Neuropsychologia 47 (2009) 2942–2947

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Object priming and recognition memory: Dissociable effects in left frontal cortex at encoding

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ARTICLE INFO

Article history:
Received 6 July 2008
Received in revised form 19 June 2009
Accepted 21 June 2009
Available online 27 June 2009

Keywords:
Implicit memory
fMRI
Repetition priming
Inferior prefrontal cortex
BA47

ABSTRACT

Functional magnetic resonance imaging (fMRI) studies have implicated the left prefrontal cortex in priming. We tested the hypothesis that object encoding activity in different prefrontal cortex regions selectively predicts subsequent object priming and recognition respectively. Participants were scanned whilst making semantic category judgements about novel object pictures. One week later priming and recognition of these objects were tested. Encoding that produced long-lasting priming in the absence of recognition memory was associated with increased activity in left inferior prefrontal (BA 47) and superior frontal (BA 8) cortices. In contrast, encoding that produced object recognition one week later activated the left middle frontal cortex (BA 9). This is consistent with other evidence indicating that object priming and recognition are independent kind of memory. Problems of measuring item-by-item recognition and priming together are discussed.

1. Introduction

Prior processing of an object often facilitates its subsequent processing. This phenomenon, called repetition priming, can be measured behaviourally when subjects are faster at naming or making decisions about repeated objects compared with novel objects. Priming can occur in the absence of aware memory for the learning episode (Schacter, Chiu, & Ochsner, 1993) and is therefore thought to reflect the influence of implicit (unaware) memory for the earlier exposure of the primed stimulus.

Neuroimaging studies of priming have found reduced haemodynamic responses in left inferior prefrontal cortex (LIFC) and occipitotemporal regions during processing of repeated relative to novel objects (Simons, Koutstaal, Prince, Wagner, & Schacter, 2003; van Turennout, Ellmore, & Martin, 2000; see Henson, 2003 for a review). Several studies have investigated how priming relates to subsequent recognition memory with early work suggesting that priming's presence during encoding has a negative impact on later recognition (Wagner, Maril, & Schacter, 2000; although see Stark, Gordon, & Stark, 2008). In contrast, little is known about the neural correlates of encoding processes that lead to object priming and whether these processes differ from those that lead to later recognition memory. If priming is the consequence of neural processing during the first exposure of a stimulus, then encoding activity should be able to predict subsequent object priming. This is analogous to the 'subsequent memory' approach where brain responses at encoding are associated with later recognition memory (Brewer, Zhao, Desmond, Glover, & Gabrieli, 1998; Wagner et al., 1998).

One candidate brain region that might mediate encoding that leads to priming is the LIFC. A recent study by Wig, Grafton, Demos, and Kelley (2005) provides evidence that activity in the LIFC during encoding of objects is necessary to produce subsequent behavioural priming of those objects. In this study, transcranial magnetic stimulation was applied to subjects' LIFC whilst they made living/non-living judgements about objects. Disruption of neural processing in LIFC at encoding abolished both later behavioural priming and repetition-related haemodynamic decreases in the LIFC. This suggests LIFC activity at encoding is important for later object priming. Consistent with this view, Schott et al. (2006) have shown that reduced activity in LIFC is associated with later word-stem completion priming. Their study was able to distinguish between the encoding of words that were either remembered, primed but not remembered, or forgotten (neither primed nor remembered). This design was unable to examine words that were later primed *and* remembered, i.e., priming in the context of recognition.

The present study was designed to test the hypothesis that activity in the LIFC at encoding predicts subsequent object priming, but that different frontal activity predicts subsequent object recognition (Brewer et al., 1998). To do this we scanned participants with fMRI whilst they performed semantic category judgements about novel object pictures. One week later participants completed a

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doi:10.1016/j.neuropsychologia.2009.06.022

priming task followed by a surprise recognition test. This allowed us to classify each object at encoding as later primed or later unprimed, and also as later recognized or unrecognized. This design allowed us to examine the neural correlates of encoding that lead to later priming and compare them with correlates of encoding that lead to recognition. Direct measures of priming (reaction time (RT)) and recognition were made for each trial, rather than calculating means across subjects as other studies have done (Wagner et al., 2000). This approach is novel and allowed encoding effects leading to priming in the context of recognition or non-recognition to be examined separately.

2. Methods

2.1. Subjects

Twelve right-handed participants with no history of neurological or psychiatric illness gave informed consent to participate in the study (nine women; mean age 22.6 years; age range 19–34 years). All the participants underwent a medical examination before taking part in the study, which had received local ethics committee approval.

2.2. Stimuli and experimental procedure

Stimuli consisted of 240 black and white line drawings of common objects (120 representing man-made objects and 120 representing natural objects). 200 objects were taken from a standardised set (Snodgrass & Vanderwart, 1980) and a further 40 natural objects were drawn in the same style. Pictures were counterbalanced across participants so that, at test, each picture was novel for some participants and repeated for the others. During the study phase, participants were scanned using fMRI whilst they saw a series of 160 object pictures. The subjects' task was to decide whether each picture represented a man-made or a natural object as quickly and as accurately as possible by pressing one of two response buttons. Pictures were presented every 6 s (2 s presentation, 4 s inter-stimulus interval) using Psyscope software (Cohen, MacWhinney, Flatt, & Provost, 1993). RTs were recorded from response boxes connected to a Psyscope button box and a Power Mac G3 computer. Response buttons were counterbalanced across subjects.

One week later the same participants returned for the test phase of the experiment and were scanned whilst performing two tasks; a priming task followed by a surprise recognition test. In the priming task, participants saw all the object pictures presented at study plus 80 novel objects randomly intermixed. They again categorised each one as man-made or natural as quickly and as accurately as possible. During the recognition test, participants saw all the object pictures again, but this time they were asked to decide whether each object was the one they recognized from the study phase. Participants were also strongly instructed only to respond that they did not recognize an object if they were very confident that they had not seen it one week earlier. In order to ensure that familiarity was used as well as recollection (source memory), participants were told to respond 'recognized' even without source memory, provided familiarity was sufficiently strong. Stimuli for the priming and recognition tasks were presented using the same parameters as at study (see above). Objects were presented in the same order during the priming and recognition tests to guarantee that the delays between priming and recognition tests for each object were equal, minimising noise in the recognition measure. The study, priming and test phases were split into 8-min sessions (two at study and three each at priming and recognition) with 80 object pictures presented in each session and a 2-min interval between each session.

2.3. Image acquisition

A 1.5T LX/Nvi Neuro-Optimised MR imaging system (General Electric, Milwaukee, USA) was used to acquire T2* weighted gradient-echo echoplanar images with blood oxygenation level dependent (BOLD) contrast. A total of 384 volumes were acquired at study (192 per session). Each volume comprised 20, 6 mm axial slices (64×64, 3 mm $\times$ 3 mm pixels, echo time = 40 ms) oriented parallel to the AC-PC line and positioned to cover the entire brain except the most superior part. Volumes were collected continuously with a repetition time of 2.5 s/volume.

2.4. fMRI analysis

Data were analysed using Statistical Parametric Mapping (SPM99, Wellcome Department of Cognitive Neurology, London, UK). The time series for each voxel was realigned temporally to acquisition of the first slice and spatially to the first volume using sinc interpolation. Images were normalised to a standard EPI template based in Talairach space (Ashburner & Friston, 1999) using nonlinear basis functions. The normalised images were smoothed with an isotropic 8 mm FWHM Gaussian kernel and proportionally scaled to a grand mean of 100 across all voxels and scans within a session. The time series were high-pass filtered to 1/120 Hz and low-pass smoothed by a 4-s FWHM Gaussian kernel.

Statistical analysis was carried out in two stages. In the first stage, the BOLD response to each event-type was modelled by convolving a series of delta functions corresponding to each stimulus onset with the canonical haemodynamic response function and its partial derivative with respect to time (Friston et al., 1998). These functions, together with a constant term for each session, were modelled as participant specific covariates in a fixed effects general linear model. Parameter estimates were calculated for each covariate from a least mean squares fit of the model to the data. Pairwise contrasts between the canonical parameter estimates for event-types generated statistical parametric maps (SPMs) of the *t*-statistic, which were subsequently transformed into maps of the Z statistic. Contrast images generated for each participant were used in second stage, one-sample *t*-tests treating participants as a random effect.

Events of interest in the study phase were defined for objects correctly classified as man-made or natural; incorrect responses were modelled separately. Each object was classified as recognized or unrecognized during the recognition test, and then classified as primed or unprimed depending on whether it was categorised as man-made or natural faster at test than at study ('inclusive' analysis condition). A consequence of using this definition of priming was that primed items had longer RTs at study than unprimed items. Any speed-up from study to test could thus reflect either priming or regression towards the mean. To minimize effects of regression to the mean an unbiased selection procedure was used to ensure that primed and unprimed objects had matched RT distributions at study ('matched' analysis condition). The rationale is that regression to the mean should operate equally for primed and unprimed stimuli with matched study RTs. Use of the 'matched' analysis condition also ensured that encoding was more similar between later primed and unprimed stimuli. An algorithm written in Matlab (version 5.3, Mathworks) took primed and unprimed response distributions for each subject and binned them every 50–70 ms based on their study RT. For corresponding pairs of primed and unprimed bins the minimum number of trials in either bin was selected. A matched number of trials was then randomly selected from the corresponding bin of the other distribution. This procedure was conducted separately for both recognized and unrecognized objects. The resultant trials had matching RT distributions and did not differ in terms of study median RTs. Study RT matched and non-matched objects were modelled separately in the design matrix. Even if regression to the mean is not fully ruled out by this method, regression should only add noise to the data and reduce the chance of identifying real encoding effects that predict priming (type 2 error), but should not produce false positive fMRI findings. Convergent findings from the 'inclusive' and 'matched' analyses predicting priming can be treated with confidence. The inclusion analysis should be more subject to noise from stronger regression effects, whereas matching will have reduced numbers because of the selection process.

In the 'inclusive' analysis, second-level contrast images were analysed in a 2(primed/unprimed) $\times$ 2(recognized/unrecognized) ANOVA to assess main effects of recognition and priming at encoding as well as any interaction between recognition and priming. To further assess encoding effects predicting later recognition of objects, second level correlations were performed between contrast images for the Recognized > Unrecognized contrast and subjects' proportion of hits minus proportion of false alarms score (pHits − pFA). To examine the neural correlates of encoding that lead to priming without recognition, planned comparisons between unrecognized primed and unrecognized unprimed second-level contrast images were performed. Two versions of this contrast were conducted. The first combined matched and unmatched unrecognized objects, and the second used only unrecognized objects with matched study RTs to control for regression towards the mean. Similar comparisons between recognized primed and recognized unprimed objects were also performed. Regions in SPMs were considered significant if five or more contiguous voxels survived a $P < 0.001$ uncorrected threshold. There is a risk of making type I errors with uncorrected thresholds; however, given that this is the first study to examine neural correlates of visual object priming at encoding, specifying a precise a priori anatomical search area to correct for multiple comparisons proved difficult. The approach adopted here is a reasonable trade-off between making type I and type II errors (see Schott et al., 2006).

3. Results

3.1. Behavioural results

Performance was close to perfect on the man-made/natural task (96% accuracy, SEM 0.4%). Objects with RTs less than 250 ms or greater than 2.5 standard deviations above the subject's mean categorisation RT were considered outliers and were not analysed. Performance on the recognition test was significantly above chance, the group mean corrected recognition score (proportion recognized − proportion false alarms) was 0.28 [$t(11) = 8.61$, $P < 0.001$]. Across the group of 12 participants, repeated objects were categorised more quickly (675 ms) than novel objects (692 ms) [$F(1,11) = 13.62$, $P < 0.005$] showing a significant group priming effect of 17 ms. Significant priming effects were also found when recognized (678 ms) and unrec-