

Selecting Among Competing Alternatives: Selection and Retrieval in the Left Inferior Frontal Gyrus

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It has been widely argued that the left inferior frontal gyrus (LIFG) is involved in the control of retrieval of information from long-term memory. Recent claims that the LIFG is involved in selecting among semantic alternatives have been challenged on the grounds that the manipulation of selection demands may have been confounded with controlled retrieval. The current study used an event-related functional magnetic resonance paradigm to re-examine the possibility that LIFG activation is involved in selection processes. In order to minimize potential confounding effects of controlled retrieval, we used an automatic retrieval task (picture naming) and held retrieval demands constant, while varying selection demands by way of competitor priming from earlier semantically related trials. We found significant activation in LIFG as a function of increased selection demands; activation centred on two peaks, one in anterior LIFG and a second more superior and posterior region. These data support the view that LIFG plays a role in selection among semantic information, even in the absence of controlled retrieval processes.

Keywords: competition, LIFG, retrieval, selection, semantic

Introduction

The representation and processing of semantic information support a wealth of cognitive abilities, including language comprehension and production, object recognition, thinking and memory. For this reason, understanding the neural basis of the semantic system is a central goal of cognitive neuroscience. Lesion-deficit studies and neuroimaging of healthy brains have established that semantic processing recruits an extensive, largely left lateralized network of temporal, frontal and parietal regions (Vandenberghe *et al.*, 1996; Mummery *et al.*, 1998; Tyler *et al.*, 2001). The question remains, however, as to the precise contributions of, and interactions among, the components of such a system.

In this paper we focus on the role of a region that has attracted considerable attention: the left inferior frontal gyrus (LIFG). Neuroimaging studies have frequently found the LIFG to be activated during semantic tasks (Petersen *et al.*, 1989; Demonet *et al.*, 1992; Demb *et al.*, 1995; Martin *et al.*, 1995; Thompson-Schill *et al.*, 1997; Gabrieli *et al.*, 1998; Poldrack *et al.*, 1999; Tyler *et al.*, 2001). Recent studies have also shown that transcranial magnetic stimulation (TMS) of the anterior portion of the left inferior prefrontal cortex slows responses in a semantic decision task (Devlin *et al.*, 2003; Kohler *et al.*, 2003). However, in the neuropsychological literature, LIFG lesions have not typically been reported to result in semantic deficits, being traditionally associated with the morpho-syntactic and/or speech output impairments of Broca's aphasia (Goodglass, 1976; Zurif, 1995; Grodzinsky, 2000) although the

lesion-deficit associations here are controversial (Dronkers *et al.*, 2000). Semantic impairments are generally associated with temporal lobe damage (Hodges *et al.*, 1992; Gainotti *et al.*, 1995). It is widely argued, therefore, that the LIFG may support processes that operate over semantic representations rather than the representations themselves (Poldrack *et al.*, 1999; Fletcher and Henson, 2001).

Two major hypotheses have recently emerged as to the nature of the semantic processes supported by the LIFG. The first is that LIFG is involved in selecting among competing semantic alternatives held in working memory; for example, in deciding which of many possible attributes of a word's meaning are relevant for a specific decision task (Thompson-Schill *et al.*, 1997, 1998, 1999; Desmond *et al.*, 1998; Gabrieli *et al.*, 1998). The second is that LIFG guides the controlled retrieval of semantic information that cannot be generated on the basis of automatic stimulus-response associations; for example, retrieving the semantic information necessary to find a connection between two weakly related words (Buckner, 1996; Fiez, 1997; Bokde *et al.*, 2001; Wagner *et al.*, 2001; Gold and Buckner, 2002).

In the current study we examine the LIFG role in semantic selection when potentially confounding effects of controlled retrieval are minimised. Before discussing these issues further, we note that there is variation in the exact regions of interest across studies, with some researchers focusing specifically on the LIFG (e.g. Thompson-Schill *et al.*, 1997, 1999), while others suggest that semantic processing is limited to only the more anterior portion of ventrolateral frontal cortex (Poldrack *et al.*, 1999) and yet others refer more generally to left inferior prefrontal cortex (LIPC). For consistency, we use the term LIFG throughout this paper.

Semantic Selection and Retrieval

Drawing on theoretical accounts of prefrontal cortex function in non-semantic domains (e.g. Kimberg and Farah, 1993), Thompson-Schill *et al.* (1997) suggested that the LIFG is involved in selecting among competing semantic alternatives, rather than retrieval of semantic information *per se*. In a similar vein, Gabrieli *et al.* (1998) suggested that the LIFG is activated to the extent that a greater amount of semantic information must be held in working memory in order to select among alternative answers. To test their hypothesis, Thompson-Schill *et al.* (1997, 1999) carried out a series of functional magnetic resonance imaging (fMRI) studies, manipulating selection demands in several tasks, while aiming to hold semantic retrieval constant, and reported a significant increase in LIFG activation in conditions that increased selection demands, as well as a decrease in activation when selection demands were reduced

by repetition of task demands. They also found that patients with lesions including the LIFG were impaired specifically in the high selection conditions of a verb generation task (Thompson-Schill *et al.*, 1998). Further evidence in support of left frontal involvement in selection processes comes from a stem completion study (Desmond *et al.*, 1998), although activation centred on left middle rather than inferior frontal cortex, and from a recent study employing a proactive interference paradigm (Dolan and Fletcher, 1997; Fletcher *et al.*, 2000).

An alternative view is that the LIFG supports the controlled retrieval of semantic information (Buckner, 1996; Fiez, 1997; Bokde *et al.*, 2001; Wagner *et al.*, 2001; Gold and Buckner, 2002; reviewed in Poldrack *et al.*, 1999). On this view, it is claimed that the cases where LIFG activation is not observed — such as the low-selection conditions of Thompson-Schill *et al.*'s studies — involve *automatic* rather than *controlled* retrieval and it is this variable that accounts for the lack of LIFG recruitment. Controlled retrieval of semantic information is an example of a more general process of *cognitive control* (Norman and Shallice, 1986; Miller, 2000; Wagner *et al.*, 2001; Miller *et al.*, 2002). The claim is that the prefrontal cortex is a source of top-down signals, which guide goal-directed behaviours and processes that are not automatically triggered by strong associations to environmental stimuli. Controlled behaviours, including the strategic interrogation of conceptual knowledge to generate specific pieces of information for a given task, are attention-demanding and driven by internal goals and knowledge. Automatic behaviours, in contrast, are well-learned responses triggered by environmental stimuli (Miller *et al.*, 2002).

Wagner *et al.* (2001) suggest that in Thompson-Schill *et al.*'s studies, controlled retrieval and selection were confounded such that increases in LIFG activation observed in 'high selection' conditions could be attributed to simultaneous increase in controlled retrieval demands. For example, in Thompson-Schill *et al.* (1997)'s classification task, the high selection condition involved judging whether a specific attribute was true or false of a pictured object (e.g. *car-expensive*), while the low selection condition involved judging whether a word was the appropriate basic level name for a pictured object. The logic of the task is that in the former case, participants must select the relevant attribute from the many possible semantic properties of *car* in order to make the correct response, whereas in the case of the picture-name match, only one name is appropriate, so no selection is required. However, the difference between the tasks could be reinterpreted as a manipulation of controlled versus automatic retrieval, i.e. the controlled retrieval of a specific, task-relevant piece of information in order to decide that a car is expensive in contrast to the automatic stimulus-response association of an object and its name. In Thompson-Schill *et al.* (1999)'s attribute generation study, participants generated either a colour or action associated with a stimulus word such as *apple*. When they were subsequently asked to produce a different attribute to the same concept (e.g. first the colour of the apple and then an action associated with an apple), LIFG activation increased, presumably as a function of the selection demands associated with competition from the previously generated, now irrelevant, information. Thompson-Schill *et al.* argue that if LIFG supported retrieval of semantic information rather than selection, its activity should be reduced when the same concept (e.g. *apple*) is repeated, regardless of whether the same or different attribute is generated, since

retrieval of this concept has been primed. However, proponents of the retrieval hypothesis could, again, reinterpret the 'different attribute' trials as involving greater controlled retrieval demands, since access to semantic memory in this task could be viewed as guided search for specific pieces of information associated with a word, rather than as a passive spread of activation to a range of attributes from which one is then selected. Searching for an action associated with an apple may be more difficult when it is necessary to suppress the irrelevant search criterion from an earlier 'colour' trial [see also Badre and Wagner (2002) for other interpretations of this study].

In summary, several studies strongly suggest that the LIFG plays a role in selecting among semantic information. However, an alternative explanation in terms of controlled retrieval remains a possibility in any task where subjects are required to retrieve a specific piece of information that is not automatically activated by an existing stimulus-driven association; in each case, an increase in selection demands can be reinterpreted as the need to retrieve more information, more distantly related information or to change search criteria from trial to trial. We avoided this problem in our study by manipulating selection demands in the context of a task that exploits a strong pre-existing stimulus-response association, so minimizing the role of controlled retrieval and therefore any possibility that it could inadvertently covary with selection manipulations.

If we find LIFG activation associated with increased selection in an automatic task, this does not, of course, rule out the possibility that left prefrontal cortex *also* plays a part in controlled retrieval. It is plausible that there is functional heterogeneity within the LIFG, such that different subregions may be associated with either controlled retrieval or selection. For example, Wagner *et al.* (2001) suggest that controlled retrieval is centred upon the anterior regions of left inferior frontal cortex, leaving the possibility for selection processes to be localized to the more posterior LIFG region. As mentioned above, the peak activations reported by Thompson-Schill *et al.* fall in a dorsal posterior region of the LIFG, an area suggested by Poldrack *et al.* (1999) to be commonly activated for phonological and lexical, as well as semantic processing — perhaps reflecting a domain-general selection and/or retrieval process (Gold and Buckner, 2002). The area associated most strongly with controlled retrieval in Wagner *et al.*'s study is more anterior — within the ventral anterior region (essentially BA 45/47) of the LIFG suggested by Poldrack *et al.* to be selectively associated with semantic processing. It is possible that this region subserves controlled retrieval (Fiez, 1997; Price *et al.*, 1997; Wagner *et al.*, 2001), although it is not clear that this would be a semantic-specific process, as suggested by Poldrack *et al.*'s analysis (see also Bokde *et al.* 2001) or a more general process of retrieval operating over different types of information (Gold and Buckner, 2002). If such regional fractionation of processes within the LIFG can be reliably observed, this would lend credence to the view that selection and controlled retrieval are distinct cognitive processes, which are recruited under different conditions.

The Current Study

We conducted an fMRI study, using a competitor priming task (Wheeldon and Monsell, 1994), which allowed us to manipulate semantic selection demands in a situation where retrieval of semantic information was (i) automatic rather than controlled and (ii) did not covary with high versus low selection demands.

The participants' task was to provide the basic level name to a line drawing of a familiar, easily nameable object — so exploiting automatic retrieval only. Picture naming is an automatic task in the current context, in that there is a strong association between the stimulus — the pictured object — and the response — its name (Miller, 2002). [Note: We acknowledge that the automatic/controlled distinction is a controversial one, and that these terms are not always defined in the same way in different contexts. In the current study, we are using the term 'automatic' to refer to the stimulus-driven activation of the basic level name of a picture of a common object. Although one may decide whether to actually produce that name aloud, or may decide to output a different response to the picture (e.g. to label it as a living or non-living thing), we suggest that the activation of the name itself remains an automatic by-product of object recognition. In contrast, we do not claim that the competitor priming process is necessarily an automatic one. It is often argued in the priming literature that producing interference as well as facilitation of responses may be at least partially dependent on controlled or strategic processes, although a strategy-based account of the competitor priming effect is rejected by Wheeldon and Monsell (1994). Either way, the logic of our study rests on the automatic nature of the object naming task, and not of the competitor priming process.] Most cognitive theories of word production (including the more specific case of picture naming) include a well-defined process of selection, in which the correct abstract word representation (or lemma) must be activated by the semantic specification of the pictured object (e.g. Schriefers *et al.*, 1990; Roelofs, 1992; Levelt, 1993; Wheeldon and Monsell, 1994; Levelt *et al.*, 1999). Accounts differ as to whether lemma selection involves lateral inhibition among coactivated words, or whether a differential threshold must be reached in the absence of direct inhibition, but concur that there is a process of competition among coactivated candidates until one emerges as the 'winner' and goes on to activate its lexical form information and drive speech output. Consistent with this claim, imaging studies of picture naming typically report LIFG activation (e.g. van Turennout *et al.*, 2000; Burgund *et al.*, 2003), which may reflect this competition and selection process. Critically for our study, selection demands in picture naming can be manipulated by increasing the degree of competition among lemmas, for example by priming a related but incorrect picture name, using various word-picture interference or competitor priming paradigms.

We introduced three conditions in order to manipulate selection demands in the picture naming task:

Competition Condition

The picture to be named was preceded several trials earlier by a written definition of a highly related word (e.g. participants would produce the word *whale* in response to the definition *the largest mammal that lives in the sea* several trials before naming a picture of a shark). Several studies have shown that prior production of semantically related object names increases the degree to which they compete with the correct name for output (Brown, 1979; Vitkovitch and Humphreys, 1991; Vitkovitch *et al.*, 1993, 2001; Wheeldon and Monsell, 1994; Levelt *et al.*, 1999; Tree and Hirsh, 2003). Since the primes and targets are semantically similar (e.g. *shark*, *whale*) but not phonologically similar, competition for naming responses can be attributed to selection among coactivated lemma representations activated by similar conceptual representations, rather than

form-based selection of the correct phonological specification for output (e.g. Vitkovitch *et al.*, 1993; Wheeldon and Monsell, 1994).

Repetition Condition

The picture was preceded several trials earlier by a written definition of the same word (e.g. a definition of a shark before the picture of a shark). This condition should have the effect of reducing the demands on the selection of the appropriate candidate for output, since the correct name has just been produced, increasing its activation relative to possible competitors. Many earlier studies have demonstrated robust repetition priming (e.g. Durso and Johnson, 1979) and, more specifically that prior production of the same name in response to a written definition reliably facilitates picture naming (Wheeldon and Monsell, 1992; Monsell *et al.*, 1992). [The hypothesized reduction of selection demands among competing semantic alternatives may be only one component of any such facilitation effect, since this condition also involves repeated activation of the same lexical and phonological representations. Repetition effects persist over a much longer time course than do competition priming effects, and so must be supported, at least in part, by different processes (Wheeldon and Monsell, 1994).]

Unrelated Control Condition

The picture to be named is preceded by unrelated definitions only (e.g. the picture of a shark is preceded by the definition, *organ for pumping blood*).

Our hypothesis is that LIFG activation will vary as a function of the selection demands of the picture naming task, as manipulated by the three priming conditions. Our main prediction is an increase in LIFG activation in the competition condition relative to the unrelated control condition. In addition we expect a reduction in LIFG activation in the repetition condition. It is important to note that our predictions are about increases or decreases in LIFG activation relative to the unrelated control condition, which may itself produce a degree of activation in this region relative to a low level baseline condition. In other words, there is a certain degree of selection required when participants name a picture, even in the absence of an explicit competitor prime; this may reflect competition among alternative names for the same object (e.g. sofa versus couch; bird versus robin) or unintended competition from other previous items in the test list. Previous studies have generally found that LIFG is activated in picture naming tasks relative to a fixation baseline (e.g. van Turennout *et al.*, 2000; Burgund *et al.*, 2003; although see Thompson-Schill *et al.*, 1997).

Materials and Methods

Participants

Fifteen right-handed native English speakers between the ages of 18 and 35 were tested. Each gave informed consent and was paid for their participation.

fMRI Parameters

Scanning was carried out on a 3 T Bruker Medspec Avance S300 system at the Wolfson Brain Imaging Center, Cambridge, UK, using a gradient-echo EPI sequence ($T_R = 3600$ ms; $T_A = 1100$ ms; $T_E = 27.5$ ms; flip angle = 90° ; FOV = 200 mm \times 200 mm), 21 oblique slices, 4 mm thick (1 mm gap between slices, 64×64 in-plane resolution) with head coils, 100 kHz

bandwidth and spin echo guided reconstruction). T_1 -weighted scans were acquired for anatomical localization.

In this experiment it was important to be able to record participants' overt naming responses to the pictures so that we could analyse the number of incorrect names generated in each condition and enter the error rate on each picture as a modulator into the analyses. Therefore we used a start-stop event-related imaging paradigm with a condensed T_A (1.1 s) and extended T_R (3.6 s). This allowed scanning acquisition phases to follow just after naming responses in the period during which the magnet gradient was not operating, so avoiding the head movement artefacts associated with speech production (Huang *et al.*, 2001).

Materials

Participants produced a name in response to an alternating series of written definition sentences and line drawings presented on the screen in front of them. Probe pictures were preceded by definition primes, of one of three types (i) unrelated, (ii) competition, (iii) repetition. Primes and probes were interleaved such that there were always two items between a prime and its corresponding probe.

There were 60 prime-probe pairs in each of the three conditions. The 60 competitor priming pairs were predominantly those used by Wheeldon and Monsell (1994). Each pair consisted of a line drawing of an easily nameable object along with the written definition of a related competitor word. For example, a picture of a shark would be preceded by a definition of a whale (*The largest creature that swims in the sea*). These pairs were established in Wheeldon and Monsell's study to provide robust competitor priming effects as indexed by significant increases in naming latencies to the pictures when preceded by the primes over a range of prime-target intervals and numbers of intervening items (from 2 to 30+ intervening items).

In addition to the 60 competitor prime trials, we generated an equal number of repetition and unrelated pairs, matched as closely as possible to the competitor prime pairs. Pictures were taken from the sets of line drawings compiled by Wheeldon and Monsell (1994) and Snodgrass and Vanderwart (1980). For the repetition condition, we generated definition sentences that participants could reliably name with the intended word (for example, the sentence *A spiky desert plant* was paired with a picture of a cactus). Unrelated definitions were generated that reliably produced a name that had no semantic relation to the picture (for example, the definition *Organ for digesting food* was paired with a picture of a padlock). Repetition and unrelated definitions were of a similar length to the competition definitions. As shown in Table 1, all pictures and sentences were closely matched across the three priming conditions on word/picture familiarity, word frequency, visual complexity of pictures and naming agreement for definitions. Where not already available from earlier norming studies (Snodgrass and Vanderwart, 1980), familiarity and visual complexity ratings for each picture were obtained from pre-tests in which 14 participants were asked to give ratings on a scale of 1-5. Naming agreement for the definitions was established on the basis of the number of correct names generated in the pilot behavioural experiment.

Table 1

Materials in each of the three priming conditions. Normative data come from the following sources: word frequency (Baayen *et al.*, 1995); picture familiarity (Snodgrass and Vanderwart, 1980, and data collected at Centre for Speech and Language); word familiarity (Coltheart, 1981); visual complexity and definition naming agreement (data collected at Centre for Speech and Language).

Variable	Priming condition		
	Competition	Repetition	Unrelated
Probe picture			
Word frequency of name	38.9	41.3	40.7
Length of name (syllables)	1.55	1.65	1.5
Picture familiarity	3.24	3.14	3.01
Picture visual complexity	2.86	2.91	2.90
Prime sentence			
Word frequency of name	49.6	41.3	44.8
Word familiarity of name	542	539	523
Definition naming agreement (%)	84	87.5	86

Procedure

The scanning session for each participant was divided into four blocks, each containing 15 trials in each of the three conditions. Blocks were separated by a period of 8.8 s, during which participants saw a fixation cross on the screen. The conditions were randomly ordered within a block. In addition to the 45 test pictures and 45 test definitions in each block, one filler item was introduced at the beginning and one at the end to complete the interleaving. We also included a fixation point (+) continuously presented in the centre of the screen for the duration of seven scans at the start and end of each block (i.e. 14 fixation scans per block), although this was not modelled. The division of items into blocks was solely for the purposes of varying presentation order to avoid practice and/or fatigue consistently affecting specific items: half the participants saw blocks 1 and 2 followed by 3 and 4 and the other half saw 3 and 4 followed by 1 and 2. Thus the experiment had a fully between-items, within-subjects design. A practice block of 23 items preceded the main experimental sessions.

In order to avoid head movement artefacts associated with speech production, we used a 'stop-start' scanning technique in which a 1.1 s volume acquisition phase occurred shortly after participants named the definition or picture. In this way we were able to obtain overt naming responses and thus ensure that participants showed the behavioural effects of competition/repetition priming in terms of increased/reduced naming errors relative to the unrelated condition. Moreover, overt naming allowed us to determine whether participants produced the correct or incorrect name to each picture target, so that we could enter this information as a modulator into our analyses of the imaging data. The onset of each picture was jittered so that it occurred at any time between 0 and 800 ms from the offset of the previous acquisition phase. The picture remained on the screen for 250 ms and participants had until the next scanner acquisition period to respond (between 1700 and 2500 ms, depending on the jitter). To encourage participants to respond quickly and so increase the requirement for rapid selection of the correct name, there was also a deadline tone at 600 ms after picture onset. Participants were instructed to try to 'beat the beep' and name the picture before they heard the tone. Written definition sentences were presented for 1600 ms, with a deadline tone at 2020 ms. The interval between the onset of a definition prime and its corresponding picture probe was between 11.05 and 11.85 s, depending on the degree of jitter for a given picture. These timings are summarized in Table 2 and illustrated Figure 1. Participants' naming responses were recorded through a sound delivery system onto a DAT recorder and later transcribed, so that error rates on picture trials in each condition could be computed.

fMRI Analysis

Pre-processing (slice timing correction, image realignment into standard stereotactic space and smoothing) and statistical analysis of the data were performed using SPM99 software (Wellcome Institute of Cognitive Neurology, www.fil.ion.ucl.ac.uk), implemented in Matlab (Mathworks Inc. Sherborn, MA). Four time series were acquired for each subject (111 scans per series). The first three scans of each time series were discarded to allow for T_1 equilibrium before the test trials started. Slice timing correction was followed by image realignment to account, respectively, for different slice acquisition times and head

Table 2

fMRI study: timing parameters for each picture and sentence

	Time from onset of trial (ms)	Duration/timing of event (ms)
Scanning	0	1100
Picture onset	1100-1900 (jittered)	250
Deadline tone	1700-2600 (jittered)	600 after picture onset
Scanning	3600	1100
Sentence onset	4450	1600
Deadline tone	6470	2020 after sentence onset
Scanning	7200	1100
Picture onset	8300-9100	250
Etc.		

Table 3

Behavioral data in the scanner: Overall error percentages in each condition and breakdown of errors by type in each priming condition

Error type	Prime condition		
	Unrelated	Competition	Repetition
All errors as percentage of all trials	8.2	19.9	4.2
Error breakdown: Percentage of total error score made up by each error type			
Omission	34	17.6	47.8
Perseveration of prime name	0	57.4	n/a
Perseveration of any other prior name	19.5	7.8	15.9
Other incorrect name	46.2	17.5	37.8
Significant hesitation	8.5	5.2	7.9
Late response (cut off by onset of scanner noise)	1.2	0.6	0

Table 4

Left inferior frontal gyrus activations

Regions	Cluster level		Voxel level		Coordinates		
	$P_{corrected}$	Extent	$P_{corrected}$	Z	x	y	z
Competition minus repetition							
BA 47	0.014	34	0.101	3.24	-38	22	-8
Competition minus control							
BA 45	0.039	14	0.085	3.25	-38	28	18
BA 46			0.103	3.17	-46	34	20
Additional cluster size/activation peaks for clusters significant at a lower threshold of $P = 0.01$							
Competition minus repetition							
BA 44	0.056	75	0.293	2.75	-54	4	24
BA 44			0.329	2.69	-52	10	32
BA 44			0.454	2.84	-40	6	32
Competition minus control							
BA 46			0.072	3.31	-48	38	16
BA 47			0.145	3.03	-36	26	-4
Repetition minus control							
BA47	0.037	90	0.221	2.93	-30	14	-20

All clusters containing any voxels significant at $P < 0.05$ after statistical correction are reported. Cluster extents are presented at an uncorrected threshold of 0.001. Multiple peaks within an extent are shown on subsequent lines.

LIFG centring on BA 45 and 46. Second, we asked whether the competitor prime produced activation in the LIFG relative to the repetition condition. This was indeed the case with a larger cluster of significant activation relative to the repetition condition, peaking at a more inferior point in BA 47. The fact that the competitor condition produced a significant increase in LIFG activation relative to the repetition condition, as well as the control condition, suggests that this effect is due to the increased selection demands that are engendered by the competitor prime (but not by the repetition prime), rather than by other processes such as evocation of a memory of a related prior event — which would be common to both competition and repetition conditions compared to the unrelated control. The two regions of activation associated with the competitor priming condition are plotted in Figure 2a,b.

As a further comparison of competition, repetition and control conditions, we fitted percent signal change against peristimulus time (PST) at the activation peaks for competition versus control and competition versus repetition conditions (see Fig. 3). Also shown are plots of raw parameter estimates (plus standard error to indicate variability in response across individuals) in the three conditions. In both locations, a robust positive response is shown for competition relative to the other conditions. For the competition versus control peak (BA 45), a negative response is found for repetition and control

conditions. At the competition versus repetition peak (BA 47), a positive response is shown for all three conditions, but for competition, the response peak is higher and occurs earlier than for repetition and control conditions. The parameter estimate plots are consistent with the random effects results, with a disproportionately larger and non-overlapping response in both locations for competition over control conditions.

As noted in the Materials and Methods, the error rate associated with each picture was included in the analysis as a parametric modulator, since errors were not evenly distributed over conditions. A direct assessment of the effects of error across all conditions, modelled independently of other task elements, produced significant activation of LIFG (peak: -38 -32 -6), although this was anterior to that found in our competition versus repetition contrast. However, even with the effects of task error included in the model in this way, the competitor condition (relative to repetition and control) was associated with greater activation of LIFG.

In contrast, there were no significant activations associated with the repetition condition, when compared with either the unrelated control or the competition condition. This is not surprising, since the prediction for the repetition conditions was *reduced* activation in the LIFG relative to the unrelated control due to the correct naming response having already been produced on the prime trial. However, there was no statistical evidence for deactivation in the repetition condition either: the reverse contrasts (repetition minus control or repetition minus competition) revealed no significantly activated voxels or clusters.

In order to investigate the extents of activations further, we lowered the threshold to an uncorrected $P = 0.01$. At this very low threshold there was an additional cluster of activation in LIFG for the contrast of competition minus repetition (Fig. 2c). This region of superior and posterior LIFG (BA 44) overlaps in part with coordinates presented by Thompson Schill *et al.* (1997) which were related to high over low selection conditions (see below). Additional activation peaks were also found for the competition minus control condition in the more inferior area (BA47) which had shown up only in the competition-repetition contrast at the higher threshold.

In summary, we found two small but significant regions of activation in the LIFG associated with naming pictures in the competitor priming condition relative to the competition and repetition conditions. It may be that these are peaks within a single extent rather than two distinct and independent activations. The wider activations revealed when the threshold was lowered suggests that this is the case.

Comparisons with Earlier Studies

Our next question was whether our areas of activation are consistent with those associated with selection processes in earlier studies. Thompson-Schill *et al.* (1997) reported peak activations for the high selection conditions of three tasks, all of which clustered in a dorsal region of the LIFG. We have plotted these peaks in Figure 4a, to provide a comparison with the activations observed in the current study. It is clear that the Thompson-Schill peaks are located in a region considerably superior and posterior to either of our significant clusters. Nevertheless, when we plotted the percent signal change for each of the experimental conditions in our study at each of the peak coordinates identified by Thompson-Schill *et al.* (1997),

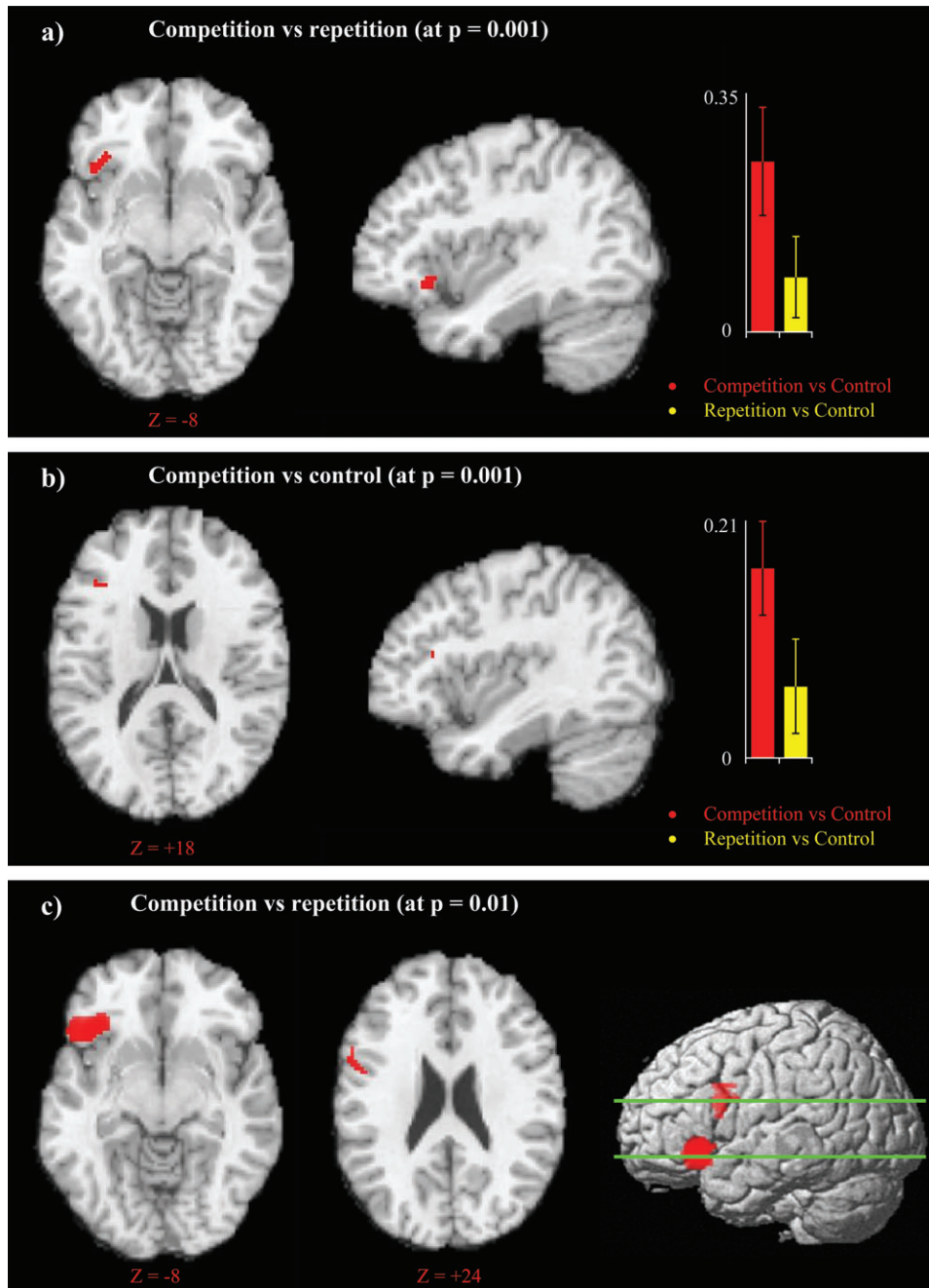


Figure 2. (a) Plot showing LIFG activation for competition minus repetition contrast. The colour bars indicate strength of activation (beta values). The areas shown survived $P < 0.05$ correction for multiple comparisons at the cluster level and were thresholded at 0.001. Coordinates presented in MNI space. (b) Plot showing LIFG activation for competition minus control contrast. The colour bars indicate strength of activation (beta values). The areas shown survived $P < 0.05$ correction for multiple comparisons at the cluster level and were thresholded at 0.001. Coordinates presented in MNI space. (c) LIFG activation for competition minus repetition contrast at a lower threshold ($P = 0.01$). Coordinates presented in MNI space.

we found greater activation in the competition priming condition than the repetition priming condition, consistent with the results of the competition minus repetition contrast at a reduced statistical threshold (Table 4, and Fig. 2c). This indicated that although our activations were centred on a more inferior region than in the earlier study, their extent overlaps to some degree.

We then carried out a similar analysis focusing on the coordinates for which activation was greatest in the weak >

strong contrast in the Wagner *et al.* (2001) study. This contrast was intended to reflect increased demands on controlled retrieval while holding selection constant. The peak activation was in anterior LIFG and was suggested to be specifically associated with controlled retrieval of semantic information. We also include percent signal change for the conditions in our study at the peak coordinates presented in an earlier investigation of semantic retrieval found to be associated with the semantic processing of subsequently remembered relative

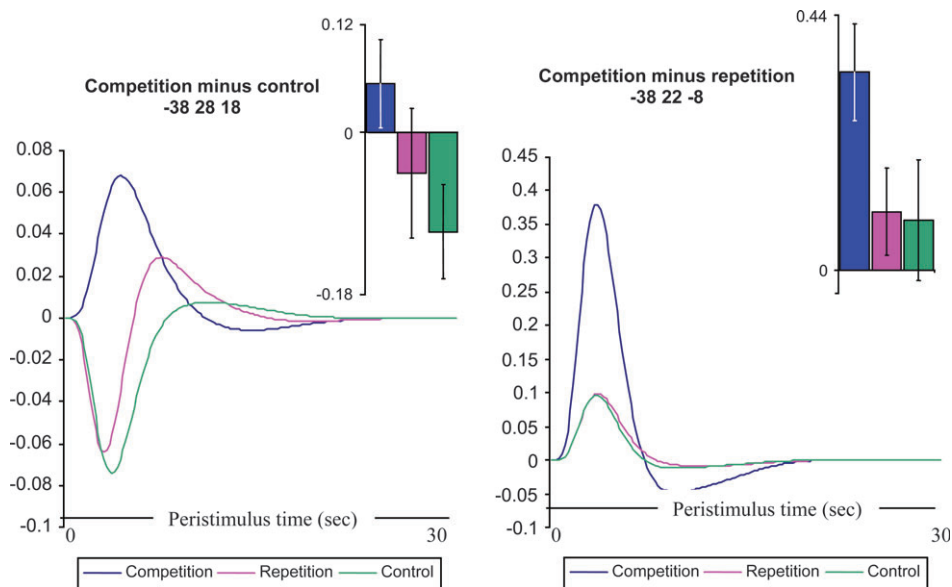


Figure 3. Fitted responses averaged across all subjects showing a simple plot of mean (fitted) response against peristimulus time (PST) at activation peaks for the competition versus control and competition versus repetition contrasts. Note: The fitted response is not corrected for confounds (global flow and high pass filtering). Individual (adjusted) data were not available in all conditions at these peaks. Also shown are plots of raw parameter estimates (plus standard error to indicate variability in response across individuals) in the three conditions.

to subsequently forgotten words (Wagner *et al.*, 1998). Figure 4b shows the signal change in our competition and repetition conditions (relative to the unrelated control baseline) for the peaks in both Wagner *et al.*'s studies. Surprisingly, we find that there was greater activation in our competition than our repetition condition, at the anterior coordinate (-45 +27 -12) — the peak that Wagner *et al.* (2001) suggested was strongly associated with controlled retrieval of semantic information. Thus, we are finding significant activation for semantic selection without controlled retrieval in a very similar area to that previously suggested to be specifically associated with controlled retrieval without selection. In more superior peaks reported by Wagner *et al.* (1998) (associated with processing of words later remembered relative to words later forgotten), there was also more activation for competition relative to repetition conditions.

Discussion

In this fMRI study regions within the LIFG were activated as a function of increasing demands on the process of selecting among semantic alternatives. Unlike previous studies, there was no potential confounding of selection with controlled retrieval, since the task exploited the automatic retrieval of a name in response to a picture, and this did not vary across high and low selection conditions. Moreover, the LIFG activations in the competition condition cannot simply be assigned to an increase in some non-specific difference between conditions, such as task difficulty, since the effect was significant even with error rate independently modeled as a parametric modulator. Also, a non-specific difficulty factor is unlikely to be the basis for our results, since a number of studies suggest that tasks engaging semantic processing are associated with LIFG activation, even when the control tasks are subjectively more difficult and are associated with longer reaction times (e.g. Otten *et al.*, 2001). Multiple regions of activation were associated with high

selection (BA 47, 45, 46), consistent with selection processes extensively represented throughout LIFG rather than associated with a specific subregion. Indeed, at a lowered statistical threshold, additional recruitment of superior and posterior LIFG (BA 44) was observed during competition relative to repetition conditions.

Before discussing our interpretation of the competition and selection in the LIFG further, we first turn briefly to the issue of why we did not observe a reduction in LIFG activation in the repetition condition compared to the unrelated control condition. We predicted that the increased availability of the name of the target picture, brought about by activating that same name in response to a definition on a preceding prime trial, would make selection of the target lemma more efficient and so reduce LIFG activation. Several studies have found evidence of decreased neural activity — or repetition suppression — in regions including LIFG when stimuli and responses are repeated (Schacter and Buckner, 1998; Koutstaal *et al.*, 2001; see Henson, 2003, for a review). However, the most robust effects are generally found when both stimulus and task are identical across trials (Thompson-Schill *et al.*, 1999). Mixed results have been found when, for example, different exemplars of the same object are shown (Koutstaal *et al.*, 2001; Vuilleumier *et al.*, 2002). In our experiment, repetition trials were not identical, as the prime was a definition and the target a picture. The different modality of stimulus presentation may have reduced repetition suppression [although see Lebreton *et al.* (2001) for evidence of reduced but significant repetition suppression effects in left prefrontal regions for cross-format (word-picture) repetition presentations]. Moreover, there are mixed results as to whether repetition suppression is found in LIFG for a picture naming task, even when repeated trials are identical. While Chao *et al.* (2002) and van Turennout *et al.* (2000) report decreases in LIFG activation, Burgund *et al.* (2003) report transient *increases* in LIFG activation as a function of repeated trials in a picture naming task. Thus, although we did expect to see

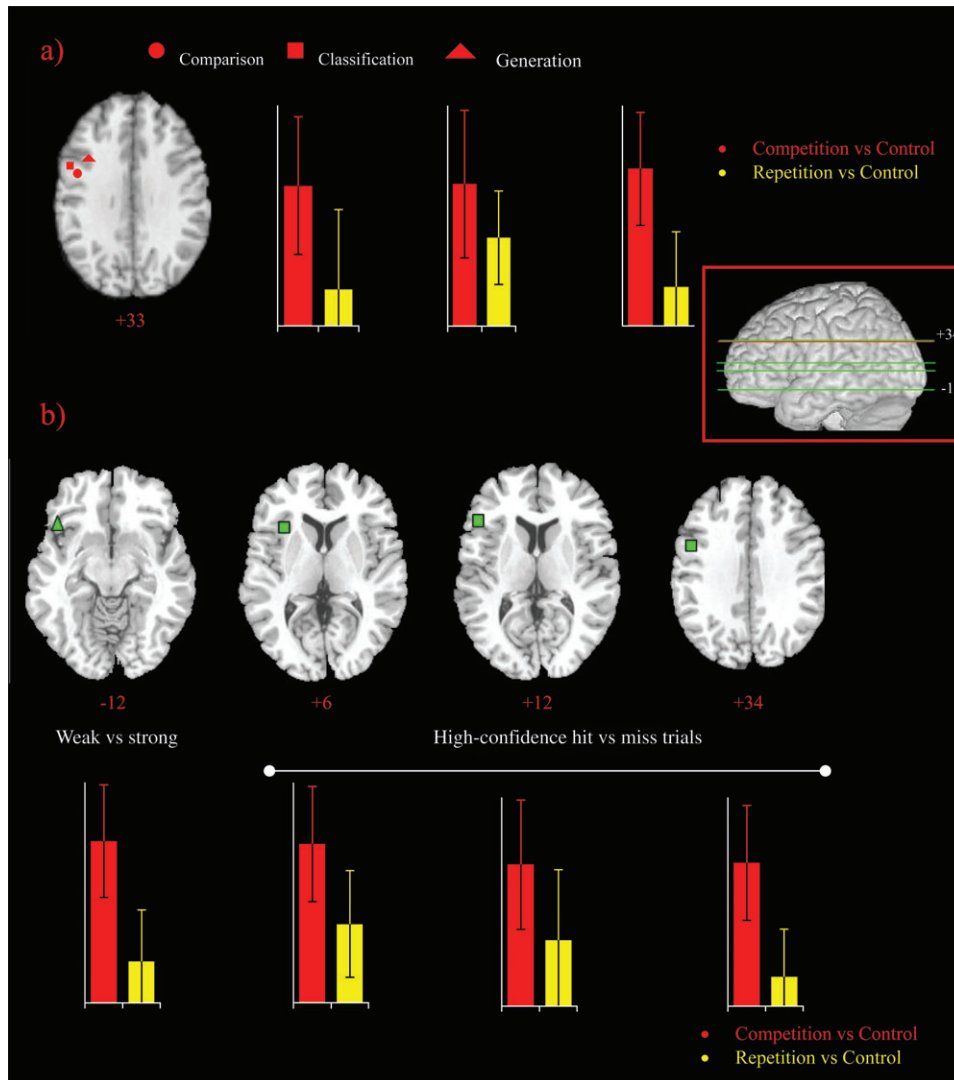


Figure 4. (a) Location of peak LIFG activations reported in Thompson Schill *et al.* (1997) superimposed on an axial brain slice. The plots show the results of competition minus control and repetition minus control contrasts from the present study at each location. Coordinates presented in MNI space. Approximate slice location indicated by red line on the three-dimensional rendered brain. (b) Plots show the results of competition minus control and repetition minus control contrasts from the present study at earlier reported activation peaks for words with weak versus strong semantic associations (Wagner *et al.*, 2001) and semantic classification of words subsequently remembered (high confidence hits) versus words subsequently forgotten (misses; Wagner *et al.*, 1998). Coordinates of axial brain slices, presented in MNI space. Approximate slice locations indicated by green lines on the three-dimensional rendered brain.

reduced LIFG activation in our repetition condition, it is possible that any such effect was reduced by the non-identical presentation format, or that any suppression in activation as a result of reduced competition in the selection phase was masked by possible priming related increases in activation that emerged from some other aspect of the task.

Returning to the main focus of the study, in line with many previous researchers, we have interpreted the interference effect of semantic primes on picture naming as emerging from competition within the process of selecting among coactivated lemmas in order to produce the target name (Brown, 1979; Schriefers *et al.*, 1990; Vitkovitch and Humphreys, 1991; Roelofs, 1992; Vitkovitch *et al.*, 1993, 2001; Levelt, 1993; Wheeldon and Monsell, 1994; Burke, 1999; Levelt *et al.*, 1999). However, there is an alternative possible interpretation of the competitor priming paradigm that would locate the effect within the initial activation of semantic information on the

basis of the picture, and so allow an explanation of both the behavioural effect and the increased LIFG activation in the fMRI study in terms of increased demands on controlled retrieval, rather than selection (Badre and Wagner, 2002). On this account the semantic similarity between the competitor prime and the target picture would lead to competition in the process of activating the correct semantic representation for the target; the increased accessibility of the semantic information associated with the competitor increases the probability that this set of semantic representation ‘wins’ the automatic retrieval stage. If this were the case, it would be plausible that to access the correct semantic and/or lexical representation for the target picture, a top-down control process is required to guide retrieval of this knowledge in the face of competition. On this account, the increased LIFG activation in the competitor condition would be attributable not, as we have claimed, to selection among coactivated semantic representations following

automatic retrieval, but rather to the operation of a controlled retrieval process that is initiated in order to overcome competition within the automatic retrieval process itself.

This 'retrieval' account of the competitor priming paradigm is a logical possibility and similar accounts have been suggested previously to explain picture-word interference effects (Lupker and Katz, 1981; Rayner and Springer, 1986). However, it is called into question by considerable evidence that the semantic competition effect is reduced or disappears when a task is used that measures the activation of a semantic representation from a picture, without requiring a naming response. In this case, the effect of prior semantically related prime stimuli is generally facilitatory, not inhibitory (Kroll and Potter, 1984; Schriefers *et al.*, 1990; Humphreys *et al.*, 1995; cf. Bajo *et al.*, 2003). For example, in data collected in our laboratory, we found a facilitatory effect of prior presentation of related trials in word-picture matching task. Participants' reaction times to decide whether a picture represented the same concept as a written word were facilitated as a function of the number of preceding trials from the same category ($R^2 = 0.394$ $P < 0.001$; Raposo *et al.*, 2003). In fact, even when the target picture does have to be named, facilitatory semantic priming can outweigh competitor effects if the interval between prime and target is very short (Wheeldon and Monsell, 1994), if prime and target are associatively related rather than being semantically similar (Alario *et al.*, 2000; Tree and Hirsh, 2003) and possibly, if the prime is not itself named (Damian and Bowers, 2003; Tree and Hirsh, 2003; although see Bajo *et al.*, 2003). This transient facilitatory effect is thought to stem from spreading activation within the semantic system, which increases the availability of the semantic representation of the target concept to be named (Wheeldon and Monsell, 1994). Thus, we would question Badre and Wagner's assumption that 'multiple representations [within semantic memory] can compete for processing through mutually inhibitory interactions' (p. 207). In contrast, the interference or competitor effect of semantically related primes in picture naming tasks like the one used in our study seems to be located in the requirement to select a single lemma to drive the output of the correct name, rather than in any competition at the level of activating the correct semantic information for the picture. Further direct evidence that semantic interference is located at the lemma selection level comes from a recent study in which prior presentation of a semantically related prime slowed performance in a task in which Spanish subjects made a grammatical gender decision in response to pictured objects (Bajo *et al.*, 2003). Grammatical gender is claimed to be a syntactic feature linked to the lemma level of representation (Jescheniak and Levelt, 1994), and as such, competition effects in this task can be quite specifically tied to lemma selection rather than semantic activation.

For these reasons, we do not believe that the increased LIFG activation in the competition condition of our fMRI study can be attributed to the need for controlled retrieval processes such as top-down bias mechanisms to overcome competition from the prime at the level of activating representations within semantic memory. We turn now to an examination of potential selection processes, which remain rather imprecisely defined. In the current study we have assumed that selection demands vary as a function of the degree of competition among alternative candidates for a response. Thus, selection demands were argued to be high when one must name a picture of a *shark* on trials

where an incorrect related response, such as *whale*, has been given an activation boost shortly beforehand. In other words, *whale* has become a pre-potent response that must be inhibited or ignored. Therefore, within the context of the current task, we have used the terms *competition* and *selection* interchangeably. However, the term *selection* has often been used in the literature to refer to more metalinguistic, effortful processes, in which participants must choose among, for example, different semantic attributes on which to base a response. It remains an open question as to whether these different interpretations of selection are referring to the same underlying process, or should be distinguished, and similarly, whether a distinction should be drawn between processes of competition on the one hand, and selection on the other.

The term *competition* is widely used in models of language comprehension and production to describe the emergence of a unique candidate as the 'winner' from a pool of coactivated representations. In normal circumstances, competition processes are rapid and automatic and not subject to conscious control. For example, when a spoken word starts to be heard, a cohort of candidate word representations is activated — e.g. on hearing, the sequence /ka.../, there is an increase in activation for the matching candidates *cat*, *candle*, *cab*, etc. Over time, these representations continue to accrue or lose activation as a function of their match or mismatch with the unfolding phonological sequence. Candidates compete with each other in proportion to their degree of activation, whether this be in terms of direct lateral inhibition between them, or the requirement for one to reach a sufficiently large advantage over other the others (e.g. Marslen-Wilson, 1990). Similarly, there is parallel activation of, and competition among, lexical representations (at lemma and/or lexeme level) in word production (Stemberger, 1985; Levelt *et al.*, 1999).

In all the cases described above, a single candidate emerges automatically as the winner of the competition process, without involving controlled processing. In the broadest sense of the word, this candidate has been *selected*. However, we may want to reserve the term *selection* for the more specific case where it is necessary to carry out some additional processing relevant to current task goals. For example, in natural speech, the competition among cohort candidates is automatic and almost invariably the correct word is recognized either before or shortly after the end of the word, without any noticeable difficulty for words with large cohorts (e.g. *cat*) versus small cohorts (e.g. *ocean*). We could think of this as competition without selection. However, if a task were introduced in which the word were truncated after the initial two phonemes and people asked to guess which word they were hearing, as in the 'gating paradigm', then there would be a greater selection demand associated with generating a single response among all the possibilities for /ka.../ (Grosjean, 1980; Tyler and Wessels, 1983). In this case, there is competition *and* selection; task-related selection demands increase in line with the underlying competitor dynamics. This was also the situation in the speeded picture-naming task used in the current study. By demanding a speeded 'beat the beep' response, we forced people to select a naming response before the process of competition among possible candidates was fully resolved. Other things being equal, it will be relatively straightforward to select the correct name for production, since it will receive the majority of activation from the object recognition system; if it is clearly a picture of a shark, the lemma *shark* will be activated more strongly than all

others. However, in the competitor priming condition, the activation of a highly related lemma has been boosted, so that when the picture is presented, it reaches a level similar to that of the correct word — making it more difficult to reject in favour of the correct response; i.e. increasing selection demands. It is possible that with time, and continued activation from the pictured object, the competition between target and incorrect distracter would resolve such that the correct candidate emerges as the winner, but the task demands of speeded naming force participants to make a choice from within the unresolved competitor space. Within this framework we suggest that there is a task-specific process of selection that operates on the competition among candidates. Selection is defined relative to a particular task or goal. Note that it is possible to construct tasks that operate over the same competitor set (e.g. word candidates) but which do not require selection, at least within the same level of representation. For example, making a lexical decision simply requires a participant to decide whether there is a real word present or not. There is no need to discriminate among competing neighbours to select one of them among others; indeed, the more activation there is in the system as a whole, the more likely it is that there is a word present (Forster and Shen, 1996). Similarly, lexical decision is easier for words with many senses (e.g. *twist* as in twisted ankle versus *twist* in a story) rather than few senses (e.g. *hotel*) since there is no need to select just one sense from all those possible in order to make the decision (Rodd *et al.*, 2002).

Although we suggest that selection in this sense is more than just competition, it is still a relatively rapid, automatic process. The tasks described above, such as picture naming and word identification, do not require that multiple possibilities be held in working memory, nor do they involve effortful, metalinguistic judgements — as do many tasks previously used in the investigation of LIFG function. We cannot determine at this stage whether these two kinds of selection are qualitatively different processes — one automatic and the other controlled — perhaps subserved by distinct subregions within the left prefrontal cortex, or whether they are endpoints of a continuum, in which a single underlying process may be subject to varying degrees of explicit control. The location of the LIFG activation we found to be specifically associated with an increase in automatic selection demands was in a more anterior inferior region of the LIFG than those reported by Thompson-Schill *et al.* (1997, 1999), which is consistent with the interpretation that we are tapping different kinds of selection process.

What we can conclude on the basis of the current results is that the selection process involved in naming a picture to deadline recruits the LIFG. It is unlikely in this case that LIFG activation can be attributed to confounding controlled retrieval demands with selection demands — since we used an automatic retrieval task, and there was no potential increase in controlled retrieval with the selection demands of the task. We have also argued against the potential reinterpretation of this effect as controlled retrieval operating to resolve inhibitory interactions among semantic representations (Badre and Wagner, 2002). Finally, we reiterate that the scope of our study was an investigation of the effect of increasing selection demands on LIFG activation when retrieval demands were held constant. Thus we do not attempt to make claims about whether or not any or all regions within the left prefrontal cortex are *also* involved in controlled retrieval (or indeed several other

candidate processes). This question is not addressed by the design of the study.

Badre and Wagner (2002) have recently proposed that apparent selection effects should be reinterpreted along with controlled retrieval as reflecting the operation of a single top-down bias mechanism. In support of this claim, they cite a study in which they also found anterior LIFG activity associated with both selection and control demands — suggesting a unitary process rather than separate processes subserved by dissociable subregions within the left prefrontal cortex. This result is echoed in our own study, in which the activation cluster for a selection task is centred on the anterior inferior LIFG region identified by Wagner *et al.* (2001) to be most strongly associated with controlled retrieval of semantic information. Thus, very similar regions seem to be activated for processes that are apparently very different — both in terms of selection versus retrieval and in terms of their degree of automaticity. While we do not wish to claim that our results refute Badre and Wagner's elegant synthesis of the selection and retrieval approaches into a single mechanism, they nevertheless highlight just how broad a spectrum of apparently different processes must be spanned by any proposed unitary mechanism.

Notes

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