

Face Repetition Effects in Implicit and Explicit Memory Tests as Measured by fMRI

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Recent parallels between neurophysiological and neuroimaging findings suggest that repeated stimulus processing produces decreased responses in brain regions associated with that processing — a ‘repetition suppression’ effect. In the present study, volunteers performed two tasks on repeated presentation of famous and unfamiliar faces during functional magnetic resonance imaging (fMRI). In the implicit task, they made fame-judgements (regardless of repetition); in the explicit task, they made episodic recognition judgements (regardless of familiarity). Only in the implicit task was repetition suppression observed: for famous faces in a right lateral fusiform region, and for both famous and unfamiliar faces in a left inferior occipital region. Repetition suppression is therefore not an automatic consequence of repeated perceptual processing of stimuli.

Introduction

Recent functional imaging studies have reported a phenomenon of ‘repetition suppression’, whereby the repeated processing of a stimulus produces a decreased response in brain regions associated with that processing. This decreased regional haemodynamic response may be a consequence of decreases in the mean firing rate of neuronal populations, analogous to the phenomenon of ‘response suppression’ recorded directly from single cells in monkey inferior temporal cortex (Desimone, 1996). This neuronal suppression has been observed across a range of different tasks (Brown and Xiang, 1998) and is believed to be an automatic property of perceptual learning in the cortex (Wiggs and Martin, 1998). Such suppression has also been posited as the neuronal correlate of priming – the facilitation or bias in behavioural responses to repeated stimuli (Schacter and Buckner, 1998).

In a previous imaging study (Henson *et al.*, 2000b), we showed that repetition effects can be sensitive to the familiarity of the stimuli. Subjects were shown faces, which were either familiar (belonged to famous people), or unfamiliar (faces of people that had not been seen prior to the experiment). Repetition of familiar faces was associated with a reduced response in a right lateral fusiform region previously associated with face processing (Kanwisher *et al.*, 1997), consistent with previous findings. Repetition of unfamiliar faces was, however, associated with an increased response in this region – a ‘repetition enhancement’ effect. We attributed the suppression to lowered thresholds for activating perceptual representations of familiar faces, producing faster recognition when those faces were repeated. This proposal is consistent with ‘abstractionist’ theories of repetition priming, which predict priming effects only for stimuli with pre-existing representations (Tenpenny, 1995; Bowers, 2000). We attributed the repetition enhancement for unfamiliar faces to the gradual formation of new perceptual representations. These new representations might allow additional recognition processes to occur on repeated presentations of unfamiliar faces that did not occur on their initial

presentation, producing the response increase – see Henson *et al.* (Henson *et al.*, 2000b) for more details.

These repetition effects were observed in the context of an indirect monitoring task. Subjects responded only when they saw a pre-specified target (an inverted face). This rare target was not of theoretical interest, serving only to ensure that attention was given to each face. The main advantage of this task, which has been advocated in event-related potential (ERP) studies of repetition effects (Rugg and Doyle, 1994), is that the dimensions of interest – repetition and familiarity – are incidental to task performance. This means there is no a-priori reason for subjects to give differential attention to familiar or unfamiliar faces, or initial versus repeated presentations. This is important because attention can modulate responses in perceptual regions: Directing attention to faces increases the response in fusiform regions for example (Wojciulik *et al.*, 1998). A disadvantage, however, is that there is no explicit manipulation of the subject’s attention, or of their processing of the stimuli (other than that required to distinguish targets from nontargets). Furthermore, there is no concurrent behavioural measure of priming.

The present experiment was intended to address these limitations of our previous paradigm by examining the effect of different tasks on the pattern of repetition-related brain responses. More specifically, we used two tasks that encouraged attention to either the familiarity or the repetition of stimuli. Subjects viewed a sequence of familiar and unfamiliar faces, each of which was presented twice in a randomly intermixed fashion (Fig. 1A). In one task, they decided whether or not each face belonged to a famous person (regardless of whether they had seen it previously in the experiment); in the other task, they decided whether or not they had seen each face before in the experiment (regardless of whether it was famous). Thus only the task instructions varied, while the nature of the stimuli remained constant. Following the terminology of Roediger and McDermott (Roediger and McDermott, 1993), we call the former task an implicit memory task, because it makes no reference to the repetition of stimuli, and the latter an explicit memory task, because it makes direct reference to repetitions. The implicit task corresponds to the fame-judgement task used in previous studies of face priming (Ellis *et al.*, 1990) and for which reaction times provided an online index of priming. The explicit task corresponds to a continuous episodic recognition memory task. Together with the dimensions of familiarity and repetition, these tasks comprise a $2 \times 2 \times 2$ factorial design (Fig. 1B).

Materials and Methods

Subjects

Twelve right-handed volunteers (six male; aged 22–42 years, median 29 years) gave informed and written consent to participate in the experiment. All volunteers reported themselves to be in good health with no history of neurological illness.

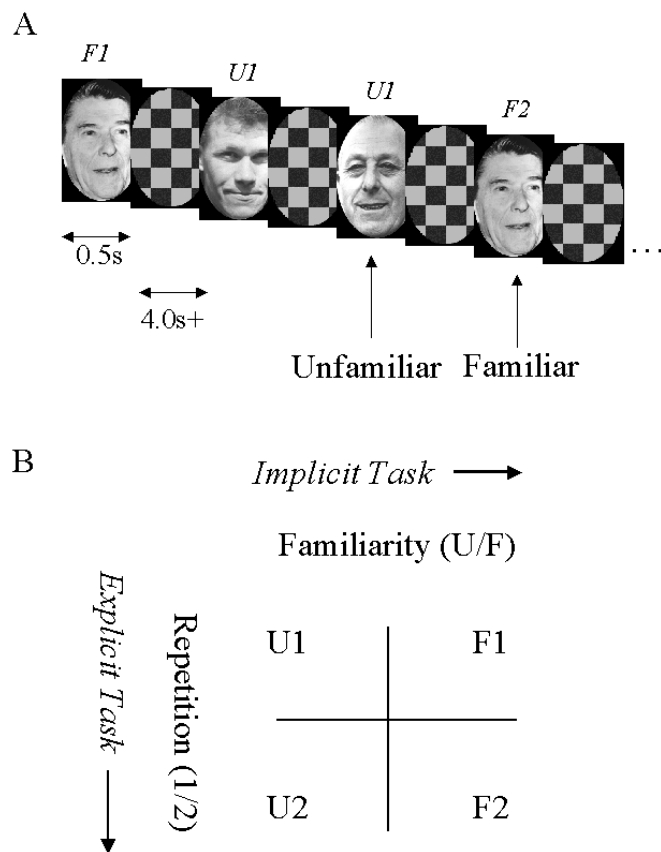


Figure 1. Schematic of the stimuli (A) and tasks (B).

Procedure

Famous and nonfamous (unfamiliar) greyscale faces (52 of each) were taken from the set created by Gorno-Tempini *et al.* (Gorno-Tempini *et al.*, 1998). These faces were split into two sets of 26 familiar (famous) and 26 nonfamous (unfamiliar) faces (eight female and 16 male in each set). A random sequence of two presentations of each face was created from each set for each subject (different faces were thus used for different tasks). The faces were presented for 500 ms, replacing a baseline of an oval checkerboard present throughout the interstimulus interval, with a stochastic distribution of stimulus onset asynchrony (SOA) determined by a minimal SOA of 4.5 s and 52 randomly intermixed null events (Josephs and Henson, 1999). Each stimulus was presented on a mirror 30 cm above the participant, subtending a visual angle of $\sim 10^\circ$.

Each subject was scanned during two sessions (one immediately after the other), each session involving a different task. Subjects were instructed to press one of two keys with either the index or middle finger of their right hand as a function of the task. In both tasks, they were told that some faces would be famous and that faces would be repeated at various intervals. In the implicit (fame-judgement) task, subjects used the keys to indicate whether a face was famous or nonfamous, regardless of whether they had seen it before during the experiment. In the explicit (recognition) task, subjects indicated whether it was the first or second time they had seen each face during the experiment, regardless of whether or not it was famous. The assignment of stimulus sets to each task, the assignment of keys to positive and negative responses and the order of tasks were counterbalanced across subjects.

Scanning Parameters

A 2T VISION system (Siemens, Erlangen, Germany) was used to acquire 24 T_2^* -weighted transverse echoplanar (EPI) images ($64 \times 64 \times 3 \text{ mm}^2$ pixels, $T_E = 40 \text{ ms}$) with blood oxygenation level dependent (BOLD) contrast. EPIs comprised 3 mm thick axial slices taken every 4.5 mm, acquired sequentially in a descending direction and continuously during each 12 min session. Two sessions of 356 volumes were collected with an

effective repetition time (T_R) of 2 s/volume. The first five volumes were discarded to allow for T_1 equilibration effects. The ratio of SOA to T_R ensured an effective sampling rate of the impulse response over trials of $T_R/4$ (2 Hz).

Behavioural Analysis

The four basic trial-types were the first and second presentation of familiar and unfamiliar faces (F1, F2, U1 and U2 respectively). Median correct reaction times (RTs) between 200 and 4000 ms from stimulus onset were calculated for each trial-type for each subject (responses outside this time-window were included with the errors).

One aspect of the random intermixing of the two presentations of each face is that second presentations are necessarily later in time, on average, than first presentations. To control for this potential time confound, a subset of correct trials was selected (the 12 latest first presentations and the 12 earliest second presentations), for which the mean time since the start of each session did not differ significantly ($P > 0.05$ for each trial-type). The average lag between repetitions in this subset was 3 min (27 intervening faces). Analyses of RTs were restricted to these trials.

Median correct RTs were subjected to a 2 (task) \times 2 (familiarity) \times 2 (repetition) repeated measures analysis of variance (ANOVA). The same ANOVA was performed on error proportions (over all trials) after a square-root transform. Effects were deemed reliable at $P < 0.05$, though are not necessarily reported in the presence of higher-order interactions. Planned, pairwise, two-tailed *t*-tests on the RTs were performed for the repetition effect at each level of the other factors.

Imaging Analysis

Imaging data were analysed using statistical parametric mapping (SPM99, Wellcome Department of Cognitive Neurology, London, UK) (Friston *et al.*, 1995) implemented in Matlab5 (The Mathworks Inc., USA). All volumes were realigned spatially to the first volume and the time-series for voxels within each slice realigned temporally to acquisition of the middle slice. Resulting volumes were normalized to a standard EPI template based on the MNI reference brain in Talairach space (Talairach and Tournoux, 1988) and resampled to $3 \times 3 \times 3 \text{ mm}^3$ voxels. No subject moved more than $\pm 2 \text{ mm}$ in any direction during a session. The normalized images were smoothed with an isotropic 8 mm full-width half-maximal Gaussian kernel. The time-series in each voxel were highpass-filtered to 1/120 Hz to remove low-frequency noise and scaled to a grand mean of 100 over voxels and scans within each session.

Statistical analysis was performed in two stages, assuming a balanced mixed effects design. In the first stage model, 12 event-types were defined for each session. Four of these represented correct responses to the four basic trial-types when matched for time of occurrence (see Behavioural Analysis). The remaining event-types represented other correct responses for each trial-type (unmatched for time) and errors for each trial-type. The BOLD impulse response to events of each type was modelled by a canonical haemodynamic response function (HRF) (Friston *et al.*, 1998). This function was convolved with a sequence of delta functions for events of each type in a high resolution time space and downsampled at the midpoint of each scan to form covariates for the general linear model. Also included for each session were six covariates to capture residual movement-related artefacts (the three rigid-body translations and rotations determined from the realignment stage) and a single covariate representing the mean (constant) over scans.

Parameter estimates for each covariate were determined by a least-mean-square fit of the model to the data. The parameter estimates for the canonical HRF comprised the data for the second stage of analyses. For the exploratory, whole-brain analysis, contrast images of the repetition effect (a planned comparison of first versus second presentations, collapsed across familiarity) for each subject were entered into one-sample *t*-tests for each task, treating subjects as a random variable. The resulting statistical parametric maps (SPMs) of the *t*-statistic at each voxel were thresholded at $P < 0.001$ uncorrected for multiple comparisons. To restrict analysis to voxels in which the canonical HRF provided a reasonable fit to the data, these second-stage SPMs were masked with voxels that survived $P < 0.001$ uncorrected in reduced *F*-tests (separable across trial-types, pooled across subjects) from the first-stage SPMs. Thus, voxels for which a significant proportion of the total variability in the

evoked response to one or more event-types was not captured by canonical HRF were not included in the analysis.

To test for differences in the repetition effects across the two tasks (the interaction between task and repetition), further paired *t*-tests were performed on the contrast images of the repetition effect. To test for commonalities, the SPMs from the one-sample tests for the implicit task were masked inclusively with those from the explicit task (maintaining only voxels that survived $P < 0.01$ in both SPMs). For regions showing such task differences or commonalities, *post hoc* analyses were performed in three-way ANOVAs (as in the behavioural analyses) on the canonical parameter estimates (and for which the *P*-values are descriptive only, given the selective sampling of the voxels). The maxima of activated regions were checked on a mean normalized EPI, localized as best as possible on a normalized structural image and labelled using approximations to the systems of Talairach and Tournoux (Talairach and Tournoux, 1988) and Brodmann (Brodmann, 1909).

Results

Behavioural Results

Median correct reaction times (RTs) and error proportions are shown in Figure 2A. Priming occurred in the implicit task, as shown by faster RTs to second than first presentations, particularly for familiar faces. Subjects also responded faster to second than first presentations of familiar faces in the explicit task. These findings were confirmed by an interaction between familiarity and repetition [$F(1,11) = 6.10$, mean square error (MSE) = 0.008, $P < 0.05$]. Planned pairwise tests on the repetition

effects were significant for familiar faces in the implicit [$t(11) = 4.51$, $P < 0.001$] and explicit [$t(11) = 2.63$, $P < 0.05$] tasks, but did not quite reach significance for unfamiliar faces in the implicit test [$t(11) = 2.15$, $P < 0.10$]. RTs were longer to unfamiliar than familiar faces, particularly in the implicit task, as confirmed by an interaction between task and familiarity [$F(1,11) = 5.01$, MSE = 0.015, $P < 0.05$]. There were also main effects of familiarity and repetition [$F(1,11) > 18.6$, MSE < 0.025, $P < 0.001$], but no other effects reached significance.

More errors were made to familiar than unfamiliar faces in the implicit task (i.e. more famous faces were unidentified than unfamiliar faces were falsely identified), but more errors were made to unfamiliar than familiar faces in the explicit task. This pattern was confirmed by an interaction between task and familiarity [$F(1,11) = 11.2$, MSE = 0.034, $P < 0.01$]. More errors were also made for repetitions of unfamiliar than familiar faces, as confirmed by an interaction between familiarity and repetition [$F(1,11) = 23.2$, MSE = 0.009, $P < 0.005$], particularly for missed repetitions of unfamiliar faces in the explicit task; there was little evidence of a 'false fame' effect in the implicit task, (Buchner *et al.*, 2000). The hit-false-alarm rate for second presentations in the explicit task was 0.81 for familiar and 0.46 for unfamiliar faces. There was no obvious speed-accuracy trade-off in the pattern of errors.

Imaging Results

We first report a focal analysis restricted to the right lateral

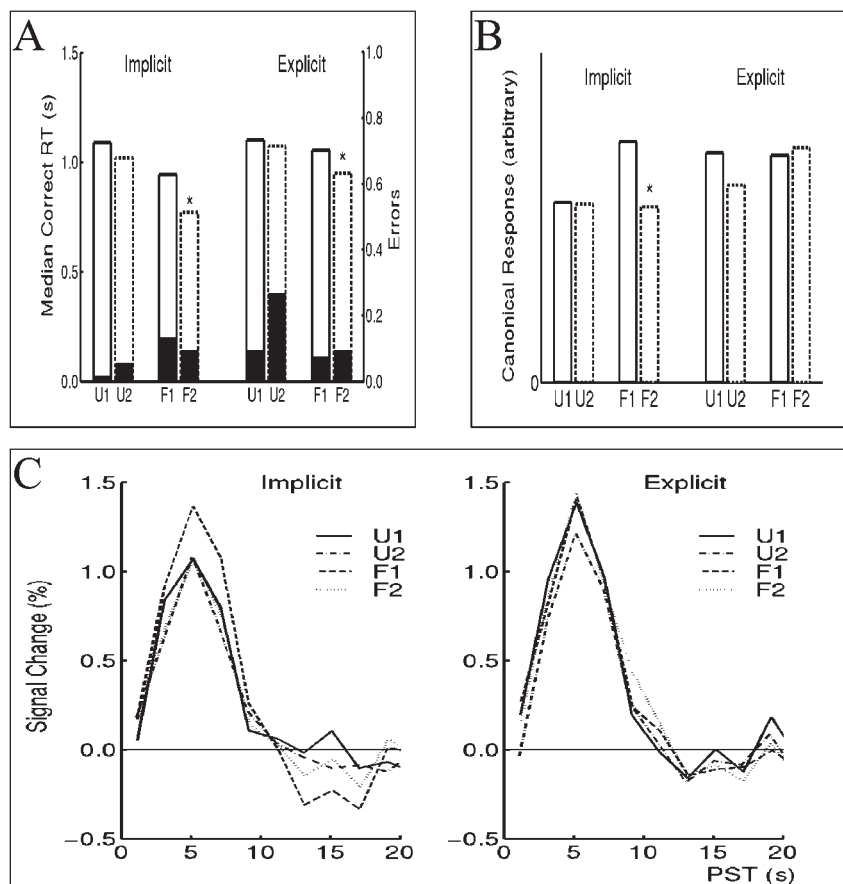


Figure 2. (A) Median correct reaction times (open bars) and median error proportions (solid bars). (B) Parameter estimates for the best-fitting canonical HRF in the right fusiform region of interest. Repetition effects (difference between first and second presentations) significant at $P < 0.05$ are indicated by an asterisk. (C) Event-related data, adjusted for confounds, binned every 2 s and averaged over subjects, from the region of interest in terms of percentage signal change (relative to grand mean over voxels and scans) against peristimulus time (PST).

midfusiform region of interest ($x = +45, y = -57, z = -24$), defined from our previous experiment on repetition effects for two presentations of faces (Henson *et al.*, 2000b). We then report an exploratory analysis extended to repetition effects across the whole brain.

Region of Interest

The event-related responses of the right fusiform region of interest are shown in Figure 2C. In the implicit task, this region showed a greater response to first presentations of familiar than unfamiliar faces, which was reduced following repetition. In the explicit task, the region showed little effect of familiarity or repetition. This pattern was confirmed by a three-way interaction between task, familiarity and repetition on the canonical parameter estimates (Fig. 2B) [$F(1,11) = 5.05$, $MSE = 0.014$, $P < 0.05$]. No other effects reached significance. The only significant pairwise repetition effect was the response suppression for familiar faces in the implicit task [$t(11) = 4.15$, $P < 0.005$]. The response to first presentations was also greater for familiar than unfamiliar faces in the implicit (but not explicit) task [$t(11) = 4.18$, $P < 0.005$].

Whole-brain Repetition Effects

Other regions showing repetition effects in either the implicit or explicit task are shown in Figure 3. Regions showing repetition suppression are shown in blue; regions showing repetition enhancement are shown in orange.

An extensive right fusiform region (region a), encompassing the region of interest discussed above, and a left posterior extrastriate occipital region (region b, most probably in the inferior occipital sulcus) showed repetition suppression in the implicit but not explicit task. Indeed, both regions evidenced a task \times repetition interaction: $F(1,11) = 27.8$, $P < 0.001$ and $F(1,11) = 16.7$, $P < 0.005$, respectively. However, whereas the right fusiform region ($x = +36, y = -51, z = -24$) only showed suppression for familiar faces, as confirmed by a task \times familiarity \times repetition interaction [$F(1,11) = 6.90$, $P < 0.05$] (as with the above predefined region of interest), the left occipital region showed a pattern suggestive of suppression for both familiar and unfamiliar stimuli in the implicit task (no interactions with familiarity reached significance). This was confirmed by repetition suppression effects in the implicit task for familiar faces in the right fusiform [$t(11) = 3.35$, $P < 0.01$] and, in the left occipital region, for unfamiliar faces [$t(11) = 2.34$, $P < 0.05$] and a trend for familiar faces [$t(11) = 1.91$, $P < 0.10$]. We note that the occipital region has previously been associated with structural processing of faces prior to identification (Haxby *et al.*, 2000), facilitation of which might explain the repetition suppression common to both types of faces (though it is unclear why such suppression did not occur in the explicit task too).

Several regions showed repetition enhancement (Table 1). In the implicit task, these included foci in posterior cingulate and bilateral parietal cortex (the latter including lateral intraparietal sulcus and supramarginal gyri). In the explicit task, similar intraparietal regions were found, as well as regions in left anterior and posterior inferior prefrontal cortex, bilateral dorsal superior frontal sulci (possibly including the frontal eye fields), left insula, bilateral precentral and postcentral sulci, and right dorsal cerebellum.

The bilateral intraparietal regions were the only regions showing reliable repetition effects in both tasks, namely repetition enhancement (regions c and d in Fig. 3). The left parietal region showed main effects of repetition [$F(1,11) = 31.6$, $P < 0.001$] and task [$F(1,11) = 6.11$, $P < 0.05$], the latter reflecting

mainly greater responses to first presentation of faces in the explicit than implicit task. Repetition effects were significant for familiar and unfamiliar faces in the implicit task and for familiar faces in the explicit task [$t(11) > 2.96$, $P < 0.05$]. In the right parietal region, repetition enhancement tended to be greater for familiar than unfamiliar faces, particularly in the explicit task, consistent with an interaction between familiarity and repetition [$F(1,11) = 8.12$, $P < 0.05$]. There was also suggestion of greater repetition enhancement in the implicit than explicit task in a marginal interaction between task and repetition [$F(1,11) = 4.79$, $P = 0.05$]. Repetition effects were significant for familiar faces in both tasks [$t(11) > 3.68$, $P < 0.01$].

Discussion

The main finding of the present study was that decreased BOLD responses in temporal/occipital regions were observed to repeated faces in an implicit fame-judgement task, but not in an explicit recognition task. The implication of this finding is that repeated visuoperceptual processing of stimuli is not always associated with response decreases in posterior temporal/occipital regions. This would appear counter to claims, derived from neurophysiology, that neuronal response suppression ‘... happens automatically in the cortex ...’ and is ‘... an intrinsic property of cortical neurons providing a form of perceptual learning that allows us to identify previously encountered objects quickly’ (Wiggs and Martin, 1998). Rather, the pattern of stimulus repetition effects, even in relatively early visual regions, depends on the specific task. A second finding was that several regions, including parietal cortex, showed repetition-related BOLD increases in one or both tasks. Such repetition enhancement has been associated with recollection of the prior occurrence of stimuli (see below), which may be automatic in that it was incidental to the implicit task requirements.

Fusiform Repetition Effects and Priming

The present implicit task replicated the interaction between familiarity and repetition in the right fusiform that we found previously (Henson *et al.*, 2000b), with greater repetition suppression for familiar than unfamiliar stimuli. Furthermore, unlike the monitoring task used in our previous study, which did not provide a behavioural measure of priming, the present fame-judgement task confirmed the presence of concurrent priming effects. The reaction time improvements following repetition were greater for familiar than unfamiliar faces, consistent with previous behavioural studies (Ellis *et al.*, 1990) and mirroring the fusiform interaction. It should, however, be noted that, though a task like fame-judgement was necessitated by the factorial nature of our design, it is not an ideal task to examine interactions between familiarity and priming, since the familiarity dimension is confounded by the response requirements.

The precise role of the lateral fusiform cortex in visual object processing is controversial. Researchers debate whether it is specialized for perceptual categorization (e.g. distinguishing faces from nonfaces) and/or exemplar discrimination, e.g. recognizing familiar faces (Kanwisher *et al.*, 1997; Gauthier *et al.*, 2000; Haxby *et al.*, 2000). Though some imaging studies have found greater fusiform activation for familiar than unfamiliar faces (Sergent *et al.*, 1992; Andreasen *et al.*, 1996; Henson *et al.*, 2000a,b; Katanoda *et al.*, 2000), others have not (Kapur *et al.*, 1995; Gorno-Tempini *et al.*, 1998; Dubois *et al.*, 1999; Leveroni *et al.*, 2000; Nakamura *et al.*, 2000), discrepancies that may reflect differences in the tasks employed (as suggested by the

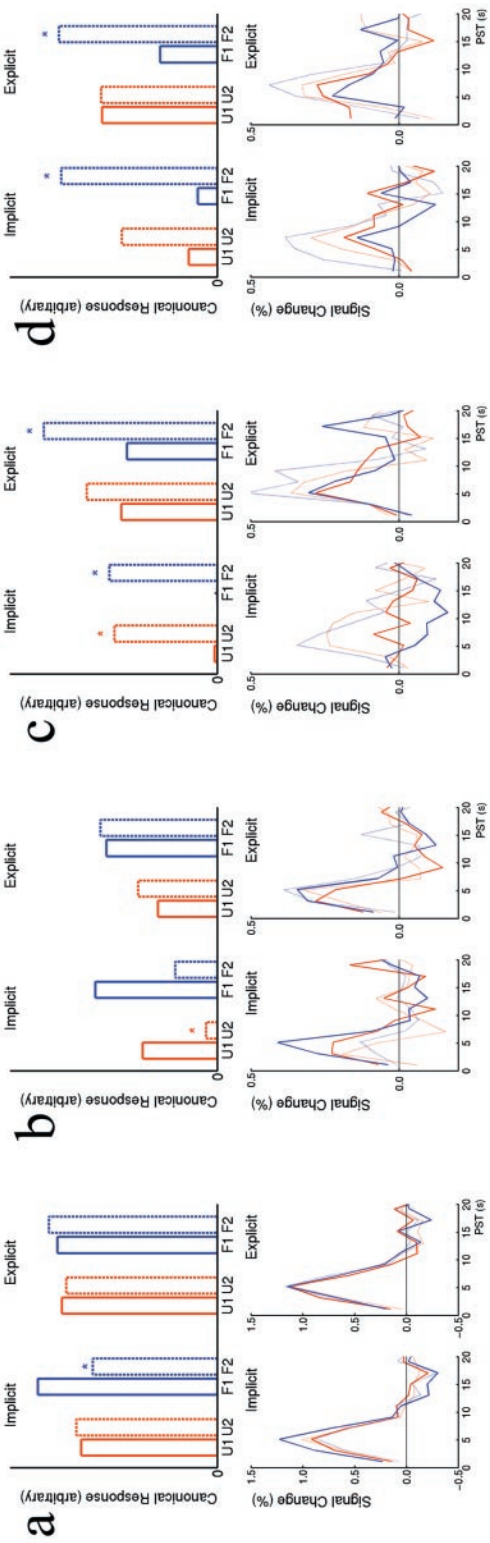
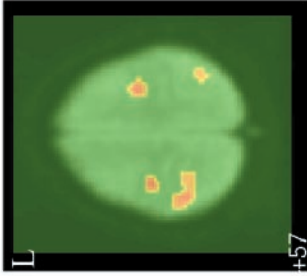
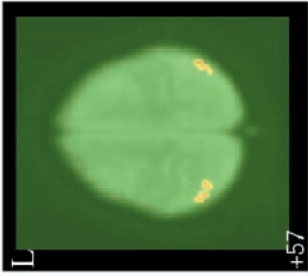
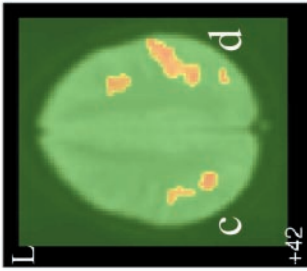
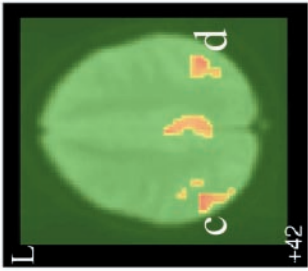
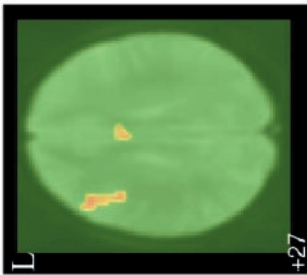
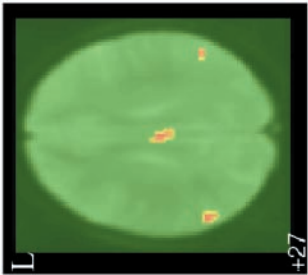
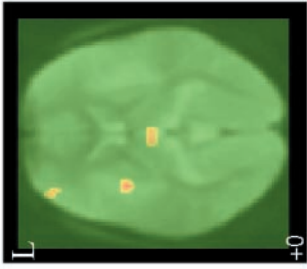
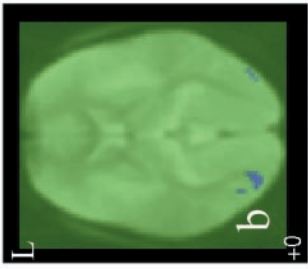
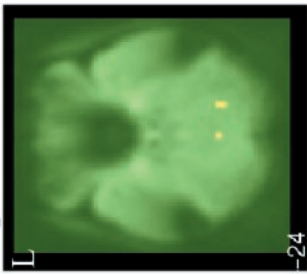
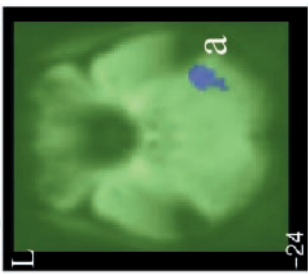


Figure 3. Transverse slices through regions showing repetition effects in implicit (top row) and explicit (middle row) tasks (decreases in blue; increases in orange). Slices derive from the mean normalized EPI across subjects at $z = -24, 0, +27, +42, +57$ mm. Only regions of at least 10 contiguous voxels surviving $P < 0.01$ are shown (for purposes of illustration). Event-related data (bottom) derive from maxima of regions showing an interaction between task and repetition at $P < 0.001$ (regions a and b) or repetition effects at $P < 0.01$ in both tasks (regions c and d). These regions were in right fusiform (a), $x = 36, y = -51, z = -24, Z(\text{interaction}) = 3.65, Z(\text{implicit}) = 3.12, Z(\text{explicit}) = 3.12, Z(\text{implicit}) = 3.12, Z(\text{explicit}) = 2.99$; and right parietal (d) $x = 45, y = -48, z = 42, Z(\text{implicit}) = 3.12, Z(\text{explicit}) = 2.98$, cortices. The event-related data are binned every 2 s. See Figure 2 legend for more details about plots.

Table 1
Maxima of regions showing repetition effects in implicit and explicit tasks

Region of activation	BA	L/R	Implicit				Explicit			
			x	y	z	Z	x	y	z	Z
Suppression										
Fusiform	37	R	39	-51	-27	3.44				
Occipital	18/19	L	-36	-78	-9	3.49				
Enhancement										
Anterior frontal	10/11	L					-42	51	-12	4.65
Inferior frontal	9/46	L					-45	27	27	3.31
Superior frontal	6	L					-21	6	51	3.69
		R					33	9	48	4.10
Insula	–	L					-36	0	0	3.41
Precentral	4/6	L					-33	-18	60	3.81
		R					30	-9	57	3.57
Posterior cingulate	23	B	0	-21	27	3.75				
		R	6	-48	42	3.99				
Postcentral		L					-30	-36	63	3.53
		R					54	-27	42	3.53
Parietal	40	L	-45	-51	39	3.95	-33	-57	45	3.51
	40	R	51	-51	45	4.18	39	-45	42	3.53
Cerebellum		R					24	-60	-30	3.41

L = left, R = right, B = bilateral, BA = Brodmann area. Regions in bold show differential or common repetition effects across tasks (see Fig. 3).

present findings). Though the classical definition of (associative) prosopagnosia is an inability to recognize familiar faces (De Renzi, 1986), the precise localization of the critical lesion (e.g. to lateral fusiform cortex) is unknown and there have been reports that such patients are impaired at finer discriminations in perceptual categorization tasks (Davidoff and Landis, 1990). Intracranial ERPs have shown that later temporal components recorded from fusiform electrodes (but not the early 'face-specific' component) can be modulated by familiarity (Puce *et al.*, 1999), raising the possibility that familiarity-related fusiform responses reflect feedback from other regions.

We previously attributed the fusiform interaction to a visual recognition process, specific to individual objects. This could explain the greater response to initial presentations of familiar than unfamiliar stimuli and the enhanced response associated with repetition of unfamiliar stimuli (assuming that the initial presentation of unfamiliar stimuli was sufficient to create a new representation that allowed them to be recognized subsequently). The decreased response following repetition of familiar stimuli could then be attributed to the facilitation of the recognition process when it is repeated. One difference between the current and previous studies, however, is that repetition enhancement was not found for unfamiliar faces in the present study. This may be another example of a task effect, in that our previous indirect monitoring task may have engendered processing of unfamiliar faces that differed from that engendered by the present fame-judgement task. The lack of repetition effects in the present explicit task suggests, at least, that the repetition enhancement in our previous monitoring task did not reflect differential effects of episodic memory. Further experiments are required to characterize conditions under which fusiform repetition enhancement is observed.

One possible explanation for the fusiform repetition effects is that they are a consequence of the different reaction times, i.e. an effect rather than a cause of the behavioural priming. Such an account is not entirely adequate, in that the pattern of reaction times was not a perfect match to the pattern of right fusiform responses (cf. Fig. 2A,B): reaction times in the implicit task were longer to unfamiliar than familiar faces for example, yet the fusiform response to unfamiliar faces was weaker. Moreover, other

regions in which processing would presumably correlate with reaction times, such as early visual and motor regions, did not show repetition effects in the implicit task. None the less, the question of cause and effect is better addressed with neuropsychological data and in this case it is noteworthy that at least two patients have been reported with impaired perceptual priming following posterior occipital/temporal lesions (Gabrieli *et al.*, 1995; Keane *et al.*, 1995).

Interactions between Task and Repetition Effects

The results of previous imaging comparisons of repetition effects in implicit and explicit memory tasks have been mixed, particularly with regard to ventral temporal-occipital regions. In two studies, completion of partial word cues with previously studied words was associated with response decreases in occipital regions in both implicit and explicit versions of the task (Squire *et al.*, 1992; Blaxton *et al.*, 1996). In a study using 2-D object-drawings (Schacter *et al.*, 1995), however, response increases were found in fusiform regions associated with repetition of possible (but not impossible) object-drawings in both an implicit (possible/impossible object decision) and an explicit (recognition) task. In a study using random-dot patterns (Reber *et al.*, 1998), Reber *et al.* found response decreases in occipital regions associated with exemplars of the same versus different category in an implicit task (categorization), but response increases associated with repeated versus new patterns in an explicit task (recognition). Previous imaging comparisons of repetition effects in implicit and explicit tests thus provide little guidance for interpreting the present pattern of fusiform responses. None the less, while we are unable to offer a conclusive account, we consider three possibilities below.

A Processing Account

The first account makes the assumption adopted by most previous imaging studies of priming – that repetition suppression reflects the facilitation of a process that is repeated (Schacter and Buckner, 1998). The question relevant to the present fusiform responses is then: what is the precise process that is facilitated?

One candidate process is the identification that a face belongs

to a known individual. Such identification is a prerequisite for naming a face and is likely to occur in fame-judgements. This is a modification to the fusiform recognition process that we suggested previously (Henson *et al.*, 2000b), the difference being that unfamiliar faces cannot be identified even after repetition, which can explain the lack of repetition effects for unfamiliar faces in the present study. In other words, this proposal implicitly distinguishes between ‘familiarity’ and ‘fame’, in that multiple repetitions may be sufficient to make an initially unfamiliar face familiar, but are not sufficient to make it identifiable; the face may also need to be associated with semantic information, such as a name, or ‘PIN’ (Bruce and Young, 1986). Such information might be represented in other brain regions, in which case fusiform activity would depend on top-down feedback from these regions (see above). This account resembles that given for the inferotemporal activations found when naming objects (Friston *et al.*, 1996).

This proposal might also explain the absence of repetition effects in the explicit task, by virtue of the fact that the recognition memory task does not require identification of faces, only that a particular photograph of a face has been seen before in the experiment. There are several problems with the proposal, however. Firstly, the fusiform response was generally greater in the explicit than the implicit task, which is problematic if no identification occurs in the explicit task. Secondly, it is unlikely that subjects did not identify famous faces in the explicit task, even if not required to by the task instructions. Identification (and often naming) of famous faces appears to be an automatic process (Ellis *et al.*, 1990), consistent with the evidence that fame influenced the pattern of errors and reaction times in the explicit task (Fig. 2A). Indeed, automatic identification would be needed to explain the greater responses to initial presentations of famous than unfamiliar faces in our previous indirect monitoring task (Henson *et al.*, 2000b).

A Task-relevance Account

A second possible account is that the absence of repetition suppression in the explicit task is a consequence of making the repetition of stimuli task-relevant. Neurophysiological studies of delayed-match-to-sample (DMS) tasks have shown at least two distinct types of repetition-sensitive cells in monkey inferior temporal cortex (Miller and Desimone, 1994). One type shows decreased firing rates to repetition of stimuli whether or not they are task-relevant (i.e. to both targets and repeated distractors). Another type shows increased firing rates to task-relevant repetitions (targets), but little change in firing rate for task-irrelevant repetitions (repeated distractors). For related findings in a human fMRI study of DMS for faces, see Jiang *et al.* (Jiang *et al.*, 2000).

Thus, in the present implicit task it is possible that only decreases in cell firing occurred to repeated stimuli, because the repetition was not task-relevant. In the explicit task, however, where repetitions were task-relevant, there may have been a balance between cells of both types, such that there was no net change in the BOLD response. This account might explain why fusiform suppression to repeated faces was found in a one-back location-repetition task (Gauthier *et al.*, 2000), where repetition of face identity was irrelevant, but not in a one-back face-repetition task (Epstein *et al.*, 1999), where repetition of face identity was relevant. A problem with this account, however, is why repetition suppression was not seen for unfamiliar faces in the present implicit task (one might suggest that the firing of cells in the present fusiform region is selective for familiar faces,

but then it is unclear why no familiarity effects were seen in the explicit task).

A further problem with the task-relevance account concerns the distinction between a working memory task, requiring the detection of repetition of a single target in a short series of distractors (as in the DMS task) and a long-term memory task, requiring the detection of any repetition in a long series of items (as in the present explicit task). This distinction is important because increased neural firing rates to repetitions are rarely seen in serial recognition tasks directly analogous to the present explicit task (Brown and Xiang, 1998), which invariably produce larger numbers of cells showing response suppression. Furthermore, the cells in monkey cortex that show the longest-lasting suppression are in anterior temporal regions (such as TE and perirhinal cortex); cells in more posterior temporal regions tend to have short-lived suppression effects (Brown and Xiang, 1998), some not lasting more than one intervening stimulus, though the precise monkey analogue of the fusiform ‘face area’, as functionally defined in humans, remains unclear (Gauthier and Logothetis, 2000).

An Attentional Account

The final possibility considered here is an attentional account. Directed visual attention to faces can increase responses in fusiform regions (Wojciulik *et al.*, 1998). Thus, for the pattern of fusiform responses in Figure 2B to be explained, an attentional account must justify why more attention was given to all four conditions in the explicit task and to the first presentation of familiar faces in the implicit task, than was given to the remaining three conditions in the implicit task.

One possibility is that the increased attention to both first and second presentations of faces in the explicit task reflected either an attempt to retrieve a memory for prior occurrence of a face or, failing that, an attempt to encode that face effectively into episodic memory. This is consistent with episodic encoding and retrieval being attention-demanding processes (Craik *et al.*, 1996) and would be examples of endogenously driven attention. In the implicit task, the increased attention to the first presentation of a familiar face may have been exogenously driven, in that the presentation of a famous face may be sufficient to capture attention.

The problem with this account is then to explain why less attention was given to the second presentation of familiar faces in the implicit task. One might argue that repeated judgements on the same face require less endogenous attention, or that repetitions are less likely to capture exogenous attention. This would not, however, explain the lack of repetition suppression for unfamiliar faces. Moreover, such a proposal appears to beg the question, in that it does not specify why repeated presentations require less attention.

In summary, none of the accounts considered above appears sufficient to explain the complete pattern of repetition effects across the implicit and explicit tasks. A combination of two accounts is, of course, possible: for example, an automatic repetition suppression effect associated with repeated perceptual processing that is obscured by a top-down attentional repetition enhancement effect in the explicit task. Indeed, because the BOLD impulse response effectively integrates over several seconds of neural activity, it may obscure dissociable repetition effects that operate over different sub-second timescales (James *et al.*, 2000; Henson and Rugg, 2001), as suggested by MEG/EEG studies (Dale *et al.*, 2000; Dhond *et al.*, 2001).

Repetition Effects in other Brain Regions

Several regions showed repetition enhancement in one or other task. Some of these, such as parietal, posterior cingulate and left anterior prefrontal cortices, have previously shown repetition enhancement (or 'old-new' effects) in explicit memory tasks using words (Rugg and Henson, 2001). Bilateral parietal regions showed old-new effects in both the implicit and explicit tasks of the present study. These regions have been implicated in recollection of episodic memories (Rugg and Henson, 2001), which have may have been incidental in the present implicit task, or even intentional, as subjects tried to remember the response they made last time, in an attempt to be consistent in their fame-judgements. Old-new effects in frontal regions were only seen in the explicit task. Though any interaction with task did not reach significance, it is noteworthy that frontal old-new effects have been attributed to post-retrieval processes, such as the monitoring of retrieved information in relation to old-new decision criteria (Henson *et al.*, 2000a), which may have been specific to the explicit task.

Notes

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