In this positron emission tomography study, we investigated the neural correlates of semantic priming, where response to a word is facilitated when preceded by a semantically related word. Nine normal subjects were scanned while performing a lexical decision task. Within this condition, the proportion of related prime-target word pairs was varied across scans from 0 to 100%. The control task involved letter decision on consonant letter strings, controlling orthographic processing and response selection. First, lexical decision (relative to letter decision) activated regions previously observed in lexicosemantic tasks, i.e., the left anterior and inferior temporal lobe and left inferior frontal gyrus. Behavioral analysis confirmed significant facilitation of lexical decision to related targets (mean priming effect 68 ms). It also suggested the contribution of both automatic and strategic processes, consistent with theoretical accounts of priming. Automatic priming was indicated by consistent RTs to related targets irrespective of the proportion of related word pairs per scan. Strategic processing was indicated by decreases in RTs to nonwords as the proportion of related targets increased. Nonlinear correlational analysis of cerebral activity during lexical decision revealed a neurophysiological correlate of these behavioral effects in (i) the left anterior temporal lobe (BA 38), a region involved in lexicosemantic processing; (ii) the anterior cingulate cortex, right premotor region (BA 6), and right superior parietal lobe (BA 7), regions associated with attentional processes. We conclude that in this experimental context, semantic priming involves both automatic and strategic processing. © 1999 Academic Press

Key Words: semantic priming; lexical decision; automatic processing; attentional processing; PET.

INTRODUCTION

Semantic priming refers to the facilitating effect seen on the response to a word (target) when preceded by a semantically related word (prime), compared to an unrelated word (e.g., Meyer and Schvaneveldt, 1971; Moss et al., 1995). The shortened latency and improved accuracy is thought to reflect automatic, implicit access to semantic information, in contrast to many standard semantic tests that rely on voluntary, explicit access and retrieval of semantic information. The facility that priming offers to examine implicit processing has led to the widespread use of priming paradigms in the study of disordered semantic processing in patients. For example, patients with “semantic access” deficits, but not patients with a “degraded store” of semantic knowledge, can explicitly retrieve the meaning of a word when preceded by presentation of a semantically related word (Warrington and Shallice, 1979; Shallice, 1988). In contrast, “degraded store” patients such as those with progressive aphasia (Tyler et al., 1997) or Alzheimer’s disease (Chertkow et al., 1989) show intact implicit semantic priming, as indicated by speeded lexical decision latency when a related word is presented prior to the target word. This effect can be present to an abnormally high degree, so called hyperpriming (Chertkow et al., 1989; see also Moss and Tyler, 1995). Priming paradigms therefore provide a means to distinguish different types of semantic deficit.

Theoretical accounts of semantic priming have been of two broad types: automatic (e.g., Collins and Loftus, 1975; McClelland and Rumelhart, 1985) and strategic/attentional (Posner and Snyder, 1975; McKoon and Ratcliff, 1992). Neither type of account can individually explain all the complex behavioral phenomena associated with semantic priming, leading to hybrid proposals comprising elements of several accounts (e.g., Posner and Snyder, 1975; Neely, 1977, 1991). It is now generally accepted that there are both automatic and attentional processes involved that can be differentially weighted according to experimental variables. For example, behavioral studies have shown that automatic effects predominate when the interval between prime and target is less than 400 ms (short stimulus onset asynchrony (SOA) (Neely, 1977)), and that at longer SOAs strategic processes take over (de Groot, 1984;
SOAs (Henik et al., 1995). In addition, the proportion of related prime-target pairs can have an effect, with strategic processes becoming more involved when the proportion of related prime-target pairs is high (Neely, 1991). It appears that while the relative contribution of automatic and strategic processes varies, a hybrid mechanism underpins semantic priming.

The physiological corollary of priming will differ both quantitatively and qualitatively depending upon the relative contribution of automatic and strategic processes. Automatic processes should cause changes in activity in semantic regions. Connectionist models predict decreased activation for a related target compared to an unrelated target, either because less activation is necessary to reach the threshold (due to partial activation by the preceding prime) or because the activation threshold is reached more rapidly (as pathways are more easily utilizable) (Collins and Loftus, 1975; Plaut and Shallice, 1993). Finally the neuropsychological phenomenon of repetition suppression, which may well be related to the processes involved in perceptual identity priming (Wiggs and Martin, 1998), has been found to have a correlate in reduced cell firing in studies of macaque inferior temporal cortex (e.g., Miller et al., 1991). It is plausible that semantic priming could have a similar neurophysiology based on overlapping semantic features in the prime and target words.

Any of these hypothesized mechanisms should lead to less activation in a semantic region for a scan involving related word pairs than for a scan involving no related word pairs. A purely “automatic account” of priming therefore predicts a decrease in activation in lexicosemantic regions with increasing proportions of related targets, i.e., an inverse correlation. Strategic theories, on the other hand, suggest activation changes both in regions specialized for semantic processing and in regions involved in attentional modulation of such processing. In contrast to automatic priming, such attentional modulation of semantic activation could reasonably be expected to produce summed increases in activity with increases in the proportion of related targets. Increasing attention also increases the degree of priming behaviorally; it is therefore possible that in semantic regions, no overall change in activity would be seen when attentional and automatic processes exert an equal influence. Finally, if a hybrid of automatic and strategic processing underpins semantic priming, with automatic processes dominating in low proportions of related prime-targets, and strategic processes dominating in high proportions, then a complex pattern of variation in activation is possible. In short, there are three possible outcomes of increasing the proportion of related targets: automatic processing predicts decreases in activation, attention predicts increases (or no overall change in activity), and a combination of the two predicts a complex relationship.

To our knowledge, there have been no functional neuroimaging studies published investigating short-term semantic priming. Neuroimaging studies of priming thus far have focussed exclusively on long-lasting repetition priming, both conceptual identity and perceptual identity (for a current review see Schacter and Buckner, 1998). While repetition/identity priming and semantic priming (as defined here) differ behaviorally (e.g., in the duration of effect; attentional mechanisms involved (Farah, 1989), they also share common features: both are forms of implicit memory and may be intact in patients with deficits in explicit/declarative memory; both show facilitation of the identification of primed stimuli and inhibition of the identification of nonprimed stimuli. Findings from previous repetition priming studies may therefore have some bearing on the current study.

Several of the studies on repetition/identity priming have investigated changes in neural activity associated with repeating items during the same task and during different tasks. The responses are mainly anatomically and task specific, with extrastriate occipital regions showing reduced activation when recall from visually presented stimuli is primed (using word-stem completion: e.g., Buckner et al., 1995; Squire et al., 1992), and prefrontal regions showing reduced activation when an item is repeated during a semantic retrieval task (e.g., Demb et al., 1995). The essential findings have therefore been a decrease in regional cerebral blood flow in regions specific to the task performed, implying facilitation of perceptual processing in perceptual identity priming, and facilitation related to semantic processing in conceptual identity priming. Of note, other regions have been found in repetition priming studies. For example, Schacter et al. (1996), using a stem-completion task, replicated the findings in extrastriate cortex, but in addition found significant decreases in the right prefrontal cortex and right parietal cortex, areas thought to be involved in attentional mechanisms (Mesulam, 1990).

Given the huge body of neuropsychological literature examining “automatic” and “controlled” mechanisms in semantic priming in normals and patients, it seemed timely to attempt an initial definition of these mechanisms in terms of brain regions involved. We investigated the neural correlates of semantic priming using lexical decision, a task recognized as sensitive to priming, and one which has been investigated before with functional imaging, where it has activated left inferior frontal and anterior temporal regions (Price et al., 1994; Rumsey et al., 1997). Cognitive components such as orthographic processing and response selection were controlled by contrasting activity during lexical deci-
sion and a letter decision task on consonant letter strings. To maximize semantic analysis in the lexical decision task, category coordinate stimuli were used with pure semantic relationships rather than associated/semantic relationships (see Moss and Tyler, 1995), and the nonword stimuli were made as word-like as possible in order to strongly engage semantic processing. We expected that the categorical comparison of lexical decision versus letter decision would reveal lexicosemantic regions involved in lexical decisions on visually presented words. For this contrast we predicted left lateralized activations, involving the inferior frontal and anterior/inferior temporal lobes (Vandenberghe et al., 1996).

**METHODS**

Subjects/Scanning

Nine healthy males (age range 27–31 years) took part. All were strongly right-handed on the Edinburgh Handedness Inventory. The study was approved by the local hospital ethics committee and the Administration of Radioactive Substances Advisory Committee (UK). Each subject underwent 12 PET scans measuring distribution of brain activity. Scans were obtained using an ECAT EXACT HR+ PET Scanner (CTI, Knoxville, TN) over a 2-h period, with collimating septa retracted. Before each scan, volunteers received a 20-s intravenous bolus of H$_{2}^{15}$O at a concentration of 55 Mbq ml$^{-1}$ at a flow rate of 10 ml min$^{-1}$ through a forearm cannula.

Tasks

Stimuli consisted of letter strings presented visually in the center of a screen (Fig. 1). Each target was highlighted by pairs of lines at the side of the stimulus. A single-word lexical decision presentation was used, simplifying the subject's task, and also allowing a short prime-target interval, emphasizing automatic semantic processing (de Groot 1984, Posner and Snyder, 1975). The initial stimulus (prime) was shown for 200 ms, followed by a blank screen for 50 ms, then the target was presented for 400 ms. Stimulus pairs were presented every 2500 ms with 18 pairs of stimuli shown per scan. Each target was highlighted by pairs of lines at the side of the stimulus. Twelve pairs were word–word pairs, and 6 were word–nonword pairs. Nonwords were made up from words by altering one letter, making the lexicosemantic decision more pertinent. The word series were matched across all scans for frequency and length, and all categories were mixed equally across scans. The proportion of prime-target-related pairs varied across the lexical decision scans in the proportions 0:12, 3:9, 6:6, 9:3, and 12:0.

Subjects were told they would see pairs of letter strings presented serially, and were instructed to respond only to the second stimulus seen of each pair (target). In response to the target stimulus, subjects had to perform one or two tasks: (a) In two scans, the primes and targets were consonant letter strings and the task was letter decision ("is there a 'b' present?"). (b) In 10 scans, the primes were words, the targets were either words (concrete nouns) or nonwords, and the task was lexical decision ("is it a real word?").

For the lexical decision task, the concrete words used for word pairs were category coordinate stimuli (within category, e.g., horse-dog), because priming effects have been shown to be robust with these stimuli. Twelve stimulus pairs were word–word pairs, and 6 were word–nonword pairs. Nonwords were made up from words by altering one letter, making the lexicosemantic decision more pertinent. To ensure semantic processing occurred rather than low-level lexical processing, we used pure semantic relationships (e.g., pig-horse) as opposed to associated/semantic relationships (e.g., dog-cat) (Moss and Tyler, 1995). The word series were matched across all scans for frequency and length, and all categories were mixed equally across scans. No prime-target pair was repeated, to avoid the possible confound of "episodic" or repetition priming.

To look for possible nonlinear (complex) priming effects, a correlational design was used within the active task: the proportion of related word pairs varied from 0 to 100% (i.e., in the ratios 0:12, 3:9, 6:6, 9:3, and 12:0) across the lexical decision scans. Reaction times and error rates were recorded throughout. Subjects practised prior to scanning until they could perform the
tasks. Scan order was pseudo-counterbalanced within and across subjects.

Analysis

The data were analyzed with statistical parametric mapping (SPM96—Wellcome Department of Cognitive Neurology, London, UK: http://www.fil.ion.ucl.ac.uk/spm/spm_reference). The reconstructed images were realigned, normalized, and smoothed (16 mm) as previously described (Friston et al., 1995a). The generated statistical images had a full-width half-maximum (FWHM) resolution of $9.5 \times 9.7 \times 9.9$ mm. Main effects of condition were assessed using ANCOVA and linear contrasts as described elsewhere (Friston et al., 1995b). Two types of analysis were performed: (i) Categorical comparisons of lexical decision with letter decision. (ii) Nonlinear correlational analysis (using lexical decision data only) looking for regions showing variation in activity with varying proportions of related targets, i.e., both linear and possible complex responses to priming. First and second order polynomials were derived from the proportions of related targets used and entered as covariates of interest. The resulting SPM(F) map displayed all brain areas showing significant variance correlating with these covariates either singly or in combination (Buechel et al., 1996). For both analyses, confounding order effects were removed by using scan order as a covariate of no interest. Results are reported in terms of (i) areas showing effects of task; (ii) areas showing effects of priming. Significance was set at uncorrected $P < 0.001$ for regions previously implicated in semantic tasks (e.g., Vandenberghe et al., 1996).

RESULTS

Behavioral Data

Table 1 shows mean error rates and reaction times (RTs) for each task. The letter decision (control) task produced significantly longer RTs than those for the semantic tasks ($P < 0.005$), though there was no difference in the error rates. No significant differences in errors were seen between any of the conditions.

Within the lexical decision (active) conditions, there was a significant difference between RTs for words and nonwords, both related and unrelated word targets showing significantly shorter RTs than nonword targets. A priming effect was seen for all proportions of related targets, with a significant mean decrease in reaction time of 68 ms for related relative to unrelated word targets ($P < 0.0001$) as measured by subtracting the RTs for related word-pairs from unrelated RTs in each condition. RTs for related targets were remarkably consistent, suggesting automatic priming was occurring. However, for unrelated targets and nonword

<table>
<thead>
<tr>
<th>TABLE 1</th>
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<tr>
<td>Behavioral Effect of Task and Proportion of Related Targets on Individual Stimulus RTs</td>
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<tr>
<td><strong>Lexical decision</strong></td>
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<tr>
<td>Percentage related word pairs</td>
</tr>
<tr>
<td>Mean (ms) (SE)</td>
</tr>
<tr>
<td>None</td>
</tr>
<tr>
<td>25%</td>
</tr>
<tr>
<td>50%</td>
</tr>
<tr>
<td>75%</td>
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<tr>
<td>100%</td>
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<tr>
<td>Mean over scans</td>
</tr>
<tr>
<td><strong>Letter decision</strong></td>
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<tr>
<td>All stimuli</td>
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</table>

Note. Mean reaction times (RT) and standard error (SE) (as mean percentage correct for each condition) for subjects during the different scanning tasks.
targets there was an effect of the proportion of related targets on RTs, indicating the influence of strategic processes (see Discussion). RTs to nonwords decreased significantly ($P < 0.05$) with increasing proportion of related targets, using a nonparametric trend test (Page’s L trend test). RTs for unrelated targets showed (i) a 69-ms decrease between the conditions containing no related primes and 25% related primes, and (ii) a 48-ms increase between the conditions containing 25 and 75% related primes (which resulted in a corresponding increase in the size of the priming effect as the proportion of related word-pairs was increased, though this did not reach significance)—see Table 1.

**PET Results**

(a) Categorical analysis: Task effects. Contrasting lexical decision with letter decision revealed that relative increases in activity for lexical decision were mainly left lateralised, involving the predicted temporal regions (inferior temporal gyrus (BA 20), anterior temporal lobe (BA 38), posterior middle temporal gyrus (BA 21), and left inferior frontal/insular region (see Table 2 and Fig. 2). Midline activation was seen in the orbitofrontal gyrus (BA 11) extending into the anterior cingulate cortex. The reverse contrast (letter decision–lexical decision) revealed increased activity for letter decision in the left supramarginal gyrus (BA 40), bilateral superior parietal lobes (BA 7), right occipitotemporal junction (BA 19/39), and right superior frontal gyrus (BA 8). Table 2 lists coordinates and peak z scores for these contrasts.

(b) Priming effects. Nonlinear correlational analysis revealed significant variations in response to differing proportions of related targets in two regions (Fig. 3) that were also identified in the main effect of lexical decision relative to letter decision (see above): the left anterior temporal lobe (BA 38) and anterior cingulate cortex. As can be seen from the plots depicted in Fig. 3, the response in the left anterior temporal lobe (BA 38) consisted of a decrease in activation with increasing proportions of related targets, except for the highest proportion of priming where activation increased. The anterior cingulate cortex showed a nonlinear decrease in activity with increasing proportion of related targets (Fig. 3). This decrease was only pronounced when the proportion of related targets was high. Two other regions that were not differentially active for lexical decision (in the categorical contrast) showed significant variation in response that survived a corrected threshold: the right superior parietal lobe (BA 7) and right premotor region (BA 6). These two regions showed a nonlinear decrease in activity with increasing proportion of related targets that differed in shape to that seen for the anterior cingulate, and to an extent mirrored the shape of the plot for the anterior temporal lobe. Table 3 lists the coordinates and peak z scores for the regions showing significant variance in the SPM(F) map.

**DISCUSSION**

**Behavioral Effects**

Behavioral data confirmed a significant priming effect, i.e., responses during lexical decision were facilitated when the target was preceded by a related prime. A short prime-target interval was used to emphasise automatic processing. Consistent with this the speed of responses to related primes remained constant as the proportion of related primes changed (Faureau and Segalowitz, 1983).

However, the behavioral data also suggested the additional contribution of strategic processes. First, as

![FIG. 3. Priming effects. Regions of significant regional cerebral blood flow (rCBF) change in the nonlinear analysis of the lexical decision data displayed on a 3D rendering of a standard brain MRI. Regions showing enhanced activity for lexical decision and nonlinear decrease in activity with increasing relatedness proportion are circled in blue. Regions surviving a corrected threshold and showing a nonlinear decrease in activity are circled in green.](image-url)
FIG. 2. Lexical decision–letter decision. Regions of significant regional cerebral blood flow (rCBF) change in the categorical contrast of lexical decision–letter decision. The threshold was set at $Z > 3.1 (P < 0.001)$ in this and all other contrasts. The results are shown in two sections: (i) the top images display sagittal and transverse glass brain sections showing significant activity, with a typical plot of the adjusted response in the anterior temporal lobe (coordinates $-40, -28, -18$) for all tasks; (ii) slices through local maxima as in the table presented on standard MRI brain sections, at the given z coordinate. N.B. For this and Fig. 3: L, left; R, right; A, anterior; P, posterior; B, baseline task, i.e., letter decision.
previously shown by Neely (1991), there was a significant decrease in the nonword RTs as the proportion of related prime-targets increased, even though the number of nonwords remained constant. This effect is consistent with the criterion for producing a "No" response being under strategic control (Seidenberg and McClelland, 1989). Second, there was an increase in RTs to unrelated word targets when the proportion of primes increased from 25 to 75%. This increase in the RTs to unrelated targets (while the RTs to related targets stayed constant) resulted in a nonsignificant increase in the size of the priming effect (see Table 1). Overall, the behavioral data indicate automatic and strategic effects in our experimental design, even with the short SOA. Consistent with previous behavioral findings, the strategic effect becomes increasingly important with higher proportions of related word pairs.

PET DATA

Our primary aim was to discover whether there is a physiological correlate of the behavioral phenomenon of semantic priming. The experimental design allowed us (i) to ensure lexical decision was activating regions involved in semantic processing, and (ii) to examine the data for nonlinear variations in activity with changes in the proportion of related targets. The task effect (categorical analysis) is discussed prior to the effect of priming (nonlinear analysis).

Lexical Decision

The left inferior temporal gyrus, anterior temporal lobe, posterior middle temporal gyrus, temporal operculum, inferior frontal/insula region, and orbitofrontal cortex were activated for lexical decision relative to letter decision, consistent with previous studies using this task (Price et al., 1994; Rumsey et al., 1997), semantic categorization tasks (Vandenberghe et al., 1996; Price et al., 1997), and word retrieval tasks (e.g., Mummery et al., 1996). Patient data (Hodges et al., 1992; Hodges and Patterson, 1997; Kapur et al., 1994) has also shown that anterior temporal regions are involved in semantic processing. In contrast, frontal lobe lesions do not generally result in semantic deficit. Hagoort et al. (1997) have demonstrated that frontal lobe lesions cause impaired strategic priming but intact automatic priming. These observations from patients plus recent imaging findings (Thompson-Schill et al., 1997) have led to the view that the inferior frontal lobe plays an executive role during semantic tasks (Fiez, 1997). It is noteworthy that, in our study, the inferior frontal region activated for lexical decision does not show sensitivity to semantic priming. It is possible that this is due to the nature of the role of frontal cortex in lexical decision when block design is used. If it is important in setting up a mode of operation for performance of a task, then no differential activity would be expected within the lexical decision conditions. The orbitofrontal cortex has been previously activated by semantic decisions (Vandenbergh et al., 1996; Price et al., 1997), and there are patient studies (Bechara et al., 1998) that indicate a role for this region in decision making.

We conclude that lexical decision in this context requires semantic processing when the distractors are very wordlike and does not, as some have argued (e.g., Shelton and Martin, 1992), rely solely on presemantic processes.

Letter Decision

The reverse contrast (letter decision–lexical decision) revealed activation in bilateral superior parietal lobes (BA 7), right superior frontal gyrus (BA 8), right temporo-occipital junction, and left supramarginal gyrus (BA 40). This pattern of relative deactivations for lexical decision has been shown previously in language tasks (e.g., Shulman et al., 1997; Rumsey et al., 1997). The left supramarginal gyrus is thought to be important in sublexical processing (Price, 1997).

Prime-Target Relationship

As discussed in the introduction, we predicted certain patterns of response dependent on the processes involved in semantic priming. Purely automatic processing should lead to decreases with increasing priming; purely attentional processing should lead to increases or no change; a hybrid of automatic and attentional mechanisms suggests a complex pattern of activation response.

We looked for linear and nonlinear changes in activity as the proportion of related targets increased. The areas that are sensitive to priming fall into two categories: one left lateralized region (anterior temporal lobe; BA 38) normally associated with semantic processing

<table>
<thead>
<tr>
<th>Table 3: Significant Cortical Regions Showing Nonlinear Changes in Activity with Increasing Proportion of Related Targets</th>
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<tbody>
<tr>
<td>Area</td>
</tr>
<tr>
<td>Left anterior temporal lobe</td>
</tr>
<tr>
<td>Anterior cingulate cortex</td>
</tr>
<tr>
<td>Right superior parietal lobe</td>
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<tr>
<td>Right premotor cortex</td>
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Note. Regions of significant activation in the nonlinear analysis: (a) regions showing enhanced activity in lexical decision and (b) regions surviving a corrected threshold (P < 0.05).
and three regions associated with attention. The involvement of "attentional" regions confirms that strategic postlexical semantic matching occurs in addition to automatic processing when performing this task. The areas associated with attention and semantic processing are discussed separately below.

(a) "Semantic" regions. In most regions that were more active for the lexical decision task (relative to the letter decision task), there was no effect of semantic priming (e.g., in BA 20, the inferior temporal cortex). However, one temporal region (the anterior temporal lobe) showed variation in activity with increasing proportion of related prime-target pairs. Support for a role for the anterior temporal lobe in semantic priming comes from studies using diverse methodologies. For instance, cortex in this region is thought to be the neural generator of the N400 (Nobre et al., 1994), an electrophysiological signal that is attenuated by semantic priming (Kutas and Hillyard, 1984). Lesion data have shown that left temporal lobectomy patients have impaired individual item recollection while retaining intact information about semantic attributes (Seidenberg et al., 1993). These findings taken together imply that the anterior temporal lobe (BA 38) is important in the identification of a concept denoted by a word, acting in concert with other semantically associated regions that are insensitive to semantic priming (such as the inferior and middle temporal gyrus (BA 20/21)).

In descriptive terms, the response in the left anterior temporal lobe (BA 38) consisted of a decrease in activation with increasing proportions of related targets, except for the highest proportion of priming where activation increased (see Fig. 3). A similar U-shaped function over a range of values has been observed previously in at least one functional imaging study, where it was explained by two different effects maximal at the two ends of the continuum (Fletcher et al., 1996). The nature of the nonlinear response in this experiment together with the behavioral data also raises the possibility that it is derived here from two processes acting concurrently. Automatic priming leads to decreases in semantic activation but this effect is attenuated and ultimately reversed as strategic mechanisms become involved with higher proportion of related targets. One speculative explanation for this is that semantic priming effects include a direct automatic effect with an indirect influence of strategic processing principally affecting the nonword responses. Although the behavioral data support our hypothesis, the nature of our experiment precludes separation of the neural response to individual stimuli. The most critical finding, however, is that at least two different patterns exist in the regions held to be involved in semantic processing.

(b) "Attentional" regions. The anterior cingulate cortex showed increased activity during lexical decision (relative to letter decision) and a nonlinear decrease in activity with increasing proportion of related targets (Fig. 3). This decrease was only pronounced at high priming densities, that is at the priming densities where the reduction in nonword response RTs occurred. This pattern fits with a change in the way the task was carried out, from greater to lesser supervisory control in the terminology of Norman and Shallice (1986). This perspective relates to a variety of characterizations of anterior cingulate cortex function (e.g., Paus et al., 1998; Carter et al., 1998), which suggest that the more active the anterior cingulate is, the less routine the task is. In other words, when the proportion of related words is low, there is little strategic expectation and the task is not routine. In such a situation, activity in the anterior cingulate would be high. Conversely, when the proportion of related words is high, expectation is high, and the task is routine, leading to less activity in the anterior cingulate cortex.

Two further regions showed no differential activity in the categorical analysis, but survived correction for multiple comparisons in the nonlinear analysis. The right superior parietal lobe (BA 7) and the right premotor region (BA 6) revealed equivalent activity for lexical and letter decision when no priming was occurring. However, these regions were sensitive to priming, showing a nonlinear decrease in activity with increasing proportion of related targets. These regions are thought to be involved in visuo-spatial attention, and along with the anterior cingulate have been previously associated with attentional mechanisms in previous anatomical (Mesulam, 1990) and imaging studies (Nobre et al., 1997). Our experimental design has allowed us to differentiate between these regions in the type of response seen, albeit at a descriptive level. A more precise definition of the functional roles these regions play in semantic priming will require further research. However, the sensitivity of attentional regions to varying degrees of priming suggests the importance of attention in priming, even at short SOAs.

Finally, these findings suggest certain similarities between semantic and repetition priming. Previous repetition priming studies have also shown decreases in activation in task-specific regions and decreases in right superior parietal lobe and right premotor regions, very close to the regions we describe (Schacter et al., 1996). While there are substantial differences between these two forms of implicit memory, our result suggests that attentional brain areas may be involved in both semantic and repetition/identity priming, while there are unique responses to semantic priming in the left anterior temporal lobe, possibly due to automatic processing.
CONCLUSIONS

We have shown a nonlinear physiological response to priming correlating with a significant behavioral effect, and differential sensitivity within semantic regions to semantic priming. The behavioral data and PET findings together support a dual-process theory of semantic priming with coexistent automatic and attentional mechanisms. Finally, taken together with previous neuroimaging results on repetition priming, the data suggest that attentional mechanisms underlying semantic priming may be common to different types of priming, while the automatic component is task-specific.

ACKNOWLEDGMENTS

We are grateful to R. Frackowiak for his helpful comments. This work was supported by the Wellcome Trust. C.J.M. is an MRC Clinical Training Fellow; C.J.P. is a Welcome Senior Research Fellow.

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