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Repetition suppression and semantic enhancement: An investigation of the neural correlates of priming

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Abstract

The priming of a stimulus by another has become an important tool for exploring the neural underpinnings of conceptual representations. However, priming effects can derive from many different types of relationships and it is important to distinguish between them in order to be able to develop theoretical accounts of the representation of conceptual knowledge. While it is well known that repetition priming (the repeated presentation of the same stimulus) is associated with a reduced neural response, called repetition suppression (RS), the neural correlates of *semantic* priming (when two stimuli are related in meaning but not identical) are not so well established. We compared the neural correlates of repetition and semantic priming using written words, independently manipulating form and meaning. In an fMRI study, subjects saw single words and made a concrete–abstract decision. Two consecutive words were identical (*town–town*) or varied along a continuum of semantic relatedness, from highly related (*cord–string*) to unrelated (*face–sail*). We found distinct patterns of activation for repetition and semantic priming. Repetition priming was associated with RS in LIFG, bilateral parahippocampal gyrus and R fusiform gyrus. We also observed increased activation for word repetition in the RMFG and RMTG/STG, which may reflect recognition of item's earlier presentation. There was *no* evidence of suppression for semantic relatedness. Semantic priming was associated with *enhanced* activation in multiple bilateral fronto-temporal areas, i.e. semantic enhancement. The results suggest that repetition and semantic priming in visual word recognition depend on distinct cognitive processes and neural substrates.

Keywords: Priming; Repetition suppression; Semantic enhancement

1. Introduction

Priming has been one of the most valuable techniques for investigating the functional properties of conceptual representation and processing. Priming refers to the facilitated processing of a stimulus, as indexed by faster reaction times (RTs) and/or greater response accuracy, following prior encounter with the same or a related stimulus (Henson, 2003; Richardson-Klavehn & Bjork, 1988; Schacter & Buckner, 1998; Tulving & Schacter, 1990). This facilitatory priming suggests that when a prime stimulus is encountered, information about the stimulus becomes rapidly and automatically available and this influences the processing of the target (Moss & Gaskell, 1999; Neely, 1991). Several kinds of relationship between stimuli have been shown to support priming, including repetition of the item (e.g. prime *table*, target *table*; Henson, 2003; Schacter & Buckner, 1998; Wiggs & Martin, 1998), morphological overlap between prime and target (e.g. prime *happy*, target *happily*; Marslen-Wilson, Tyler, Waksler, & Older, 1994), and semantic overlap between two stimuli (e.g. prime *tiger*, target *lion*; Meyer & Schvaneveldt, 1971; Moss, Ostrin, Tyler, & Marslen-Wilson, 1995; Neely, 1991; Tulving & Schacter, 1990). By varying the nature of the semantic relationship between prime and target, priming is a useful tool for investigating the kinds of information which become activated when the prime is processed and for drawing inferences about the content of concepts and their interrelationships (Moss et al., 1995; Rossell, Price, & Nobre, 2003).

Given the clear behavioural evidence that priming reflects the nature of the relationships between concepts, if priming is associated with changes in neural response, then it is potentially a useful tool to elucidate the neural representation and organisation of concepts. Neuroimaging investigations of priming have revealed priming-related effects in numerous regions of the human brain, with the specific regions depending on the type

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of stimulus, e.g. words or pictures, and the manner in which the stimulus is processed, e.g. whether the task requires semantic or perceptual processing (Henson, 2003). This paper is concerned with the neural correlates of priming in visual word recognition, as observed in neuroimaging studies with healthy volunteers. We focus on the two main sets of priming studies that have contributed the most to questions about the neural representation and organisation of concepts – repetition priming, i.e. when the prime and target stimulus are identical, and semantic priming, i.e. when prime and target are related in meaning.

In the case of repetition priming, the most consistent finding is a decrease of the haemodynamic response for repeated, primed stimuli, compared to novel stimuli. Following the neuroimaging literature of priming effects, we will refer to this haemodynamic reduction as *repetition suppression* or RS (see Henson, 2003 for a review). Previous fMRI studies have shown that repetition-related decreases of activation occur at different processing levels. For example, RS has been observed in regions involved in perceptual (e.g. Koustaal et al., 2001; Simons, Koustaal, Prince, Wagner, & Schacter, 2003; Vuilleumier, Henson, Driver, & Dolan, 2002; Wiggs & Martin, 1998), phonological (Badgaiyan, Schacter, & Alpert, 1999, 2001; Buckner, Koustaal, Schacter, & Rosen, 2000), morphological (Bozic, Marslen-Wilson, & Tyler, 2005), semantic (e.g. Buckner et al., 2000; Demb et al., 1995; Schacter & Buckner, 1998; Thompson-Schill, D'Esposito, & Kan, 1999) and numerical processing (Naccache & Dehaene, 2001). In the particular case of visual word recognition, various studies have reported consistent reductions of activation in higher-order prefrontal brain regions when subjects perform the same semantic task on repeated words. For example, Demb et al. (1995) observed RS in the left inferior frontal gyrus (LIFG) for repeated compared to novel words when participants performed a semantic task (i.e. concrete–abstract decision), but not when they performed a non-semantic task (e.g. deciding whether words were printed in lower or upper case). Likewise, Wagner, Koustaal, Maril, Schacter, and Buckner (2000) reported reduced activation in the anterior LIFG, as well as in the mid-lateral temporal cortex, for words on which subjects had previously made the same concrete–abstract decision, but not when subjects had previously made a non-semantic (upper-lower case) decision. These studies suggest that RS in the LIFG is process-specific, depending not only upon stimulus repetition but also the maintenance of the same semantic task across repetitions. Similar results were reported by Thompson-Schill and colleagues in a study using a words generation task. They found RS in the LIFG when subjects performed the same semantic task (either colour or action generation) on repeated words, but not when subjects performed different tasks (colour generation followed by action generation or vice-versa). In another set of studies, Henson investigated priming effects for familiar and unfamiliar words and observed RS for repeated familiar words in left fusiform regions, but increased activation (often called *repetition enhancement*, RE) in the same regions for repeated unfamiliar representations (Henson, 2001). These findings have been interpreted as suggesting that RS occurs when the same processes operate on both primed and unprimed stimuli, whereas RE reflects different/additional processes such as those related to the formation of new representations, as in the case of unfamiliar stimuli.

In contrast to repetition priming, the neural correlates of semantic priming in word processing are not so well established. Some studies have reported decreases in the haemodynamic response for semantic priming, but the regions where suppression occurs are not consistent across studies. Kotz, Cappa, von Cramon, and Friederici (2002) using a lexical decision task, have found decreased activation for semantically related words in several regions of the frontal cortex and bilateral temporal operculum, but, using similar tasks, other authors have reported suppression effects in bilateral middle frontal gyrus, left posterior temporal gyrus, left precentral gyrus and right caudate (Rissman, Eliassen, & Blumstein, 2003), while still others have found decreased activation in the left anterior medial temporal gyrus (Rossell et al., 2003). In a prime–target relatedness judgement task, Giesbrecht and colleagues also found reduced activation for related relative to unrelated words in several regions of the frontal, temporal and parietal cortex, including the left middle and inferior temporal gyrus, left prefrontal cortex and left inferior parietal cortex (Giesbrecht, Camblin, & Swaab, 2004). Some of these studies have also reported enhanced activation associated with semantic priming. Kotz et al. (2002), for example, have found increases in left posterior middle temporal gyrus, inferior parietal cortex and cuneus, while Rossell et al. (2003) have reported activation in the left supramarginal gyrus.

Given the differences in the stimuli, task demands and methodological characteristics (such as interstimulus interval, proportion of related items and the type of semantic relation between words), direct comparisons between studies are difficult. Our current understanding of the neural correlates of semantic priming remains therefore largely speculative. Given that some studies show reduced neural activity for semantic priming, just like others have shown for repetition priming, some authors have proposed that both types of priming share the same neural basis (Copland et al., 2003; Kotz et al., 2002; Mummery, Shallice, & Price, 1999). In contrast, the finding that semantic priming also generates enhancement effects suggests that the neural correlates of semantic and repetition priming may be distinct. Consistent with this latter view, behavioural studies show some striking differences between these two types of priming; for example, whereas repetition priming is long lasting, semantic priming is not (Henson, 2003; Schacter & Buckner, 1998), and distinct forms of processing appear to be associated with different types of priming, e.g. perceptual versus semantic processing (Copland et al., 2003).

Thus, it remains unclear what the neural correlates of semantic priming are and whether semantic and repetition priming share the same neural correlates. Although some studies have suggested that repetition and semantic priming share the same neural bases, no direct comparison between the two types of priming has so far been conducted. By directly comparing the neural correlates of repetition and semantic priming, we were able to investigate which neural regions show common and distinct effects (whether suppression or enhancement of activation), which in turn may help to determine the nature of semantic and repetition priming effects in visual word recognition. These are critical questions that need to be addressed before priming can be confidently used to investigate the neural representation and processing of meaning.

In this event-related fMRI study, subjects saw a list of words and made an abstract/concrete decision on each word, a task that requires access to semantic information and therefore taps into the semantic system. Within the list, two consecutive words were either identical (e.g. *town–town*) or they varied along a continuum of semantic relatedness, from highly related (e.g. *cord–string*) to unrelated (e.g. *face–sail*). Semantic relatedness was treated as a continuum (rather than a discrete variable) to better reflect the nature of the semantic relation between words that we encounter in the world. By including a repetition and semantic condition in the same experiment, we were able to compare the two kinds of effects using the same task, the same group of participants and comparable materials.

2. Methods

2.1. Subjects

We tested fifteen right-handed, native English speakers (mean age was 22 years; six males and nine females). Each gave informed consent and was paid for their participation. The study was approved by Addenbrookes NHS Trust Ethical Committee.

2.2. Stimuli and design

We used a semantic categorisation task, in which subjects saw a written word (presented in lowercase, in the middle of the screen) and made a speeded decision as to whether the word was concrete or abstract. We manipulated the semantic relationship between two consecutive words which were either identical (e.g. prime-*town* followed by target-*town*) or varied along a continuum of semantic relatedness, from highly related (e.g. prime-*cord* followed by target-*string*) to unrelated words (e.g. prime-*face* followed by target-*sail*).

Degree of semantic relatedness between prime and target was determined by means of scores in a pretest, in which 15 subjects who did not take part in the fMRI study made relatedness judgements on pairs of written words using a nine-point scale where 1 denoted unrelated and 9 denoted highly related words. From these ratings we chose pairs of words along a continuum of semantic relatedness, ranging from the most unrelated (e.g. *face–sail*, rated as 1.3) through to medium relatedness (e.g. *brush–pliers*, rated as 4) to the most highly related (e.g. *cord–string*, rated as 7.3). Words were related by virtue of their similarity in meaning (i.e. feature overlap) rather than co-occurrence, so that priming effects resulted from activation within the semantic system rather than from associative links (McKoon & Ratcliff, 1992; Moss et al., 1995; Plaut, 1995). All word pairs had low association strength (mean = .059), as measured by free association norms (Moss & Older, 1996). Word-pairs were matched for frequency (CELEX database, Baayen & Pipenbrook, 1995), familiarity (MRC Psycholinguistics databases, Coltheart, 1981) and number of letters along the continuum of semantic relatedness. Half of the prime–target pairs were concrete, the other half abstract according to concreteness ratings in the MRC Psycholinguistics database (Coltheart, 1981). Words with ratings between 100 and 400 were considered abstract and between 400 and 700 as concrete. Within the subsets of concrete and abstract words, pairs were matched for the relevant variables along the continuum of semantic relatedness. Word-pairs in the identity condition were matched for frequency, familiarity and number of letters, with pairs in the unrelated condition, which was composed of pairs drawn from the lower end of the semantic continuum (rated between 1 and 2 in the pretest of semantic relatedness). Half of the pairs in the identity and unrelated conditions were concrete, the other half abstract. Concrete identity and concrete unrelated pairs were matched on the relevant variables. A similar matching was carried out for the abstract pairs. *T*-tests confirmed that there were no significant differences between conditions on any of the variables listed above ($p > .05$ in all cases). All paired words were either both concrete or both abstract, in order to elicit the same response on the abstract/concrete judgement task for prime and target, thus avoiding a potential confound between priming effects and congruity of response effects.

We used fixation as a baseline condition, in which subjects saw a cross in the middle of the screen and no response was required. There were 50 prime–target pairs in the identity condition (25 concrete and 25 abstract) and 150 along the continuum of semantic relatedness (75 concrete and 75 abstract), from which 50 pairs (drawn from the lower end of the continuum) were used as the unrelated condition, 100 fixation items and 200 filler items. Fillers were included to offset the fact that all test word-pairs were congruent (either two abstract words or two concrete words in succession). Pairs were interspersed with filler items in order to have an equal number of congruent and incongruent transitions across the entire set. Moreover, filler items were semantically unrelated to the experimental pairs, giving an equal proportion of related and unrelated transitions.

2.3. Procedure

Each event consisted of a written word presented for 500 ms followed by a 2 s delay during which the participant made a concrete–abstract judgment by pressing a left button if the word was concrete and a right button if it was abstract. In the baseline condition, a cross was presented in the middle of the screen for 500 ms followed by a 2 s delay and no response was required. Presentation and timing of stimuli were controlled by DMDX software (Forster & Forster, 1990). Items were pseudorandomly organised into four sessions, with session order counterbalanced across subjects. Each session comprised of 175 trials with five lead-in trials. Each session lasted approximately 7.5 min, with 1–2 min rest between each session. The first session was preceded by a short practice session of 24 items before scanning started. We recorded both reaction times and accuracy.

2.4. MRI acquisition and imaging analysis

Scanning was carried out on a 3-T Bruker Medspec Avance S300 system at the Wolfson Brain Imaging Centre, Cambridge, England, using a gradient-echo EPI sequence (TR = 1100 ms; TE = 30 ms, flip angle 65°, matrix size 64 × 64, FOV 24 cm × 24 cm, 21 oblique slices away from the eyes, 4 mm thick, 1 mm gap between slices, 3.1 × 3.1 in-plane resolution, 405 repetitions) with head coils, 144 kHz bandwith, and spin-echo-guided reconstruction. T1-weighted scans were acquired for anatomical localisation. The trial duration (i.e. 2500 ms) was not an interger multiple of the TR (i.e. 1100 ms) and therefore data were sampled at various points along the HRF ensuring an effective sampling rate (Josephs, Turner, & Friston, 1997).

Preprocessing and statistical analysis of the data were performed using Statistical Parametric Mapping software (SPM99, Wellcome Institute of Cognitive Neurology, www.fil.ion.ucl.ac.uk), implemented in Matlab (Mathworks Inc., Sherborn, MA, USA). Initial preprocessing consisted of slice timing correction by resampling slices in time relative to the first slice collected. All images were realigned to the first image (after excluding five dummy images to allow T2 equilibrium) to account for head motion. The images were spatially normalised to a standard EPI template based on the Montreal Neurological Institute (MNI) reference brain, using a 12-parameter linear affine transformation (translation, rotation, zoom and shear in x, y and z directions) and a linear combination of three-dimensional discrete cosine transform basis function to account for non-linear deformations. The spatially normalised images were smoothed with an isotropic 8 mm full-width half-maximal Gaussian kernel.

The data were analysed using the general linear model as implemented in SPM99. We performed two types of analysis on the data, a contrast analysis and a correlation analysis. The contrast analysis investigated repetition priming effects, by identifying the regions that showed suppression and enhancement of activation associated with the second item of the pair. Following Josephs and Henson (1999), we modelled the target of each condition separately (identity concrete, identity abstract, unrelated concrete and unrelated abstract) and collapsed primes across conditions. As has been shown previously, modelling primes into the various conditions would lead to a correlation between the regressors of the primes and targets within a condition (mainly because they always occur one after the other and close together in time). In contrast, by modelling targets from each condition separately and collapsing primes across conditions, we were able to maximize sensitivity to differential effects between conditions, as the resulting regressors are not correlated.

Table 1
Mean RTs (and standard deviations) to the targets of the identity and unrelated conditions for both concrete and abstract words

	Identity	Unrelated	Mean
Concrete	637 (53.6)	870 (200.1)	754
Abstract	664 (41.2)	935 (98.9)	800
Mean	651	903	

In a separate analysis, we examined the regions that showed modulation in activity as a function of the degree of semantic relatedness. In this model, we entered the degree of semantic relatedness between prime and target (as determined by our pretests) as a parametric modulator with linear expansion for each item in the target conditions. For both the contrast and correlation analyses, trials were entered as events and modelled using a canonical hemodynamic response function (HRF). The time series in each voxel were highpass-filtered to remove low frequency noise. Each analysis was performed for each subject and results were combined into a group random effects analysis. Results were voxel thresholded at $p < .001$ and $p < .01$ uncorrected and only clusters that survived $p < .05$ corrected for multiple comparisons across the entire brain volume were considered significant. Since SPM coordinates are given in MNI space, the results reported here were converted to Talairach space with a nonlinear transform (Brett, 2001).

3. Results

3.1. *Behavioural data*

Subjects' reaction time (RT) data was inverse transformed prior to statistical analyses in order to reduce the effects of outliers (Ulrich & Miller, 1994). Incorrect and timed-out responses (>1900 ms) were excluded from the analyses. RTs were analysed by participants (F1) and items (F2). In order to replicate the neuroimaging analysis, priming effects were investigated by analysing differences between targets in the different conditions. This analysis assumed that there were no differences between primes in different conditions, as they were matched in all relevant variables. To confirm this assumption we ran a series of statistical tests, which showed no significant differences in RTs to primes of different conditions ($p > .05$ in all cases). Thus differential effects between targets should reflect the relationship with the previous prime.

We first investigated *repetition priming effects* by comparing the mean RT of all targets in the identity condition with targets in the unrelated condition (Table 1), which showed (a) significantly faster RTs for the identity compared to the unrelated condition ($F1(1,14) = 120.021, p < .001; F2(1,96) = 283.368, p < .001$), (b) an effect of concreteness, with faster RTs for concrete compared to abstract words ($F1(1,14) = 14.476, p = .002; F2(1,96) = 7.964, p = .006$), and (c) no significant interaction between semantic condition and concreteness, suggesting that repetition priming effects occurred equally for both concrete and abstract words. There was no evidence of increased priming across experimental sessions ($F2(3,270) = 2.58$, $p = .855$), suggesting that subjects were not developing strategies across the experiment.

We next investigated *semantic priming effects* by performing an analysis of covariance (ANCOVA) between the degree of semantic relatedness between prime and target and the mean RT to the target for concrete and abstract words (Fig. 1). This analysis included all target words in the continuum of semantic relatedness, from highly related to unrelated targets and both concrete and abstract words (i.e. 150 data points). There was a significant effect of semantic relatedness ($r = .585$, $t(147) = 4.684, p < .001$), with faster RTs as a function of increasing semantic relatedness, and a main effect of concreteness ($t(147) = 7.220$, $p < .001$), associated with faster RTs for concrete than abstract words. Separate analysis carried out on concrete words showed significant semantic priming effects ($r = .459$, $t(73) = 4.417$, $p < .001$). Similar analysis carried out on abstract words also showed a marginally significant semantic priming ($r = .219, t(73) = 1.919, p = .059$). The priming effect for concrete words was significantly larger than for abstract words ($t(146) = 2.637$, $p = .009$). We also investigated priming effects across subjects by binning the levels of relatedness into three conditions (unrelated, medium related and highly related words). Similarly to the analysis of covariance, we found (a) significantly faster RTs for increased semantic relatedness ($F2(1,14) = 29.085$, $p < .001$), (b) faster RTs for concrete compared to abstract words ($F2(1,14) = 40.618$, $p < .001$ and (c) an interaction between semantic condition and concreteness, due to larger semantic priming effects for concrete than abstract words ($F2(1,14) = 23.5$, $p < .001$). Once again, there was no evidence of subjects developing strategies across the experiment since priming did not vary across sessions ($t(585) = .759$, $p = .448$). Interestingly, repetition and semantic priming correlated across participants, that is, the participants whose performance most benefited from item repetition also benefited the most from semantic overlap between items (for concrete words $F1(1,13) = 11.53$, $p = .005$; for abstract words $F1(1,13) = 6.306$, $p = .026$). In summary, the behavioural results showed significant repetition and semantic priming effects for both concrete and abstract words. Semantic priming effects were larger for concrete than abstract words.

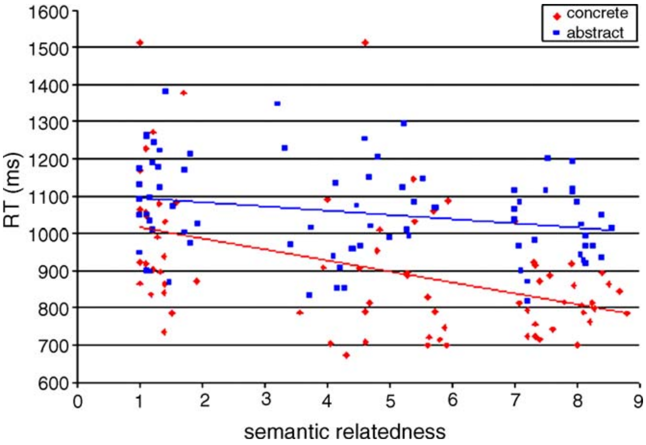

Fig. 1. Mean RTs to the targets along the continuum of semantic relatedness (where 1 = unrelated and 9 = highly related) for both concrete and abstract words.

3.2. *Imaging data*

3.2.1. *Repetition priming effects*

To investigate whether repetition of a word was associated with decreased brain activity (i.e. RS) we contrasted the unre-

Table 2
Brain areas showing RS (unrelated minus identity) and RE (identity minus unrelated)

Region	Cluster level		Voxel level		Coordinates		
	$p_{\text{corrected}}$	Extent	$p_{\text{corrected}}$	Z	x	y	z
(A) Unrelated minus identity (RS)							
R cerebellum*	**.000**	**1315**	**.762**	**3.99**	**8**	**−48**	**−18**
R cerebellum*			.769	3.98	20	−67	−22
R cerebellum			.923	3.79	26	−59	−24
R thalamus	**.014**	**405**	**.962**	**3.70**	**26**	**−25**	**10**
R parahippocampal gyrus (BA 18 and 37)			.994	3.53	36	−39	4
R cingulate gyrus (BA 23)			1.000	3.35	30	−56	12
L precentral gyrus (BA 6)	**.046**	**319**	**1.000**	**3.21**	**−40**	**1**	**28**
L inf. frontal gyrus (BA 45)			1.000	3.13	−48	20	16
L inf. frontal gyrus (BA 44 and 45)			1.000	2.60	−50	11	20
L parahippocampal gyrus (BA 27)	**.054**	**307**	**.938**	**3.76**	**−4**	**−31**	**−2**
L cerebellum			1.000	3.10	−10	−41	−10
L hippocampus			1.000	2.89	−32	−37	−2
(B) Identity minus unrelated (RE)							
R middle temporal gyrus (BA 21)*	**.000**	**2795**	**.015**	**5.27**	**61**	**−33**	**0**
R middle temporal gyrus (BA 21)*			.131	4.69	63	−41	4
R inf. parietal lobule (BA 40)*			.137	4.67	59	−51	32
R inf. frontal gyrus (BA 9)*	**.000**	**2786**	**.042**	**5.00**	**40**	**15**	**27**
R inf. frontal gyrus (BA 45)*			.561	4.17	46	31	6
R medial frontal gyrus (BA 9)			.818	3.93	10	46	31

Activations shown for whole brain analysis. All clusters are significant at $p < .05$ after statistical correction for multiple comparisons. Cluster extents are presented at an uncorrected threshold of .01; *clusters also significant at height threshold of .001. The highest three peaks within an extent are shown on subsequent lines, with the most significant shown in boldface. L: left; R: right; inf.: inferior.

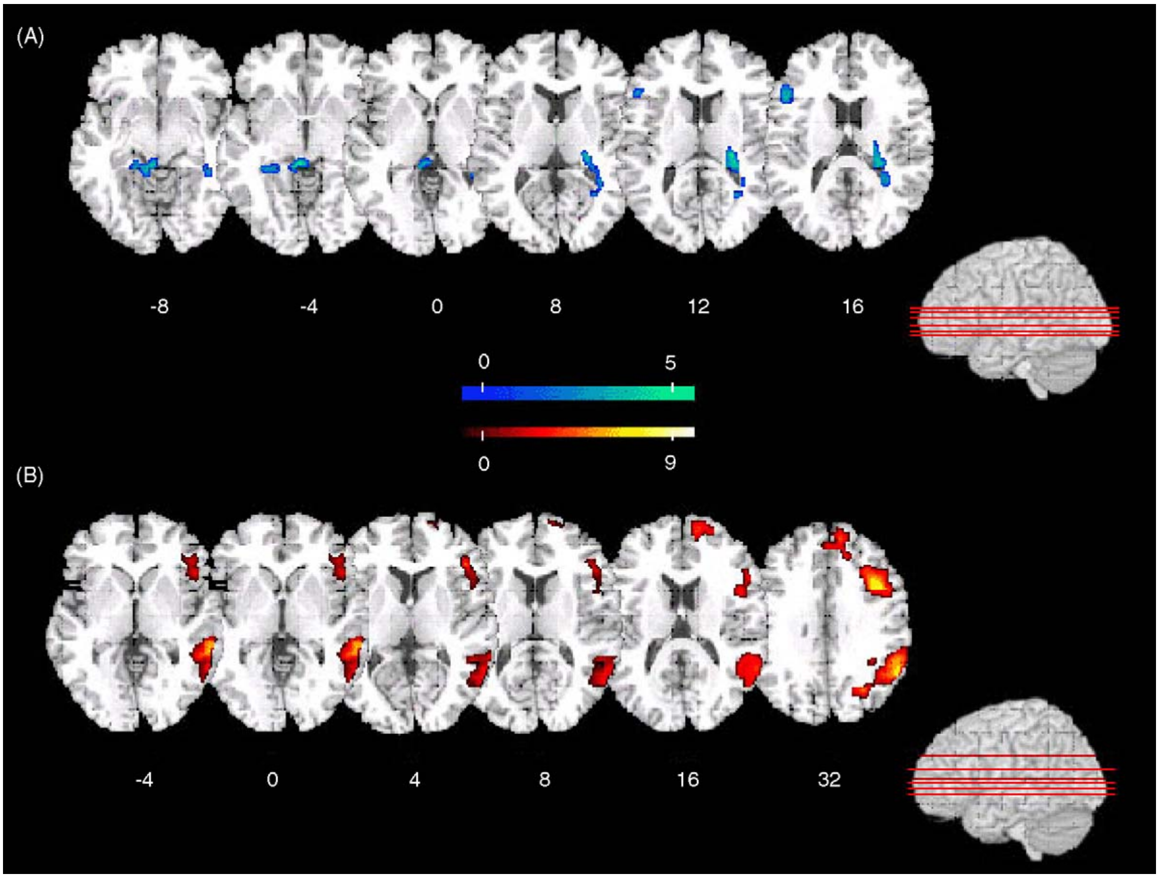

Fig. 2. Panel A: unrelated minus identity (RS); panel B: identity minus unrelated (RE) ($p = .01$).

Table 3
Brain areas showing increase of activation when semantic overlap increased

Region	Cluster level		Voxel level		Coordinates		
	$p_{\text{corrected}}$	Extent	$p_{\text{corrected}}$	Z	x	y	z
R middle frontal gyrus (BA 9)	**.000**	**993**	**.655**	**3.99**	**44**	**25**	**30**
R middle frontal gyrus (BA 9)			.709	3.94	38	21	39
R inf. frontal gyrus (BA 44)			.883	3.74	44	13	31
R middle temporal gyrus (BA 21)*	**.000**	**887**	**.974**	**3.54**	**59**	**−41**	**2**
R middle temporal gyrus (BA 21)*			.988	3.47	61	−33	−2
R supramarginal gyrus (BA 40)			.995	3.39	55	−47	34
R medial frontal gyrus (BA 8)*	**.002**	**689**	**.416**	**.421**	**6**	**37**	**37**
R medial frontal gyrus (BA 9)*			.810	.384	0	46	31
L medial frontal gyrus (BA 9)*			.997	.337	−6	40	27
R inf. frontal gyrus (BA 45)	**.007**	**568**	**.796**	**3.85**	**51**	**33**	**9**
R inf. frontal gyrus (BA 47)			.832	3.81	48	19	−8
R inf. frontal gyrus (BA 47)			1.000	3.23	44	21	−1
L middle frontal gyrus (BA 9)	**.008**	**558**	**.996**	**3.38**	**−42**	**23**	**26**
L inf. frontal gyrus (BA 44)			.998	3.33	−36	13	23
L middle frontal gyrus (BA 9)			1.000	3.23	−44	23	36
L middle temporal gyrus (BA 21)	**.014**	**507**	**.973**	**3.55**	**−48**	**−29**	**−5**
L middle temporal gyrus (BA 21)			1.000	3.21	−63	−39	4
L middle temporal gyrus (BA 21)			1.000	2.94	−51	−12	−8

Activations shown for whole brain analysis. All clusters are significant at $p < .05$ after statistical correction for multiple comparisons. Cluster extents are presented at an uncorrected threshold of .01; *clusters also significant at height threshold of .001. The highest three peaks within an extent are shown on subsequent lines, with the most significant shown in boldface. L: left; R: right; inf.: inferior.

lated minus identity conditions, combining concrete and abstract words, given that the behavioural data showed significant repetition priming effects for both concrete and abstract words and no differences between them. The only significant cluster of activation at a height threshold of 0.001 was in the R cerebellum. We found RS, at a height threshold of .01, in the L precentral gyrus (BA 6) and LIFG (BA 44–46), and in the L parahippocampal/lingual gyrus (BA 27), hippocampus and cerebellum. RS also occurred in some regions of the right hemisphere, including one cluster in the fusiform gyrus (BA 19) and cerebellum and another cluster in the thalamus, extending to the parahippocampus (BA 18 and 37), fusiform (BA 37) and cingulate gyrus (BA 23) (Table 2 and Fig. 2).

We found increased activation to repeated compared to novel unrelated words in two regions of the right hemisphere, including a cluster in the middle temporal gyrus (MTG, BA 21) extending to the superior temporal gyrus (STG, BA 22 and 39) and R inferior parietal lobule (RIPL, BA 40), and another cluster in the R inferior frontal gyrus (RIFG, BA 45) extending to R middle frontal gyrus (RMFG, BA 9), R superior frontal gyrus (RSFG, BA 9) and bilateral medial frontal gyrus, for both thresholds of .001 and .01 (Table 2 and Fig. 2).

3.2.2. *Semantic priming effects*

We first looked at the brain areas that showed modulation of activity associated with increasing degree of semantic relatedness for concrete and abstract words together. Increasing semantic relatedness was associated with increased activation in the LIFG (BA 47), RMFG (BA 9), bilateral medial frontal gyrus (BA 9) and RMTG (BA 21 and 22) at a height threshold of .001. At a lower threshold ($p = .01$), we observed increased neural responses associated with increases in semantic relatedness in several bilateral fronto-temporal-parietal regions, including IFG (BA 44 and 45 in the left hemisphere and BA 44, 45 and 47 in the right hemisphere); MFG (BA 9 and 46); MTG (BA 21) extending to the STG (BA 21 and 22), supramarginal gyrus (BA 40) and RIPL (BA 40); and medial frontal gyrus (BA 8 and 9) extending to cingulate gyrus (BA 32) (Table 3 and Fig. 3). There

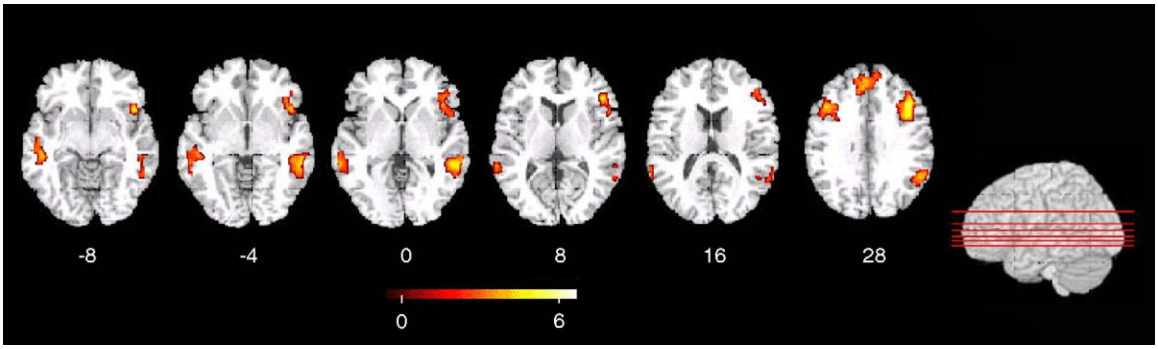

Fig. 3. Increased activation as a function of increasing semantic relatedness (SE) ($p = .01$).

Table 4
Brain areas showing increase of activation when semantic overlap increased for concrete words

Region	Cluster level		Voxel level		Coordinates		
	$p_{\text{corrected}}$	Extent	$p_{\text{corrected}}$	Z	x	y	z
R inf. frontal gyrus (BA 47)	**.000**	**1767**	**.125**	**4.68**	**26**	**22**	**−14**
R inf. frontal gyrus (BA 47)			.334	4.37	48	23	−10
R inf. frontal gyrus (BA 44)			.505	4.20	36	13	32
L inf. frontal gyrus (BA 44)*	**.000**	**817**	**.664**	**4.06**	**−40**	**13**	**21**
L middle frontal gyrus (BA 9)			.993	3.51	−34	27	39
L inf. frontal gyrus (BA 44)			1.000	3.32	−48	15	29
R medial frontal gyrus (BA 8)*	**.000**	**719**	**.117**	**4.70**	**6**	**37**	**39**
R medial frontal gyrus (BA 10)			.873	3.84	−8	57	14
R medial frontal gyrus (BA 9)			1.000	3.28	8	58	25
R middle temporal gyrus (BA 21)*	**.002**	**603**	**.015**	**5.24**	**65**	**−29**	**0**
R middle temporal gyrus (BA 21)*			.578	4.13	61	−43	4
R inf. temporal gyrus (BA 37)*			.760	3.97	55	−49	−4
L middle temporal gyrus (BA 21)	**.008**	**469**	**.975**	**3.63**	**−57**	**−27**	**−2**
L sup. temporal gyrus (BA 22)			1.000	3.34	−63	−40	9
L middle temporal gyrus (BA 21)			1.000	3.33	−50	−39	−6
R supramarginal gyrus (BA 40)*	**.017**	**408**	**.855**	**3.86**	**53**	**−49**	**34**
R inf. parietal lobule (BA 40)*			.999	3.39	46	−47	23
R sup. temporal gyrus (BA 22)			1.000	2.82	63	−48	19

Activations shown for whole brain analysis. All clusters are significant at $p < .05$ after statistical correction for multiple comparisons. Cluster extents are presented at an uncorrected threshold of .01; *clusters also significant at height threshold of .001. The highest three peaks within an extent are shown on subsequent lines, with the most significant shown in boldface. L: left; R: right; inf.: inferior; sup.: superior.

were no regions showing decreases of activation as a function of increases in semantic relatedness (at either thresholds of .001 or .01).

Given that the behavioural results showed larger semantic priming effects for concrete compared to abstract words, we examined the neural correlates of semantic priming for concrete and abstract words separately. For concrete words, we found increased activation as function of increasing semantic relatedness in six clusters at a height threshold of .001, including bilateral IFG (BA 44 in the left hemisphere and BA 45 and 47 in the right hemisphere), medial frontal gyrus (BA 8 and 9), RMFG (BA 9), RMTG (BA 37 and 21) and R supramarginal gyrus (BA 40). Lowering the threshold to .01, we found activation in bilateral IFG (BA 44 and 47) extending to the LMFG (BA 9), bilateral medial frontal gyrus (BA 8–10), bilateral MTG (BA 21 and 37) extending to the LSTG (BA 22) and R inferior temporal gyrus (RITG, BA 37) and R supramarginal gyrus (BA 40) extending to the RSTG (BA 22) and RIPL (BA 40) (Table 4 and Fig. 4). Abstract words only activated the RMFG (BA 9 and 46) extending to the RIFG (BA 44), at $p = .01$ only (Table 5 and Fig. 4). There were no regions showing decreases of activation as a function of semantic relatedness for either concrete or abstract words (for $p = .001$ and .01).

For comparability with previous studies, we analysed the data in a contrast analysis, comparing related (pairs rated 3–9 in pretest) with unrelated items (pairs rated 1–2). Concrete words produced greater activation for related compared to unrelated items in five clusters at a height threshold of .001. Three of these clusters were located in the RIFG in BA 45, 47 and 44 (extending to the RMFG, BA 9), respectively. A fourth cluster was located in the RMTG (BA 21), extending to the RSTG (BA 22) and another cluster in the L medial frontal gyrus (BA 10). At a lower threshold of .01 we found significant activation bilaterally in several fronto-temporal regions including IFG (BA 44–47), medial frontal gyrus (BA 10) and middle/superior temporal gyrus (BA 21 and 22) (Table 6). There were no significant activations for the contrast unrelated minus related (at either threshold of .001 and .01). For abstract words, there were no differences between related and unrelated words (for both thresholds of .001 and .01).

Taken together, our results showed distinct patterns of neural activity for repetition and semantic priming. Repetition priming was associated with repetition suppression in the LIFG, bilateral

Table 5
Brain areas showing increase of activation when semantic overlap increased for abstract words

Region	Cluster level		Voxel level		Coordinates		
	$p_{\text{corrected}}$	Extent	$p_{\text{corrected}}$	Z	x	y	z
R middle frontal gyrus (BA 9)	**.012**	**487**	**.993**	**3.46**	**40**	**18**	**40**
R middle frontal gyrus (BA 46)			.999	3.33	40	21	23
R middle frontal gyrus (BA 9)			1.000	3.18	48	29	28

Activations shown for whole brain analysis. All clusters are significant at $p < .05$ after statistical correction for multiple comparisons. Cluster extents are presented at an uncorrected threshold of .01. The highest three peaks within an extent are shown on subsequent lines, with the most significant shown in boldface. R: right.

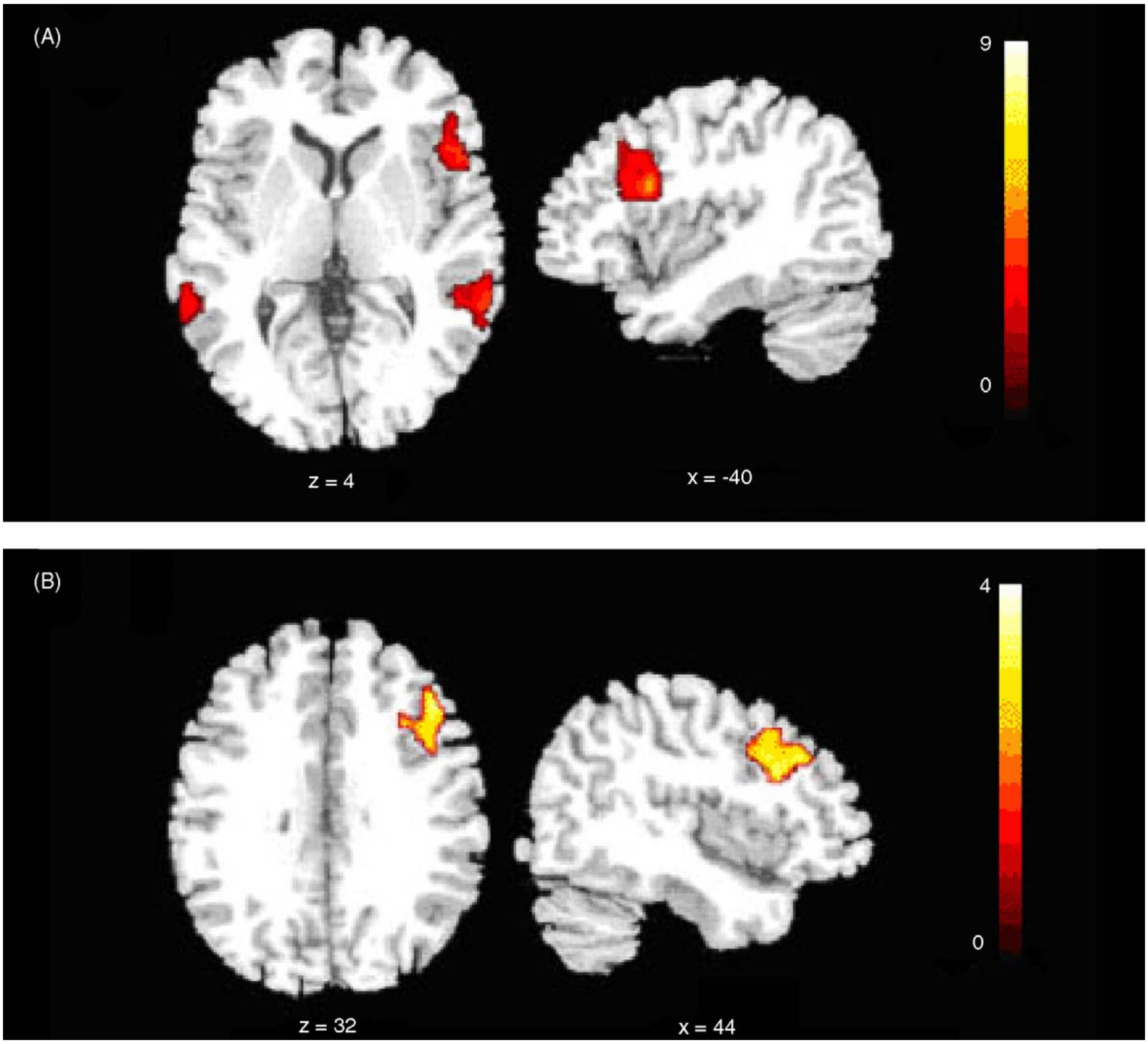

Fig. 4. Increased activation as a function of increasing semantic relatedness (SE) for (A) concrete words and (B) abstract words ($p = .01$).

Table 6
Brain areas of activation for the contrast related minus unrelated for concrete words

Region	Cluster level		Voxel level		Coordinates		
	$p_{\mathrm{corrected}}$	Extent	$p_{\mathrm{corrected}}$	Z	x	y	z
R inf. frontal gyrus (BA 45)*	**.000**	**2026**	**.334**	**4.39**	**53**	**22**	**6**
R inf. frontal gyrus (BA 45)*			.390	4.33	51	30	8
R inf. frontal gyrus (BA 44)*			.394	4.32	42	3	22
L inf. frontal gyrus (BA 45)	**.000**	**1129**	**.621**	**4.12**	**−40**	**22**	**19**
L inf. frontal gyrus (BA 47)			.926	3.78	−44	25	−8
L inf. frontal gyrus (BA 47)			.982	3.62	−34	21	−11
L medial frontal gyrus (BA 10)*	**.001**	**894**	**.729**	**4.02**	**−6**	**59**	**14**
L medial frontal gyrus (BA 10)*			.978	3.64	−8	51	7
L medial frontal gyrus (BA 10)*			.999	3.41	−2	49	14
R middle temporal gyrus (BA 21)*	**.007**	**622**	**.335**	**4.38**	**57**	**−31**	**0**
R middle temporal gyrus (BA 21)*			.470	4.25	51	−37	0
R sup. temporal gyrus (BA 22)*			.855	3.89	65	−41	6
L sup. temporal gyrus (BA 22)	**.045**	**435**	**.780**	**3.97**	**−59**	**−38**	**9**
L middle temporal gyrus (BA 21)			.983	3.62	−63	−37	2
L middle temporal gyrus (BA 21)			.993	3.54	−55	−33	−2

Activations shown for whole brain analysis. All clusters are significant at $p < .05$ after statistical correction for multiple comparisons. Cluster extents are presented at an uncorrected threshold of .01; *clusters also significant at height threshold of .001. The highest three peaks within an extent are shown on subsequent lines, with the most significant shown in boldface. L: left; R: right; inf.: inferior; sup.: superior.

parahippocampus and R fusiform gyrus, and repetition enhancement in R-lateralised regions including RMTG extending to STG and R frontal regions. Semantic priming for concrete and abstract words produced increased activation in bilateral IFG, MFG and MTG. We found the same effect when we looked at concrete words only.

4. Discussion

The current study was motivated by the lack of consensus concerning the neural correlates of semantic priming for written words. Some studies have suggested that semantic and repetition priming may share the same neural correlates, based on the finding of reduced neural activity for both types of priming. However, other studies have reported enhancement of activation for related words in different neural regions (e.g. Rossell, Bullmore, Williams, & David, 2001; Rossell et al., 2003), suggesting that priming-related neural responses are not unitary, but instead depend on the nature of the processing in hand. To address these issues, we investigated the neural correlates of repetition and semantic priming in visual word recognition, using a single task and similar materials.

4.1. Repetition priming

The behavioural priming results showed that subjects were significantly faster when performing a semantic judgement to repeated words relative to novel words. This behavioural facilitation induced both suppression (RS) and enhancement (RE) of neural activity for repeated words in different neural regions. RS was observed in the LIFG and in multiple temporal regions, including bilateral parahippocampal gyrus, R fusiform cortices and cerebellum, regions that are typically associated with written word processing (e.g. Bright, Moss, & Tyler, 2004; Mummery, Patterson, Hodges, & Price, 1998; Price, 2000; Rossell et al., 2001; Tyler et al., 2003). Our findings are consistent with many other studies which have reported RS in many of the same areas, using a variety of tasks, such as concrete/abstract decision and colour/action generation (e.g. Buckner et al., 1998; Demb et al., 1995; Thompson-Schill et al., 1999; Wagner et al., 2000). Reductions in activation due to repetition have been explained as being due to two different mechanisms. On the one hand, it has been claimed that RS may reflect the facilitation of the processing of the repeated items, possibly due to lowered thresholds for activating repeated representations, as suggested by the neural tuning view (Henson, Shallice, & Dolan, 2000). On the other hand, according to the response-learning hypothesis, RS may occur on the basis of a learned association between the word and the prior response, as participants may rapidly produce a repeated response from short term memory when the lexical or orthographic representations match across exposures (Dobbins, Schnyer, Verfaellie, & Schacter, 2004; Schacter, Dobbins, & Schnyer, 2004).

We also observed *increased* activation in right frontal (RMFG) and temporal (RMTG/STG) regions for repetition priming, consistent with some previous research (e.g. Koustaal et al., 2001). These findings have been interpreted as suggesting that increased activation for repeated items may reflect the recognition of an item's earlier presentation, which may be an automatic process, incidental to the task requirements. Consistent with this hypothesis, numerous studies of recognition memory using words have associated correct retrieval of information with several R-lateralised activations, namely in the R prefrontal cortex (Fletcher, Frith, & Rugg, 1997; Rugg, Fletcher, Frith, Frackowiak, & Dolan, 1996). However, since these studies focused on long term episodic retrieval, further research is required to investigate whether similar recognition processes occur when items are repeated shortly after the initial presentation.

4.2. Semantic priming

We investigated the neural correlates of semantic priming by manipulating the degree of semantic relatedness between prime and target in a continuum from highly related to unrelated words. The behavioural results showed significantly faster RTs for increased semantic relatedness. The neuroimaging results showed *increasing* activation as a function of increasing semantic relatedness in several bilateral fronto-temporal-parietal regions, including the middle and superior temporal gyrus, supramarginal gyrus, inferior parietal lobule, inferior and medial frontal gyrus. We refer to this increased neural activity as a function of increased semantic relatedness as *semantic enhancement* (SE).

Activations in similar regions, mainly left-lateralised, have previously been reported in semantic priming studies. For example, Kotz et al. (2002) using an auditory lexical-decision task observed increased activation for related compared to unrelated words in the LMTG. Rossell et al. (2003) using a lexical decision task with written words reported SE for related words in the L supramarginal gyrus. In addition to the clear involvement of the L fronto-temporal regions in semantic processing, the strong right-lateralised response to semantically related words observed in the present study is consistent with the view from both cognitive models of semantic processing and neuroimaging studies that semantic knowledge is processed bilaterally (Bright et al., 2004; Beeman & Chiarello, 1998; Pilgrim, Fadili, Fletcher, & Tyler, 2002; Rossell et al., 2001). For example, Kotz et al. (2002) found bilateral STG activation for semantically related words, while Rossell et al. (2001) found increased activation in the RSTG and bilateral MTG. These results are also consistent with lesion studies, which have shown that the processing of semantic information requires right-hemisphere involvement. For instance, some studies have reported reduced semantic priming in patients with broad right hemisphere lesions (Hagoort, Brown, & Swaab, 1996; Kotz, Friederici, & von Cramon, 1999; Swaab, Brown, & Knight, 1998). Investigations of split-brain patients have also provided evidence for the role of the right hemisphere in the semantic processing of words (Neininger & Pulvermuller, 2003; Zaidel, 1998).

However, although our results are consistent with a role for the right hemisphere in semantic processing, an alternative interpretation of the semantic enhancement effect for words in the right hemisphere is also possible. Most of these right-lateralised regions overlapped with the areas that showed repetition enhancement effects in the identity condition, including the RIFG, RMFG and RMTG. As outlined above, these effects have been interpreted as reflecting subjects' recognition of items earlier presentation (Fletcher et al., 1997; Koustaal et al., 2001; Rugg et al., 1996). The same process may be responsible for the effects in the semantic priming conditions, if we assume that subjects are as likely to recognise the prior presentation of a related stimulus as of an identical stimulus.

In this study, we were able to compare priming effects for concrete and abstract words and found that, in common with many other studies, concrete words primed more robustly than abstract words. Many behavioural studies have shown that concrete words are typically processed more rapidly than abstract words, in tasks ranging from lexical decision (de Groot, 1989; Schwanenflugel, Harnishfeger, & Stowe, 1988) to sentence verification (Belmore, Yates, Bellack, Jones, & Rosenquist, 1982; Holmes & Langford, 1976) and sentence comprehension (Haberlandt & Graesser, 1985). Moreover, semantic priming effects are also larger for concrete relative to abstract words (Tyler, Moss, Galpin, & Voice, 2002). Thus, concrete words clearly display a processing advantage over abstract words. In the fMRI data, we found more extensive activation for concrete compared to abstract words. Semantic priming for concrete words was associated with increased activation in bilateral fronto-temporal regions, consistent with many studies of semantic processing of concrete nouns (Bright et al., 2004; Devlin et al., 2002; Friederici, Opitz, & von Cramon, 2000; Rossell et al., 2001; Tyler et al., 2003). In contrast, semantic priming for abstract words was restricted to frontal cortex (RMFG extending to RIFG). These findings are consistent with previous work showing the recruitment of right hemisphere frontal regions in the processing of abstract words (Beauregard, Chertkow, Bub, & Murtha, 1997; D'Esposito et al., 1997; Kiehl et al., 1999), possibly due to the extra cognitive demands required for the more difficult task of judging abstract words (Grossman et al., 2002; Kiehl et al., 1999). The longer RTs for abstract compared to concrete judgments supports this interpretation. An alternative possibility is that semantic information associated with abstract words is coded more coarsely than concrete words, thereby recruiting multimodal association regions in the right hemisphere to help integrate information related to abstract concepts (Beeman et al., 1994; Grossman et al., 2002).

Finally, we turn to perhaps the most striking result of the study: all neural correlates of *semantic* priming consisted of increases in activation. Our results show that the behavioural facilitation induced by priming is not necessarily linked to suppression of neural activation. In our study, the behavioural results showed faster RTs for both repetition and semantically related conditions compared to the unrelated condition. However, suppression effects were specific to repetition priming. These results suggest that repetition and semantic priming may be underpinned by different types of processing. While semantic priming has a conceptual basis, repetition priming may have a more perceptual or orthographic nature. If this is the case, then repetition priming may not be an adequate tool to investigate the semantic processing of concepts.

The lack of suppression effects for semantic priming may seem surprising given that some studies have linked semantic priming with reduced neural activity (Copland et al., 2003; Giesbrecht et al., 2004; Rossell et al., 2001, 2003). However, the neural correlates of semantic priming in written word processing have so far shown little consistency across studies, with suppression effects reported in a variety of different neural regions. Moreover, while some studies report only suppression effects, others have also reported increases of activation associated with semantic priming (Kotz et al., 2002; Rossell et al., 2001). These differences in results may be due to the wide variation in methods, tasks and materials across studies. One important consideration, often ignored, is the nature of the relationship between prime and target. In the current study, word-pairs were related by their similarity in meaning (i.e. feature overlap), whereas in other studies, word-pairs are mostly related by virtue of their co-occurrence, i.e. they are lexical associates (e.g. *key-chain*, Kotz et al., 2002) and are not semantically related, or only weakly semantically related. It is well-established that associative (lexical) and semantic priming reflect different types of relationship and potentially different types of process (Moss et al., 1995; Neely, 1991). The question of how associatively related pairs might differ from semantic relations and the implications this may have for neural activity warrant further investigation. Another important consideration concerns whether priming effects are associated with more automatic or controlled processes. In this study, the high proportion of related pairs throughout the experiment (i.e. 50%), along with the long SOA (i.e. 2500 ms), may have induced a more controlled semantic processing of the words, which may have resulted in a post-lexical semantic matching of the words (de Groot, 1983; Neely, 1991; Neely, Keefe, & Ross, 1989). In contrast, previous studies, using shorter SOAs and lower proportion of related pairs may have tapped into automatic semantic priming effects (Moss et al., 1995; Neely, 1991).

One possible interpretation for the semantic priming effects found in this study is that put forward by Henson and colleagues that while suppression of neural activation occurs when the *same process* is performed on the repeated stimulus, enhancement of neural activation is observed when an additional process operates on the target (Henson, 2001; Henson et al., 2000). This notion of process repetition versus process change was proposed for specifying the conditions under which RS and RE will be observed in repetition priming, but it is unclear if this framework can be applied to semantic priming. In our study, subjects performed the same task on each word – deciding whether it was concrete or abstract – so, at face value, the processes could be considered identical for prime and target. However, it is also possible that when a word follows a related prime (e.g. *lion–tiger*) the semantic relationship between the two words modulates the processing of the target word, perhaps by prompting more fine-grained analysis of its meaning. The current experiment does not enable us to determine the nature of these additional or novel processes, and this remains a speculative interpretation. In future studies, a detailed analysis of the underlying cognitive processes involved in each trial is required to evaluate potential modulators of processing in the context of prior trials.

In summary, we have identified differential patterns of neural activity for repetition and semantic priming, suggesting that priming-related neural responses are not unitary. Repetition priming was associated with a decrease of neural activity (RS) in several fronto-temporal regions, including LIFG, bilateral parahippocampal gyrus and R fusiform gyrus. We also observed increased activation for word repetition in the RMFG and RMTG/STG, which may reflect recognition of item's earlier presentation. In contrast, there were no suppression effects for semantic priming. We observed increased neural activation for increased semantic relatedness (SE) in the IFG and the MTG, bilaterally. The results suggest that repetition and semantic priming in written word recognition depend on distinct cognitive processes and neural substrates. Further studies will be needed to determine whether SE is the result of process change in semantic priming.

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