The role of the left prefrontal cortex in sentence-level semantic integration

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Whether left inferior frontal gyrus (LIFG) activation during sentence comprehension reflects semantic integration or domain-general cognitive control remains unclear. To address this issue, 26 participants were presented with sentences word by word during fMRI scanning and were asked to perform two semantic tasks, one explicit (semantic congruency judgment) and one implicit (font size judgment). In the two language tasks, semantic integration load was parametrically manipulated with high close, low close and semantically violated sentences. Participants also performed a classical Stroop task during scanning. Conjunction analysis of the explicit and implicit tasks revealed two regions in left inferior frontal gyrus associated with semantic integration load: one anterior region (aIFG) and one posterior region (pIFG). However, only the pIFG region was also activated during the Stroop task. These results indicate that different regions in the LIFG play different roles in semantic integration, with aIFG more important for domain-specific processing and pIFG more important for domain-general cognitive control.

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Introduction

To comprehend a sentence, the reader needs to combine the semantic activations of the individual words to form a coherent, meaningful representation. Such a process is usually referred to as semantic integration (e.g., Jung-Beeman, 2005; Rogalsky and Hickok, 2009). The representation constructed from the words read so far forms a context into which the next word has to be connected or bound, a process referred to as information binding (Hagoort, 2005). In addition, semantic integration also includes a selection process (Hagoort, 2005; Lau et al., 2008). For example, many words are ambiguous, and their appropriate meaning has to be selected out of several possible meanings for a specific context. Further, the reader would constantly make predictions about the incoming words based upon the present context, either intentionally or unintentionally. In cases in which the incoming word differs from the predicted word, the more appropriate meaning must be selected over the inappropiate meanings for successful integration.

There is a large body of evidence suggesting that left inferior frontal gyrus (LIFG) plays a critical role in sentence-level semantic integration. LIFG activation is found when a critical word semantically violates the overall sentence context (e.g., Newman et al., 2001; Ni et al., 2000; Zhu et al., 2009) or does not fit sentence expectations, though its role can be semantically acceptable (e.g., Baumgaertner et al., 2002; Huang et al., 2012). Moreover, LIFG activation is observed when a specific word meaning needs to be selected from multiple meanings of an ambiguous critical word to fit the sentence context (e.g., Rodd et al., 2005, 2012; Zempleni et al., 2007).

Theoretical models have linked sub-regions in the LIFG, including pars orbitalis (BA 47), pars triangularis (BA 45), pars opercularis (BA 44) and deep frontal operculum, with varied linguistic processes (review see Bookheimer, 2002; Price, 2012; Rogalsky and Hickok, 2011). Friederici (2012) proposes that pars triangularis and pars orbitalis support semantic processing, while pars opercularis and the frontal operculum (FOP) subserve syntactic processing. Hagoort (2005) proposes an anterior-ventral to posterior-dorsal gradient in LIFG responsible for a “unification” operation of semantics, syntax and phonology. Some researchers propose that LIFG contributes to controlled semantic processing. Specifically, the anterior portion of LIFG (aIFG) is suggested to be involved in controlled semantic retrieval, while the posterior portion of LIFG (pIFG) supports competition and selection (Jung-Beeman, 2005; Lau et al., 2008).

Beyond its role in language, LIFG is known to be important for domain-general cognitive control (Duncan and Owen, 2000; Miller and Cohen, 2001), such as selection between competitors and regulation of conflicts (January et al., 2009; Novick et al., 2005). There is, thus, the possibility that LIFG activation in semantic integration could be solely explained by general cognitive control, i.e., to select a propitiates candidate from among competitors and to implement reanalysis in the face of misinterpretation. In the presence of ambiguity, cognitive control is needed to select a proper meaning and to resolve the conflict between context and other potential meanings that are context irrelevant. Empirically, overlap was found between activation related to

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general cognitive control and to syntactic ambiguity resolution (January et al., 2009) and semantic integration (Ye and Zhou, 2009a).

Instead of attributing LIFG activation in semantic integration solely to general control, Badre and Wagner (2007) propose a dual-account theory that divides lexical semantic processing into separate processes involving accessing stored conceptual representations and selecting among active competitors. While the access process is proposed to be specific to semantics, the selection process is considered to be domain-general. In support of this theory, their study showed anterior LIFG activation for semantic access and middle LIFG activation for selection (Badre et al., 2005).

Although the dual-account theory was developed for word processing, it also suggests a possible way to understand LIFG function in sentence-level semantic integration. That is, semantic integration includes both domain-specific processes and domain-general processes, which may be associated with different parts of LIFG. In the present study, we tested this possibility by comparing brain activations associated with semantic integration and with cognitive control. Key to the present study, the classical Stroop paradigm was used to measure cognitive control free from sentence-level linguistic processing.

Another feature of the present study was the use of a 3-condition design manipulating semantic integration load parametrically, as in Zhu et al. (2012). Zhu et al. constructed high cloze (HC), low cloze (LC) and semantically violated (SV) sentences. They showed that both N400 amplitude (an index for semantic integration) and LIFG activation were modulated parametrically across the three conditions. In the literature, most studies of semantic integration compare only two conditions to identify semantic integration, and their contrasts are often confounded by cognitive control. For example, incongruent sentences may capture more attention and trigger automatic semantic recovery, a process not necessarily engaged for congruent sentences (Kaan and Swaab, 2003; Zhu et al., 2009). Such processes are less likely to be a problem in a 3-condition parametric design, which would only identify processes common to all conditions across different levels of processing.

Third, the present study used both an explicit and an implicit language task for localizing regions for semantic integration, following Zhu et al. (2012). Previous studies have mostly exclusively used explicit language tasks in which participants could adopt task-specific strategies (Caplan et al., 2008; Newman et al., 2009; Zhu et al., 2012). Such strategies may inately involve attentional control, which is highly dependent upon the prefrontal cortex, especially the pLIFG (Crimion et al., 2003; Van Petten and Luka, 2006; Vuong and Martin, 2011). When comparing violated or unexpected critical words with control words, attentional control and other task-specific processing would confound the semantic integration effect (Zhu et al., 2009). In the current study, a font size judgment task is used as the implicit semantic task. Focusing on font size helps to reduce a task-induced attentional effect, as attention was comparable across conditions. Zhu et al. (2012) observed semantic integration modulation with the font size task, indicating its validity as an implicit semantic task. Given that both the explicit task and the implicit task engage semantic integration, a conjunction analysis of the two would effectively eliminate brain activations associated with task-specific strategies including attentional control and would provide a purer depiction of the neural basis of semantic activation.

Briefly, the present study was intended to understand how LIFG contributes to semantic integration during sentence comprehension and, more specifically, to address the relationship between semantic integration and general cognitive control. Both explicit and implicit semantic tasks were used to better localize brain regions for semantic integration, and the Stroop task was used to localize brain regions for general cognitive control. We are interested in whether there is a sub-region in LIFG that is sensitive to semantic task but not to cognitive control. If such a region is found, our results would suggest the presence of a domain-specific process for semantic integration. If, instead, all semantic tasks as well as the Stroop task show completely overlapping regions of activation in the LIFG, our results would instead suggest that the role of LIFG in semantic integration can be solely attributed to domain-general cognitive control processes.

Methods

Participants

Twenty-six healthy native Chinese speakers participated in the experiment (16 female, 10 male; age range 20–28 years, mean age 23.2 years). All were right-handed with normal or corrected-to-normal vision, and none showed neurological impairment. All signed a written informed consent form approved by the local ethics committee.

Stimuli

Following previous studies (Hagoort and Brown, 1994; Zhu et al., 2012), semantic integration load was manipulated by changing the fitness between context constraints and a critical word. We modified a common two-condition contrast (congruent vs. incongruent sentences) to a parametric design to include three types of sentences: high cloze (HC), low cloze (LC), and semantically violated (SV) sentences. Prior EEG research has shown that such sentence-type manipulations significantly modulate N400 amplitude, an index of semantic integration load (Hagoort et al., 2009).

First, 144 sentences (each 8 to 13 words in length) with highly constraining contexts were constructed (HC, e.g., 强盗们在商量抢劫银行的时候被逮捕了, “The robbers were arrested by the policemen when they were planning to rob the bank”). Each sentence was then modified by replacing a noun (i.e., 银行, bank) with a semantically unexpected noun (电脑, computer) that was nevertheless semantically congruent within the context (LC condition). Next, the same noun was replaced with a noun (鼻涕, snot) that was anomalous within the semantic context of the sentence (SV condition). Importantly, the critical words (CWs) in the HC, LC and SV conditions were counterbalanced so that the same word (e.g., computer) appeared once in each of the HC, LC and SV conditions. Cloze probabilities of the sentences were rated by another 58 participants from the same subject pool. The cloze probabilities of the high cloze condition (the ratio of the most frequently appearing word in all self-generated responses) ranged from 59% to 100% (mean = 89.5%, SD = 10.7%). The cloze probabilities of the high cloze condition were significantly higher than the low cloze condition (which ranged from 0 to 8.6%, mean = 1.0%, SD = 1.8%, t(143) = 91.7, p < .001) and the violation condition (0, i.e., the response was not generated by any participant, t(143) = 96.7, p < .001). The cloze probabilities of the low cloze condition were also significantly higher than the violation condition (t(143) = 6.9, p < .001). The critical words were matched across conditions for the number of word strokes (akin to word length in English) to control visual complexity (mean and SD for HC, LC and SV were 16.3 ± 4.5, 15.9 ± 4.3 and 16.3 ± 4.2, respectively, F < 1) and frequency (mean and SD of log frequency for HC, LC and SV were 2.6 ± 0.7, 2.5 ± 0.7 and 2.6 ± 0.7, respectively, F < 1) (Cai and Brysbaert, 2010). Semantic acceptability ratings for all sentences were obtained on a 6-point Likert scale (1 = entirely unacceptable, 6 = fully acceptable). The average ratings for the HC, LC and SV conditions were 5.2 ± 0.6, 4.9 ± 0.6, and 1.6 ± 0.5, respectively. The acceptability ratings were significantly different across sentence type (F(2, 290) = 2182.8, p < .001) and between condition contrasts (p values < .001).

Sentence presentation was counterbalanced across tasks and participants in two steps. First, the 144 sets of sentences were split into two groups of 72, one for the SEM task and one for the FONT task. The mapping between the groups and the tasks was counterbalanced between participants. Second, in each task, the three sentence conditions were also counterbalanced between participants. Therefore, each sentence
frame would be presented only once to each participant without repetition.

In the FONT task, as the seventh word presented served as the critical word, the word with an altered font size was presented between the eighth and final word in the experimental sentences to avoid confounds from response preparation. There were 36 experimental sentences with a word altered in font size, equally distributed across conditions. To further discourage adoption of specific response strategies, 36 additional filler sentences were included, in which one word between the second and seventh position (before the critical word) was randomly selected to feature a changed font size. The size of the changed word was either smaller (font SONG at size 28) or larger (SONG 54) than the other words (SONG 40).

In addition, a classical Stroop task was adopted with 60 trials for each condition: congruent (Con), incongruent (Incon), and neutral (Neutral). In the Con trials, color words (green, red, yellow and blue) were printed in a color that matched the meaning of the word (green, red, yellow and blue, respectively). In the Incon trials, the color words were printed in a color of an inconsistent color name (e.g., the word green printed in yellow color), with equal combination probability. In the Neutral trials, color-neutral words (e.g., ball) were printed in black.

Procedure

All stimuli were presented with the E-Prime software. The procedure for the FONT and SEM tasks is shown in Fig. 1. Sentences were presented word by word, with words displayed for 300 ms and a 200 ms blank between words (SOA = 500 ms). There was also a 300 ms fixation and a 200 ms blank period prior to the first word presentation. After the sentence presentation, participants were asked to press a button within a 3000 ms response window to indicate whether there was a word with a change in font size in the FONT task or whether the sentence was semantically acceptable in the SEM task. Participants viewed a blank screen after responding on each trial. The total length of each trial was 10 s.

In the Stroop task, a 300 ms fixation was followed by a 200 ms blank screen, and words were then presented for 2000 ms. Participants were asked to indicate whether the printed color was red or yellow (left button) or blue or green (right button). The color-button correspondence was counterbalanced across participants. If the response was completed within 2000 ms, the color word was replaced with a blank screen for the entire 2000 ms duration. Before the next trial started, there was a variable interval of 2000, 2500 or 3000 ms (mean = 2500 ms).

After a short practice session, there were two functional imaging runs with an equal number of trials for each of the FONT, SEM and Stroop tasks. The FONT task was always presented first to the participants, who were not informed that there would be semantic tasks to come; this design was adopted to encourage participants to focus on font size without attending to the semantic information explicitly. The presentation order of the SEM and Stroop tasks was counterbalanced across participants.

fMRI data acquisition

Data acquisition was performed using a Siemens 3 T Trio MR scanner. Whole-brain echo-planar images (EPIs) were acquired in an interleaved manner with ascending slice order (TR = 2000 ms, TE = 30 ms, flip angle = 90°, 32 slices, slice thickness = 4 mm, voxel size 3 x 3 x 4 mm³). A high-resolution T1-weighted scan was acquired for each participant after the functional runs using an MP-RAGE sequence (192 slices, TE = 3.03 ms; slice thickness = 1 mm; voxel size 1 x 1 x 1 mm³).

Preprocessing and whole brain analyses

Data were analyzed with SPM8 (www.fil.ion.ucl.ac.uk/spm). Preprocessing included motion correction by means of rigid body registration along 3 rotations and 3 translations, coregistration between EPI and structural images, normalization to a standard MNI T1 template (interpolation to a voxel size of 2 x 2 x 2 mm³), high-pass filtering (cut-off cycle = 128 s), and spatial filtering with an isotropic Gaussian kernel (FWHM = 6 mm). All statistical analyses were performed within a general linear model framework, first at the single-subject level and then at the random-effect group level.

At the first-level of analysis, parametric modulation of BOLD responses across experimental conditions during presentation of the critical word (500 ms, the stimulus onset asynchrony in the experiment) was estimated for the FONT and SEM tasks separately. This analysis was to reveal voxels showing a monotonic increase in activity as a function of semantic integration load. Following Zhu et al. (2012), −1, 0 and 1 were used in the design matrix for the HC, LC and SV to model the monotonic trend across the conditions. As in previous studies (Hagoort et al., 2004; Zhu et al., 2012), the critical words but not the entire sentences were modeled as regressors as different sentences differed from each other only in the critical words. Words in a sentence other than the critical word, the response period, the trial interval, the filler sentences (in the FONT task), and motion parameters were modeled as nuisance regressors.

At the second-level of analysis, the parametric modulation contrast was set as input for the FONT and SEM task analysis. The group level results revealed monotonic changes with an increased semantic integration load in each task. Then, a conjunction analysis of the FONT and SEM task was used to define regions in which the activation was parametrically modulated by semantic integration load in both tasks. For the Stroop task, an Incon/Con contrast was conducted to localize brain regions associated with the Stroop congruency effect. Independent regions of interest (ROI) analyses were then performed, as described in the ROI analysis section.

Monte Carlo simulations with the AlphaSim program were used to determine the threshold, taking into account both native space voxel dimensions and the effective smoothness of the preprocessed data (http://afni.nimh.nih.gov/pub/dist/doc/manual/AlphaSim.pdf). The simulations used 1000 iterations and indicated a significance level of p < .001 and cluster threshold of 25 voxels for a corrected significance level of p < .05. Activation coordinates reported were in MNI-space. In determining Brodmann Areas for peak activations, the icbm2tal function
ROI analyses

To further investigate the relationship between activation associated with the semantic integration effect and the Stroop congruency effect, a cross-over ROI analysis was conducted. Separate spherical ROIs with a 6-mm radius were drawn based upon the peak coordinates from the activations revealed in the FONT and SEM conjunction analysis and the Stroop congruency effect. The beta values of the Incon and Con conditions were extracted for each participant within these ROIs, derived from the conjunction analysis of the FONT and SEM tasks, and the parametric modulation beta values of the FONT and SEM tasks were extracted within the ROI derived from the Stroop task. These beta values were entered into analyses in SPSS 18.0. In the ROI defined by the Stroop task, a one-sample t-test was performed to test whether there was significant parametric modulation in the SEM and FONT tasks, and the beta values of the Con and Incon conditions were compared to test whether there was a significant Stroop congruency effect in the ROIs defined in the conjunction analysis.

Results

Behavioral results

A one-way repeated-measures analysis of variance (ANOVA) was performed for behavioral data analysis, with pairwise comparison threshold set at $p = .05$ after Bonferroni correction.

In the FONT task, there was no significant main effect by condition of either accuracy ($96.5 \pm 0.8$, $96.5 \pm 0.9$, $94.4 \pm 1.1%$ for HC, LC and SV, respectively, $F(2, 50) = 3.16, p = .07$) or RT ($469 \pm 26$, $470 \pm 25$, $476 \pm 24$ ms for HC, LC and SV, respectively, $F(b1)$).

In the SEM task, there was a significant main effect of accuracy ($98.1 \pm 0.6$, $87.7 \pm 2.0$, $94.6 \pm 1.2%$ for HC, LC and SV, respectively, $F(2, 50) = 15.10, p < .001$). Further comparisons showed that HC > LC, SV > LC, and HC > SV (all $p$ values < .05). There was also a significant main effect of RT ($523 \pm 31$, $592 \pm 38$, $463 \pm 29$ ms for HC, LC and SV, respectively, $F(2, 50) = 15.57, p < .001$, HC < LC, SV < HC, SV < LC, all $p$ values < .05).

For the Stroop task, there was a significant effect by condition for RT ($575 \pm 15$, $664 \pm 18$, $603 \pm 18$ ms for Con, Incon and Neutral, respectively, $F(2, 50) = 96.29, p < .01$, all pair-wise comparisons were significant with $p < .001$). The condition effect did not reach significance for accuracy ($99.2 \pm .3$, $98.1 \pm .5$, $99.0 \pm .3%$ for Con, Incon and Neutral, respectively, $F(2, 50) = 2.96, p = .06$).

fMRI results

Regions of activation showing parametric modulation by semantic integration load in the FONT and SEM tasks are shown in Fig. 2.

Table 1

<table>
<thead>
<tr>
<th>Task</th>
<th>Region</th>
<th>BA</th>
<th>MNI</th>
<th>Peak t value</th>
<th>Voxels</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>x</td>
<td>y</td>
<td>z</td>
<td></td>
</tr>
<tr>
<td>Semantic parametric effect</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FONT</td>
<td>MFG</td>
<td>9/46</td>
<td>−40</td>
<td>20</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td>MTG/supramarginal gyrus</td>
<td>21</td>
<td>−64</td>
<td>−46</td>
<td>−4</td>
</tr>
<tr>
<td></td>
<td>STG</td>
<td>20/22</td>
<td>−46</td>
<td>−10</td>
<td>−20</td>
</tr>
<tr>
<td></td>
<td>R medial FG/SFG</td>
<td>6/8</td>
<td>−4</td>
<td>22</td>
<td>52</td>
</tr>
<tr>
<td>SEM</td>
<td>MFG/SFG</td>
<td>9/46</td>
<td>−46</td>
<td>22</td>
<td>34</td>
</tr>
<tr>
<td></td>
<td>precuneus</td>
<td>7</td>
<td>−8</td>
<td>−70</td>
<td>38</td>
</tr>
<tr>
<td></td>
<td>IPL</td>
<td>40</td>
<td>−36</td>
<td>−58</td>
<td>42</td>
</tr>
<tr>
<td></td>
<td>CG</td>
<td>32</td>
<td>0</td>
<td>26</td>
<td>38</td>
</tr>
<tr>
<td></td>
<td>MFG/IFG</td>
<td>8/9</td>
<td>46</td>
<td>26</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td>R MFG/SFG</td>
<td>10/11</td>
<td>−24</td>
<td>50</td>
<td>−12</td>
</tr>
<tr>
<td></td>
<td>PCG</td>
<td>23</td>
<td>4</td>
<td>−26</td>
<td>26</td>
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<tr>
<td>FONT &amp; SEM conjunction</td>
<td>MFG</td>
<td>9</td>
<td>−40</td>
<td>24</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td>IFG/MFG</td>
<td>47/11</td>
<td>−38</td>
<td>40</td>
<td>−10</td>
</tr>
<tr>
<td>Stroop Incon vs. Con</td>
<td>SFG</td>
<td>6</td>
<td>−4</td>
<td>4</td>
<td>58</td>
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<tr>
<td></td>
<td>MFG/IFG</td>
<td>6/9</td>
<td>30</td>
<td>−2</td>
<td>50</td>
</tr>
<tr>
<td></td>
<td>STG/IFG</td>
<td>13/40</td>
<td>−48</td>
<td>−50</td>
<td>18</td>
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<tr>
<td></td>
<td>IFG</td>
<td>37</td>
<td>−46</td>
<td>−62</td>
<td>−12</td>
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<tr>
<td></td>
<td>IPL/precuneus</td>
<td>7/40</td>
<td>−26</td>
<td>−62</td>
<td>38</td>
</tr>
<tr>
<td></td>
<td>STG/insula</td>
<td>13</td>
<td>50</td>
<td>−46</td>
<td>14</td>
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<tr>
<td></td>
<td>insula/IFG</td>
<td>13/47</td>
<td>32</td>
<td>24</td>
<td>−2</td>
</tr>
</tbody>
</table>

Note: L, left; R, right; IFG, inferior frontal gyrus; MFG, middle frontal gyrus; MTG, middle temporal gyrus; STG, superior temporal gyrus; SFG, superior frontal gyrus; IPL, inferior parietal lobule; PCG, posterior cingulate gyrus; FFG, fusiform gyrus.
Table 1. In the FONT task, a modulation effect was found in the left middle frontal gyrus, left middle temporal gyrus/supramarginal gyrus, left superior temporal gyrus, and bilateral medial/superior frontal gyrus. In the SEM task, a modulation effect was found in the left middle/superior frontal gyrus, left precuneus, left inferior parietal lobule, cingulate cortex, right middle frontal gyrus, right middle/superior frontal gyrus, and right posterior cingulate cortex.

Conjunction analysis of the FONT and SEM tasks revealed significant parametric modulation of semantic integration in two LIFG regions as follows: aIFG and pIFG. Table 2 presents the mean beta estimates, showing a monotonic increase from HC, to LC and finally to SV in both tasks and in both ROIs.

In the Stroop task (Fig. 2 and Table 1), the contrasts between the Incon and Con trials and between the Incon and Neutral trials revealed similar activations bilaterally in the frontal gyrus and in the left temporal-parietal junction, with additional activations in the left inferior temporal gyrus and right superior temporal gyrus in the Incon vs. Con contrast.

To explore whether there was overlap between the semantic integration effects and Stroop congruency effects, we plotted the Stroop Incon vs. Con contrast. No significant overlap was observed in the left IFG, while the present conjunction analysis revealed both aIFG and pIFG ROIs.

Importantly, cross-over ROI analysis found overlap as well as dissociation between the semantic integration effect and the Stroop effect. As shown in Fig. 4, in the ROI defined by the Stroop task (pIFG), there was a significant semantic integration load effect in both the FONT and SEM tasks (p values < .05). However, in the ROIs defined by the semantic integration effect, the Stroop congruency effect was only shown in pIFG ROI (p < .05) but not in aIFG ROI (p > .5).

Discussion

To examine the role of LIFG during sentence comprehension, the present study tested the hypothesis that there are both domain-specific and domain-general processes in semantic integration associated with different regions in LIFG. We asked participants to perform two tasks tapping into semantic integration either explicitly or implicitly, the SEM task and the FONT task, and one task tapping into general cognitive control, the Stroop task.

In the FONT task, our behavioral results showed no significant effects of semantic integration load. This finding replicated a previous study (Zhu et al., 2012) which suggested that behavioral performance is not affected by semantic integration load in the FONT task, as this task involves implicit semantic processing.

For the SEM task, the LC condition was less accurate than the HC and SV conditions, and responses in the SV were faster than in the HC and LC conditions. The finding that the incongruent condition (SV) was no more difficult – and perhaps even easier than – the congruent condition (HC or LC) at first appears confusing, as we would expect the behavioral responses to track the semantic integration load, with the manipulation becoming increasingly difficult from HC, LC to SV. However, similar findings have been reported in the literature in several languages (e.g., in European languages: Kuperberg et al., 2000, 2003, 2008; Osterhout and Nicol, 1999; in Chinese: Schirmer et al., 2005; Wang et al., 2008; Zhu et al., 2012).

Apparently, behavioral measures such as RT may be affected by factors other than semantic integration load, e.g., task strategy. Explicit semantic tasks such as semantic congruency judgments place high demands on participants to attend to linguistic features, potentially eliciting strategic processing (Van Petten and Luka, 2006). Strategic processes unrelated to language processing may interact with the experimental manipulation; for example, “Yes” and “No” responses may recruit different processes, and this may have differential effects on the congruent and incongruent conditions and thus affect behavioral performance (Zhu et al., 2009). Given these confounds, RT may not always track semantic integration, and our analysis was focused on brain imaging data.

The imaging results revealed parametric modulation of LIFG activation by semantic integration load. A conjunction analysis of the FONT and SEM tasks revealed two key clusters: one in aIFG and one in pIFG. This pIFG activation (broadly BA 9, 44, 45) has been previously found for semantic integration (Constable et al., 2004; Dien et al., 2008; Rodd et al., 2012; Zempleni et al., 2007). The aIFG activation has also been reported in explicit sentence comprehension studies (e.g., Kiehl et al., 2002; Ruschemeyer et al., 2005; Tesink et al., 2009) and in an implicit language task (Crinion et al., 2003; Zhu et al., 2012).

In a similar conjunction, Zhu et al. (2012) observed activation only in aIFG, while the present conjunction analysis revealed both aIFG and pIFG. This difference may be due to the different magnetic field strength in the two studies, which was 1.5 T in the previous study.
and 3.0 T in the present one. Increased field strength would enhance the signal to noise ratio, potentially revealing additional pIFG activation in the FONT task. Consistent with this possibility, both aIFG and pIFG activations were also found in the FONT task in another 3.0 T study of ours (Zhu et al., unpublished data).

Note that the negative beta values in some conditions should not be interpreted as suppression in LIFG during semantic integration (see also Ye and Zhou, 2009a; Zhu et al., 2012 for similar results of negative signals). The computed BOLD signal values reflect relative as opposed to the absolute levels of activity, being positive or negative dependent upon baseline estimation (Gusnard and Raichle, 2001) as well as other regressors in the statistical model.

For the Stroop task, the congruency effect was evident in both the behavior and the imaging results. Compared to the Con condition, the Incon condition elicited greater activation in LIFG, mainly in the posterior portion of LIFG. This finding was in line with previous studies (January et al., 2009; Ye and Zhou, 2009a; see review, Nee et al., 2007) and confirmed the role of LIFG in selection between simultaneously activated competitors.

More critical in the imaging results was the pattern of overlap and dissociation between brain activations for the semantic integration effect and the Stroop congruency effect. While both aIFG and pIFG were found to be associated with semantic integration, only the pIFG was found for the Stroop congruency effect. Given that the Stroop congruency effect is a relatively pure index of general cognitive control, these results suggest that the pIFG activation identified during the semantic integration tasks may also be associated with a domain-general role of cognitive control. Such control processes may include cognitive regulation, such as the selection and inhibition of irrelevant information, important for language comprehension (Novick et al., 2005, 2010; Ye and Zhou, 2009b). For example, when there are violations to highly constrained contexts, inhibitory functions must be engaged to override the activation of predicted words or to resolve the conflict between predicted words and the actually presented words (January et al., 2009; van de Meerendonk et al., 2011; Vuong and Martin, 2011; Ye and Zhou, 2009a).

That the aIFG was activated for semantic integration but not for the Stroop congruency effect suggests that this region is associated with a domain-specific process in semantic integration. Such a process may be related to information binding as proposed by Hagoort (2005). In Hagoort’s model (2005), binding is defined as combining independent elements into a coherent overall representation. The binding process may be closely related to inhibition/selection in semantic processing, but can be completely independent from inhibition or selection. That is, there are situations requiring information binding even though there is no ambiguity or competition (cf. Hagoort et al., 2009), in which significant activation in LIFG, including aIFG, is observed (Tesink et al., 2009).

Similar to the present study, Fedorenko et al. (2011) also found language specific activation in LIFG during sentence comprehension, when compared with tasks engaging cognitive control and working memory load. However, they used nonwords in their control baseline. Such stimuli differ from sentence stimuli at multiple linguistic processing levels, in lexical-semantic processing, syntactic processing, and in sentence-level semantic processing. This makes it hard to determine whether the LIFG activation they found was specific to semantic, syntactic or pragmatic processing.

In general, the finding of dissociation between aIFG and pIFG activation in sentence reading and in the Stroop task supports the functional heterogeneity of the LIFG (Badre and Wagner, 2007; Hagoort, 2005; Huang et al., 2012; Lau et al., 2008). They do not, however, fully fit into the unification model in Hagoort (2005). In Hagoort’s model, the pIFG was proposed to support syntactic and phonological processing rather than semantic related processing. Neither did the results fully fit the two-process account in Badre and Wagner (2007), which associates the middle portion of the LIFG (BA45) with domain general selection, different from the larger region including BA45 and the more posterior region found here. These discrepancies will have to be addressed in future research.

In summary, the present study indicates that different regions within LIFG play different roles in semantic integration, with aIFG important for domain-specific processing and pIFG for domain general cognitive control.

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Conflict of interest

The authors declare no competing financial interests.

References