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The effect of repetition lag on electrophysiological and haemodynamic correlates of visual object priming

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The modulation of repetition effects by the lag between first and second presentations of a visual object during a speeded semantic judgment task was examined using both scalp event-related potentials (ERPs) and event-related functional magnetic resonance imaging (efMRI). Four levels of lag were used within a single session, from zero to one, to tens of intervening stimuli, and which allowed partial separation of the effects of interference from the effects of time. Reaction times (RTs) showed that the magnitude of repetition priming decreased as lag increased. The ERP data showed two distinct effects of repetition, one between 150 and 300 ms post stimulus and another between 400 and 600 ms. The magnitude of both effects, particularly the earlier one, decreased as lag increased. The fMRI data showed a decrease in the haemodynamic response associated with repetition in several inferior occipitotemporal regions, the magnitude of which also typically decreased as lag increased. In general, and contrary to expectations, lag appeared to have mainly quantitative effects on the three types of dependent variable: there was little evidence for qualitative differences in the neural correlates of repetition effects at different lags.

Keywords: Repetition effects; Lags; ERPs

The effects of incidental repetition of a stimulus have been used to investigate both memory and perception (Henson, 2003). Such effects are often associated with "priming", indexed behaviourally as a change in the speed, bias or accuracy of processing the stimulus after repetition. From the memory perspective, priming is interesting because of evidence that it can occur in the absence of awareness of the repetition (Warrington and Weiskrantz, 1974), and that it may reflect operation of a memory system separate from that impaired in global amnesia (Schacter and Tulving, 1994; Squire and Cohen, 1984). From the perception perspective, the degree to which priming generalises across changes in certain properties of the stimulus (e.g. changes in the viewing angle of a visual object) has been used to infer the nature of the underlying perceptual representations (e.g. Biederman and Cooper, 1991).

The haemodynamic correlate of stimulus repetition is typically a decreased response (so-called "repetition suppression") in brain regions associated with processing the stimulus in a given task (Schacter and Buckner, 1998). For visual stimuli, the main such regions are within occipitotemporal cortex; cortex that is typically intact in amnesics but damage to which has been associated with impaired visual priming (Keane et al., 1995). In analogy with behavioural measures of priming, repetition suppression has also been used as a tool to map out the brain regions associated with different stages of visual object processing (Grill-Spector et al., 1999; Kourtzi and Kanwisher, 2000; Koutstaal et al., 2001; Vuilleumier et al., 2002). Indeed, it has been proposed that this technique offers a higher spatial resolution than conventional comparisons of different stimulus categories (Grill-Spector et al., 1999; Naccache and Dehaene, 2001).

A potentially important parameter for repetition effects is "lag": the interval between first and second stimulus presentations. Behavioural priming can be very long lived. For example, the time taken to name a visual object can show priming up to a year later (Cave, 1997). The size of priming effects does tend to decrease with lag however, depending on the nature of the stimulus and manner in which it is processed (Bentin and Moscovitch, 1988). Moreover, there may be qualitative rather than simply quantitative differences in the causes of priming at different lags. For example, a qualitative difference has been suggested between "immediate" repetition (in the absence of intervening stimuli) and repetition after intervening items (Bentin and Moscovitch, 1988; Ratcliff et al., 1985). Priming of immediate repetitions, for example, may include contributions from motor response preparation (Bentin and Peled, 1990) and, for short temporal intervals, contributions from a short-lived sensory store, such as a visual iconic memory (Sperling, 1960). In physiological terms, such priming might be mediated by transient neural activity rather than synaptic change. There may also be an important distinction between "short" lags of one to four intervening items (and intervals of several seconds) and longer lags (e.g. McKone, 1995). This distinction may partly reflect whether stimuli are still in visual/working memory (Phillips,

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1974). There may even be a distinction between "long" lags of several minutes, beyond working memory span but within the same experimental session, and "very long" lags across sessions and days. Studies of perception have tended to use immediate or short lags, whereas studies of memory have tended to use long or very long lags.

A further question is whether the critical factors determining the effects of lag are the presence of intervening items, the passage of time, or both. In other words, do the mechanisms underlying lag effects reflect active interference from other items, or passive decay over time? In addition to their theoretical importance, the presence of qualitative (e.g. mechanistic) differences across lags would have practical implications for the use of repetition suppression as a tool to dissociate brain regions according to different stages of perceptual processing. Some imaging studies of visual object processing, for example, have used immediate repetition (Grill-Spector et al., 1999; Kourtzi and Kanwisher, 2000), whereas others have used long-lag repetition (Koutstaal et al., 2001; Vuilleumier et al., 2002). Any discrepancies across these studies could therefore reflect the different lags employed rather than implying different conclusions regarding the invariant aspects of visual object representations.

Qualitative differences across lags are difficult to demonstrate with a unidimensional behavioural measure like reaction time, though they might include interactions of lag with another independent variable (such as stimulus familiarity or task, Bentin and Moscovitch, 1988). For multidimensional measures such as electroencephalography (EEG) and functional magnetic resonance imaging (fMRI), evidence of qualitative differences can be defined as an interaction between lag and one or more dimensions of the dependent variable, such as time or space. Such an interaction can be viewed as a necessary, though not sufficient, condition for different functional interpretations (Rugg and Coles, 1995). This is the approach taken by the present study.

Using event-related fMRI (efMRI), we previously found repetition effects in occipitotemporal cortex in response to visual stimuli that decreased over 1 to 147 intervening stimuli, paralleling the effect of such lags on behavioural priming (Henson et al., 2000). This was a post hoc analysis however, which did not explicitly manipulate different categories of lag (e.g. the "short" and "long" lags defined above), and could not dissociate the effects of intervening items from the effects of time. Other efMRI studies found that the magnitude of occipitotemporal repetition suppression during covert naming of visual objects did not appear to differ for "long" lags of 30 s (10 or more intervening items) and "very long" lags of 3 days (van Turennout et al., 2000, 2003). These studies did find a repetition-by-lag interaction in left inferior prefrontal cortex, in which the amount of repetition suppression was actually greater for very long than for long lags. The authors attributed this to a gradual procedural learning of object naming that took time to develop.

The effects of repetition lag have been explored in EEG studies that examine stimulus-locked event-related potentials (ERPs), providing additional information about the latency of repetition effects. Using an indirect monitoring task, Nagy and Rugg (1989) found a widespread positive shift associated with repetition of words, onsetting approximately 300 ms, which did not appear to vary across lags of 0, 6 and 19 intervening words. An earlier transient negative deflection over frontal sites however, onsetting approximately 200 ms poststimulus, was found for the lag 0 condition, but not for the other conditions, suggesting a qualitative difference between immediate and short lag repetitions. Using a lexical decision task, Karayanidis et al. (1991) reported the same widespread positive shift onsetting 300 ms for immediate and short lags (of four intervening words), but failed to find the earlier negative deflection for immediate repetition. Instead, the authors proposed that lag had quantitative rather than qualitative effects on the ERP repetition effects.

In the present study, participants saw pictures of common objects and decided whether each object could (in real life) fit into a shoebox. Priming was indexed by the difference between second

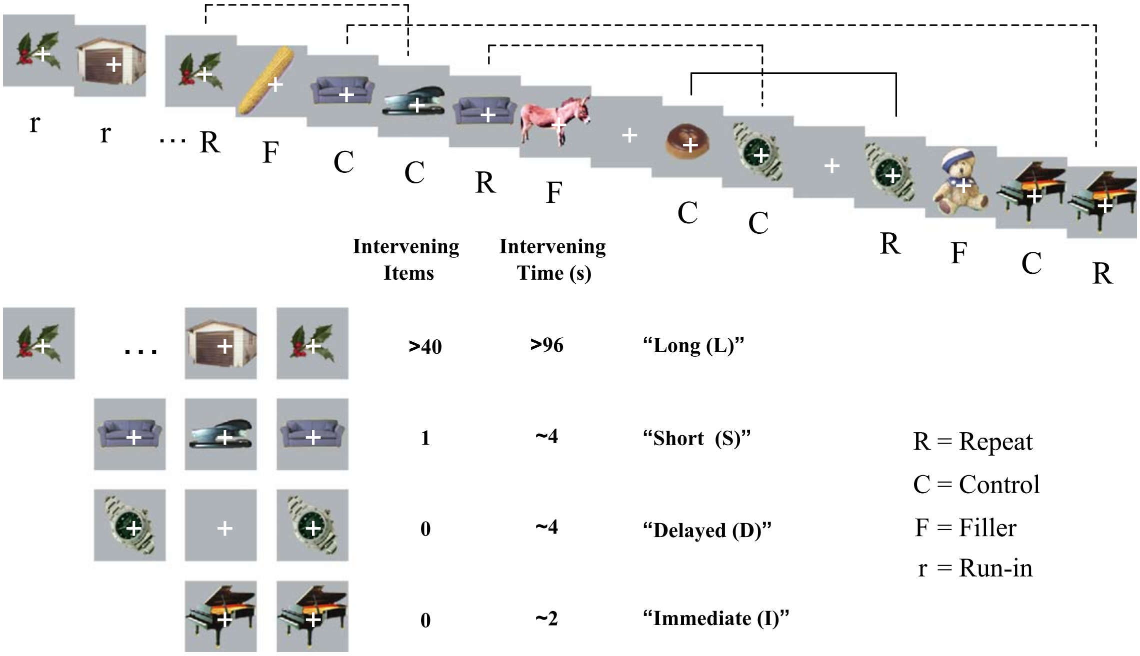

Fig. 1. Schematic of the experimental design.

vs. first presentations of objects in the reaction time (RT) to make this decision. There were four conditions, each corresponding to a different repetition lag (see Fig. 1): (1) Long lags, when at least 40 stimuli or 96 s occurred between the repetition of an object, (2) Short lags, when only one stimulus and at least 4 s occurred between a repetition, (3) Delayed lags, when at least 4 s but no stimuli occurred between a repetition and (4) Immediate lags, when at least 2 s but no stimuli occurred between a repetition. Equal numbers of nonrepeated control stimuli were also assigned a ‘lag’ (see Materials and methods), giving independent measures of the repetition effect (the difference between each Repeat and its matched Control), unconfounded by time. The effects of multiple intervening stimuli (beyond the typical range of working memory) could be tested by comparing repetition effects at Long vs. Short lags. The effect of interference from intervening stimuli, while holding the temporal delay constant, could be tested by comparing repetition effects at Delayed vs. Short lags (at least for a single intervening stimulus). The effect of decay over time could be tested by comparing repetition effects at Immediate vs. Delayed lags (at least over the range of 2 and 4 s). These comparisons were made on both ERP and efMRI data, acquired from different groups of participants.

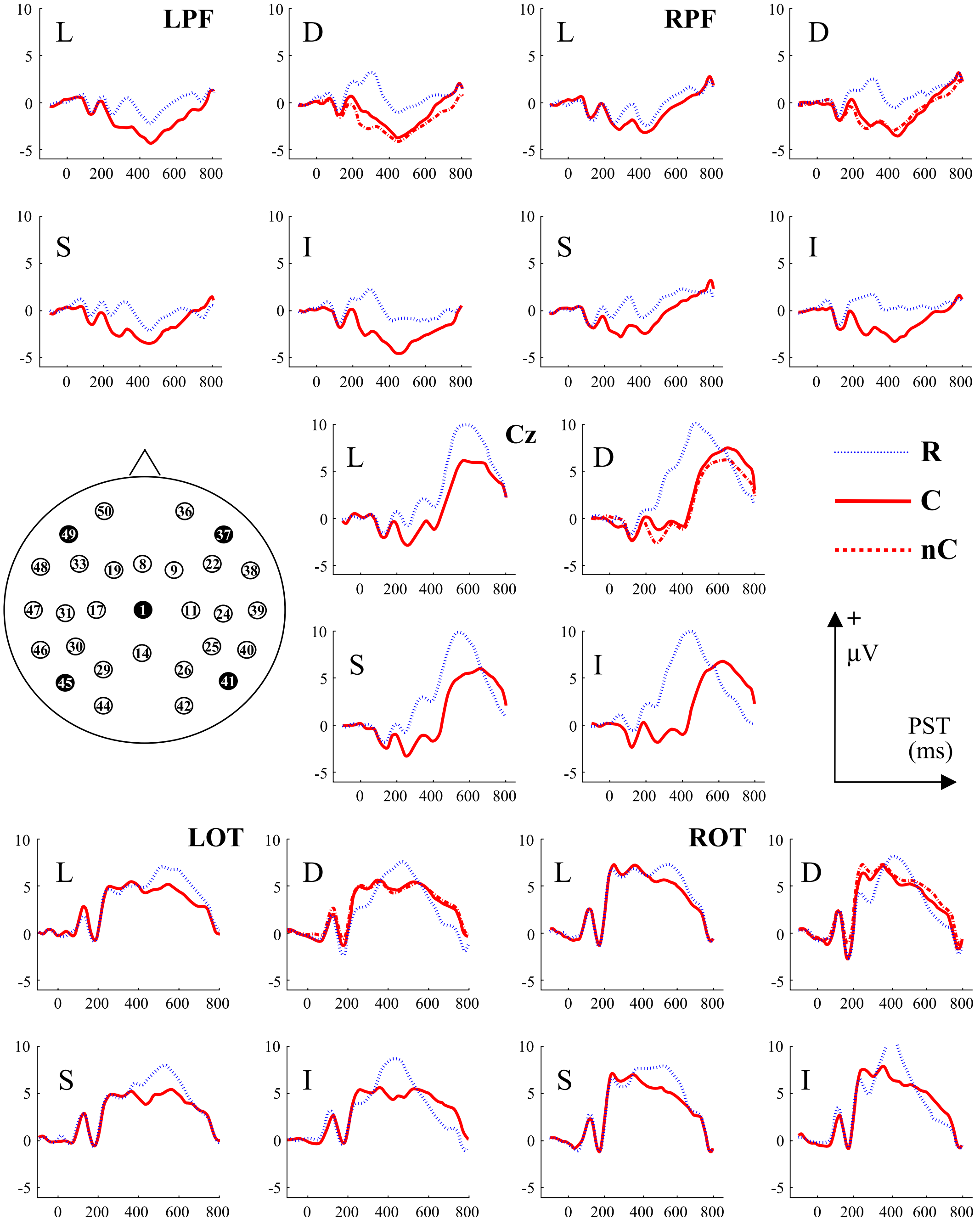

Fig. 2. ERP data from selected electrodes in the montage (inset): left and right prefrontal (LPF/RPF, Easycap sites 49/37), central (Cz, Easycap site 1), and left and right occipitotemporal (LOT/ROT, Easycap sites 45/41). L = Long, S = Short, D = Delayed, I = Immediate conditions; R = Repeat, C = Control, nC = non-delayed Control (see text); PST = poststimulus time.

Materials and methods

Participants

Thirty-one volunteers gave written consent to participate in the study: 19 for the EEG experiment and 12 for the fMRI experiment. The data from three participants in the EEG experiment, and from one in the fMRI experiment, were not analysed because of technical problems or data artifacts (e.g. excessive movement). The 16 remaining participants in the EEG experiment contained 7 men and 9 women, aged 20–25, 3 left-handed; the 11 participants in the fMRI experiment contained 6 men and 5 women, aged 22–33, 2 left-handed. All volunteers reported themselves to be 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).

Basic design

There were four lags of interest: (1) Long lags, when at least 40 stimuli and 96 s intervened between the repetition of an object, (2) Short lags, when only one stimulus/two Stimulus Onset Asynchronies (SOAs), corresponding to 4.80 s in the EEG experiment and 4.56 s in fMRI experiment, occurred between a repetition, (3) Delayed lags, when two SOAs, but no stimuli, intervened between a repetition and (4) Immediate lags, when one SOA (2.40 s in the EEG experiment; 2.28 s in fMRI experiment), but no stimuli, intervened between a repetition. Equal numbers of nonrepeated control stimuli were also assigned a lag (see below), giving eight conditions of interest.

Materials

Stimuli were coloured pictures of everyday nameable objects selected from Robb and Rugg (2002) and from the Hemera Photo Objects collection (Volumes 1 and 2; http://www.hemera.com), presented within a gray square against a black background and with a white fixation cross in the centre of the square. In the EEG experiment, the stimuli were displayed for 600 ms with an SOA of 2400 ms on a computer screen approximately 90 cm from the participant, subtending a visual angle of approximately 3°. In the fMRI experiment, the stimuli were displayed for 700 ms with an SOA of 2280 ms, projected onto a mirror 30 cm above the participant, with the gray square subtending a visual angle of approximately 5°.

Procedure

The participants' task was to decide whether each stimulus could, in real-life, fit in a shoe box. We chose this task because it requires object identification without appearing to be confounded by systematic visual differences between objects that fall into one or other response category, and because this task has been used in previous fMRI studies of object priming (Koutstaal et al., 2001). Participants responded "yes" or "no" by pressing a key with the index finger of either their left or right hand, with both speed and accuracy emphasised. The assignment of hand to response was counterbalanced across participants; the assignment of objects to conditions was randomised. Participants were told that some objects were repeated, but that this did not affect their task. Each participant received a short practice session that included examples of each repetition condition.

The EEG experiment was run as two sessions of approximately 12 min, separated by a short rest, with 15 replications of each condition per session (except the Delayed Control condition, which had 30 replications per session; see below). The fMRI experiment was run as a single session of approximately 14 min, with 20 replications of each condition. Each session, though a continuous sequence, consisted of two phases (unknown to participants). The first, shorter phase was a "run-in" period, lasting approximately 1 min in the EEG experiment and 2 min in the fMRI experiment. The purpose of the run-in was to present the first occurrences of repeated objects in the Long lag condition. The run-in also included stimuli from the other Lag conditions, including delayed lags, to maintain stationary probabilities of stimulus repetition (0.29 in EEG experiment; 0.31 in fMRI experiment) and stimulus delay (0.18 in EEG experiment; 0.13 in fMRI experiment). None of the run-in objects were of interest.

The second phase in each session contained of three basic stimulus types: Repeats, Controls and Fillers (Fig. 1). Only Repeats and Controls were of interest. The assignment of lag to Controls was determined by random selection of nonrepeated objects from the second phase, with the constraints that (1) Controls (like Repeats) were preceded by a nonrepeated stimulus, (2) Controls for the Delayed lag condition (like Repeats for that condition) were also preceded by a delay. The remaining nonrepeated stimuli became Fillers (Fig. 1). For the EEG experiment, additional Control delays were added so that the probability of a Repeat following a delay (0.29) was the same as that without a delay (so that delays did not "cue" any change in the predictability of different stimulus types). The presentation order of trials of each condition was randomised.

EEG acquisition

The electroencephalogram was recorded from silver/silver chloride electrodes on 31 scalp sites, 29 in an elasticated cap (Falk Minow Easycap "montage 10", http://www.easycap.de./easycap) and one on each mastoid process. Recording was continuous, with reference to a mid-frontal electrode (Fz). Impedances were less than 10 kΩ. Vertical and horizontal electrooculograms (VEOG and HEOG) were recorded from electrode pairs situated above and below the right eye and on the outer canthi. Recordings were amplified with a bandwidth of 0.03–100 Hz (3-dB points) and digitised (12 bit, 0.122 μV/bit; 0.6 μV/bit for VEOG) at a sampling rate of 500 Hz.

fMRI acquisition

A 2-T Vision system (Siemens, Erlangen, Germany) was used to acquire 24 T2*-weighted transverse echoplanar (EPI) images (64×64 3×3 mm^2 pixels, TE = 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. The slices were oriented parallel to the inferior temporal lobes, and excluded the inferior cerebellum and superior frontal/parietal cortex (min and max z-coordinates were −42 mm and +27 mm in normalised images; see below). A total of 465 volumes were collected continuously with a repetition time (TR) of 1824 ms. The first 5 volumes were discarded to allow for equilibration effects. An additional 64-slice, whole-brain EPI with

$2 \times 2 \times 2$ mm^2 voxels was also acquired for each participant to aid spatial normalisation (see below). The ratio of SOA to TR ensured that the impulse response was sampled every 456 ms (over trials).

Basic analysis strategy

The same basic analyses—repeated-measures analyses of variance (ANOVAs)—were performed on the behavioural, ERP and efMRI data, in the following hierarchical manner. An initial, omnibus 2×4 ANOVA included the factors of repetition (Repeats and Controls) and lag (Long, Short, Delayed and Immediate). Any significant interactions between repetition and lag were examined in more detail by three 2×2 ANOVAs across consecutive levels of lag (Long/Short, Short/Delayed and Delayed/Immediate). Any significant interactions in these ANOVAs were followed by two one-way ANOVAs on the repetition effect at each corresponding lag. A significant main effect of repetition in the omnibus ANOVA, in the absence of an interaction, was followed by a one-way ANOVA for the Long condition, to test for a repetition effect at even the most extreme lag.

In the behavioural analyses, the above two ANOVA factors were supplemented by a third factor of participant group (ERP/efMRI). In the ERP analyses, the factors were supplemented by a third factor with 31 levels, one per scalp site, and repeated for time windows of interest. In the efMRI analyses, the ANOVAs were 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). All analyses used a Greenhouse–Geisser correction for nonsphericity (or a variant thereof in the case of the efMRI data; see below). Significance was defined as a P value below 0.05; significant effects were only reported in the absence of significant higher-order interactions.

Behavioural analysis

Trials with reaction times (RTs) less than 200 ms or greater than 2250 ms were excluded. Trials with repeated objects were restricted to "consistent" responses, in which the same response was given on first and second presentations.

ERP Analysis

Preprocessing was automated using EEG functions from SPM2 (Kiebel and Friston, 2003; http://www.fil.ion.ucl.ac.uk/spm); statistical analysis was performed using additional code written in Matlab (The Mathworks, http://www.mathworks.com/products/matlab). To correct for VEOG contamination of the EEG caused by blinks, the data were initially epoched from 800 to 2400 ms relative to stimulus onset. This epoch was beyond the −100 to 800 ms range that comprised the ERPs of interest (see below), so that contamination of blink estimates by ERP signal was minimised. Epochs containing an artefact were rejected. Artefacts were defined as a site from which the signal had "blocked" owing to A/D saturation (a value of zero for at least eight consecutive time points), exceeded an absolute threshold of 200 μV or "drifted" (a linear regression with a correlation coefficient greater than 0.8 and range over the epoch greater than 100 μV). Remaining epochs were lowpass-filtered to a 3-dB attenuation at 20 Hz using a zero-phase shift filter. Blinks were defined by a VEOG deflection exceeding 200 μV with a full-width-at-half-maximum (FWHM) less than 200 ms (mean number of blinks = 211; range = 21–335). A "blink profile" for a 100-ms window straddling the peak of each blink in the VEOG was then created by averaging over all epochs containing blinks. A correction weight for each EEG site was then defined by the parameter estimate for the slope of a linear regression of that site's blink profile against the blink profile for the VEOG (Picton et al., 2000).

The data were then re-epoched from −100 to 800 ms, baseline-corrected relative to the 100 ms prestimulus period, and epochs with artefacts removed (defined as above; mean number of artefacts = 8; range = 0–32). Each EEG epoch was corrected for blinks by subtracting the VEOG for that epoch multiplied by the corresponding blink correction weight calculated above. The data were re-referenced to the average of the left and right mastoids (for consistency with most previous studies of stimulus repetition effects).

ERPs were calculated by averaging trials according to condition and behaviour as described above (mean number of trials contributing to each ERP, averaging across participants and all conditions except Delayed Controls = 27, range = 19–30; mean for Delayed Controls = 58). ANOVAs were performed for each of four time windows, based on the mean amplitude (with respect to mean prestimulus baseline) within that time window. The time windows were 110–140 ms (encompassing a P120 component over occipitotemporal sites), 160–190 ms (encompassing an N170 component over occipitotemporal sites), 200–300 ms (encompassing the early repetition effect described by Nagy and Rugg, 1989) and 400–600 ms (encompassing a central positive peak described by Henson et al., 2003).

For display purposes (i.e. Fig. 2), the ERPs were lowpass-filtered to a 3-dB attenuation at 10 Hz using a zero-phase shift filter. Scalp potential maps were created by spline interpolation [calculation of current source density (CSD) maps did not add any additional information]. Differences in scalp topographies were tested by ANOVAs over all sites after normalising amplitude differences to the mean min–max range over sites and participants (McCarthy and Wood, 1985). Though the practice of amplitude normalisation before topographic analysis has recently been criticised by Urbach and Kutas (2002), their criticisms regarding baseline artefact and the effects of residual noise apply only when data are normalised with respect to squared amplitude ("vector scaling"), and do not apply to data normalised with respect to amplitude range, as in the present study. Nonetheless, we note that such scaled topographic analyses do not typically have high power.

efMRI analysis

Analysis of the efMRI data was performed with SPM (http://www.fil.ion.ucl.ac.uk/spm). All volumes were coregistered to the first volume and then unwarped to allow for EPI distortions owing to movement (Andersson et al., 2001). Spatial normalisation parameters were estimated by warping each participant's high-resolution EPI to a standard EPI template based in Talairach space (Ashburner and Friston, 1999), using an initial EPI orientation determined by approximate manual matching to the template. The functional EPIs were then coregistered to the high-resolution EPI, deformed with the normalisation parameters, and resampled to $3 \times 3 \times 3$ mm^3 voxels. These normalised images were smoothed with an isotropic 8-mm FWHM Gaussian kernel (final estimated smoothness was $10 \times 10 \times 10$ 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 (Holmes and Friston, 1998). 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 canonical HRF (Friston et al., 1998). The resulting time courses were downsampled at the midpoint of each scan to form covariates in a General Linear Model. Separate covariates were modelled for the eight conditions of interest (according to behaviour), plus four additional covariates for fillers, run-in fillers, run-in repeats and inconsistent/missed responses, 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.

Contrasts of the parameter estimates for the eight conditions of interest comprised the data for the second-stage analyses, which treated participants as a random effect. More specifically, images of the repetition effect for each lag and each participant were entered into a 1 × 4 ANOVA without an intercept term. A Statistical Parametric Map (SPM) was created of the F statistic for an "effects of interest" contrast. This contrast identified regions in which there was a significant repetition effect across one or more lags. In other words, the contrast included regions showing a main effect of repetition and/or a repetition-by-lag interaction. The SPM was thresholded for 5 or more contiguous voxels surviving $P < 0.001$, using the nonsphericity correction described in Friston et al. (2002). This SPM was used to identify "regions of interest" (ROIs) for further analysis, defined as maxima within the SPM that were at least 10 mm apart. The parameter estimates for each ROI maximum were then subjected to the same ANOVAs as the behavioural and ERP data (see Basic analysis strategy). The maxima were localised on a normalised high-resolution EPI, averaged across participants. Stereotactic coordinates correspond to the standard Montreal Neurological Institute brain. These coordinates bear a close, but not exact, match to the atlas of Talairach and Tournoux (1988), which was used to estimate Brodmann Areas (Brodmann, 1909).

Results

Behavioural results

Less than 10% of responses on average were inconsistent or missed; subsequent analyses were confined to consistent responses. The omnibus ANOVA on median RTs showed a significant repetition-by-lag interaction [$F(2.37,59.3) = 25.8$, $P < 0.001$]. There were no significant effects of participant group (ERP/efMRI), so the mean RTs in Table 1 were collapsed across groups. Subsequent ANOVAs showed that priming (the RT difference of Controls minus Repeats) increased across each successive level of lag, with repetition-by-lag interaction (F's > 5.40, P's < 0.05). This reflected a priming increase of approximately 50 ms across each level of lag and suggests that priming was sensitive to both the number of intervening items and the amount of intervening time. Priming remained significant even at the Long lag [$F(1,26) = 24.2$, $P < 0.001$].

An ANOVA on Controls only showed no significant effect of lag [$F(2.63,65.8) = 2.04$, $P = 0.12$]. If Delayed and Immediate Controls were restricted to those trials in which the same response was given as the previous trial (as was necessarily the case for Delayed and Immediate Repeats; see Materials and methods), the mean Control RTs decreased, but only slightly (see Table 1). The ANOVA for Delayed and Immediate lags still showed a main effect of priming, [$F(1,25) = 115$, $P < 0.001$], demonstrating that priming across consecutive trials involved more than simple motor preparation, though the repetition-by-lag interaction no longer reached significance [$F(1,25) = 2.36$, $P = 0.14$]. The ANOVA for Short and Delayed lags continued to show a repetition-by-lag interaction [$F(1,25) = 4.93$, $P < 0.05$], demonstrating that the presence of an intervening item did more than simply disrupt the degree of motor preparation.

Table 1
Mean and standard error (in smooth parentheses) of median RTs (ms) for consistent responses to Controls and Repeats, and their difference (priming), for each lag, collapsed across participant group ($N = 27$)

	Long	Short	Delayed	Immediate
Controls	759 (36)	744 (36)	779 (36) [772]	760 (39) [744]
Repeats	699 (35)	642 (36)	611 (37)	555 (37)
Priming	60 (12)	102 (15)	168 (15) [162]	205 (18) [190]

Numbers in square parentheses are corresponding mean RTs when Delayed and Immediate Controls are conditionalised on same response as previous trial.

ERP results

The ERPs for Controls and Repeats at each lag are shown for selected sites in Fig. 2; the results of the ANOVAs for each of the four time windows are shown in Table 2. In brief, there was some evidence for a repetition effect in the earliest (P120) time window of 110–140 ms, but only for Immediate lags. There was clear evidence for repetition effects for Immediate and Delayed lags in the second (N170) time window of 160–190 ms, and for all lags in the 200–300 and 400–600 ms time windows. The size of the 200–300 ms repetition effect was significantly smaller for Short than Delayed lags, and the repetition effect in the 400–600 ms window appeared to reflect an earlier latency of a positive-going peak.

110–140 ms (P120) window

The omnibus ANOVA for the occipitotemporal P120 latency interval showed a repetition-by-site interaction [$F(3.8,56.5) = 2.5$, $P < 0.06$] and a main effect of repetition [$F(1,15) = 3.8$, $P < 0.07$] that approached significance. No repetition effects were found for the Long lag however, which prompted tests for the remaining lags. Only the Immediate lag showed a main effect of repetition [$F(1,15) = 5.9$, $P < 0.05$], which took the form of a more positive-going deflection for Repeats than Controls that was maximal over central sites, and corresponding to an enhanced P120 at occipitotemporal sites. Given the post hoc nature of these tests however, this early repetition effect should be treated as tentative.

160–190 ms (N170) window

The omnibus ANOVA for the occipitotemporal N170 latency showed a repetition-by-site interaction [$F(2.9,43.4) = 6.1$, $P < 0.005$]. No repetition effects were found for the Long lag

Table 2
Significant effects in ANOVAs on the mean ERP amplitude in time windows of interest, two-tailed $P < 0.05$

Window	LSDI	LS	SD	DI	L	S	D	I
110–140	(RS)	–	–	–	ns	ns	ns	R
160–190	RS	–	–	–	ns	ns	RS	R
200–300	RLS	RS	RLS	RS	RS	RS	RS	RS
400–600	(RLS)	(RLS)	RS	RS	RS	RS	RS	RS

L/S/D/I = one-way ANOVAs for Long/Short/Delayed/Immediate lags; LS/SD/DI = two-way ANOVAs across consecutive levels of lag; LSDI = omnibus ANOVA across all four lags. R = main effect of repetition, RS = repetition-by-site interaction, RLS = repetition-by-lag-by-site interaction, – = not tested, ns = nonsignificant, () = $P < 0.05$ one-tailed.

however, which prompted tests for the remaining lags. Only the Delayed and Immediate conditions showed repetition effects, in the form of a repetition-by-site interaction [$F(3.4,51.0) = 4.8$, $P < 0.005$] and a main effect of repetition [$F(1,15) = 7.6$, $P < 0.05$], respectively. Both repetition effects reflected a positive-going divergence for Repeats relative to Controls over most sites, which continued into the subsequent time window. The positive deflection was maximal over frontal sites in the Delayed condition, accompanied by an enhancement of the N170 over occipitotemporal sites (Fig. 3A), and maximal over left central sites in the Immediate condition (Fig. 3B). Despite the apparent differences between Figs. 3A and B, however, there was no evidence for different topographies of these two repetition effects [$F(4.3,65.0) < 1$].

Interestingly, the presence of a longer delay before the stimulus affected the ERP to Controls alone (compare dotted and solid red lines for the Delayed condition in Fig. 2). The ERPs were less positive-going over frontal sites for non-delayed controls (dotted line; the average of Controls from the Long, Short and Immediate conditions) than for Delayed Controls (solid line). This was confirmed by a delay-by-site interaction [$F(4.5,68.0) = 5.1$, $P < 0.001$] (emphasising the importance of using matched controls for Delayed Repeats). This effect of delay was also seen for the 200–300 ms time window (below) [$F(3.3,49.2) = 5.4$, $P < 0.005$], but not the earlier 110–140 time window, or the later 400–600 ms time window (F's < 1.7, P's > 0.18).

200–300 ms window

The omnibus ANOVA for the 200–300 ms time window showed a repetition-by-lag-by-site interaction [$F(6.9,104.8) = 3.4$, $P < 0.005$]. Follow-up ANOVAs across consecutive levels of lag showed a repetition-by-site interaction for Long vs. Short [$F(2.7,40.1) = 11.0$, $P < 0.001$], a repetition-by-site-by-lag interaction for Short vs. Delayed [$F(3.3,49.5) = 3.6$, $P < 0.05$] and a repetition-by-site interaction for Delayed vs. Immediate [$F(4.4,66.3) = 36.1$, $P < 0.001$]. This pattern reflected a repetition effect at each lag, including the Long lag, as confirmed by pairwise tests (F's > 4.2, P's < 0.01) together with a reliable increase in the size of this effect from one to no intervening stimuli (i.e. from Short to Delayed conditions).

The topography of the effect was a positive-going difference maximal over frontocentral sites, accompanied by a transient negative-going difference over left and right occipitotemporal sites for Delayed and Immediate conditions (Figs. 3C–F). The topography did not differ reliably in any comparison across successive lags (F's < 1.4, P's > 0.26), suggesting that the above repetition-by-lag interactions reflected quantitative differences in the magnitude of a common set of generators rather than a qualitative difference in the set of generators. Nor did the topography of the Immediate and Delayed repetition effects differ reliably from those for the corresponding effects in the earlier 160–190 ms time window (F's < 1.5, P's > 0.22), suggesting that they too reflected the same generators.

400–600 ms window

The omnibus ANOVA for this time window, which encompassed a central positive peak, showed a repetition-by-site interaction [$F(3.9,58.8) = 12.1$, $P < 0.001$] and a trend for a repetition-by-site-by-lag interaction [$F(7.6,114.0) = 2.0$, $P < 0.06$]. The latter interaction most likely included a contribution from an interaction across Long and Short lags, which also approached significance [$F(3.6,54.8) = 2.4$, $P < 0.07$]. Repetition effects were found for all lags separately (F's > 4.0, P's < 0.01).

Repeats were more positive-going than Controls over all sites, with a central maximum (e.g. Figs. 3G and H). The effect of

Table 3
Significant effects in ANOVAs on the fMRI data in the regions of interest, two-tailed $P < 0.05$

Region	l/r	BA	Coordinates			LSDI	LS	SD	DI	L	S	D	I
			x	*y*	*z*								
Mid. front.	r	46	+51	+45	+9	R+	–	–	–	ns	–	–	–
Inf. front.	l	44	−48	+12	+21	R+	–	–	–	R	–	–	–
Parahipp.	l	35	−27	−27	−24	RL	(RL)	R	R	ns	R	–	–
	r	35	+30	−27	−24	(RL)	RL	R	R	ns	R	–	–
Parahipp.	r	36	+39	−36	−12	R+	–	–	–	R	–	–	–
Ant fus.	l	20/37	−30	−45	−24	R	–	–	–	ns	–	–	–
	r	20/37	+33	−39	−21	R	–	–	–	R	–	–	–
Midfus.	l	37	−42	−51	−27	RL+	ns	R	R+	–	–	–	–
Midfus.	l	37	−45	−57	−15	RL	ns	ns	R	–	–	–	–
	r	37	+45	−60	−12	RL	ns	R	RL	–	–	R	R
Lat. inf. occ.	l	19/37	−48	−75	−6	RL+	RL+	R	R	ns	R	–	–
	r	19/37	+51	−72	−6	R	–	–	–	ns	–	–	–
Lat. mid. occ.	l	19	−39	−81	+21	R	–	–	–	ns	–	–	–
	r	19	+42	−84	+15	R	–	–	–	R	–	–	–
Post. cing.	r	23	+9	−36	+24	RL	RL	ns	ns	R	ns	–	–

l = left, r = right, BA = Brodmann Area, + = lateralised. See Table 2 legend for more details.

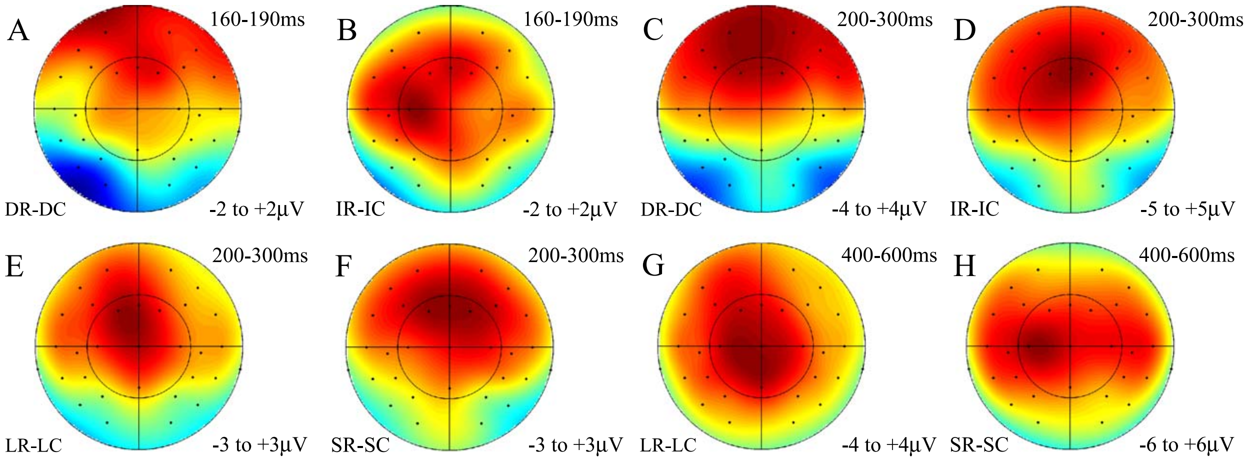

Fig. 3. Scalp potential difference maps for repetition effects in (A) Delayed condition from 160 to 190 ms, (B) Immediate condition from 160 to 190 ms, (C) Delayed condition from 200 to 300 ms, (D) Immediate condition from 200 to 300 ms, (E) Long condition from 200 to 300 ms, (F) Short condition from 200 to 300 ms, (G) Long condition from 400 to 600 ms and (H) Short condition from 400 to 600 ms. Colours scaled to max/min of differences, red = positive, blue = negative.

decreasing lag on Repeats was almost certainly to decrease the latency of a positive peak in the ERP (e.g. peaking at approximately 400 ms for Immediate Repeats, relative to approximately 600 ms for Controls; Fig. 2). This latency shift may correlate with the faster RTs for Repeats than Controls (e.g. approximately 550 ms for Immediate Repeats, relative to 750 ms for Controls; Table 1), and with the increase in this priming effect with decreasing lag.

Topographic analyses showed no interaction between repetition and lag [$F(7.4,110) = 1.6$, $P = 0.13$], suggesting a common set of generators. However, the 400–600 ms repetition effects did differ

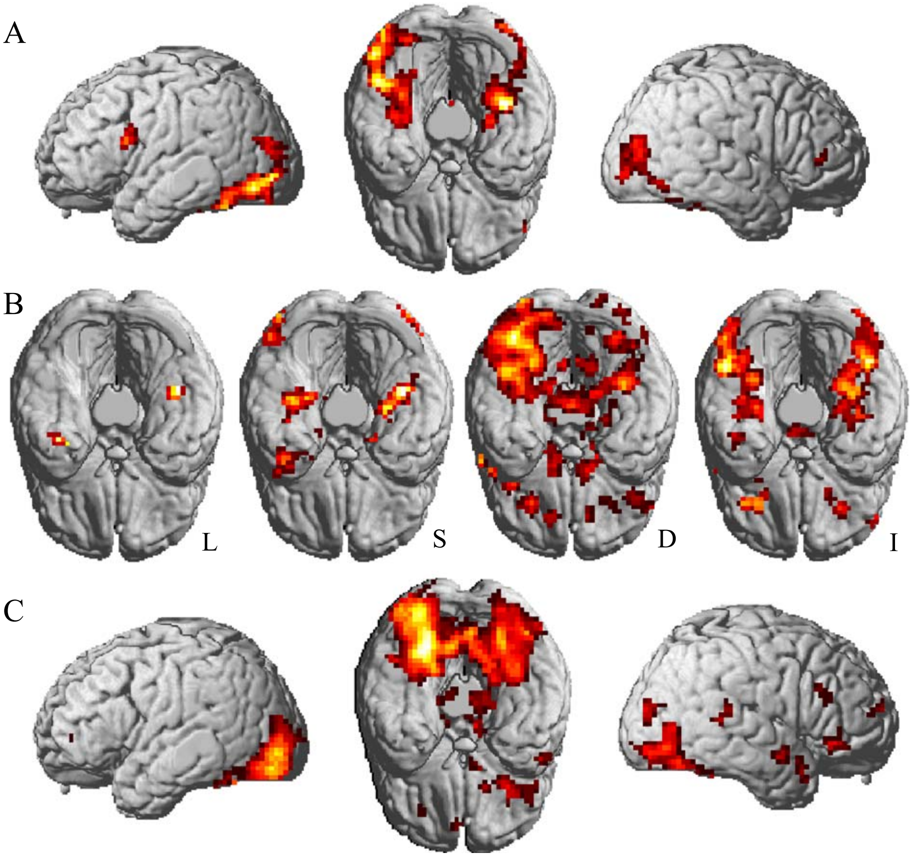

Fig. 4. Surface renderings of fMRI data onto a canonical normalised brain (with cerebellum artificially removed) for (A) omnibus F-contrast, thresholded at $P < 0.001$ uncorrected, (B) t tests of Controls–Repeats (repetition suppression) for each lag separately (see Fig. 1 legend for definitions), thresholded at $P < 0.01$ for illustrative purposes and (C) t test of Delayed–Non-delayed controls (see text for details), thresholded at $P < 0.01$ for illustrative purposes.

significantly from those from the earlier 200–300 ms time window, for all lags (F's > 8.1, P's < 0.001), except the Long [$F(2.6,49.4) = 1.4$, $P = 0.26$]. This suggests that the generators of the repetition effects change over time, and that an earlier onset of a central 600-ms positive peak following repetition is not sufficient to account for the repetition effects in the earlier 200–300 ms time window.

efMRI results

Voxels identified by the omnibus F-contrast for main effects or interactions between repetition and lag are shown in Fig. 4A; the results of the ANOVAs for each ROI maxima within these voxels are shown in Table 3. Most ROIs lay within bilateral bands of voxels extending from medial inferior temporal cortex (parahippocampal and fusiform gyri) to lateral parts of the inferior occipital cortex and posterior parts of lateral occipitotemporal cortex. The three exceptions were ROIs in left posterior inferior frontal cortex, right mid-lateral frontal cortex and posterior cingulate. All repetition effects, except that in the posterior cingulate, reflected decreased responses for Repeats relative to Controls (i.e. repetition suppression).

Occipitotemporal ROIs

Four ROIs within the occipitotemporal cortex showed interactions between repetition and lag: in bilateral parahippocampal cortex (close to collateral sulcus, most likely BA 35), bilateral midfusiform (ascending the lateral occipitotemporal sulcus, most likely BA 37), a slightly more inferior aspect of left midfusiform (fusiform gyrus, most likely BA 37) and left lateral inferior occipital cortex (most likely in inferior occipital sulcus and BA 19/37). The bilateral parahippocampal regions showed a greater repetition effect for Short than Long lags (Fig. 5A), significantly so on the right [$F(1,10) = 7.5$, $P < 0.05$] and marginally so on the left [$F(1,10) = 3.9$, $P = 0.08$]. This corresponded to repetition suppression at the Short (F's > 11.0, P's < 0.01), but not Long (F's < 1.1, P's > 0.3) lags.

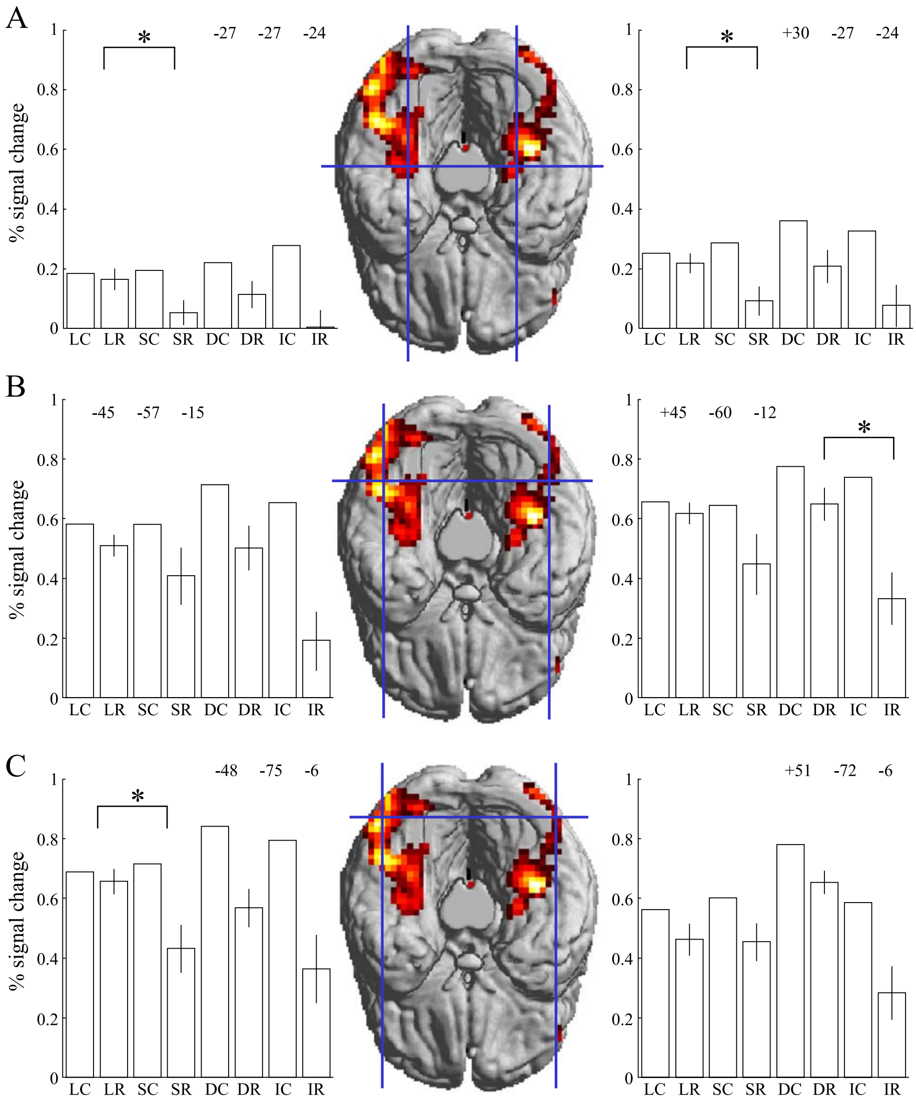

Fig. 5. Plots of peak percentage signal change (relative to mean over all voxels) for the eight conditions from the peak of the bilateral occipitotemporal ROIs (localised by cross-hairs on the SPM of the omnibus F-contrast from Fig. 4A). ROIs are in (A) parahippocampal, (B) midfusiform and (C) lateral inferior occipital cortices. Error bars show the standard error of the repetition effect at each lag (i.e. subtraction of successive Control and Repeat conditions). *, interaction between repetition and successive lags significant at $P < 0.05$ (one-tailed).

The repetition-by-lag interactions in the bilateral midfusiform ROIs reflected a more graded pattern, with decreasing amounts of repetition suppression with increasing lag (Fig. 5B). The only significant repetition-by-lag interaction across consecutive levels of lag was across Delayed and Immediate lags in the right midfusiform region [*F*(1,10) = 5.5, $P < 0.05$]. The more inferior left midfusiform gyrus ROI showed a similar pattern, though with evidence of lateralisation in this case, as defined by a region-by-repetition interaction when data from homologous coordinates in the opposite hemisphere were used as an additional factor in the ANOVA [*F*(1,10) = 5.4, $P < 0.05$].

The repetition-by-lag interaction in the left lateral inferior occipital ROI reflected greater repetition suppression for Short than Long lags ($F = 6.8$, $P < 0.05$). Indeed, repetition suppression was significant for Short ($F = 12.5$, $P < 0.005$), but not Long ($F < 1$) lags (Fig. 5C), similar to the parahippocampal ROIs. A homologous right lateral inferior occipital region showed a main effect of repetition, but no evidence of any lag effects. Indeed, the presence of a region-by-repetition-by-lag interaction [*F*(2.2,22.6) = 4.7, $P < 0.05$] suggested a left lateralisation of repetition effects in this cortical area.

The remaining ROIs in Table 3 showed only a main effect of repetition (though most showed nonsignificant trends for decreasing amounts of repetition suppression with increasing lag). Three showed repetition suppression even at the Long lag (*F*’s > 5.7, *P*’s < 0.05). These ROIs were in right lateral middle occipital cortex (BA 19), possibly extending into the horizontal posterior segment of the superior temporal sulcus, right anterior fusiform (BA 20/37), rostral to the bilateral fusiform ROIs considered above and right parahippocampal cortex (most likely BA 36), extending more superiorly up the collateral sulcus than the bilateral parahippocampal ROIs considered above. The latter is shown in Fig. 6C, and was right-lateralised with a repetition-by-region interaction [*F*(1,10) = 10.1, $P < 0.01$].

Qualitative differences in topography

To test whether the influence of lag on repetition effects differed reliably across occipitotemporal cortex, an ANOVA was performed across all eight bilateral occipitotemporal ROIs (Table 3), with additional factors of anterior–posterior (four levels) and laterality (two levels). There was a repetition-by-lag-by-laterality interaction [*F*(2.3,22.8) = 4.35, $P < 0.05$]. This reflected a greater effect of lag on repetition suppression in the left vs. right hemisphere (i.e. longer-lasting repetition suppression in ROIs on the right than on the left). Follow-up ANOVAs on left and right hemisphere ROIs separately showed repetition-by-lag interactions in both hemispheres (*F*’s > 3.9, *P*’s < 0.05) but no interactions among repetition, lag and anterior–posterior extent (*F*’s < 1.9, *P*’s > 0.11).

Remaining ROIs

The two prefrontal regions were in left posterior inferior frontal cortex (within the inferior frontal sulcus, most likely BA44) and right midlateral frontal cortex (on the lip of the inferior frontal sulcus, most likely BA 46). Both showed main effects of repetition

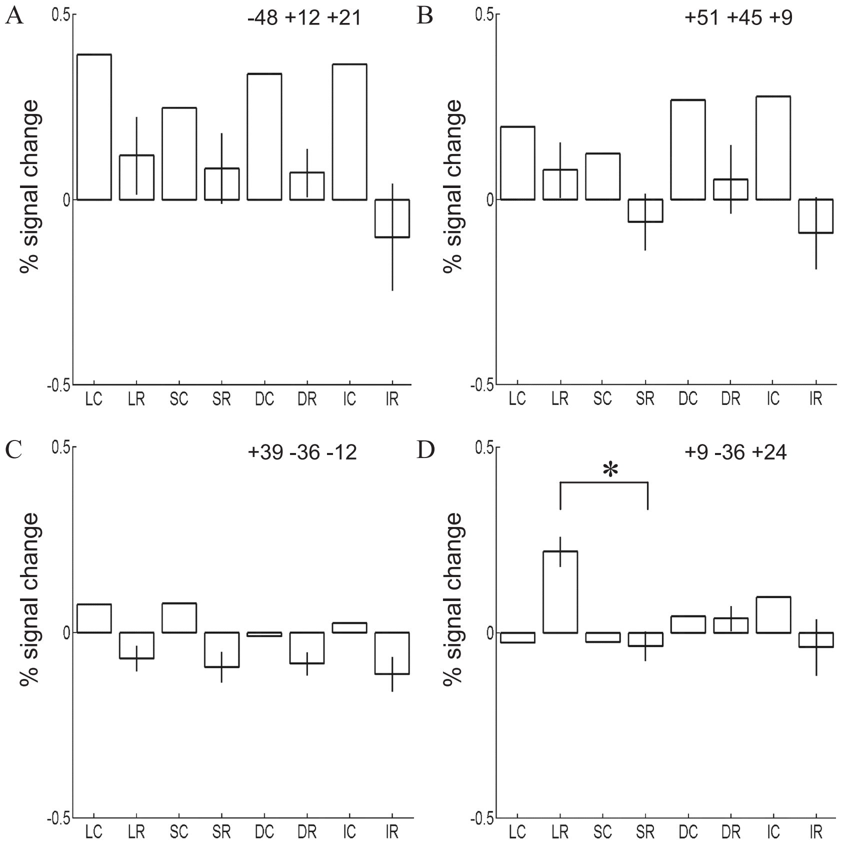

Fig. 6. Plots of peak percentage signal change for the four lateralised ROIs: (A) left posterior inferior frontal, (B) right midlateral frontal, (C) superior right parahippocampal and (D) posterior cingulate cortices. See Fig. 5 legend for more details.

(*F*'s > 15.5, *P*'s < 0.005) in the absence of detectable interactions with lag (Figs. 6A and B). Repetition suppression was significant in the left posterior inferior frontal region even for the longest lag [$F(1,10) = 6.8$, $P < 0.05$]. Both regions showed evidence of lateralisation using homologous coordinates from the opposite hemisphere (*F*'s > 6.4, *P*'s < 0.05).

The posterior cingulate ROI was the only region to show an increased response for Repeats relative to Controls. This ''repetition enhancement'' was seen only for the Long lag condition (Fig. 6D), as confirmed by repetition-by-lag interactions in both the omnibus ANOVA [$F(2.0,19.6) = 10.5$, $P < 0.001$] and the ANOVA across Long and Short lags [$F(1,10) = 17.5$, $P < 0.005$]. Pairwise tests confirmed repetition enhancement for Long [$F(1,10) = 37.2$, $P < 0.001$], but not Short [$F(1,10) < 1$] lags.

Whole-brain analyses

SPMs of the T-contrast for repetition suppression at each lag were also calculated and are shown, for voxels surviving one-tailed $P < 0.01$ on the ventral surface of the brain, in Fig. 4B. Note that comparisons across lags cannot be made from these SPMs (such comparisons are reported in the ROI analyses above); they are shown here for illustrative purposes only (see Discussion). For the Long lag, the only significant voxels were in the right anterior fusiform/superior parahippocampal ROIs, a left anterior temporal region (not in the ROI analyses above), and the right lateral middle occipitotemporal and left prefrontal ROIs (not shown). For the Short lag, additional repetition suppression was seen bilaterally in the lateral inferior occipital, anterior fusiform and parahippocampal ROIs. For the Delayed and Immediate conditions, most of the inferior occipitotemporal ROIs were present, including the appearance of the midfusiform ROIs (in addition to some orbitofrontal regions not identified in the omnibus ANOVA).

The spatial extent of regions showing repetition suppression also appeared greater for the Delayed than Immediate condition. This may relate to greater responses to Delayed Controls than other types of Controls, as illustrated in an SPM of the T-contrast of Delayed Controls vs. the average of the other three types of Controls in Fig. 4C. The majority of the posterior occipitotemporal voxels showed a greater response to objects preceded by a 4.56-s SOA than a 2.28-s SOA. Indeed, most of the above occipitotemporal ROIs (but not those in prefrontal cortex) showed numerically greater responses to Delayed Controls than non-delayed Controls (again reinforcing the importance of using matched Controls).

Discussion

The present study showed clear effects of the lag between first and second presentations of an object on the repetition effects measured with RTs, with ERPs and with efMRI. Taken as a whole however, the repetition effects at different lags appeared to differ quantitatively rather than qualitatively; any evidence for spatially distinct repetition effects in the ERP or efMRI data at different lags was only suggestive. We summarise the main findings below before considering them in relation to previous ERP and fMRI studies.

Summary of repetition effects

The behavioural data showed that priming of RTs increased as lag decreased. This was the case across each successive lag condition, suggesting effects of both the number of intervening items and the amount of intervening time.

The ERP data showed a repetition effect from 200 to 300 ms poststimulus that increased in magnitude as lag decreased. This was certainly the case across the Short and Delayed conditions, demonstrating an effect of a single intervening stimulus. An earlier repetition effect from 160 to 190 ms was observed for the Delayed and Immediate conditions, but the topography of this effect did not differ reliably from that in the 200–300 ms time window. A later repetition effect from 400 to 600 ms was found for all lags, with limited evidence for a modulation by lag. The topography of this later repetition effect did differ from that of the earlier time windows, suggesting at least two qualitatively different effects of repetition as a function of peristimulus time. Importantly however, the topography of these repetition effects did not differ reliably as a function of lag, suggesting that lag has quantitative rather than qualitative effects.

The fMRI data revealed repetition effects in several regions, primarily in ventral occipital and temporal cortices, but also in posterior cingulate and prefrontal cortices. With the exception of the posterior cingulate, this repetition effect took the form of a decreased response for second vs. first presentations (repetition suppression), the size of which tended to increase as lag decreased, although this interaction only reached significance in a subset of brain regions. The clearest cases of repetition-by-lag interactions were across Long and Short lags in parahippocampal and lateral inferior occipital regions. When all bilateral occipitotemporal regions of interest were analysed together, there was evidence that repetition suppression decreased with lag more rapidly in the left than in the right hemisphere.

ERP findings

The widely distributed, positive-going shift in the 400–600 ms time window resembles the typical electrophysiological correlate of stimulus repetition (Rugg and Doyle, 1994). Unlike in Nagy and Rugg (1989), there was a trend for the magnitude of this shift to increase as lag decreased. This most likely reflected differences in the onset latency of the prominent positive deflection evident in Fig. 3, which onset earlier as lag decreased (consistent with Karayanidis et al., 1991).

We failed to replicate the early frontal negative deflection associated with immediate repetition by Nagy and Rugg (1989). Indeed, we found a centrofrontal repetition-related deflection from 200 to 300 ms that was of the opposite polarity (similar findings were reported by Penny et al., 2001; Schendan and Kutas, 2003). Moreover, though the magnitude of this frontal positive shift decreased as lag increased, it was still reliable even for lags exceeding the longest used by Nagy and Rugg (1989). The reason for this discrepancy across studies is not clear, but could relate to differences between stimuli (objects vs. words) or task (semantic decision vs. target monitoring).

The repetition-related positive shift over frontal sites from 200 to 300 ms was accompanied by a negative deflection over occipitotemporal sites. The latter resembles the ''N250r'' (using an average reference) associated with short-lag repetition of familiar faces (Schweinberger et al., 1995). This transient negative deflection was only evident at occipitotemporal sites for Delayed and Immediate conditions, consistent with the proposal that the N250r is short-lived (Schweinberger et al., 2002a). Nonetheless, the accompanying frontal positive shift was significant for long lags of 40 or more intervening stimuli. This pattern of results could reflect two distinct but temporally overlapping repetition effects within the 200–300 ms time window. Alternatively, the difference between the present findings and those of Schweinberger et al. (2002a) could reflect a difference between long and very long lags (across session), or between objects and faces.

The 200–300 ms repetition effect had a topography that differed from the repetition effect that peaked between 400 and 600 ms, suggesting that the two effects reflect the activity of at least partially distinct neural generators. This finding is consistent with a study by Itier and Taylor (2002), who estimated an orbitofrontal source from 250 to 450 ms for immediate/short-lag repetition of faces, but an occipitoparietal source for a later repetition effect from 400 to 600 ms. (We did not attempt source localisation given the relatively low density of electrode coverage and lack of coregistration of electrode locations with cortical anatomy.)

We also found evidence of an earlier repetition effect from 160 to 190 ms for immediate repetition without intervening items (in our Delayed and Immediate conditions). The absence of any detectable difference in the topography of this effect compared with that in the 200–300 ms window suggests that the former might simply reflect an earlier onset of a repetition-related modulation of the same set of generators. Campanella et al. (2000) and Itier and Taylor (2002) found that immediate repetition decreased the magnitude of the N170 to faces, an effect comparable to the present occipitotemporal N170 modulation (though see Schweinberger et al., 2002b). The lack of significant repetition effects in our Long and Short conditions suggests that such an early repetition effect (expressed in terms of magnitude) is not apparent when another stimulus intervenes, though this suggestion is tempered by the lack of a significant interaction with lag for the 160–190 ms time window.

Doniger et al. (2000) described an occipital negative deflection they termed the "Ncl" (using a nose reference), onsetting 230 ms and peaking 290 ms, which was associated with explicit identification of fragmented objects (using the ascending method of limits, Snodgrass and Feenan, 1990). The CSD of the Ncl suggested a generator in the lateral occipital complex (see below). This might correspond to the occipitotemporal repetition-related negativity from 200 to 300 ms in the present study. Furthermore, when Doniger et al. (2001) repeated object sequences across trials within the ascending method of limits, they found a priming effect on an earlier N170 component (when the level of degradation associated with object identification in primed trials was compared with same level of degradation, before identification, in unprimed trials). This priming effect had a topography similar to the later Ncl, implicating the same generators. These findings are reminiscent of the negative deflection from 160 to 190 ms found for Immediate and Delayed repetition in the present study. Given that Doniger et al. (2001) did not find any difference between primed and unprimed trials at degradation levels before identification, these data suggest that repetition (priming) simply causes earlier identification of visual objects.

Schendan and Kutas (2003) reported a frontocentral positivity from 140 to 250 ms, similar to that in the present study, associated with repetition of intact visual objects. (These were long-lag repetitions, though their measurement window encompassed both the 160–190 and 200–300 ms windows of the present study). Importantly, the size of this effect was greater when objects were repeated in the same vs. a different view, suggesting that these early repetition effects arise from view-specific representations (analogous to face repetition effects onsetting 200 ms that are modulated by whether repetitions are of the same or a different view of the faces, e.g., Jemel et al., 2003; Schweinberger et al., 2002b). If ERPs during this time window do reflect explicit identification, as Doniger et al. (2000) suggest (though see Schendan and Kutas, 2002, and Viggiano and Kutas, 1998), the speed-up in identification of objects following repetition may be greater for repetition of identical views of those objects.

Schendan and Kutas (2003) also reported a repetition-related frontal positivity from 300 to 400 ms, which they attributed to a modulation of a frontal "N350". Though the topography of this effect did not differ from that in their earlier time window, its functional properties may have because it was sensitive to long-term view familiarity (the repetition effect was greater for "unusual" than "canonical" views of objects). The authors attributed this effect to selection of object models/structural descriptions (Schendan and Kutas, 2003). However, an anterior positive-going deflection from 225 to 325 ms has also been associated with semantic priming of objects (McPherson and Holcomb, 1999), which does not seem to be affected by the degree of visual similarity among objects (Barrett and Rugg, 1990). Together, these data suggest that object-elicited frontal repetition effects may be more conceptual than perceptual in origin.

The later repetition effect from 400 to 600 replicates our previous finding for long-lag, incidental repetition of faces (Henson et al., 2003). The different topography of this effect from the earlier repetition effects (consistent with Schendan and Kutas, 2003) suggests functional dissociation. Schendan and Kutas (2003) attribute the later effect to parallel view compensation processes (Ullman, 1996), possibly related to mental rotation (Tarr and Pinker, 1989) or to view-specific representations in the dorsal stream (James et al., 2002; Turnbull et al., 1997). Alternatively, the ERP effect may reflect a speeding of decision processes owing to priming of prior perceptual processing (reflected in the early ERP repetition effects). This latter account is consistent with the latency shift of a positive peak, with greater shifts for shorter lags, consistent with the RT priming data. A further possibility is that the repetition effect from 400 to 600 reflects explicit recollection of the previous presentation of an object (Allan et al., 1998), incidental to the task, or of the previous response to that object, to maintain consistency across trials.

Finally, we note that some weak evidence was found for a very early repetition effect in the Immediate condition, in the form of widespread positive-going deflection from 110 to 140 ms (within the time scale of the occipitotemporal P120). Such an early repetition effect is not typically found for long lags (though see George et al., 1997; Tsivilis et al., 2001), but may occur for very short temporal lags (Schweinberger et al., 1995; indeed, Seeck et al., 1997, reported a face repetition effect over lags of one to two intervening faces that onset as early as 50 ms). Early ERP repetition effects for short lags could reflect the influence of a short-lived visual iconic store. We note however that even the immediate lag condition of the present ERP experiment had an interstimulus interval of 1800 ms, which is relatively long compared with the duration of a few hundred milliseconds typically associated with a visual iconic store (Efron, 1970; Sperling, 1960; testing such very short SOAs was not possible given the response requirements of the present study).

fMRI findings

The present findings of occipitotemporal repetition suppression are consistent with most previous neuroimaging studies using familiar visual stimuli (Henson, 2003). There was a general trend for decreased amounts of repetition suppression as lag increased, particularly across the Short vs. Long conditions (e.g. in the lateral inferior occipital cortex, consistent with our previous parametric analysis using faces, Henson et al., 2000). There was little evidence for specific effects of time or interference across lags of zero to one intervening stimulus. Only two regions of interest within occipitotemporal cortex showed significant repetition suppression for the Long condition alone (in right parahippocampal and anterior fusiform cortices). This may reflect a lack of power for comparisons at individual lags in the present study, since previous studies have reported repetition suppression in more posterior occipitotemporal regions over much longer lags (Henson et al., 2002; van Turennout et al., 2000, 2003).

An interaction was found among repetition, lag and the laterality of the occipitotemporal ROIs, with a greater effect of lag on repetition suppression in the left hemisphere relative to the right hemisphere. Note that the presence of regional interactions could reflect differences in the biophysics of the BOLD response across different brain regions (e.g. different gains in the transduction of neural/synaptic activity into the BOLD response might cause a multiplicative interaction in an additive model like ANOVA). However, this caveat is less likely to apply to interactions across homologous regions in left and right hemispheres, for which biophysical differences (e.g. in vasculature) are less likely. Nonetheless, though the laterality by lag (by repetition) interaction might be viewed as an example of a qualitative effect of a lag on the neural correlates of repetition—a necessary condition for claiming functional segregation of repetition effects in the occipitotemporal cortex—it is unclear whether it comprises sufficient evidence for such a conclusion.

We failed to find any reliable difference in the longevity of repetition effects from posterior to more anterior occipitotemporal regions (in that this factor, unlike laterality, did not interact with repetition and lag). This is contrary to what one might have expected from repetition effects indexed by neuronal firing rates in the Macaque, which appear to last longer in anterior than in posterior inferior temporal regions (Brown and Xiang, 1998). This discrepancy could reflect differences between the two measures. For example, the fMRI BOLD signal, because it integrates over several seconds of underlying neural/synaptic activity, will be blind to qualitative differences in repetition effects within such a time scale (Henson and Rugg, 2002).

Though the occipitotemporal ROIs (the main interest of the present study) showed a qualitatively similar pattern of lag effects (apart from a lateralisation), the left inferior prefrontal and posterior cingulate ROIs showed a different pattern. The opposite sign of the repetition effect in the posterior cingulate in particular (and its restriction to the Long lag condition) is unlikely to be attributable to biophysical differences across brain regions. These data suggest functions (e.g. retrieval from long-term explicit memory for the posterior cingulate region, or object naming for the left inferior frontal region; see below) that differ from the more perceptual functions assumed to occur in inferior occipitotemporal cortex.

Previous studies using a covert object naming task have found repetition suppression in occipitotemporal regions that did not appear to vary across lags from 30 s to 3 days (van Turennout et al., 2000, 2003). The 30-s conditions of those studies still entailed up to 12–15 intervening stimuli however. Thus, all lags used in those studies were beyond working memory span (i.e. correspond to "long" and "very long" lags using the terminology in the introduction). If the critical factor for lag effects in occipitotemporal cortex is whether the object is still present within working memory (or, more generally, that only a few other objects have intervened), then one would not expect to have seen lag effects in the van Turennout et al. studies, but would expect to do so, at least across Long vs. Short conditions, in the present study. Alternatively, the effect of lag in occipitotemporal cortex in the present study, but its absence in the van Turennout et al. studies, might reflect differences in the tasks (Bruce et al., 2000).

The left posterior inferior frontal ROI showed repetition suppression across all lags, including the longest. This may reflect facilitation of covert naming of objects, or facilitation of retrieval of semantic information about the objects (Wagner et al., 1997). Unlike van Turennout et al. (2000), we did not find greater repetition suppression at longer lags; if anything, there was a nonsignificant trend for less repetition suppression at longer lags (as found by Wagner et al., 2000, using words). Again however, this could reflect a difference between the present long lags and the very long lags of van Turennout et al. (2000). The posterior cingulate ROI that showed repetition enhancement in the Long lag condition may reflect episodic retrieval (see Rugg and Henson, 2002), possibly incidental to the present task. It is interesting that this enhancement was not found when objects could still be in working memory, suggesting that the posterior cingulate is only engaged in retrieval from long-term memory.

Other implications

The present efMRI repetition effects suggest that lag may not be a critical factor for studies that use repetition suppression to map the functional anatomy of different stages of object processing, in the sense that there was little evidence that different occipitotemporal regions within the same hemisphere exhibited lag effects to different degrees (as might arise if repetition effects in different regions reflected different mechanisms). Nonetheless, most occipitotemporal regions showed a quantitative effect of lag, with greater repetition suppression for smaller lags. This raises the issue of statistical power for comparisons of repetition effects across studies using different lags. This is apparent from the SPMs in Fig. 4B, which raise the possibility that one might see significant repetition suppression in lateral inferior occipital cortex (the posterior part of the lateral occipital complex, Malach et al., 1995) in a study using short lags, but not in one using long lags.

The present study failed to disambiguate fully the roles of interference and temporal decay in repetition effects. Both factors affected priming of RTs, to an approximately equal extent (i.e. across the Immediate, Delayed and Short conditions). The presence of an intervening stimulus may have a greater effect than the passage of time on early ERP repetition effects (from 160 to 190 ms), but the data were only suggestive in the sense that a significant repetition effect was found for Delayed but not Short lags (in the absence of an interaction). The only interaction between repetition and lag in the fMRI data (other than across the Long and Short conditions, for which time and intervening stimuli were confounded) was in a right midfusiform region, which showed an effect of the passage of time (across the Delayed vs. Immediate conditions). Note that the present study allowed only a limited test of the interference/decay hypotheses, in that these could only be distinguished across zero or one intervening item, and from approximately 2 to 4 s. Future studies might vary the two factors across a greater range. Furthermore, tests of the two hypotheses in the present design necessarily involved the Delayed condition, which may have had unwanted confounds, despite the use of a matched control (see Other considerations).

Though our ERP and efMRI data provided little evidence for qualitatively different mechanisms underlying repetition effects at different lags, such qualitative differences might emerge through interactions with other independent variables. McKone (1995), for example, found that word frequency affected long-lag priming in lexical decision, but not short-lag priming over zero to three intervening items, and Bentin (1989) found that the effects of phonological and orthographic priming during lexical decision dissociated across 0 to 15 intervening items. Another common independent variable is a change in physical depiction when an object is repeated. Itier and Taylor (2002), for example, found a qualitative difference between zero and one intervening stimuli, in that a positive shift for repeated faces from 250 to 450 ms was modulated by spatial or contrast inversion for immediate, but not short-lag, repetition. Another potential qualitative difference across lags occurs when the first presentation of a stimulus is subliminal (“masked priming”). Schnyer et al. (1997), for example, found an N400 attenuation under masked priming for immediate word repetition, but not when one word intervened. This is consistent with the finding of behavioural evidence of masked priming for immediate but not short-lag repetition (Humphreys et al., 1988). More recently however, attenuation of the N400 has been reported for short-lag (as well as immediate) masked priming of words (Misra and Holcomb, 2003), suggesting a quantitative rather than qualitative difference between immediate and nonimmediate repetition.

The onset latency of the present long-lag ERP repetition effect (from 200 to 300 ms) is earlier than is typically found using word or faces (Henson and Rugg, 2002; Puce et al., 1999). This may pose problems for hypotheses regarding the temporal evolution of long-term priming effects (Henson and Rugg, 2002), though it is noteworthy that the earlier “sensory” evoked components (e.g. occipitotemporal P120 and N170) did not appear to show long-lag repetition effects. Such components did show repetition effects in the Delayed and Immediate conditions, suggesting that sensory (e.g. “bottom-up”) processes can be affected by immediate repetition. Because the same picture of an object was repeated, the present study does not distinguish whether such early effects result from relatively abstract object-based representations, or are restricted to short-lived image-based representations.

Other considerations

Clear effects were seen in both the ERP and efMRI data when the gap among objects was longer than the modal interstimulus interval. This was apparent from comparing Delayed Controls against the other Controls. This is an interesting finding in its own right, and may be a consequence of a “missing stimulus” effect (Sutton et al., 1967): in this case, the effect of a rare gap on the processing of the subsequent stimulus. For the fMRI data, it could also be a consequence of reduced saturation of the BOLD response following a longer period among stimulations (possibly reflecting the “balloning” of blood vessels, Friston et al., 2000). It is for reasons like these that we used matched Controls for the Delayed Repeats. However, we note that it is possible that the additional delay interacted with whether the subsequent object was a repetition. For example, participants may have been particularly watchful for a repetition after noticing a gap (although the probability of such a repetition was unaffected by the gap in the EEG experiment).

Finally, there were some procedural differences between the EEG and fMRI experiments. These included small differences in the SOAs, plus one session in the fMRI experiment vs. two in the EEG experiment, resulting in a slightly longer average lag in the Long condition and fewer total trials in the fMRI experiment. The overall probability of a gap (for the Delayed conditions) also differed, and the probability of a repetition increased after a gap in the fMRI experiment (from 31%, on average, to 50% following delay), but not in the EEG experiment. These differences may prevent direct comparisons between the two modalities.

Conclusion

The present study confirmed robust effects of the lag between two presentations of an object on behavioural, electrophysiological and haemodynamic measures of the difference between those presentations. The study found little evidence however to support qualitatively different neural correlates of such repetition effects at the different lags used. Nonetheless, future studies that combine manipulations of lag with other independent variables may find stronger evidence of dissociable neural correlates at different lags.

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References

Allan, K., Wilding, E.L., Rugg, M.D., 1998. Electrophysiological evidence for dissociable processes contributing to recollection. Acta Psychol. 98, 231–252.

Andersson, J.L., Hutton, C., Ashburner, J., Turner, R., Friston, K., 2001. Modeling geometric deformations in EPI time series. NeuroImage 13, 903–919.

Ashburner, J., Friston, K.J., 1999. Nonlinear spatial normalization using basis functions. Hum. Brain Mapp. 7, 254–266.

Barrett, S.E., Rugg, M.D., 1990. Event-related potentials and the semantic matching of pictures. Brain Cogn. 14, 201–212.

Bentin, S., 1989. Orthography and phonology in lexical decision: evidence from repetition effects at different lags. J. Exp. Psychol., Learn., Mem., Cogn. 15, 61–72.

Bentin, S., Moscovitch, M., 1988. The time course of repetition effects for words and unfamiliar faces. J. Exp. Psychol.: Gen. 117, 148–160.

Bentin, S., Peled, B.S., 1990. The contribution of task-related factors to ERP repetition effects at short and long lags. Mem. Cognit. 18, 359–366.

Biederman, I., Cooper, E.E., 1991. Evidence for complete translational and reflectional invariance in visual object priming. Perception 20, 585–593.

Brodmann, K., 1909. Vergleichende Lokalisationslehre der Grosshirnrinde in ihren Prinzipien dargelstellt auf Grund des Zellesbaues. Barth, Leipzig.

Brown, M.W., Xiang, J.Z., 1998. Recognition memory: neuronal substrates if the judgement of prior occurrence. Prog. Neurobiol. 55, 149–189.

Bruce, V., Carson, D., Burton, M., Ellis, A., 2000. Perceptual priming is not a necessary consequence of semantic classification of pictures. Q. J. Exp. Psychol. 53A, 289–323.

Campanella, S., Hanoteau, C., Depy, D., Rossion, B., Bruyer, R., Crommelinck, M., Guerit, J.M., 2000. Right N170 modulation in a face discrimination task: an account for categorical perception of familiar faces. Psychophysiology 37, 796–806.

Cave, B.C., 1997. Very long-lasting priming in picture naming. Psychol. Sci. 8, 322–325.

Doniger, G.M., Foxe, J.J., Murray, M.M., Higgins, B.A., Snodgrass, J.G., Schroeder, C.E., Javitt, D.C., 2000. Activation timecourse of ventral visual stream object-recognition areas: high density electrical mapping of perceptual closure processes. J. Cogn. Neurosci. 12, 615–621.

Doniger, G., Foxe, J.J., Schroeder, C.E., Murray, M.M., Higgins, B.A., Javitt, D.C., 2001. Visual perceptual learning in human object recognition areas: a repetition priming study using high-density electrical mapping. NeuroImage 13, 305–313.

Efron, R., 1970. The minimum duration of a perception. Neuropsychologia 8, 57–63.

Friston, K.J., Fletcher, P., Josephs, O., Holmes, A., Rugg, M.D., Turner, R., 1998. Event-related fMRI: characterizing differential responses. NeuroImage 7, 30–40.

Friston, K.J., Mechelli, A., Turner, R., Price, C.J., 2000. Nonlinear responses in fMRI: the Balloon model, Volterra kernels, and other hemodynamics. NeuroImage 12, 466–477.

Friston, K.J., Glaser, D.E., Henson, R.N.A., Kiebel, S., Phillips, C., Ashburner, J., 2002. Classical and Bayesian inference in neuroimaging: applications. NeuroImage 16, 484–512.

George, N., Jemel, B., Fiori, N., Renault, B., 1997. Face and shape repetition effects in humans: a spatio-temporal ERP study. NeuroReport 8, 1417–1423.

Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzchak, Y., Malach, R., 1999. Differential processing of objects under various viewing conditions in the human lateral occipital complex. Neuron 24, 187–203.

Henson, R.N.A., 2003. Neuroimaging studies of priming. Prog. Neurobiol. 70, 53–81.

Henson, R.N.A., Rugg, M.D., 2002. Neural response suppression, haemodynamic repetition effects, and behavioural priming. Neuropsychologia 41, 263–270.

Henson, R., Shallice, T., Dolan, R., 2000. Neuroimaging evidence for dissociable forms of repetition priming. Science 287, 1269–1272.

Henson, R.N., Shallice, T., Gorno-Tempini, M.L., Dolan, R.J., 2002. Face repetition effects in implicit and explicit memory tests as measured by fMRI. Cereb. Cortex 12, 178–186.

Henson, R.N., Goshen-Gottstein, Y., Ganel, T., Otten, L.J., Quayle, A., Rugg, M.D., 2003. Electrophysiological and haemodynamic correlates of face perception, recognition and priming. Cereb. Cortex 13, 793–805.

Holmes, A.P., Friston, K.J., 1998. Generalisability, random effects and population inference. NeuroImage 7, 754.

Humphreys, G.W., Besner, D., Quinlan, P.T., 1988. Event perception and the word repetition effect. J. Exp. Psychol.: Gen. 117, 51–67.

Itier, R.J., Taylor, M.J., 2002. Inversion and contrast polarity reversal affect both encoding and recognition processes of unfamiliar faces: a repetition study using ERPs. NeuroImage 15, 353–372.

James, T.W., Humphrey, G.K., Gati, J.S., Menon, R.S., Goodale, M.A., 2002. Differential effects of viewpoint on object-driven activation in dorsal and ventral streams. Neuron 35, 793–801.

Jemel, B., Calabria, M., Delvenne, J.F., Crommelinck, M., Bruyer, R., 2003. Differential involvement of episodic and face representations in ERP repetition effects. NeuroReport 14, 525–530.

Karayanidis, F., Andrews, S., Ward, P.B., McConaghy, N., 1991. Effects of inter-item lag on word repetition: an event-related potential study. Psychophysiology 28, 307–318.

Keane, M.M., Gabrieli, J.D., Mapstone, H.C., Johnson, K.A., Corkin, S., 1995. Double dissociation of memory capacities after bilateral occipital-lobe or medial temporal-lobe lesions. Brain 118, 1129–1148.

Kiebel, S., Friston, K.J., 2003. Statistical parametric mapping for event-related potentials. NeuroImage, 994 (HBM 2003 Abstracts).

Kourtzi, Z., Kanwisher, N., 2000. Cortical regions involved in perceiving object shape. J. Neurosci. 20, 3310–3318.

Koutstaal, W., Wagner, A.D., Rotte, M., Maril, A., Buckner, R.L., Schacter, D.L., 2001. Perceptual specificity in visual object priming: functional magnetic resonance imaging evidence for a laterality difference in fusiform cortex. Neuropsychologia 39, 184–199.

Malach, R., Reppas, J.B., Benson, R.R., Kwong, K.K., Jiang, H., Kennedy, W.A., Ledden, P.J., Brady, T.J., Rosen, B.R., Tootell, R.B., 1995. Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. Proc. Natl. Acad. Sci. U. S. A. 92, 8135–8139.

McCarthy, G., Wood, C.C., 1985. Scalp distributions of event-related potentials: an ambiguity associated with analysis of variance models. Electroencephalogr. Clin. Neurophysiol. 62, 203–208.

McKone, E., 1995. Short-term implicit memory for words and nonwords. J. Exp. Psychol., Learn., Mem., Cogn. 21, 1108–1126.

McPherson, W.B., Holcomb, P.J., 1999. An electrophysiological investigation of semantic priming with pictures of real objects. Psychophysiology 36, 53–65.

Misra, M., Holcomb, P.J., 2003. Event-related potential indices of masked repetition priming. Psychophysiology 40, 115–130.

Naccache, L., Dehaene, S., 2001. The priming method: imaging unconscious repetition priming reveals an abstract representation of number in the parietal lobes. Cereb. Cortex 11, 966–974.

Nagy, M.E., Rugg, M.D., 1989. Modulation of event-related potentials by word repetition: the effects of inter-item lag. Psychophysiology 26, 431–436.

Penny, T.B., Mecklinger, A., Nessler, D., 2001. Repetition related ERP effects in a visual object target detection task. Cogn. Brain Res. 10, 239–250.

Phillips, W.A., 1974. On the distinction between sensory storage and short-term visual memory. Percept. Psychophys. 16, 283–290.

Picton, T.W., Bentin, S., Berg, P., Donchin, E., Hillyard, S.A., Johnson Jr., R., Miller, G.A., Ritter, W., Ruchkin, D.S., Rugg, M.D., Taylor, M.J., 2000. Guidelines for using human event-related potentials to study cognition: recording standards and publication criteria. Psychophysiology 37, 127–152.

Puce, A., Allison, T., McCarthy, G., 1999. Electrophysiological studies of human face perception: III. Effects of top-down processing on face-specific potentials. Cereb. Cortex 9, 445–458.

Ratcliff, R., Hockley, W., McKoon, G., 1985. Components of activation: repetition and priming effects in lexical decision and recognition. J. Exp. Psychol.: Gen., 114.

Robb, W.G.K., Rugg, M.D., 2002. Electrophysiological dissociation of retrieval orientation and retrieval effort. Psychon. Bull. Rev. 9, 583–589.

Rugg, M.D., Coles, M.G.H. (Eds.), 1995. Electrophysiology of Mind. Oxford Univ. Press, Oxford, pp. 27–39.

Rugg, M.D., Doyle, M.C., 1994. Event-related potentials and stimulus repetition in direct and indirect tests of memory. In: Heinze, H.J., Munte, T., Mangun, G.R. (Eds.), Cognitive Electrophysiology. Birkhauser, Boston, pp. 124–148.

Rugg, M.D., Henson, R.N.A., 2002. Episodic memory retrieval: an (event-related) functional neuroimaging perspective. In: Parker, A.E., Wilding, E.L., Bussey, T. (Eds.), The Cognitive Neuroscience of Memory Encoding and Retrieval. Psychology Press, Hove, pp. 3–37.

Schacter, D.L., Buckner, R.L., 1998. Priming and the brain. Neuron 20, 185–195.

Schacter, D.L., Tulving, E., 1994. In: Schacter, D.L., Tulving, E. (Eds.), Memory Systems 1994. MIT, Cambridge, MA, pp. 1–38.

Schendan, H.E., Kutas, M., 2002. Neurophysiological evidence for two processing times for visual object identification. Neuropsychologia 40, 931–945.

Schendan, H.E., Kutas, M., 2003. Time course of processes and representations supporting visual object identification and memory. J. Cogn. Neurosci. 15, 111–135.

Schnyer, D.M., Allen, J.J., Forster, K.I., 1997. Event-related brain potential examination of implicit memory processes: masked and unmasked repetition priming. Neuropsychology 11, 243–260.

Schweinberger, S.R., Pfutze, E.M., Sommer, W., 1995. Repetition priming and associative priming of face recognition: evidence from event-related potentials. J. Exp. Psychol., Learn., Mem., Cogn. 21, 722–736.

Schweinberger, S.R., Pickering, E.C., Burton, A.M., Kaufmann, J.M., 2002a. Human brain potential correlates of repetition priming in face and name recognition. Neuropsychologia 40, 2057–2073.

Schweinberger, S.R., Pickering, E.C., Jentzsch, I., Burton, A.M., Kaufmann, J.M., 2002b. Event-related brain potential evidence for a response of inferior temporal cortex to familiar face repetitions. Cogn. Brain Res. 14, 398–409.

Seeck, M., Michel, C.M., Mainwaring, N., Cosgrove, R., Blume, H., Ives, J., Lanids, T., Schomer, D.L., 1997. Evidence for rapid face recognition from human scalp and intracranial electrodes. NeuroReport 8, 2749–2754.

Snodgrass, J.G., Feenan, K., 1990. Priming effects in picture fragment completion: support for the perceptual closure hypothesis. J. Exp. Psychol.: Gen. 119, 276–296.

Sperling, G., 1960. The information available in brief visual presentations. Psychol. Monogr. 74, 1–29.

Squire, L., Cohen, N.J., 1984. Human memory and amnesia. In: McGaugh, J.L., Lynch, G., Weinberger, N.M. (Eds.), The Neurobiology of Learning and Memory. Guilford Press, New York, pp. 3–64.

Sutton, S., Tueting, P., Zubin, J., John, E.R., 1967. Information delivery and the sensory evoked potential. Science 155, 1436–1439.

Talairach, J., Tournoux, P., 1988. Co-Planar Stereotaxic Atlas of the Human Brain. Georg Thieme Verlag, Stuttgart.

Tarr, M.J., Pinker, S., 1989. Mental rotation and orientation-dependence in shape recognition. Cognit. Psychol. 21, 233–282.

Tsivilis, D., Otten, L.J., Rugg, M.D., 2001. Context effects on the neural correlates of recognition memory: an electrophysiological study. Neuron 31, 497–505.

Turnbull, O.H., Carey, D.P., McCarthy, R.A., 1997. The neuropsychology of object constancy. J. Int. Neuropsychol. Soc. 3, 288–298.

Urbach, T.P., Kutas, M., 2002. The intractability of scaling scalp distributions to infer neuroelectric sources. Psychophysiology 39, 791–808.

Ullman, S., 1996. High-level Vision: Object Recognition and Visual Cognition. MIT Press, Cambridge.

van Turennout, M., Ellmore, T., Martin, A., 2000. Long-lasting cortical plasticity in the object naming system. Nat. Neurosci. 3, 1329–1334.

van Turennout, M., Bielamowicz, L., Martin, A., 2003. Modulation of neural activity during object naming: effects of time and practice. Cereb. Cortex 13, 381–391.

Viggiano, M.P., Kutas, M., 1998. The covert interplay between perception and memory: event-related potential evidence. Electroencephalogr. Clin. Neurophysiol. 108, 435–439.

Vuilleumier, P., Henson, R.N., Driver, J., Dolan, R.J., 2002. Multiple levels of visual object constancy revealed by event-related fMRI of repetition priming. Nat. Neurosci. 5, 491–499.

Wagner, A.D., Desmond, J.E., Demb, J.B., Glover, G.H., Gabrieli, J.D.E., 1997. Semantic repetition priming for verbal and pictorial knowledge: a functional MRI study of left inferior prefrontal cortex. J. Cogn. Neurosci. 9, 714–726.

Wagner, A.D., Maril, A., Schacter, D.L., 2000. Interactions between forms of memory: when priming hinders new episodic learning. J. Cogn. Neurosci. 12, 52–60.

Warrington, E.K., Weiskrantz, L., 1974. The effect of prior learning on subsequent retention in amnesic patients. Neuropsychologia 12, 419–428.