

Semantic Adaptation and Competition during Word Comprehension

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Word comprehension engages the left ventrolateral prefrontal (IVLPFC) and posterior lateral-temporal cortices (PLTC). The contributions of these brain regions to comprehension remain controversial. We hypothesized that the PLTC activates meanings, whereas the IVLPFC resolves competition between representations. To test this hypothesis, we used functional magnetic resonance imaging (fMRI) to assess the independent effects of adaptation and competition on neural activity. Participants judged the relatedness of word pairs. Some consecutive pairs contained a common ambiguous word. The same or different meanings of this word were primed (e.g., SUMMER-FAN, CEILING-FAN; ADMIRER-FAN, CEILING-FAN). Based on the logic of fMRI adaptation, trials with more semantic overlap should produce more adaptation (less activation) in regions that activate meaning. In contrast, trials with more semantic ambiguity should produce more activation in regions that resolve competition. We observed a double dissociation between activity in the PLTC and IVLPFC. PLTC activity depended on the amount of semantic overlap, irrespective of the amount of semantic ambiguity. In contrast, IVLPFC activity depended on the amount of semantic ambiguity. Moreover, across participants the size of the competition effect as measured by errors was correlated with the size of the competition effect in the IVLPFC. We conclude that the IVLPFC is an executive mechanism within language processing.

Keywords: ambiguity, executive function, homonym, prefrontal, word comprehension

Introduction

The ability to comprehend words is mediated by a wide network of cortical regions including the left ventrolateral prefrontal cortex (IVLPFC) and posterior lateral-temporal cortex (PLTC). A critical, outstanding question in the cognitive neuroscience of language concerns the distinction between the contributions of these brain regions to word comprehension. One approach to this question emerges from the wider literature on the function of the prefrontal cortices and their relationship to posterior brain regions such as the PLTC. Prefrontal cortices are thought to exert executive control over posterior brain regions that store and activate information (Cohen and Servan-Schreiber 1992; Miller and Cohen 2001). Based on this framework, we hypothesized that during word comprehension the IVLPFC resolves semantic competition, whereas the PLTC activates information.

The idea that the PLTC and IVLPFC make distinct contributions to word comprehension is supported by a large body of neuropsychological research. Patients with damage to the left PLTC suffer from profound deficits in language comprehension (Wernicke 1874). For example, they are unable to match

spoken and written words to pictures of their referents or understand simple sentences (Bates et al. 2003; Dronkers et al. 2004). In contrast, patients with damage to the IVLPFC have more subtle deficits in word comprehension. For instance, they are unable to rapidly activate appropriate word meanings the face of ambiguity (Milberg et al. 1987; Swaab et al. 1998; Metzler 2001; Bedny et al. 2006).

In contrast to this neuropsychological research, neuroimaging studies have illustrated that normal word comprehension typically involves both the PLTC and IVLPFC (for a review see Martin 2003). Moreover, most experimental manipulations that lead to increased activity in the PLTC also lead to increased activity in the IVLPFC. A recent example of PLTC and IVLPFC coactivation comes from neuroimaging studies of semantic priming. In this paradigm, participants make responses (e.g., a word/nonword decision) to sequentially presented items. On some proportion of the trials, the current word is related in meaning to the previously presented word. Participants typically respond faster on “related” than “unrelated” trials (Meyer and Schvaneveldt 1971; for a review see Neely 1991).

Several accounts of semantic priming have been proposed. According to some accounts, a component of this behavioral advantage comes from strategic effects at the decision making stage. For example, the presence or absence of a related prime can inform the subject’s decision to the target through semantic matching of the prime and target (Norris 1986; Ratcliff and McKoon 1988; Neely et al. 1989). However, according to most accounts, semantic priming occurs, at least in part, because the prime leads to the preactivation of the target (Neely 1991). Preactivation of the target could occur through automatic spreading activation in a lexical network (e.g., Neely 1977), the generation of an expectancy set (e.g., Becker 1980), or the direct activation of part of the target, as part of the prime in a distributed connectionist network (Masson 1995; Plaut 1995; Thompson-Schill et al. 1998). The preactivation of the target can be thought of as activating the same semantic information twice, initially during the processing of the prime and then during the processing of the target.

In neural terms, activating the same semantic information twice might correspond to activating the same neural population twice, which leads to a reduction in neural activity (i.e., neural adaptation) (Grill-Spector et al. 2006). In accordance with this interpretation, fMRI studies of semantic priming report adaptation effects in the IVLPFC and PLTC (Helenius et al. 1998; Mummery et al. 1999; Kotz et al. 2002; Copland et al. 2003; Rissman et al. 2003; Rossell et al. 2003; Giesbrecht et al. 2004; Matsumoto et al. 2005; Van Petten and Luka 2006).

At 1st glance, evidence of semantic adaptation effects in the IVLPFC and PLTC would seem to indicate that neurons in both

of these regions code semantic information. Such an interpretation would be similar to the typical interpretation of adaptation effects. For example, in vision research regions that adapt to repeated viewing of the same direction of motion are thought to represent and retrieve information about direction of motion (Huk et al. 2001). However, this interpretation of semantic adaptation is inconsistent with neuropsychological and fMRI research suggesting that the PLTC and IVLPFC play distinct roles language processing (e.g., Thompson-Schill et al. 1997; Robinson et al. 1998; Thompson-Schill et al. 1999; Kerns et al. 2004; Novick et al. 2005).

We hypothesize that the PLTC and IVLPFC respond to distinct aspects of semantic priming that are typically confounded: 1) repeated activation of the same semantic information and 2) biasing of the semantic network toward a context-appropriate meaning—and thus a reduction in semantic competition (Thompson-Schill et al. 1999). Under this account, the semantic adaptation effects in PLTC reflect the repeated activation of semantic information, whereas adaptation in the IVLPFC reflects reduced semantic competition.

To test our hypothesis about the distinct functions of the IVLPFC and PLTC in word comprehension, we developed a paradigm that enabled us to dissociate the amount of repeated semantic information from the amount of semantic competition. To do so, we systematically varied the inherent ambiguity of experimentally presented word forms and the context in which they occurred. On each trial, participants were presented with 2 pairs of words, one after the other (see Fig. 1). We will refer to the 1st pair as the “prime pair” and the 2nd pair as the “target pair,” although the subject’s task was the same for both pairs (i.e., decide if the 2 words were related to each other in meaning). On critical trials the 2nd word in each pair was ambiguous. In order to correctly note the relation between the members of each pair on these trials (and respond “yes”), participants had to retrieve the context-appropriate meaning of the ambiguous word.

We hypothesized that when presented with an ambiguous word, participants would temporarily activate both of its

meanings, giving rise to competition. Whether multiple meanings of an ambiguous word are always retrieved, or whether a strong enough context can lead to selective access of the appropriate meaning has been a critical topic of debate in the study of lexical ambiguity. Evidence from event-related potential and eye-tracking studies has demonstrated that context effects can occur both during the early stages of lexical access, as well as during the integration of the ambiguous word into the sentence context (Duffy et al. 1988; Martin et al. 1999; Sereno et al. 2003). Yet despite the early effects of context, both meanings of an ambiguous word are transiently activated under most circumstances (e.g., Swinney 1979; Binder and Rayner 1998; Duffy et al. 2001; Swaab et al. 2003). Thus in the present experiment, the presence of an ambiguous word should lead to increased competition between meanings. We manipulated the degree of increase in competition by manipulating the context.

In the consistent condition, the 1st word of the target pair was related to the same meaning of the ambiguous word as in the prime pair (e.g., SUMMER-FAN followed by CEILING-FAN). In the inconsistent condition the 1st word in the target pair was related to a different meaning of the ambiguous word (e.g., ADMIRER-FAN followed by CEILING-FAN) (see Fig. 2). Therefore, there should be more conflict and less semantic adaptation in the inconsistent than consistent condition. Under our hypothesized account of adaptation effects in IVLPFC and PLTC, this manipulation should lead to greater activity in the inconsistent than consistent condition for the IVLPFC (due to increased competition among the 2 interpretations of FAN at the 2nd pair) and PLTC (due to decreased repetition of the semantic code activated by the word FAN at the 2nd pair). (Critically, the inconsistent and consistent conditions were matched on the average relatedness of the 1st words of the prime and target word pairs [e.g., normative data indicate that on average “SUMMER” and “CEILING” are just as related as “ADMIRER” and “CEILING”].)

To dissociate the effect of increased competition from the effect of semantic adaptation, we included a control condition

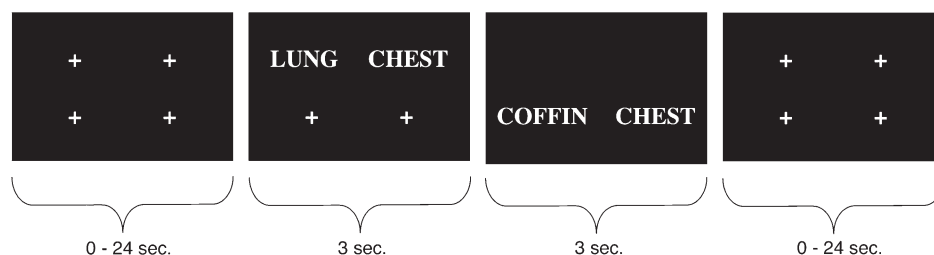


Figure 1. Relatedness judgment task.

| Trial Type | Pair 1 | Pair 2 | Semantic Competition | Semantic Adaptation |
|---------------------|----------------|-----------------|----------------------|---------------------|
| Ambiguous | | | | |
| Consistent | PIG PEN | CAGE PEN | Middle | High |
| Inconsistent | OFFICE PEN | CAGE PEN | High | Middle |
| Control | CHILD BABY | AUTUMN WINTER | Low | Low |
| Filler | GASOLINE TRUCK | FORCEPS ACROBAT | n/a | n/a |

Figure 2. Amount of semantic competition and adaptation in the inconsistent, consistent, and control conditions.

in which the prime and target word pairs did not contain ambiguous words and were unrelated to each other. Relative to the other conditions, the control word pairs are least semantically ambiguous, and are least semantically similar (because words do not repeat). Consequently, regions that respond to semantic competition should show the lowest amount of activation in the control condition. In contrast, regions that activate semantic information should show the highest amount of activation in the control condition due to the absence of semantic adaptation.

In summary, regions that respond to semantic competition should be most active in the inconsistent condition, followed by the consistent condition, and least active in the control condition. In contrast, regions that activate semantic information should be most active in the control condition, followed by the inconsistent condition, and the least activity in the consistent condition. We evaluated evidence for each of these patterns of activity in the IVPFC and PLTC (as well as other regions for which we had no a priori hypotheses).

In addition to manipulating semantic repetition and semantic competition, we also varied the type of semantic ambiguity. Half of the consistent and inconsistent word pairs contained ambiguous words with related meanings (polysemous words, such as CHICKEN which can refer to either the food or the animal), whereas the other contained ambiguous words with unrelated meanings (homonyms, such as FAN which can refer to a cooling device or an admirer). Behavioral and magnetoencephalography work suggests that there are important representational differences between these ambiguity types (Williams 1992; Rodd et al. 2002; Beretta et al. 2005; Pylkkanen et al. 2006). For example, it has been argued that unlike homonyms, the senses of polysemous words are linked to a single morphological root. Despite these representational differences, there is also evidence that both types of ambiguity can give rise to competition in a biasing linguistic context (Klein and Murphy 2001, 2002). We therefore hypothesized that both of these types of semantic ambiguity would increase semantic competition. Because most words are polysemous, the finding that related word meanings compete would illustrate how lexical-semantic competition is a pervasive part of word comprehension.

Materials and Methods

Participants

Twenty subjects (16 females) participated in the experiment. Their mean age was 23.4 (range: 19–35). All participants were right handed, native English speakers. None of the participants suffered from psychiatric or neurological disorders or had ever sustained head injury. All subjects gave informed consent and were paid \$15 an hour for taking part in the experiment.

Behavioral Procedure

Participants saw pairs of words appear on the computer screen one after the other. Their task was to read each pair to themselves and decide whether the 2 words were related in meaning. They were to respond to each pair by pressing the “Yes” or “No” button on a fiber-optic respond pad with their right and left thumb respectively, as quickly and accurately as possible. Participants were told that related words could either be similar in meaning such as “dog” and “cat,” or associated in meaning such as “dog” and “leash.” Participants were allotted 3 s to respond to each pair. If a response was not collected within 3 s, the

experiment went on to the next pair or the intertrial interval and that response was treated as an error. Trials were separated by a jittered intertrial interval 0–24 s in duration (see Fig. 1 for trial structure).

The experiment was comprised of 224 trials (37 consistent, 37 inconsistent, 38 control, and 112 filler trials). Consistent and inconsistent trials contained the same ambiguous word in the 2nd position of both word pairs. For half of the critical trials, this repeating word was a homonym (e.g., SUMMER-FAN, CEILING-FAN), and for the other half the repeating word was polysemous (e.g., CUBE-CONE, SUGAR-CONE). The ambiguous word was always paired with a non-homonym in the 1st position that was related to 1 of its meanings. In the consistent condition, the 1st and 2nd word pair made reference to the same meaning of the ambiguous word (e.g., SUMMER-FAN, CEILING-FAN). In the inconsistent condition the 1st word pair made reference to a different meaning of that ambiguous word (e.g., ADMIRER-FAN, CEILING-FAN). The 2nd word pair was identical in the inconsistent and consistent conditions (see Fig. 2).

The consistent and inconsistent conditions had identical target pairs (the 2nd pair in the quadruplet). For the target pairs, 38 pairs referenced the dominant meaning of the ambiguous word and 36 referenced the subordinate meaning. Half of the prime pairs (the 1st pair in the quadruplet) were consistent and half inconsistent. For the consistent pairs, 38 pairs referenced the dominant meaning of the ambiguous word and 36 referenced the subordinate meaning. For the inconsistent pairs 36 pairs referenced the dominant meaning of the ambiguous word and 38 referenced the subordinate meaning.

The only difference between items in the inconsistent and consistent conditions was the 1st word of the 1st pair, therefore it was important to control for unintended effects of this variation. Toward this end, the inconsistent and consistent trials were matched on the relatedness between the 1st and 3rd words through a prior rating study with a separate set of subjects. Thus referring to the example above, “SUMMER” and “CEILING” were on average as related as “ADMIRER” and “CEILING.” Words were rated in meaning on a scale of 1–7 (by 18–20 subjects per item). A rating of “7” corresponded to highly related and a rating of “1” corresponded to completely unrelated. On average the 1st and 3rd words were rated as 2.75 (SD = 1.16) in the consistent condition, and 2.74 (SD = 1.26) in the inconsistent condition. Words in the critical quadruplets were nouns 5.4 letters in length (SD = 1.0), had a mean frequency of 74.1 (SD = 58.1), and concreteness 521 (SD = 74.73). The target pairs of the critical quadruplets were on average 5.5 letters in length (SD = 1.33), had a mean frequency of 74.88 (SD = 63.69), and mean concreteness of 525.12 (SD = 75.20) (Kucera and Francis 1967).

Thirty-eight control trials were included in the experiment. The control quadruplets were similar to critical quadruplets in that words 1 and 2 were related to each other in meaning, as were words 3 and 4. However, unlike the critical quadruplets there was no relationship between the 1st word pair and the 2nd word pair. Additionally, control pairs did not contain homonyms, or word repeats. Words in the control quadruplets were nouns that were on average 6.4 letters long (SD = 1.1) had an average frequency of 47.6 (SD = 34.8), and an average concreteness of 509.12 (SD = 79.16). The words in the target control pairs, were 6.3 (SD = 1.44) letters long, had an average frequency of 30.92 (SD = 26.15), and average concreteness of 518.96 (SD = 103.71). For the target pairs, the control condition was longer and less frequent than the ambiguous conditions (length: $t(110) = 2.94$, $P < 0.005$; frequency: $t(110) = 4.65$, $P < 0.0001$) but did not differ in concreteness ($t < 1$, $P > 0.3$) (Kucera and Francis 1967).

There were a total of 112 filler triplets; of these 36 had 2 pairs of unrelated words, 38 had related words in the 1st pair and unrelated words in the 2nd pair, and 38 had unrelated words in the 1st pair and related words in the 2nd pair. Forty-one filler trials contained a repeating word, and 63 trials contained a homonym. The purpose of the filler trials was purely behavioral, to engage subjects in the relatedness judgment task and obscure the nature of the experimental design (fMRI data for these trials were not analyzed).

Each participant saw a given quadruplet once during the experiment. Which pair was seen in which condition was counterbalanced across participants. Stimuli were presented in a different random order to each of the 20 participants. The optseq algorithm (<http://surfer>.

nmr.mgh.harvard.edu/optseq/) was used to create random orders of trials and null events for each subject. The experiment took approximately 1 h and was broken up into 5 runs. Runs one through 4 contained 44 trials, and run 5 contained 48 trials.

The day before the experiment, participants came into the lab for a prescreening and to complete a 20-min practice session. In the practice session participants made relatedness judgments to word pairs and received feedback. If they made an error the word "Incorrect" was presented on the screen. If they did not respond within 3 s "Please respond as quickly as you can" appeared on the screen. None of the words that appeared in the practice session was seen in the actual experiment. During the practice session none of the trials resembled the consistent, or inconsistent conditions in the actual experiment.

The behavioral measure of interest was accuracy and reaction time to the 2nd word pair in the quadruplet as a function of condition (consistent or inconsistent). Because we were interested in the effect of context (the 1st word pair) on the processing of the 2nd word pair we excluded from analysis all trials on which participants made a "No" response to the 1st word pair in a critical quadruplet. We did the same for our analyses of control responses, so that in all cases we were measuring reaction time and accuracy of a response, immediately following a "Yes" response. For the response time and fMRI analyses we also excluded all trials where participants responded "No" to the 2nd word pair. After this procedure, the fMRI analysis included 77% (14%) of the trials for the consistent condition, 85% (10%) in the inconsistent condition, and 98% (2%) in the control condition.

fMRI Data Acquisition and Analysis

Structural and functional data were collected on a 2.89-Tesla Siemens Trio scanner using a transmit/receive gradient head coil. High-resolution T_1 -weighted structural images were collected in 160 axial slices and 1-mm isotropic voxels (time repetition [TR] = 1620 ms, time echo [TE] = 3 ms, time to inversion [TI] = 950 ms). Functional, blood oxygenation level-dependent (BOLD), echoplanar data were acquired in 3-mm isotropic voxels (TR = 3000 ms, TE = 30 ms). BOLD data were acquired in 46 axial slices, in an interleaved fashion with 53×63 in plane resolution using a Prospective Acquisition Correction sequence. The functional data were collected in 5 runs of 9 min and 30 s each. The 1st 30 s of each run consisted of a "dummy" gradient and radiofrequency pulse to allow for steady state magnetization.

Off-line data analysis was performed using VoxBo (www.voxbo.org) and SPM2 (<http://www.fil.ion.ucl.ac.uk/>) software. Using VoxBo, data were sinc interpolated in time to correct for the slice acquisition sequence. The data were realigned (SPM2), smoothed (VoxBo) with an $8 \times 8 \times 8$ mm full width at half maximum Gaussian smoothing kernel, and normalized (SPM2) to a standard template, in Montreal Neurological Institute space. Normalization maintained 3-mm isotropic voxels and used 4th degree B-spline interpolation.

The modified (for serially correlated error terms) general linear model was used to analyze BOLD activity of each subject as a function of condition, on each trial (Worsley and Friston 1995; Zarahn et al. 1997a). BOLD signal change was modeled by creating covariates for each event type including control-correct, control-incorrect, filler related-correct, filler related-incorrect, filler unrelated-correct, filler unrelated-incorrect, homonym consistent-correct, homonym consistent-incorrect, homonym inconsistent-correct, homonym inconsistent-incorrect, polysemous consistent-correct, polysemous consistent-incorrect, polysemous inconsistent-correct, polysemous inconsistent-incorrect. Neural activity was modeled as a brief impulse at stimulus onset (Zarahn et al. 1997a). Covariates of interest were convolved with a standard hemodynamic response function. Nuisance covariates included: the 1st derivative of all covariates of interest, scan effects, and an intercept term. Because the global signal covariate was correlated with the inconsistent-consistent contrast of interest for some of the subjects we did not include global signal as one of the nuisance covariates (Aguirre et al. 1998). Time series data were subjected to a high-pass (0.0055 Hz) filter, and serial correlation of error terms was modeled as previously described (Zarahn et al. 1997b).

BOLD signal differences between covariates of interest were evaluated through 2nd level analyses that treated subjects as a random effect. Second level analyses were performed on the β -values obtained

from the 1st-level models. We conducted both regions of interest (ROIs), and whole-brain analyses. We report only those effects that reached significance at $P < 0.05$ (corrected). The IVLPFC anatomical ROIs were created by resampling the standard ROIs available from the SPM toolbox. After resampling, the ROIs were adjusted where needed to conform to anatomical boundaries by a neurologist unaware of the study's hypothesis. Additionally, the 3 most inferior slices of the left orbitalis ROI were removed, as they were part of Brodmann area (BA) 47, but not part of the left frontal operculum proper.

PLTC ROIs were defined functionally through the [(inconsistent + consistent) - control] contrast. The anatomical loci of semantic effects in the temporal lobe vary considerably from person to person, and thus study to study (Thompson-Schill et al. 1999). Consequently, to examine our semantic priming hypothesis in the general location of the PLTC we defined functional ROIs specific to the present set of subjects. We identified regions in the left and right PLTC that were significantly more active in the control than in the inconsistent + consistent conditions, $P < 0.05$ (corrected) with a minimum cluster size of 10 voxels (see Fig. 4). In ROI analyses the false positive rate was controlled at $\alpha < 0.05$ by calculating a single, spatially averaged time series for each ROI for each participant.

Whole-brain, random-effects analyses were used to evaluate the following contrasts: inconsistent-consistent, inconsistent-control, consistent - control, and consistent + inconsistent - control, as well as the ambiguity type by consistency interaction. In whole-brain analyses, the false positive rate was controlled at $\alpha < 0.05$ (corrected) with a minimum cluster size of 10 voxels, by performing 2000 Monte-Carlo permutation tests on the data (Nichols and Holmes 2002).

Whole-brain, conjunction analyses were performed to identify regions that showed a competition response profile (inconsistent > consistent > control) and a semantic priming response profile (control > inconsistent > consistent). Notably, although the target words in the control condition were longer and less frequent than the ambiguous words, neither the competition nor the semantic priming predictions were confounded with a prediction based on length or frequency. Unlike the competition or adaptation predictions, according to the length and frequency prediction, control words should show greatest activity with inconsistent and consistent words showing equal responses. None of the regions discussed in the results section showed such an effect. For the competition conjunction analysis the group maps for the inconsistent-consistent contrast were overlaid with the group map of the consistent-control contrast. To identify regions that responded to semantic adaptation group maps of the control-inconsistent contrasts were overlaid with group maps of inconsistent-consistent contrasts. For the conjunction analyses each group map was thresholded by performing 2000 Monte-Carlo permutations to calculate a critical t that ensured that under the null hypothesis a single voxel would exceed threshold for both effects less 5% of the time (VoxBo www.voxbo.org). This analysis identifies voxels that show a similar effect across the 2 contrasts, but does not ensure that these voxels reach significance in both contrast independently (Price and Friston 1997; Friston et al. 2005). The latter was accomplished by testing each contrast independently as described above.

Results

Behavioral Data

The behavioral measures of interest were the accuracy and reaction time to the 2nd pair in the trial as a function of condition (consistent vs. inconsistent). Participants were faster to respond in the consistent ($M = 1185$ ms, $SD = 191$) than inconsistent condition ($M = 1301$ ms, $SD = 224$; $F_{1,57} = 23.72$, $P < 0.0001$). (There was neither an effect of ambiguity [i.e., homonymous vs. polysemous] type, nor an ambiguity type by consistency interaction in the reaction time data; $F_{1,57} = 1.1$.) The average reaction time for the control trials ($M = 1237$ ms,

SD = 199) fell between that of the consistent and inconsistent conditions and did not differ from the ambiguous trials (collapsing across consistent and inconsistent conditions, $M = 1243$ ms, $SD = 204$), $t(19) = 0.26$, $P = 0.79$). The mean reaction time for filler trials was 1357 ms ($SD = 209$).

Participants were more likely to make a yes response in the consistent ($M = 81.2\%$, $SD = 13.1$) than inconsistent condition ($M = 73.6\%$, $SD = 17.3$; $F_{1,57} = 10.73$, $P < 0.01$). The consistency effect on accuracy varied considerably across participants, ranging from a 39% difference to a -8.0% difference. There was no effect of ambiguity type, nor an ambiguity type by consistency interaction in the accuracy data ($F_{1,57} < 1$). Participants were more likely to make a “Yes” response on control trials ($M = 94.2\%$, $SD = 4.3$), than on ambiguous trials ($M = 77.4\%$, $SD = 13$; $t(19) = 6.77$, $P < 0.0001$). Participants made an accurate response to the 2nd pair of filler trials 94.3% of the time. Trials where participants made an error (i.e. responded “no”) to the 1st or 2nd word pair were excluded from the fMRI analysis.

fMRI Data

Competition Effect: Anatomical ROI Analysis in IVPFC

Based on the hypothesis that activity in the IVPFC is modulated by semantic competition, we predicted that the IVPFC would show maximal activity in the inconsistent condition, an intermediate amount of activity in the consistent condition and the lowest amount of activity in the control condition (competition response). To test this hypothesis, we examined contrasts between both the inconsistent versus consistent conditions and the consistent versus control conditions in the following IVPFC anatomically defined ROIs: the left orbitalis, left opercularis, left triangularis, and the left inferior frontal gyrus (LIFG) as a whole.

The LIFG ROI as a whole was significantly more active in the inconsistent than the consistent condition ($t(19) = 2.06$, $P = 0.05$), and more active in the consistent than control condition ($t(19) = 3.70$, $P < 0.005$). The orbitalis, opercularis, and triangularis ROIs were significantly more active in the consistent than control condition ($t(19) > 3$, $P < 0.006$). However, only the opercularis ROI showed a significant difference between the inconsistent and consistent conditions ($t(19) = 3.29$, $P < 0.005$) (Fig. 3). The inconsistent vs. consistent

effect was marginal in the orbitalis ROI ($t(19) = 1.92$, $P < 0.10$) and did not reach significance in the triangularis ROI ($t(19) = 1.54$, $P = 0.14$). Although the effect of consistency was maximal in the opercularis ROI, the region by condition interaction was not significant.

Semantic Adaptation Effects: Function ROI Analysis

In contrast to the IVPFC, we hypothesized that PLTC would show semantic adaptation as a result of semantic similarity between items in successive word pairs. Both the consistent and inconsistent conditions contained repeating words and thus should lead to some semantic adaptation relative to the control condition. However, pair 1 and pair 2 contained more overlapping semantic information in the consistent than inconsistent condition, predicting greater adaptation in the consistent condition.

Following this logic, we used the contrast of [control - (inconsistent + consistent)] to identify voxels in the PLTC that adapted to word repetition (Fig. 4, Table 1). (Because adaptation effects have also been observed in the right PLTC we examined activity in this region as well.) Functional ROIs were defined in the left and right PLTC that showed significantly lower activity for trials with repeating words relative to trials with no repeating words. These ROIs were located primarily in the superior temporal gyrus (STG) bilaterally and extended into the temporoparietal junction (see Fig. 4). If these PLTC voxels show semantic adaptation in particular, they should also be less active in the consistent than inconsistent condition. This prediction was confirmed in both the left ($t(19) = -2.89$, $P = 0.009$) and right ($t(19) = -2.54$, $P = 0.02$) ROIs, which showed significantly more adaptation in the consistent than inconsistent condition. In contrast, a region in the cuneus that also responded to word repetition did not show a specific semantic adaptation effect ($t = 1.09$, $P = 0.29$).

Competition and Semantic Priming Effects: Whole-brain Analyses

We performed a whole-brain, random-effects, conjunction analysis (Price and Friston 1997; Friston et al. 2005) to identify regions that displayed a “competition response” (inconsistent > consistent > control), and regions that displayed a “semantic adaptation response” (control > inconsistent > consistent). The LIFG, left middle frontal gyrus (LMFG), left anterior cingulate/medial frontal gyrus, and right cerebellum showed

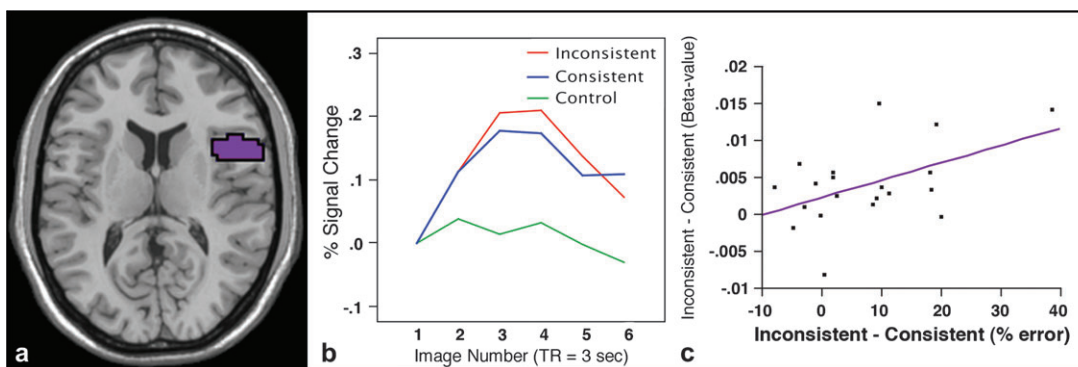


Figure 3. Competition effect in left opercularis. (a) Left opercularis anatomical ROI displayed on a template. (b) Average time series data for each of the 3 conditions: inconsistent, consistent, and control. Percent signal change from zero is on the y-axis, image number (TR) is on the x-axis. (c) Correlation between inconsistent versus consistent difference in the opercularis and the behavioral competition effect across participants. The inconsistent - consistent beta value is on the y-axis. Inconsistent - consistent percent errors is on the x-axis. Each point represents a single subject.

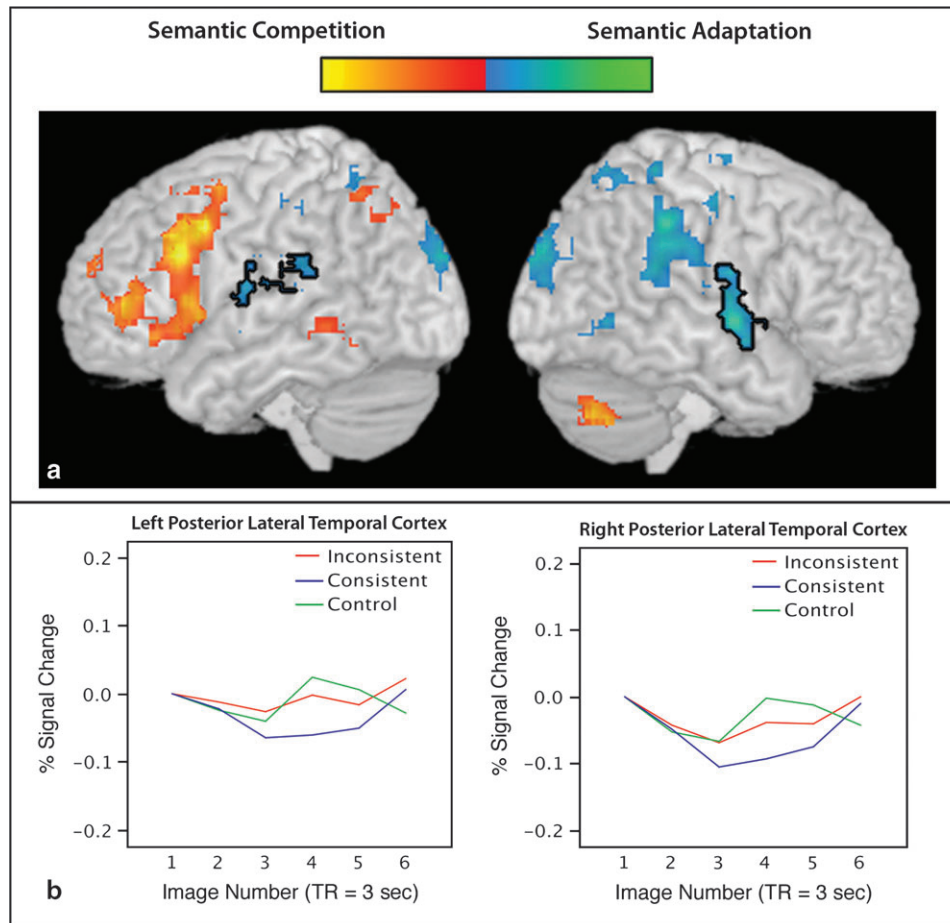


Figure 4. Semantic repetition effects in posterior temporal ROIs. (a) Group activation maps of the [(inconsistent + consistent) – control] contrast are displayed on a template. Regions that responded to competition [(inconsistent + consistent) > control] are displayed in warm colors and regions responded to semantic adaptation [control > (inconsistent + consistent)] are depicted in cool colors. The figure is thresholded at $P < 0.05$ (corrected). PLTC functionally defined ROIs are outlined in black. (b) Average time series data in PLTC function ROIs. Percent signal change from zero is on the y-axis, image number (TR) is on the x-axis.

Table 1

Brain regions activated by the [(inconsistent + consistent) – control] contrast

Brain regions activated by the (inconsistent + consistent) – control contrast

| Brain region | BA | mm ³ | x | y | z | t _{max} |
|---|--------------|-----------------|-----|-----|-----|------------------|
| (Inconsistent + consistent) > control | | | | | | |
| Left inferior/middle frontal gyri | 10/46/44/9/6 | 1908 | -54 | 9 | 39 | 8.30 |
| Anterior cingulate/ | 32/6 | 774 | -3 | 33 | 42 | 7.54 |
| Medial frontal gyrus | | | | | | |
| Right cerebellum | — | 204 | 36 | -69 | -39 | 6.53 |
| Left superior/middle frontal gyri | 10 | 81 | -24 | 57 | 24 | 5.59 |
| Left caudate nucleus | — | 39 | -12 | -6 | 18 | 5.29 |
| Left inferior/superior parietal lobules | 40/7 | 159 | -45 | -57 | 54 | 5.16 |
| Left middle temporal gyrus | 21 | 117 | -57 | -42 | -3 | 4.82 |
| Control > (inconsistent + consistent) | | | | | | |
| Right STG/insula | 22/13 | 906 | 42 | -3 | 0 | 8.62 |
| Right STG | 40/41/42 | 1017 | 57 | -36 | 21 | 8.35 |
| Inferior parietal lobule | | | | | | |
| Left STG/insula | 22/13 | 819 | -39 | -15 | 6 | 7.49 |
| Bilateral cuneus | 19/18 | 1158 | 3 | -87 | 30 | 7.37 |
| Bilateral paracentral lobule | 5/6 | 867 | -3 | -33 | 54 | 7.05 |
| Right paracentral lobule | 5/7 | 102 | 15 | -45 | 63 | 6.72 |
| Right posterior cingulate | 29 | 189 | -12 | -45 | 18 | 6.67 |
| Right middle/inferior temporal gyri | 37/19 | 105 | 48 | -60 | -3 | 6.06 |
| Right lingual gyrus | 19/18 | 204 | 9 | -63 | -9 | 5.92 |
| Right precuneus | 7 | 165 | -15 | -54 | 51 | 5.63 |
| Left lingual gyrus | 19/18 | 144 | -21 | -78 | -3 | 5.47 |

a “semantic competition” response profile. In contrast, voxels in bilateral STG and adjacent insula were sensitive to semantic adaptation (Fig. 5, Table 2).

Consistency by Ambiguity Type Interaction

We conducted whole-brain and ROI analyses to test whether regions that showed a main effect of competition and semantic adaptation also showed a consistency (inconsistent/consistent) by ambiguity type (homonymous/polysemous) interaction. No regions showed an ambiguity-type-by-consistency interaction either in the whole-brain or ROI analysis (all P 's > 0.30).

Individual Differences Analysis

After retrieving one meaning of an ambiguous word, some participants appeared to have particular difficulty retrieving a different meaning for that same word. That is, the effect of our consistency manipulation on accuracy varied considerably across participants. On average, participants were 7.43% (SD = 11.27%) more accurate in the consistent than inconsistent condition. However, the size of this accuracy effect ranged from 39% to a -8.0% difference in the opposite direction. This variability in the accuracy difference between the consistent and inconsistent conditions may reflect variability in the

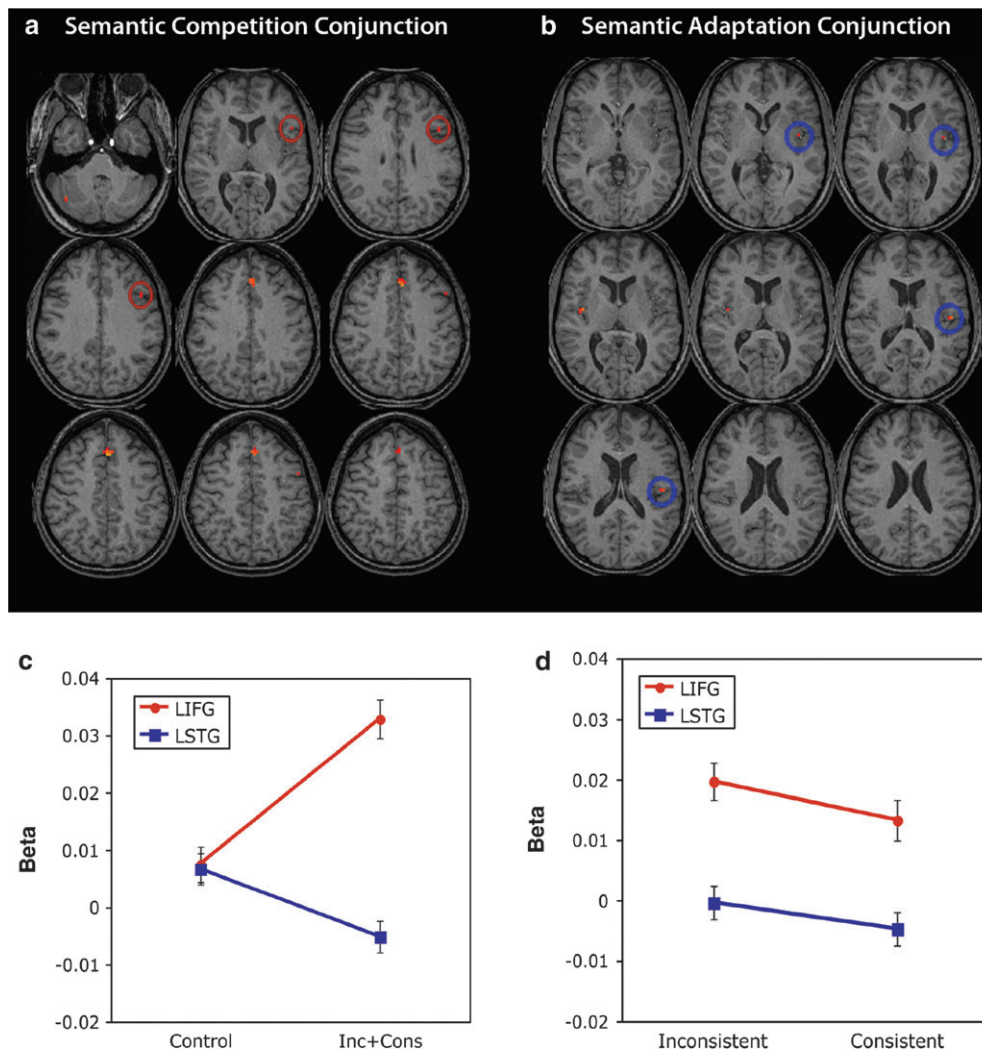


Figure 5. Semantic competition and adaptation conjunctions. Whole-brain results of the competition and adaptation conjunctions are displayed on a normalized anatomical scan of one subject. The figures are thresholded at $P < 0.05$ (corrected). (a) The competition conjunction [(inconsistent > consistent) and (consistent > control)], LIFG/MFG region is outlined in red. (b) The semantic adaptation conjunction [(control > inconsistent) and inconsistent > consistent], LSTG voxels are outlined in blue. (c) LIFG and LSTG activity for the inconsistent + consistent conditions, relative to the control. (d) LIFG and LSTG activity in the inconsistent and consistent conditions. Error bars represent the standard error of the mean.

Table 2
Competition and semantic adaptation conjunctions

| Competition and semantic priming conjunctions | | | | | | |
|---|----------|-----------------|-----|-----|-----|------------------|
| Brain region | BA | mm ³ | x | y | z | t _{max} |
| Competition conjunction | | | | | | |
| Anterior cingulate | 24 | 78 | 0 | 27 | 42 | 4.28 |
| Right cerebellum | — | 6 | 39 | -66 | -39 | 3.62 |
| Left inferior/middle frontal gyri | 44/9 | 15 | -48 | 15 | 9 | 3.34 |
| Left middle frontal gyrus | 9/6 | 6 | -51 | 6 | 45 | 3.26 |
| Semantic priming conjunction | | | | | | |
| Right insula/STG | 13/22 | 12 | 39 | -9 | 9 | 3.90 |
| Posterior left lateral sulcus | 41/43/40 | 12 | -48 | -18 | 15 | 3.84 |
| Left insula | 13 | 6 | -39 | -9 | 6 | 3.40 |

amount of competition that subjects experienced as a result of our consistency manipulation. (The difference between accuracy in the inconsistent and consistent conditions is unlikely to result from different amounts of “semantic priming” because such effects are rarely observed in accuracy data, and when

observed are typically orders of magnitude smaller than the accuracy difference observed in this experiment; Neely 1991.)

We reasoned that participants that experience more competition, as evidenced by their errors, might experience greater competition even on trials where they are able to overcome this competition and make an appropriate response. Thus we predicted that participants who experienced more competition, as evidenced by their performance, would also show a larger competition effect as measured by IVPFC activity even on correct trials.

We performed an individual differences analysis focusing on the left opercularis because this region showed the largest main effect of consistency. A correlation was calculated between the accuracy difference between the consistent and inconsistent conditions, and the BOLD difference between these conditions in the left opercularis. As predicted, the accuracy and BOLD differences between the consistent and inconsistent conditions were significantly correlated ($r = 0.49$, $P < 0.05$, Fig. 3).

To ensure that this correlation was not due to a main effect of accuracy on IVLPFC activity, we also evaluated the correlation using residual values, after modeling the effects of overall accuracy on the difference between the 2 conditions. These residualized difference scores were significantly correlated with IVLPFC activity across participants ($r = 0.52$, $P < 0.05$). (Notably, because incorrect trials were dropped from fMRI analyses, this correlation cannot be attributed to BOLD differences between correct and incorrect trials.)

We also calculated correlations between the consistency effect observed in the accuracy data and activity in regions that showed effects of semantic competition and semantic adaptation in the whole-brain, conjunction analysis. We hypothesized that activity in regions responding to semantic competition, but not semantic adaptation would correlate with this behavioral measure of competition. As predicted, the behavioral competition effect was significantly correlated with activity in regions that showed a competition profile: the IVLPFC and the right cerebellum (LIFG BA 44/9 $r = 0.52$, $P < 0.05$; right cerebellum $r = 0.65$, $P < 0.01$, see Fig. 3, Table 2). In contrast, there was no relationship between the accuracy competition effect and activity of PLTC regions identified in the semantic adaptation contrast ($-0.24 > r > -0.01$, $P > 0.30$).

Discussion

Comprehending related words in sequences engages at least 2 processes: the reactivation of the same semantic information (semantic adaptation) and biasing of semantic networks away from context irrelevant meanings in favor of the context relevant meaning (reduced semantic competition). The distinct patterns of fMRI activity we observed are most consistent with the interpretation that activity in regions of the IVLPFC (specifically, the LIFG and LMFG) varies as a function of semantic competition, whereas activity in the PLTC (specifically, the STG and adjacent insula bilaterally) varies as a function of semantic adaptation.

The IVLPFC was significantly more active in a semantically ambiguous, than a semantically unambiguous condition. This occurred despite the fact that the ambiguous condition, but not the unambiguous condition, contained repeating words. Moreover, activity was highest in the IVLPFC when participants had to retrieve a meaning of an ambiguous word after a different meaning of that word had been primed. In contrast, activity was maximal in the PLTC when participants had to retrieve an unprimed meaning irrespective of ambiguity, and the amount of PLTC activity was inversely related to the amount of repeating semantic information.

Neural Response to Semantic Competition

Previous research has shown that the IVLPFC plays a critical role in selecting context-appropriate semantic information in the face of competition (Thompson-Schill et al. 1997, 1998, 1999; Kan and Thompson-Schill 2004a, 2004b; Hirshorn and Thompson-Schill 2006). Several recent studies suggest that the IVLPFC responds to increases in several forms of linguistic ambiguity at the phonological, lexical-semantic, and sentence processing levels (Cardillo et al. 2004; Stowe et al. 2004; Blumstein et al. 2005; Rodd et al. 2005). We replicate and extend these findings by illustrating that activity in IVLPFC increases as a function of competition that arises from the interaction of context and the inherent semantic ambiguity of word forms.

The current finding is consistent with recent research showing increased IVLPFC activity to language stimuli that contain ambiguous words, compared with those that do not (Rodd et al. 2005; Copland et al. 2007; Gennari et al. 2007; Mason and Just 2007; Zempleni et al. 2007). Furthermore, patients with IVLPFC damage show a delay in selecting the context-appropriate meaning of ambiguous words (Milberg et al. 1987; Swaab et al. 1998; Bedny et al. 2006). Together, these data suggest that the IVLPFC exerts cognitive control during word comprehension by biasing posterior networks toward context-appropriate meanings.

In the present study the effect of competition within the IVLPFC was maximal in the pars opercularis on the border of the LIFG and LMFG (BA 44/9). This finding is consistent with prior research showing that competition effects within the IVLPFC are maximal in the opercularis region bordering the MFG (e.g., Badre et al. 2005). Recently, it has been proposed that the posterior aspect of the LIFG (BA 44/45) is important for resolving competition, whereas the anterior aspect of the LIFG (BA 47/45) is important in controlled retrieval of semantic information (Badre et al. 2005). Although we did not find evidence of heterogeneity in the competition effect across the LIFG (no region by effect size interaction), our findings are not inconsistent with the proposal that posterior aspects of the LIFG respond to this type of competition, whereas more anterior aspects of the LIFG are sensitive to other aspects of cognitive control (Badre et al. 2005). However, the present data are not reconcilable with the notion that other regions within the IVLPFC show effects of semantic adaptation. In all regions within the IVLPFC there was significantly greater activity when words repeated but competition between meanings was high, as compared with when there were no repeating words but competition was low (inconsistent > control). This finding indicates that previously reported semantic adaptation effects throughout the IVLPFC might have resulted from reduced competition, and not repetition suppression per se.

The size of the competition effect in the IVLPFC was correlated across participants with the size of our behavioral measure of conflict. When a context irrelevant meaning of an ambiguous word was primed, some participants had particular difficulty retrieving the context-appropriate meaning as evidence by higher error rates in the inconsistent condition. These subjects also showed a larger consistency effect in the IVLPFC on correct trials. This finding provides further evidence that the IVLPFC responds to lexical-semantic competition. Moreover, it suggests that there are important individual differences in the extent to which participants get “stuck” on a representation within semantic space. These differences may reflect either the nature of the semantic representations themselves, or the properties of the conflict resolution mechanism, and they may reflect stable, trait-like variations across individuals or temporary differences in the state of the participants (e.g., fatigue). Further research is required to understand the neural substrates of these individual differences.

In addition to the IVLPFC, the anterior cingulate and the superior right cerebellum responded to increases in competition. Like the IVLPFC, these brain regions have previously been observed to respond to competition and are frequently coactivated with the IVLPFC (Frith et al. 1991; Raichle et al. 1994; Buckner et al. 1995; Thompson-Schill et al. 1997). Our findings provide further support for idea that these regions participate in cognitive control.

However, prior evidence suggests that the anterior cingulate and the right superior cerebellum make different contributions to cognitive control from that of the IVPFC. While the IVPFC implements control, the anterior cingulate is thought to detect conflict and adjust the amount of control exerted by the prefrontal cortex (Casey et al. 2000; Cohen et al. 2000; MacDonald et al. 2000; Botvinick et al. 2001; Milham et al. 2001; Botvinick and Plaut 2002; Milham et al. 2003; Nelson et al. 2003; Botvinick et al. 2004). Consistent with this idea, a recent functional connectivity analysis suggests that the anterior cingulate modulates connectivity in frontotemporal networks during word comprehension (Stamatakis et al. 2005).

The right cerebellum also responded to semantic conflict. As in the IVPFC, activity in this region was correlated with the number of conflict-induced errors across participants. This finding is in line with a large body of research suggesting that the right cerebellum plays an important role in language processing, and executive function more generally (for a review see Marien et al. 2001; Ramnani 2006). The right cerebellum is reciprocally connected to the LIFG BA 6, 44, and 45 and is frequently coactivated with the IVPFC in functional neuroimaging studies (Leiner et al. 1986, 1989; Engelborghs et al. 1998). For example, a recent study reported increased IVPFC and right cerebellar activity when participants comprehended ambiguous as compared with unambiguous sentences (Stowe et al. 2004). Similarly, damage to the right cerebellum can lead to deficits typically associated with IVPFC lesions such as lack of spontaneous speech and receptive agrammatism (Riva and Giorgi 2000; Marien et al. 2001). In combination with prior research, the present findings support the hypothesis that the right cerebellum contributes to cognitive control during language processing. However, there is also evidence that the contributions of the IVPFC and the right cerebellum to cognitive control are qualitatively distinct. The cerebellum is thought to simulate outputs of prefrontal cortices, and apply cognitive control in a more efficient but less flexible way than those IVPFC regions to which it is functionally connected (Ramnani 2006).

In summary, a network of regions—including the IVPFC—are involved in cognitive control during language processing. These regions respond to semantic competition, and not semantic adaptation.

An interesting aspect of the present data is that, although several regions showed a main effect of competition, no regions showed an interaction between the size of the competition effect and ambiguity type. That is, homonyms and polysemous words had similar effects of semantic competition. We interpret this finding to indicate that both homonymy and polysemy have the potential to increase semantic competition. However, there are 2 important caveats to this interpretation. First, the phenomenon of polysemy has a variety of subtypes that were not examined in this study. There may be distinctions between the amounts of competition that arises from different types of polysemous ambiguity (Klepousniotou 2002). Second, the amount of competition during word comprehension is a function of the intrinsic ambiguity of a word form, and the extent to which the current context taps into this ambiguity. Consequently, it is impossible to say to what extent competition during polysemous and homonymous trials reflected the intrinsic ambiguity of these word types as opposed to the extent to which the context emphasized this ambiguity. Finally it is important to note that

the present findings do not contradict data suggesting important representational differences between homonymous and polysemous words (Williams 1992; Beretta et al. 2005; Pylkkanen et al. 2006). Rather, our findings are compatible with the notion that, despite these differences, the meanings of both homonymous and polysemous words can compete when the context favors one meaning over another (Klein and Murphy 2001, 2002).

Neural Response to Semantic Repetition

When we see or hear a word, we retrieve a meaning from long-term memory. According to neural-network models of comprehension, representations of word meanings that are similar to each other share processing units (Masson 1995; Plaut 1995). Within this framework, semantic adaptation reflects the repeated firing of neurons that participate in the retrieval of related words. We found that as more semantic information repeated, activity diminished in the PLTC (the STG and adjacent insular cortex bilaterally). This finding is consistent with prior studies that have found semantic adaptation in the PLTC (e.g., Helenius et al. 1998; Kotz et al. 2002; Wible et al. 2006). In this study we demonstrate that in contrast to the IVPFC, the PLTC does not respond to increases in semantic competition, and activity in the PLTC is not correlated with behavioral measures of conflict. The present data is therefore consistent with the hypothesis that the PLTC is important for activating lexical-semantic information.

How does the PLTC contribute to word comprehension? One possibility is that this region stores word meanings. Consistent with this idea, the PLTC responds to manipulations of semantic context. As reviewed in the introduction, and replicated in the present study, the PLTC shows semantic adaptation effects in neuroimaging studies of semantic priming (e.g., Rissman et al. 2003; Wible et al. 2006). The PLTC also shows an increased response to semantically anomalous (as compared with non-anomalous) sentences (Ni et al. 2000; Friederici et al. 2003). However, several sources of evidence cast doubt on the notion that the PLTC is the seat of lexical-semantics.

Several studies suggest that damage to the anterior, but not the posterior aspect of the LTC causes semantic deficits (Dronkers et al. 2004). Bilateral damage restricted to the posterior aspect of the STG is associated with “pure word deafness,” the inability to comprehend speech in the absence of a general deafness or a semantic deficit (Buchman et al. 1986). Furthermore, damage to a set of other regions such as the middle temporal gyrus, ventral temporal, and parietal cortices are associated with various semantic deficits (Bates et al. 2003; Dronkers et al. 2004). Additionally, a large body of neuroimaging studies implicates the PLTC in word-form processing. Subregions within the PLTC respond to speech and speech like stimuli (Corbetta et al. 2000; Hickok and Poeppel 2000; Wise et al. 2001). Although the PLTC is activated both when subjects read and hear words this could be because phonological word forms are retrieved during reading (Price 2000; Nakada et al. 2001). Based on this evidence it has been proposed that the bilateral STG represents “sound-based” speech representations that are connected via the temporoparietal junction to distributed lexical-semantic representations stored elsewhere (Hickok and Poeppel 2000). Within this framework the PLTC serves as the “entry point” between word form and lexical-semantic representations (Demonet et al. 2005).

Thus the current data can be interpreted in 3 ways, the PLTC represents semantic information or activates information stored elsewhere, or both. At present, the prior literature is more consistent with the idea that the PLTC region we identified serves as the entry point to semantic representations that are distributed throughout a cortical network (Caramazza and Shelton 1998; Tyler and Moss 2001; Thompson-Schill 2003; Damasio et al. 2004). Based on these data, we tentatively favor the interpretation that the observed repetition suppression effects in the PLTC reflect the more efficient activation of primed semantic information. If this interpretation is correct, why did we not observe semantic adaptation effects in those regions that represent semantic information? One possible reason is that the meanings of the words used in the present study are so heterogeneous that there is no brain region consistently involved in representing all of them. Alternatively, it is possible that regions involved in representing semantic information are sufficiently variable across subjects so as not to be observed in group-analyses. Distinguishing between regions involved in accessing semantic information and those involved in representing it is an important, and difficult problem for future research.

A further question concerns whether the PLTC region we observed is involved in controlled or automatic aspects of meaning activation. Both controlled and automatic processes are likely to play a role during natural language comprehension (Neely 1991). However, different psychological tasks can emphasize either controlled or automatic processes. Given the nature of the present task, the observed semantic adaptation effects could reflect either or both of these processes. Previous fMRI studies that focused on automatic aspects of semantic adaptation found adaptation in a PLTC region similar to the presently observed effect (Rissman et al. 2003). Possibly, the same brain region subserves automatic and controlled aspects of semantic adaptation. However, irrespective of whether the present data reflect automatic or controlled aspects of semantic adaptation, this adaptation reflects the more efficient activation of semantic information, rather than competition among meanings.

Conclusions

The IVPFC and PLTC are components of the neural circuit that supports normal word comprehension. The present data dissociate the functional contributions of these brain regions. We suggest that the IVPFC resolves semantic competition during word comprehension. Such competition arises through the interaction between the intrinsic ambiguity of word forms and the current context. In the present study, IVPFC activity was maximal when semantic information repeated, but semantic competition was high; and was minimal when semantic information did not repeat but semantic competition was low. In contrast, a region in the posterior aspect of the PLTC showed the opposite pattern of activation. The PLTC responded to increases in the amount of new semantic information activated, but did not respond to changes in the amount of semantic competition. These data suggest that the PLTC activates the meanings of words stored in long-term memory. In contrast the IVPFC biases posterior brain regions toward a context-appropriate meaning, thus rapidly resolving conflict.

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