid detection of social attention cues in the human STS.

Face Recognition

The frontocentral familiarity effect, onsetting ~550 ms, has been reported previously: for example, to the sample stimulus in a delayed-match-to-sample task, though left-lateralized (Barrett *et al.*, 1988), and as an enhanced 'P600' component during indirect tasks (Eimer, 2000). The present familiarity effect was found in both symmetry- and sex-decision tasks, and is unlikely to be related to RT, given that the difference between familiar and unfamiliar face RTs reversed across the two tasks. It could reflect the greater perceived symmetry of the unfamiliar than familiar faces (which was the opposite, if anything, of what one might have expected, and may relate to the specific face images used). However, the similarity of this familiarity effect to that in previous studies using different stimuli makes this possibility unlikely.

An earlier familiarity effect has also been reported as a negative deflection of the 'N400' component (Bentin and Deouell, 2000; Eimer, 2000). One reason such an effect was not seen here may be the removal of hair features, which is likely to delay recognition of familiar faces. This may have delayed the 'N400' negativity, causing it to be masked by the later positivity, though there was no evidence of a corresponding delay in the 'P600' onset.

Face familiarity also increased the haemodynamic response in the LMF to a level above that associated with face perception, replicating our previous findings (Henson *et al.*, 2000, 2002). In general, these data support the role of a ventral temporal route for processing face identity (Haxby *et al.*, 2000). For example, the increased LMF responses to familiar faces may reflect activation of pre-existing perceptual representations, such as FRUs (Bruce and Young, 1986). Such increases have not always been found however, when using faces of famous people (Gorno-Tempini *et al.*, 1998), acquaintances (Nakamura *et al.*, 2000), or faces recently familiarized through prior exposure (Dubois *et al.*, 1999; Leveroni *et al.*, 2000; Rossion *et al.*, 2001). The reason for these differences is unclear, but may relate to the task (Henson *et al.*, 2002), or whether the faces are familiar by virtue of being famous, or simply by virtue of prior exposure. Increased fusiform responses to famous faces could be a consequence of, for example, retrieval of semantic information, or even covert naming (possibly via interactions with more anterior regions), and therefore might not be expected for faces that are familiarized by prior exposure only.

The temporal pole activations to familiar faces are likely to reflect retrieval of semantic information, perhaps via access to PINs (Bruce and Young, 1986). This may not be specific to faces, since similar activations are found for other 'semantically unique' stimuli, such as famous buildings (Gorno-Tempini and Price, 2001) or familiar scenes (Nakamura *et al.*, 2000). Medial frontal activations have also been reported, for famous faces

relative to newly learned and novel faces (Leveroni *et al*., 2000), and for famous versus novel faces and names (Gorno-Tempini *et al*., 1998). The functional significance of these activations is unclear.

Face Repetition

Most previous studies of face priming have used immediate repetition and observed modulation of early ERP components between 200 and 300 ms (Barrett *et al*., 1988; Hertz *et al*., 1994; Begleiter *et al*., 1995), such as the 'N250r' (Schweinberger *et al*., 1995, 2002b). However, immediate repetition is likely to be a special case (Bentin and Moscovitch, 1988; Nagy and Rugg, 1989), including, for example, possible contributions from short-lived visual memory. Such early effects are not normally seen with the longer-lag priming of ~10 min that was used in the present design (Schweinberger *et al*., 2002a), though see George *et al*. (George *et al*., 1997).

Of those studies using long-lag priming, George *et al*. (George *et al*., 1997) found a centroparietal positivity between 450 and 550 ms associated with repetition of unfamiliar faces, resembling that in the present data. Schweinberger *et al*. (Schweinberger *et al*., 2002a) found a similar centroparietal positivity from 500 to 600 ms for familiar face repetition, but not for unfamiliar face repetition, unlike the present data. One possible reason for this discrepancy is the use of a familiarity-judgement task in the Schweinberger *et al*. (Schweinberger *et al*., 2002a) study, which may bias attention away from unfamiliar faces and towards familiar faces, which are likely to be seen as the targets (Henson *et al*., 2002). An alternative reason is that the centroparietal repetition effect for unfamiliar faces in the George *et al*. (George *et al*., 1997) and present studies is specific to repetition of the same image of a face, and would not generalize across different images of the same face (Schweinberger *et al*., 2002a).

A second repetition effect, which was only found for familiar faces in the present study, occurred over frontal electrodes from 350 to 550 ms and was interpreted as an earlier onsetting of the familiarity effect. This effect has not been reported previously. Eimer (Eimer, 2000) found a reduced familiarity effect following repetition of familiar faces in this time-range, but this was in the context of an enhanced negativity for familiar versus unfamiliar faces, the opposite polarity to the present findings.

Face repetition tended to reduce evoked haemodynamic responses, a 'repetition suppression' effect (Henson and Rugg, 2002), but only for familiar faces. Indeed, responses in the left and right LMF replicated the interaction between familiarity and repetition observed previously in indirect memory tasks (Henson *et al*., 2000, 2002). In these studies, the interaction was more significant on the right than left, but was also apparent on the left, and no laterality effects were significant in the present data. Repetition of unfamiliar faces in the present study did not produce reliable haemodynamic decreases or increases anywhere in the brain (Henson *et al*., 2000, 2002). This may reflect a type II error, the 'shallow' processing of faces in Phase 1, or the relatively long repetition lag in the present study, since temporoccipital haemodynamic repetition effects can decrease over lags of minutes (Henson *et al*., 2000).

As discussed above, the LMF may be activated in association with face recognition, as well as face perception. Repetition of familiar faces is likely to facilitate their recognition, decreasing the haemodynamic response, perhaps via a shorter duration of neural activity (Henson and Rugg, 2002). Given that early ERP components such as the scalp N170 and the intracranial fusiform N200 do not show effects of familiarity or repetition, the haemodynamic decrease is likely to be reflected in later ERP components, such as the intracranial P290 (Puce *et al*., 1999) or the scalp N250r (Schweinberger *et al*., 2002b), possibly after interactions with anterior temporal/frontal regions (Klopp *et al*., 2000).

Behavioural Priming

Priming was evident as faster RTs for repeated versus unrepeated faces in Phase 2 (as well as more accurate recognition of repeated famous faces during debriefing). The RT data confirm the findings of Goshen-Gottstein and Ganel (Goshen-Gottstein and Ganel, 2000), that priming can be found during sex-decisions, for both familiar and unfamiliar faces (Ellis *et al*., 1990). This is contrary to the standard Bruce and Young (Bruce and Young, 1986) model, according to which priming should not be found for sex-decisions. Nonetheless, the magnitude of this priming effect (20–30 ms) is considerably smaller than that found for familiarity-decisions on familiar faces (150–200 ms) (Ellis *et al*., 1990; Henson *et al*., 2002). One possibility is that priming can arise from multiple loci. For example, a perceptual process like the structural encoding of Bruce and Young (Bruce and Young, 1986) may be facilitated if the same face was perceived recently. This facilitation would occur whether or not the face is recognized, and be evident in sex-decision RTs, provided that local sex-predictive features are removed (perhaps by forcing configural processing of internal features). A second process of face recognition may also be facilitated by repetition, via reactivation of FRUs (Goshen-Gottstein and Ganel, 2000), or via strengthening of FRU–PIN connections (Burton *et al*., 1999). This facilitation would only occur for faces that can be recognized, and would quicken familiarity-decisions, but not speeded sex-decisions, for which recognition is not required.

The earlier-onsetting of the frontal ERP familiarity effect may reflect priming of this second, recognition process. Recognition of familiar faces is likely to occur automatically (Ellis *et al*., 1990), even though it is not needed for sex-decisions. In other words, neural correlates of primed recognition can be seen in the absence of behavioural correlates. Indeed, the latency decrease of the ERP effect was of the same order (200 ms) as the priming effect observed during familiarity-decisions, when recognition is required (Ellis *et al*., 1990; Henson *et al*., 2002). This facilitation may occur in the frontal or temporal pole regions that were associated with face recognition, though the evidence for haemodynamic repetition effects in these regions was only suggestive. The 400–600 ms centroparietal ERP repetition effect may then represent the ERP correlate of priming of the first, perceptual process, common to familiar and unfamiliar faces. The failure to find significant haemodynamic (or interpretable CSD) correlates of unfamiliar face repetition leaves the generator of this effect unclear. One explanation for the absence of a haemodynamic correlate may be the small size of the priming effect; another may be that the ERP repetition effect reflects reduced variability in processing times (i.e. a 'sharpening' of the peak of a positive ERP component).

Other Considerations

It is important to note that we cannot rule out contributions of explicit memory to the present repetition effects. We used an indirect memory task, and attempted to minimize explicit memory by (i) using a shallow 'study' task in Phase 1, (ii) ensuring that performance of the 'priming' task (sex-decision) was orthogonal to performance of the study task (so that the decision itself was not repeated), and (iii) requiring speeded decisions in the priming task. However, even though the behavioural data

may reflect implicit memory, the ERP and efMRI data might include correlates of explicit retrieval (e.g. subsequent to the task-relevant decision). Nonetheless, the present ERP repetition effects do not resemble those usually attributed to explicit familiarity or recollection (Rugg *et al.*, 1998; Paller *et al.*, 1999), and we did not see the repetition-related haemodynamic increases in anterior prefrontal, lateral/medial parietal or medial temporal cortices that have been associated with explicit retrieval (Rugg and Henson, 2002).

Another consideration concerns the specificity of our repetition effects. Without using different images for the first and second presentation of a face, we cannot refute the possibility that the ERP, efMRI or even behavioural effects are supported by 'superficial' pictorial codes (Bruce and Valentine, 1985). While some ERP repetition effects persist across different images of familiar faces, the size of the effects are typically reduced, and they do not always generalize across different images of unfamiliar faces (Schweinberger *et al.*, 2002a). Left fusiform efMRI repetition effects generalize across different views of objects (after small rotations), but right fusiform repetition effects do not appear to (Vuilleumier *et al.*, 2002). While behavioural priming of sex-decisions generalizes across different images of familiar faces (Goshen-Gottstein and Ganel, 2000), direct comparisons across view changes suggest a graded pattern of priming (Ellis *et al.*, 1987). These questions will be addressed in future studies.

Conclusions

Given the data and theories reviewed above, we propose the following account of our data. The presentation of a face engages at least two processes: (i) extraction of a structural representation (Bruce and Young, 1986), and (ii) rapid detection of 'social attention' cues (Perrett *et al.*, 1992). The former occurs in lateral occipital cortex, in common with visual object recognition, and in the fusiform, which may reflect additional processing demands particularly relevant to faces, such as configural or foveal processing (Malach *et al.*, 2002). The processing of social attention occurs in the STS, mainly on the right, and contributes to the N170 ERP maximal over the lateral posterior scalp.

Recognition of a familiar face typically involves multiple processes, such as semantic retrieval, covert naming and affective responses. These processes occur later (by 550 ms, at least when hair-cues are absent) in superior and orbital medial frontal cortices and temporal poles, one or more of which contribute to the ERP familiarity effect maximal over frontocentral scalp sites. These processes also involve interactions with the LMF, where structural representations of familiar faces exist [such as FRUs (Bruce and Young, 1986)]. A gradual temporal evolution of these interactions may explain why the later, but not initial, face-specific fusiform cortical ERPs are modulated by recognition (Puce *et al.*, 1999).

Recognition is facilitated if the same face has been recognized in the recent past, as would be evident in RTs to make a familiarity-decision (Ellis *et al.*, 1990). This facilitation results in an earlier-onset of the frontal ERP familiarity effect (by ~200 ms), owing to more efficient interactions between LMF and frontotemporal regions, and hence a shorter duration of neural activity in these regions, producing a decreased haemodynamic response (Henson and Rugg, 2002). Recent perception of a face, familiar or unfamiliar, can also facilitate the formation of structural representations. Under some conditions (e.g. the absence of feature-based heuristics), this facilitation is evident as a priming effect in tasks like sex-judgement, analogous to other long-lag visual object priming effects (Schacter *et al.*, 1990). This facilitation occurs by 400 ms, and is evident as an ERP repetition effect maximal over centroparietal scalp sites. The haemodynamic correlates of this effect remain to be established.

Notes

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