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Neural basis of semantic and syntactic interference in sentence comprehension

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ABSTRACT

According to the cue-based parsing approach (Lewis, Vasishth, & Van Dyke, 2006), sentence comprehension difficulty derives from interference from material that partially matches syntactic and semantic retrieval cues. In a 2 (low vs. high semantic interference) × 2 (low vs. high syntactic interference) fMRI study, greater activation was observed in left BA44/45 for high versus low syntactic interference conditions following sentences and in left BA45/47 for high versus low semantic interference conditions following comprehension questions. A conjunction analysis showed BA45 associated with both types of interference, while BA47 was associated with only semantic interference. Greater activation was also observed in the left STG in the high interference conditions. Importantly, the results for the LIFG could not be attributed to greater working memory capacity demands for high interference conditions. The results favor a fractionation of the LIFG wherein BA45 is associated with post-retrieval selection and BA47 with controlled retrieval of semantic information.

1. Introduction

During sentence comprehension, earlier information must often be linked with later information across a potentially unbounded amount of intervening material. Take as an example the sentence, in (1).

(1) The manager who knows that the owner has too much work during the month of December hires a new assistant every year.

In this sentence, "manager" has to be linked as the subject of the verb "hires" across the intervening information in the relative clause. Theories of sentence parsing have assumed different memory mechanisms that support this linkage (also termed integration). Those that emphasize capacity (e.g., Gibson, 2000; Just & Carpenter, 1992) postulate that earlier information needs to be retained in an activated state until it is successfully integrated with the rest of the sentence. According to this approach, the capacity for sentence comprehension is determined by the total amount of information that can be stored and processed simultaneously in working memory. However, several lines of evidence have recently challenged this approach, suggesting that the capacity for maintaining information is extremely limited (Cowan, 2001; McElree, 2006; Oberauer, 2002; see Van Dyke & Johns, 2012 for a review). This calls into question the notion that an entire sentence could be maintained in active memory until all linguistically dependent constituents are integrated. An alternative approach de-emphasizes capacity in favor of a cue-driven associative retrieval mechanism, which compensates for a limited memory capacity by quickly restoring information into the focus of attention as it is needed (Lewis et al., 2006; McElree, Foraker, & Dyer, 2003; Van Dyke, 2007; Van Dyke & McElree, 2011). A computational implementation (Lewis & Vasishth, 2005) has demonstrated the feasibility of this approach, relying on an active memory containing only two chunks of information (i.e., the item currently needing to be integrated, and the current state of the parse). In this parser, when a word is brought into the focus of attention, stored lexical knowledge about the word is retrieved, in the form of lexical frames that specify basic syntactic argument structure (cf. Lewis & Vasishth, 2005). These frames are similar to the lexical frames in the unification models of Tabor & Hutchins (2004) and Vosse and Kempen (2000), however they are restricted to information about core arguments only (e.g., subject, direct object) and incorporate lexical-semantic restrictions on the types of nouns that can fill those argument slots. This information becomes the cues that will enable a word to be integrated with the previously processed lexical context. For example, in sentence (1), "manager" will be encoded as a bundle of syntactic and semantic features, such as singular noun, subject, and human, along with a prediction for an upcoming verb (See Lewis et al., 2006, for further details). A similar set of features

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would be encoded for ‘‘owner’’ though the predicted slot for the verb would be filled once ‘‘has’’ was processed. When the focus of attention shifts to the verb ‘‘hires’’, it is identified as a singular tensed verb, which requires an animate subject of the type that can ‘‘hire’’ someone. These syntactic and semantic cues are combined to create a retrieval probe that will directly access all previously encoded information via a global matching associative mechanism (e.g., Clark & Gronlund, 1996).[1] Because the encoded properties of ‘‘manager’’ match the retrieval cues (i.e., it is a singular animate noun encoded as a subject, which could plausibly hire someone), it will be retrieved as a likely subject for ‘‘hires.’’ However, ‘‘owner’’ also matches the retrieval probe because it is also the subject of a sentence and refers to a human hire-er. Even though ‘‘manager’’ provides a better match because of the open slot for the verb, ‘‘owner’’ will be retrieved in error on a high proportion of trials because of the high degree of partial match. This incorrect match creates *interference* for building the correct association between ‘‘manager’’ and ‘‘hires’’ and provides an alternative, non-capacity-based, explanation for why this sentence seems difficult to understand.

A recent study of Van Dyke (2007) (see also Van Dyke & McElree, 2011) provides empirical support for the presence of syntactic and semantic interference in sentence processing. Van Dyke manipulated the semantic and syntactic properties of the intervening noun phrases to create high and low interference conditions (i.e., high vs. low semantic interference x high vs. low syntactic interference). A set of examples is as follows:

1. Low semantic–low syntactic: The worker was surprised that the resident *who was living near the dangerous warehouse* was complaining about the investigation.
2. High semantic–low syntactic: The worker was surprised that *the resident who was living near the dangerous neighbor* was complaining about the investigation.
3. Low semantic–high syntactic: The worker was surprised that *the resident who said the warehouse was dangerous* was complaining about the investigation.
4. High semantic–high syntactic: The worker was surprised that *the resident who said the neighbor was dangerous* was complaining about the investigation.

In all of these example sentences, the subject of the main clause ‘‘resident’’ needs to be integrated with the verb ‘‘complain’’ across the intervening relative clause. In the high syntactic interference conditions, the intervening noun matched the syntactic encoding of the target noun (they were both subjects), whereas in the low syntactic interference conditions, the noun was a prepositional object. In the high semantic interference conditions, the intervening noun was semantically plausible as the subject of the main verb whereas in the low semantic condition, it was not. Van Dyke (2007) reported longer reading times on the main clause verb in the high syntactic interference condition, replicating an earlier study (Van Dyke & Lewis, 2003). She also reported longer reading times in the high as compared to the low semantic interference condition, though these appeared downstream from the critical verb.

Once interference is detected, some researchers assume that a control process is initiated that allows for selection among the competing alternatives (e.g., Badre & Wagner, 2007; Thompson-Schill, D’Esposito, Aguirre, & Farah, 1997). From a computational viewpoint, different mechanisms have been proposed for this control process, such as lateral inhibition between alternative choices (Hagoort, 2005; Howard, Nickels, Coltheart, & Cole-Virtue, 2006) or the involvement of a ‘‘booster’’ mechanism which serves to amplify differences in the activation of alternative choices until a difference threshold is reached (Oppenheim, Dell, &Schwartz, 2010). Regardless of the specific mechanism, brain regions that are involved in selecting representations should be more active for high versus low interference conditions. With respect to cognitive control, regions in the left inferior frontal gyrus (LIFG) appear to play a critical role. Findings from neuroimaging studies have shown that this region is more highly activated for high as compared to low control conditions in various tasks (Badre, Poldrack, Paré-Blagoev, Insler, & Wagner, 2005; Kan & Thompson-Schill, 2004a, 2004b; Schnur et al., 2009; Thompson-Schill, D’Esposito, Aguirre, & Farah, 1997; Ye & Zhou, 2009a). For instance, Kan and Thompson-Schill (2004a) found that the LIFG (BA44 & BA45) was more engaged when a naming task required selection from multiple competing names (e.g., a picture of astove evokes many names, such as ‘‘stove’’, ‘‘oven’’, and ‘‘range’’) than when there was less competition due to high name agreement (e.g., a picture of a book evokes a single reliable response ‘‘book’’). Similarly, Badre et al. (2005) found that a single region centered at BA45 (MNI coordinate: −54, 21, 12) was associated with selection demands in four different tasks, each of which required selection among alternatives activated via an automatic associative cue-based retrieval mechanism. They argued that a post-retrieval selection process was a necessary complement to automatic retrieval, since it rarely occurs that the right conjunction of cues is present to guarantee retrieval of only the goal relevant information (Badre & Wagner, 2002; Fletcher, Shallice, & Dolan, 2000; Moss et al., 2005; Zhang, Feng, Fox, Gao, & Tan, 2004). This process is incontrast to a controlled retrieval process, which becomes necessary when desired semantic information is not automatically retrieved (Tomita, Ohbayashi, Nakahara, Hasegawa, & Miyashita, 1999). Using a factor analysis method, Badre et al. (2005) identified a region in the LIFG centered at BA47 (MNI coordinate: −45, 27, −15), which was associated with topdown use of cues to bias the activation of necessary knowledge (Badre & Wagner, 2007). Notably, this region dissociated from that centered in BA45 in that it was not activated by the selection component derived from any of the four tasks in their study.

While Badre et al. (2005) argued that at least the post-retrieval selection process is domain general (see also Kan & Thompson-Schill, 2004b; Snijders et al., 2008), the extent to which the LIFG is involved in cognitive control for all types of representations is under debate. For example, Hamilton and Martin (2005) reported a patient with LIFG damage who showed deficits in resolving interference of verbal information but not of spatial information, suggesting that this region is not involved in cognitive control of spatial information. Its role in processing competing syntactic representations in garden-path and other types of ambiguous sentences is well attested, however (Fiebach, Vos, & Friederici, 2004; January, Trueswell, & Thompson-Schill, 2009; Mason, Just, Keller, & Carpenter, 2003; Rodd, Longe, Randall, & Tyler, 2010). Also, studies of individuals with damage to the LIFG have revealed deficits in their ability to resolve lexical and syntactic ambiguities (Novick, Kan, Trueswell, & Thompson-Schill, 2009; Vuong & Martin, 2011). In all these studies, the LIFG is assumed to be involved in abandon-

[1] Global matching is a common feature of many models of recognition memory (e.g., Gillund & Shiffrin, 1984; Hintzman, 1988; Humphreys, Bain, & Pike, 1989; Murdock, 1982; Norman & O’Reilly, 2003; Shiffrin & Steyvers, 1997), and refers to the signal-detection process through which retrieval cues are compared with the contents of memory. They are referred to as ‘‘global’’ because recognition of a given item is determined both by the similarity of the retrieval probe to the target memorandum and also the similarity of the retrieval probe to all other items in memory. The comparison process occurs via direct, content-based matches to all items in memory, and is therefore speed invariant with respect to factors such as number of items in memory or hierarchical positioning among items. These factors will affect the accuracy of the match, however, and it is exactly this which gives rise to interference effects. Clark and Gronlund (1996) provide an accessible tutorial for the mathematics underlying this process. A more technical review is provided in Humphreys et al. (1989).

ing a preferred parse in favor of selecting a dispreferred parse (Novick, Trueswell, & Thompson-Schill, 2005; Vuong & Martin, 2011). These processes may involve controlled retrieval of alternative syntactic frames, and possibly the reconstruction of entire semantic interpretations, so the contribution of syntactic vs. semantic processing is unclear.

The current study contrasts with this work in examining unambiguous sentences, where the need for cognitive control relates to resolving competition from sentence elements that partially match syntactic and semantic retrieval cues, in a design that does not confound the two types of conflict. In addition, unlike much work with unambiguous sentences (Friederici, Ruschemeyer, Hahne, & Fiebach, 2003; Ni et al., 2000; Ye & Zhou, 2009a), only plausible sentences were used, which will avoid the possibility that neural activation reflects checking processes that are involved in detecting anomalies (cf., Brennan et al., 2012). These methods will allow a more direct assessment of whether particular regions in LIFG are specialized for processing particular types of linguistic information, or are sensitive to specific types of interference, during normal sentence processing. Moreover, the focus on interference resolution differentiates the present study from many others that have examined the relation of LIFG activation to working memory demands. In line with the evidence for involvement of the LIFG in standard verbal working memory paradigms (e.g., Braver et al., 1997), many have suggested that activation of the LIFG during sentence processing results from capacity demands (e.g., Just, Carpenter, Keller, Eddy, & Thulborn, 1996). In the current study, the sentences in the high and low semantic interference conditions (like those in sentences 1 vs. 2 and 3 vs. 4 above) were matched in terms of syntactic structure and in terms of the number of intervening words and unintegrated elements between the subject and main verb. Thus, to the extent that LIFG activation is greater in the high than low semantic interference conditions, the effect would be more readily attributed to interference resolution rather than capacity demands.

2. Method

2.1. Subjects

Twenty-four undergraduate students at Rice University were recruited as subjects through a web-based experiment scheduling system for a pilot behavioral study that was used to determine presentation times for the experimental sentences. Subjects received 1 credit toward the fulfillment of classroom experiment participation requirements for one-hour of participation.

Fourteen different subjects were recruited for the fMRI experiment through email announcements to undergraduate and graduate students at Rice University. Subjects were screened using a detailed questionnaire to ensure that they had no history of neurological or psychiatric problems. Subjects were compensated with $30 for a 1.5 h-participation. Data from two subjects were excluded due to uncorrectable head movement. Half of the subjects whose data were included in the analyses were female.

All subjects in the two experiments were native English speakers. In addition, all subjects were right-handed and had normal or corrected-to-normal vision. Informed consent was obtained from each subject in accordance with the guidelines and approval of the Rice University Institutional Review Board.

2.2. Materials

The stimuli included 480 experimental sentences (120 sets of 4 conditions) and 120 filler sentences. For each sentence, a comprehension question was also constructed.

The critical sentences were simplified versions of those used by Van Dyke (2007). Each sentence contained a main clause and a relative clause that separated the subject and verb of the main clause. The four conditions represented a 2 (semantic interference: low vs. high) $\times$ 2 (syntactic interference: low vs. high) design (see Table 1 for examples). As in the Van Dyke (2007) materials, in the low semantic interference conditions, the intervening noun was implausible as the agent of the main verb whereas in the high semantic interference conditions it was plausible. In the low syntactic interference conditions, the intervening noun was a prepositional object whereas in the high syntactic interference conditions, it was a subject. These four sentences that have the same main clause but belong to different conditions, depending on the properties of the intervening nouns, are referred to as a set. These 480 items were divided into four lists according to a Latin Square design, so that each list only included 30 sentences for each condition (i.e., 120 critical sentences in each list), and no two sentences in a set occurred in the same list. Each subject only read one list of critical sentences and all of the filler items (240 sentences in total; target-filler ratio is 1:1). The comprehension questions for the four conditions of each set were identical, and always asked about the subject of the verb in the main clause (see Table 1 for examples). In this way we could examine whether participants made the correct subject-verb association or were distracted by the interfering information.

Filler sentences prevented subjects from intentionally ignoring the intervening relative clause and avoiding the interference. These sentences were constructed with various syntactic structures, including the same structures as the experimental sentences, object or subject extracted relative clause sentences, simple one-clause sentences, and conjoined sentences (see Appendix A for examples). More importantly, the comprehension questions for fillers asked about information from different regions of the sentences, so that if subjects adopted a strategy of avoiding the interference by only attending to the subject of the main clause, they would have trouble answering those questions.

All sentences were presented visually phrase by phrase (five-six phrases for each sentence) at the center of a computer screen (see Appendix A for all target sentences). Table 1 provides a breakdown of the phrasal units for the experimental sentences, with separate presentation units for the head noun (first phrase) and main clause verb (phrase 5). The embedded relative clauses were presented in three phrases including one with the relative pronoun and embedded verb (phrase 2), either a prepositional phrase (in the two low syntactic conditions) or embedded sentence (in the two high syntactic conditions) (phrase 3), and an adverbial phrase (phrase 4). Following the main clause verb (phrase 5), there was a spillover region that was either an adverbial phrase or the patient of the main clause verb (phrase 6). The same experimental and filler sentences were used in the pilot experiment and the neuroimaging experiment except that all experimental sentences consisted of six phrases in the fMRI experiment while some experimental sentences did not include the sixth phrase in the pilot study (i.e., when the main clause verb was an intransitive verb). Filler sentences that were structurally similar to the experimental sentences were divided into the same phrasal units as the latter. A similar scheme was used to delimit phrases for the other types of filler sentences, with phrases for head nouns, main verbs, adverbial and prepositional phrases, and embedded noun and verb phrases. All questions were presented visually as a single unit. Presentations and response-time measurements were controlled by the PsyScope software package (Cohen, MacWhinney, Flatt, & Provost, 1993).

Table 1
Sample semantic and syntactic interference stimuli.

Sentence						Comprehension question
Phrase 1	Phrase 2	Phrase 3	Phrase 4	Phrase 5	Phrase 6	
The client	who had arrived	after the important **meeting** (LOW SEMANTIC and LOW SYNTACTIC interference)	that day	was complaining	about the investigation	Who complained?
		after the important **visitor** (HIGH SEMANTIC and LOW SYNTACTIC interference)				
	who implied that	the **meeting** was important (LOW SEMANTIC and HIGH SYNTACTIC interference)				
		the **visitor** was important (HIGH SEMANTIC and HIGH SYNTACTIC interference)				

2.3. Procedure

In the pilot behavioral experiment, subjects completed practice trials with sentences that would not appear in the actual task but had similar syntactic structures as the experimental and filler sentences. Each trial started with the first phrase of the sentence. Subjects were asked to push the spacebar to move to the next phrase once they finished reading. Each new phrase was presented immediately after the button push. The same procedure repeated until each sentence was over. Then a comprehension question appeared and subjects were instructed to verbally respond to the question as quickly and as accurately as possible. Following the verbal response, the question disappeared and a fixation cross (+) was presented on the screen until subjects pressed the spacebar again to start the next trial. The reading times for all phrases were recorded by the PsyScope software package. The verbal response times for the comprehension questions were also recorded by PsyScope with an embedded microphone. Additionally, the accuracy of the verbal responses was recorded by the experimenter who sat in during the pilot sessions.

For the fMRI experiment, subjects were told that they would see sentences presented phrase-by-phrase in the center of the screen and that they should comprehend these sentences, as they would be asked questions about their meaning following the sentence. They then completed 12 practice trials outside the scanner. The presentation format was similar to the pilot behavioral experiment except that each phrase was presented for a fixed duration. These presentation durations were determined by the phrase reading times collected in the pilot experiment, and will be listed in the results section. The total presentation duration for each sentence was 7.1s. Following the last phrase, a fixation cross (+) was presented for 400 ms. Then, a comprehension question was presented for 4s. In the scanner, the experiment employed a rapid-presentation event-related design. The intervals between trials and the intervals between each sentence and its question were both jittered (average rate of 2.5 s), so that the hemodynamic signal changes driven by the sentences and the comprehension questions could be analyzed separately. A fixation cross remained on the screen during the jittered intervals. Subjects were instructed to comprehend the phrases while they were presented and asked to verbally respond to the questions as quickly and as accurately as possible. The verbal responses in the scanner were recorded by an MRI compatible microphone (Or-Yehuda, Israel; http://www.optoacoustics.com/) and exported to the Audacity audio recording software. Accuracy was coded offline. The response times were calculated relative to the onsets of comprehension questions. The timings were determined by examining the digitally recorded waveforms in Audacity. The entire fMRI scan consisted of 10 runs, which were each comprised of 3 experimental sentences from each condition and 12 filler sentences. As such, there were 24 trials in each run, and each run lasted approximately 7 min.

2.4. Image acquisition and analysis

The scanning was conducted at University of Texas Medical School at Houston on a Philips 3T scanner using an eight-channel head gradient coil. At the beginning of each run, there was a 10s fixation to allow for stability in magnetization. At the end of each run, there was a 14 s fixation to compensate for the delay of the hemodynamic response. Anatomical images were acquired first, using a sagittal MP-RAGE T1-weighted sequence with a voxel size of $.9375 \times .9375 \times 1$ mm (TR = 8.44 ms; TE = 3.90 ms; flip angle = 8°). Functional images were acquired using an echo-planar sequence (TR = 2500 ms; TE = 30 ms; flip angle = 90°; voxel size = 2.75×2.75 in-plane resolution). During each functional run, 176 sets of 40 contiguous 3-mm thick axial images were acquired. Visual stimuli were projected onto a screen using an LCD projector and viewed through a mirror attached to the head coil.

Imaging data were analyzed using the AFNI analysis package (Cox, 1996). The first 5 TRs were excluded from the analysis. Preprocessing for each participant followed a script generated by the AFNI program afni_ proc.py. Voxel time series were aligned to the same temporal origin using the AFNI program 3dTshift and the quintic Lagrange polynomial interpolation option. For each EPI run, each 3d volume from the input dataset was registered to the volume acquired in closest temporal proximity to the T1-weighted anatomical scan (the first volume of the first EPI scan) using the AFNI program 3dvolreg with the cubic polynomial interpolation option. A 6-mm full-width half maximum (FWHM) Gaussian blur was then applied using AFNI's 3dmerge program. The data were then scaled in order to calculate the percent signal change. Preprocessed data were analyzed based on the General Linear Model (GLM; Friston, Jezzard, & Turner, 1994; Josephs, Turner, & Friston, 1997; Miezin, Maccotta, Ollinger, Petersen, & Buckner, 2000; Zarahn, Aguirre, & D'Esposito, 1997), using AFNI's 3dDeconvolve program with the TENT option. The deconvolution analysis estimated the impulse response function (IRF) for each unique condition (LoSemLoSyn vs. HiSemLoSyn vs. LoSemHiSyn vs. HiSemHiSyn), with no assumptions regarding the shape of the function, at the 11 time points (i.e., image acquisitions) immediately following the onset of the first phrase of each sentence, and at the 9 time points immediately following the onset of each comprehension question. The filler trials were modeled separately. The deconvolution analysis produced an IRF for each condition at each voxel. In addition, six motion factors and baseline drifts were also estimated and included in the model. All effects were modeled simultaneously in the GLM for eachsubject. The structural images were transformed to the Colin template (http://imaging.mrc-cbu.cam.ac.uk/downloads/Colin/) for each subject using AFNI's @auto_tlrc program, and then the functional data were aligned using the transform obtained in the previous step.

Because the presentation duration of sentences was longer than questions, the BOLD signal peak post-sentence-onset emerged later and lasted longer than the peak post-question-onset. Therefore, different time points were used to identify BOLD signal peaks for sentences and questions (7.5–15 s post sentence onset, 5–7.5 s post question onset). The intensity values for the BOLD signal peak were averaged for each condition at each voxel, and these values were submitted to an analysis of variance (ANOVA) using AFNI's 3dANOVA program. The filler trials were modeled in the deconvolution analysis, but not included in the ANOVA. The estimated hemodynamic responses were then baseline corrected such that the origin of each IRF was zero. Following the onset of sentences and following the onset of comprehension questions, regions of interference were identified through two voxel-wise contrasts (semantic interference: HiSemLoSyn + HiSemHiSyn vs. LoSemLoSyn + LoSemHiSyn; syntactic interference: LoSemHiSyn + HiSemHiSyn vs. LoSemLoSyn + HiSemLoSyn). Statistical maps were thresholded using a combined significance level of $p < 0.01$ and cluster size of 70 voxels, resulting in a corrected p-value of 0.01 (as determined by the AFNI program 3dClustSim). Then, the estimated hemodynamic response was averaged and extracted from each cluster. The interaction between the effect of interference (semantic interference or syntactic interference) and quadric contrast effect of time (across the 11 estimated time points following the onset of sentences and across the 9 estimated time points following the onset of questions) was assessed in each region. Only regions exhibiting a significant interaction effect ($p < .05$) and with the maximum BOLD signal at any time point exceeding |0.2| will be reported. These criteria were applied to ensure that the identified regions exhibit reasonable hemodynamic signal changes.

3. Results

3.1. Behavioral pilot

First, to examine the two interference effects, reading times of the critical phrase that contained the verb of the main clause and accuracy and response times to comprehension questions were submitted to a two-way repeated measures ANOVA with semantic interference (low vs. high) and syntactic interference (low vs. high) as factors. The means for response times and accuracy by condition are shown in Table 2.

For the reading times of the critical phrase, only trials with accurate verbal responses to the comprehension questions were included. After excluding extreme values (<200 ms or >2000 ms), response times ±3 standard deviations from each subject's mean were also excluded from the analysis. The main effect of syntactic interference was significant, $F(1, 23) = 7.15$, $p = 0.01$, $MSE = 1795$, but not the main effect of semantic interference, $F(1, 23) = 1.31$, $p = .26$, $MSE = 1738$, nor the interaction between semantic and syntactic interference, $F(1, 23) = .29$, $p = .60$, $MSE = 2959$. Subjects took longer to read the verb phrases in the high syntactic interference condition (mean = 719 ms) than in the low syntactic interference condition (mean = 696 ms), replicating Van Dyke (2007) and Van Dyke and Lewis (2003) who showed that integrating a subject and verb is more difficult when the intervening noun is also a subject.

For the comprehension questions, trials with no responses were counted as errors. Response times ±3 standard deviations from the mean for each subject were excluded from the analysis after excluding the extreme values (<200 ms or >5000 ms). The only significant effect was a semantic interference effect for response times, $F(1, 23) = 22.26$, $p < .001$, $MSE = 13,698$. That is, participants spent longer in responding to questions for sentences in the high semantic interference condition (mean = 1492 ms) than in the low semantic interference condition (mean = 1380 ms). The semantic interference effect for accuracy was not significant, $F(1, 23) = 1.15$, $p = .29$, $MSE = .001$. In addition, there was no significant main effect of syntactic interference for either response times, $F(1, 23) = 0.19$, $p = .26$, $MSE = 1738$, or accuracy, $F(1, 23) = 1,15$, $p = .29$, $MSE = .001$, and no significant interaction between the semantic and syntactic interference for either response times, $F(1, 23) = 1.13$, $p = .30$, $MSE = 11,769$, or accuracy, $F(1, 23) = .60$, $p = .45$, $MSE = .002$.

Additionally, reading times of phrases at each serial position of the sentences were analyzed separately for the experimental and filler sentences to determine the phrase presentation durations in the scanner that were the 75th percentile reading times for each phrase in the pilot study. The 75th percentile reading times were determined within each subject at each position (from the first to the last phrase of experimental sentences: 1343 ms, 1271 ms, 1624 ms, 1003 ms, 896 ms, and 927 ms; from the first to the last phrase of filler sentences: 1360 ms, 1339 ms, 1117 ms, 1000 ms, 1010 ms, and 930 ms). To equalize the total presentation durations for all sentences for the fMRI experiment, the 75th percentile reading times of phrases for fillers were adjusted slightly (from the first to the last phrase of filler sentences: 1360 ms, 1339 ms, 1117 ms, 1100 ms, 1110 ms, and 1030 ms). In addition, after all phrases in each sentence were presented, a fixation cross was presented at the end of each sentence (36 ms for target sentences; 44 ms for filler sentences). If a sentence only had 5 phrases, a fixation was presented as the 6th phrase. Therefore, a total presentation time of 7100 ms was applied in the fMRI experiment for each sentence.

3.2. fMRI behavioral performance

In the scanner, phrases were presented at a set rate and thus there were no RT measures for sentence reading. Consequently, only latency and accuracy for the comprehension questions were analyzed. Due to a technical problem with the microphone, response times for three subjects and accuracy data for two subjects were missing. Mean RT and accuracy by condition are shown in Table 2. Two-way repeated measures ANOVAs of semantic interference (low vs. high) and syntactic interference (low vs. high) were conducted for response times of nine subjects and for the accuracy data of ten subjects. For the analysis of accuracy, trials with no responses were counted as errors. Analyses of response times were conducted both for all trials and for trials with accurate verbal responses. As for question answering, the main effects of semantic interference were significant (response times excluding incorrect responses: $F(1, 8) = 5.80$, $p < .05$, $MSE = 10,926$; response times including incorrect responses: $F(1, 8) = 15.70$, $p < .01$, $MSE = 10,310$; accuracy: $F(1, 9) = 24.75$, $p < .001$, $MSE = .006$). That is, participants spent longer and made more errors in responding to questions for sentences in high semantic interference conditions than low semantic interference conditions. When excluding response times for incorrect responses, the means RTs were 1566 in the low semantic interference condition and 1649 in the high semantic interference condition. When including response times for incorrect responses, these means were 1628 for the low semantic interference condition and 1762 for the high semantic interference condition. The mean accuracies were 80% in the low semantic interference condition and 68% in the high semantic interference condition. Also replicating the findings from the pilot experiment for question answering, the main effect of syntactic interference and the interaction effect between the two types of interference were not significant for either accuracy or response times (the syntactic interference effect: response time excluding incorrect responses, $F(1, 8) = 3.43$, $p = .10$, $MSE = 63,420$; response time including incorrect responses, $F(1, 8) = 5.18$, $p = .052$, $MSE = 29,657$; accuracy, $F(1, 9) = 4.79$, $p = .056$, $MSE = .009$; the interaction effect: response times excluding incorrect responses, $F(1, 8) = .40$, $p = .55$, $MSE = 16,671$; response times including incorrect responses, $F(1, 8) =$

Table 2
Means of performances in the pilot behavioral experiment and in the fMRI experiment.

	During	Measure	loSem_loSyn	hiSem_loSyn	loSem-hiSyn	hiSem-hiSyn
Pilot	Sentence reading	Reading times	688 ms	703 ms	717 ms	721 ms
		(Main clause verb phrase)	(7 ms)	(8 ms)	(7 ms)	(10 ms)
	Question answering	Response times	1363 ms	1499 ms	1396 ms	1485 ms
		(Questions)	(12 ms)	(20 ms)	(23 ms)	(23 ms)
		Accuracy	94%	94%	93%	94%
		(Questions)	(1%)	(1%)	(1%)	(1%)
fMRI	Question answering	Response times	1545 ms	1602 ms	1586 ms	1697 ms
		(excluding incorrect responses)	(32 ms)	(33 ms)	(26 ms)	(40 ms)
		Response times	1615 ms	1644 ms	1640 ms	1880 ms
		(including incorrect responses)	(25 ms)	(40 ms)	(18 ms)	(65 ms)
		Accuracy	82%	75%	81%	63%
			(2%)	(2%)	(2%)	(3%)

Note: Standard errors corrected for between-subject variability are reported in parentheses.

4.66, $p = .063$, $MSE = 21{,}411$; accuracy, $F(1, 9) = 4.68$, $p = .059$, $MSE = .006$).[2]

3.3. Neuroimaging

Neuroimaging data for all trials were included in the fMRI analyses. This was motivated by the interference theory, which predicts that participants will be distracted by items that are syntactically or semantically similar to the target. Therefore, interference will result in errors or longer response times in retrieving the correct answer, so we were not interested in only successful attempts to resolve interference. Indeed, selection processes aimed at resolving interference are not guaranteed to produce the correct alternative. In fact, the likelihood of an error should be greater in high interference conditions due to the presence of close competitors, which will be selected on a high probability of trials. Hence, "interference resolution" does not necessarily imply that interference has been resolved correctly, only that the participant has made some selection from the competing alternatives. We expect that brain activations in the presence of interference, whether successfully resolved or not, will reflect the greater effort required to process these sentences.

3.3.1. Contrasts of interference effects

We conducted two voxel-wise contrasts ($p_{\text{activation}} < 0.01$ with the cluster size > 70, resulting in $p_{\text{corrected by cluster threshold}} < 0.01$) on the peak of hemodynamic signal changes following the onset of the sentences (7.5–15 s post sentence onset) in order to identify regions exhibiting the effect of semantic interference (HiSemLoSyn + HiSemHiSyn vs. LoSemLoSyn + LoSemHiSyn) or the effect of syntactic interference (LoSemHiSyn + HiSemHiSyn vs. LoSemLoSyn + HiSemLoSyn). Moreover, since interference effects were also observed in offline measures of responses to comprehension questions in the study of Van Dyke (2007) and in the behavioral data of this study, the same voxel-wise contrast analyses were also conducted on the peak of hemodynamic signal changes following the onset of questions (5–7.5 s post question onset).

We were justified in examining syntactic effects in the neuroimaging data despite the absence of syntactic effects in the behavioral data during the fMRI experiment because the syntactic effects occurred in the reading times only during the pilot experiment. As the fixed phrase-by-phrase presentation in the scanner precluded reading time data, we infer that such effects would nevertheless be present as participants read the sentences in the scanner because the reading task itself was identical aside from the presentation mode.

3.3.1.1. The syntactic interference contrast following the onset of SENTENCES. See Fig. 1 for the activation map. Two regions in the LIFG (centered at −47, 13, 16: BA44 & −45, 26, 9: BA45; coordinates in this study are all reported in MNI space) were identified that exhibited greater activation for the high syntactic interference conditions (LoSemHiSyn & HiSemHiSyn) than the low syntactic interference conditions (LoSemLoSyn & HiSemLoSyn) (see Table 3). The left superior temporal gyrus (STG; centered at −46, −24,0: BA22) (see Table 4) also showed greater activation in the high than low syntactic interference conditions. This region is of interest as some researchers have claimed that the region is involved in online syntactic processing (Friederici et al., 2003) whereas other have argued that the region is involved only in the retrieval of lexical information (both semantic and syntactic; Snijders, Petersson, & Hagoort, 2010; Snijders et al., 2008). In addition, several regions in bilateral superior frontal, right medial frontal, inferior frontal and precuneus demonstrated enhanced deactivation for the high vs. low interference conditions (see Appendix B for detailed information). Such regions have often been considered part of a default network that tends to deactivate during task performance.

3.3.1.2. The semantic interference contrast following the onset of SENTENCES. See Fig. 1 for the activation map. No region was identified in this contrast exhibiting greater activation for the high semantic conditions (HiSemLoSyn & HiSemHiSyn) than the low semantic conditions (LoSemLoSyn & LoSemHiSyn). Again, bilateral superior frontal regions showed increased deactivation for the high semantic interference conditions than the low semantic interference conditions. Detailed information about all regions that exhibited differential activation between high vs. low semantic interference conditions in this contrast is listed in Appendix C.

3.3.1.3. The syntactic interference contrast following the onset of QUESTIONS. See Fig. 2 for the activation map. No region in the LIFG was identified in this contrast exhibiting greater activation for the high syntactic conditions (LoSemHiSyn & HiSemHiSyn) than the low syntactic conditions (LoSemLoSyn & HiSemLoSyn). Significant activations for this contrast were observed in the left superior frontal gyrus, the right cuneus, middle occipital gyrus, superior temporal gyrus, and inferior frontal gyrus. Detailed infor-

[2] We note that several of these effects for question answering involving the syntactic manipulation approached significance. Given low statistical power due to a small N, 95% confidence intervals on these effects are quite wide (e.g., RTs excluding incorrect responses, CI = 68.4 ms ± 85.1 ms; accuracy, CI = 7.0% ± 7.0%). Thus we do not have strong grounds for claiming that syntactic effects on question answering were or were not greater than those in the pilot experiment.

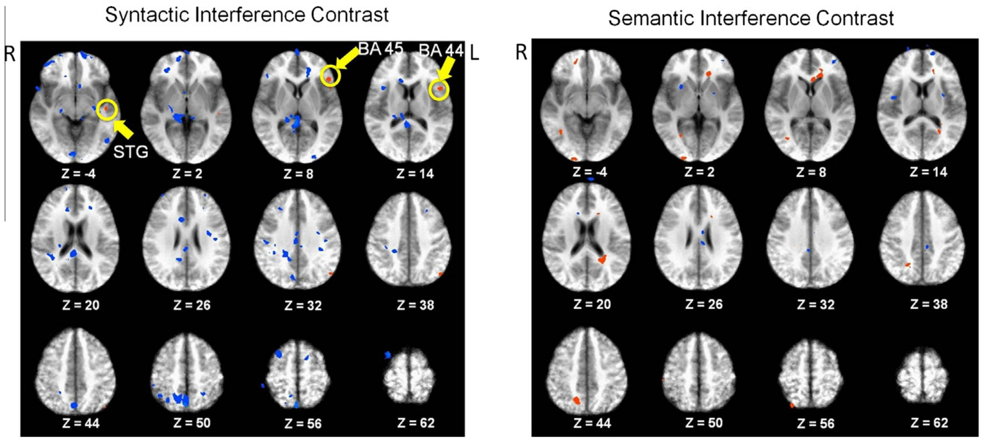

Fig. 1. The results of the contrasts based on signals immediately following the onset of sentences ($p_{\text{corrected by cluster threshold}} < 0.01$). STG standards for superior temporal gyrus. The red color represents the regions exhibiting greater activation for the high interference conditions compared to the low interference conditions. The blue color the regions exhibiting greater activation for the low interference conditions compared to the high interference conditions or the regions exhibiting greater deactivation for the high interference conditions compared to the low interference conditions.

Table 3
Regions in the LIFG exhibiting effects of semantic or syntactic interference.

Time points	Contrasts (activations relative to fixations)	Peak coordinates[a] (x, y, z)	BA[b]	Peak name	# Of Voxels
Following the onset of SENTENCES	High > low SYNTACTIC interference	−47, 13, 16	44	Left inferior frontal gyrus	235
		−45, 26, 9	45	Left inferior frontal gyrus	212
	High > low SEMANTIC interference	n.s			
Following the onset of QUESTIONS	High > low SYNTACTIC interference	n.s.			
	High > low SEMANTIC interference	−31, 19, −4	47	Left inferior frontal gyrus	193
		−50, 20, 10	45	Left inferior frontal gyrus	98

[a] Coordinates are given in MNI space.
[b] BA refers to the approximate Brodmann's area.

Table 4
Regions in the left STG exhibiting effects of semantic or syntactic interference.

Time points	Contrasts (activations relative to fixations)	Peak coordinates[a] (x, y, z)	BA[b]	Peak name	# Of Voxels
Following the onset of SENTENCES	High > low SYNTACTIC interference	−46, −24, 0	22	Left superior temporal gyrus	108
	High > low SEMANTIC interference	n.s			
Following the onset of QUESTIONS	High > low SYNTACTIC interference	n.s.			
	High > low SEMANTIC interference	−45, −27, −7	22	Left superior temporal gyrus	112

[a] Coordinates are given in MNI space.
[b] BA refers to the approximate Brodmann's area.

mation about all the regions identified in this contrast is listed in Appendix D.

3.3.1.4. The semantic interference contrast following the onset of QUESTIONS. See Fig. 2 for the activation map. Two regions in the LIFG (centered at −31, 19, −4: BA47 & −50, 20, 10: BA45) (see Table 3) were identified in this contrast exhibiting greater activation for the high semantic conditions (HiSemLoSyn & HiSemHiSyn) than the low semantic conditions (LoSemLoSyn & LoSemHiSyn). As for the syntactic contrast during sentence processing, a region in the left STG also showed greater activation in the high than the low semantic conditions (centered at −45, −27, −27: BA22; see Table 4). Other regions that exhibited this effect were in bilateral superior frontal gyrus, and the left middle frontal gyrus. Detailed information about these regions is listed in Appendix E.

3.3.2. Conjunction analysis of contrasts of interference effects

Since the LIFG and the left STG were identified in both the syntactic interference contrast and the semantic interference contrast (although at different time points, i.e., during sentence reading and during question answering respectively), a conjunction analysis was conducted between the syntactic interference contrast (following the onset of sentences) and the semantic interference contrast (following the onset of comprehension questions). Since regions that are activated in both contrasts are less likely to be noise, a conjunction map results in a smaller false alarm rate than that of each individual contrast. Therefore, a lower value of $p_{\text{corrected by cluster threshold}} < 0.05$ ($p_{\text{activation}} < 0.05$ with the cluster size > 243) was applied to each individual contrast that was included in the conjunction analysis.

A region in the LIFG (see Fig. 3; centered at BA45: −48, 24, 9 and extending to BA44; in a size of 556 voxels) was identified to be activated in both contrasts (the syntactic interference contrast following the onset of sentences & the semantic interference contrast following the onset of comprehension questions). The left STG regions (see Fig. 3; centered at BA22: −47, −9, −10; in a size of 69 voxels) that were identified in both contrasts also overlapped with the region involved in the semantic contrast extending to a more

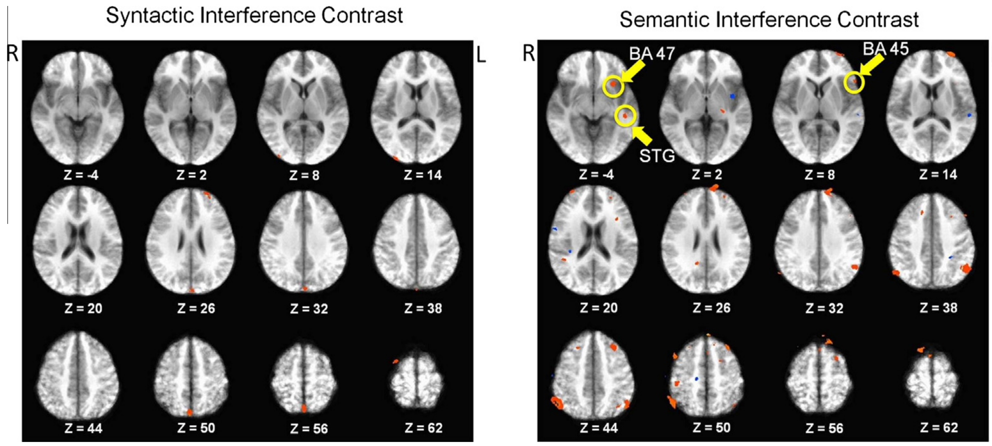

Fig. 2. The results of the contrasts based on signals immediately following the onset of questions ($p_{\text{corrected by cluster threshold}} < 0.01$). STG standards for superior temporal gyrus. The red color represents the regions exhibiting greater activation for the high interference conditions compared to the low interference conditions or the regions exhibiting greater deactivation for the low interference conditions compared to the high interference conditions. The blue color the regions exhibiting greater activation for the low interference conditions compared to the high interference conditions or the regions exhibiting greater deactivation for the high interference conditions compared to the low interference conditions.

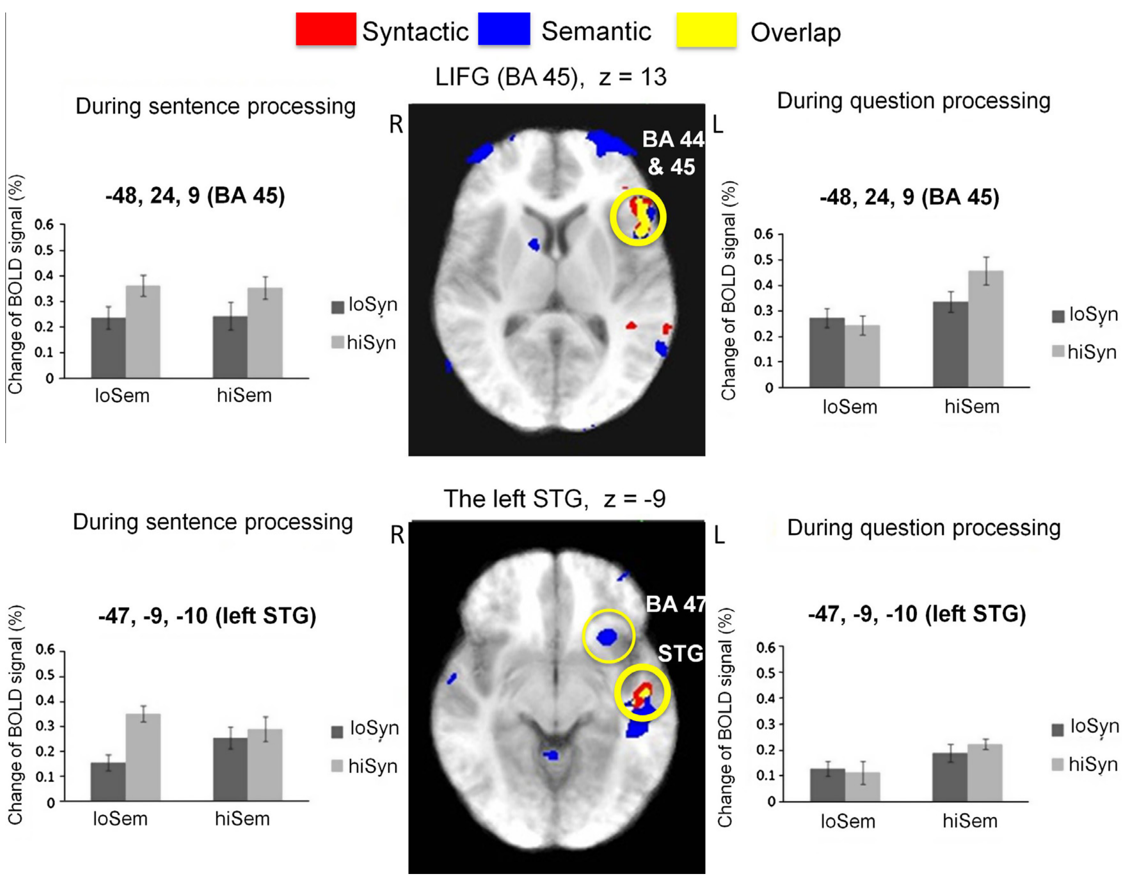

Fig. 3. The results of the conjunction analysis between the syntactic interference contrast following onset of sentences and the semantic interference contrast following onset of comprehension questions (the red color represents the regions exhibiting the syntactic interference effect; the blue color represents the regions exhibiting the semantic interference effect; the yellow color represents the overlapped regions; $p_{\text{corrected by cluster threshold}} < 0.05$), and the BOLD signal changes for each interference condition in each *overlapped* region ("loSyn" represents the low syntactic interference condition; "hiSyn" represents the high syntactic interference condition; "loSem" represents the low semantic interference condition; "hiSem" represents the high semantic interference condition). Error bars denote standard errors corrected for between-subject variability.

posterior area. Interestingly, the BA47 region that was identified in the semantic interference contrast during participants' response to comprehension questions did not show any overlap with regions exhibiting the syntactic interference effect (see Fig. 3). To further test the specific role of BA47 in semantic interference, an even lower value of $p_{\text{uncorrected}} < 0.1$ was applied to each individual contrast that was included in the conjunction analysis. The result showed that the BA47 region still only exhibited the semantic interference effect.

4. Discussion

According to the cue-based parsing theory (Lewis et al., 2006; Van Dyke, 2007; Van Dyke & McElree, 2006), when nouns that intervene between a subject and verb possess semantic or syntactic features that partially match the target subject, interference from those distractors produces increased processing difficulty. The aim of the present study was to replicate the behavioral effects of semantic and syntactic interference reported in the study of Van Dyke (2007) and, in addition, to investigate the neural basis involved in managing the two types of interference. We discuss these aims below in turn.

4.1. Time course of effects

This study did indeed find the predicted interference effects, although at different stages in processing (sentences vs. questions). Consistent with the findings of Van Dyke (2007), the syntactic interference effect was found in reading times at the critical verb phrase in our pilot experiment. Although the semantic interference effect was not observed in these reading times, it showed up later in response times for comprehension questions. A similar locus of effects was observed in the neuroimaging data: syntactic effects were observed during sentence reading, while semantic effects were observed during questions.

Van Dyke (2007) reported a similar time course, in which syntactic interference effects appeared in reading times at the critical verb, and semantic effects appeared later, although in the original experiment this effect was also in reading times (at sentence end). Although this time-course difference is consistent with other studies showing semantic effects later than the region containing the anomaly (Boland & Blodgett, 2001; Braze, Shankweiler, Ni, & Palumbo, 2002; Ni, Fodor, Crain, & Shankweiler, 1998), the low temporal resolution of fMRI makes the difference in the current study more difficult to interpret. One possibility is that the semantic interference effect observed during questions was in fact due to a continuation of processing that started during sentence reading but was not complete until past the end of the sentence. This is plausible because the integration of semantic information appears to be slower than the integration of syntactic information; McElree and Griffith (1995, 1998) found that violations of syntactic constituent structure were noticed 50–100 ms before violations of theta roles (i.e., semantic fit). This difference in time course is likely due to differences in the unification of syntactic and semantic information. As syntactic processing occurs over a finite set of grammatical features, it will take less time to determine how each noun phrase syntactically matches the critical verb. Moreover, these matching processes are simpler: required syntactic features (i.e., grammatical roles, agreement features, plurality) are either present or not. In contrast, determining the semantic fit between a noun phrase and a verb is more complex due to the possibility of varying degrees of match. For example, consider the experimental sentence "The ambassador who had exposed the known conspiracy during the meeting will arrive" which was considered to have both low semantic and syntactic interference. In this sentence "conspiracy" will unambiguously be assigned the role of object, which will thus result in a clear non-match on this syntactic feature when the comprehender tries to retrieve the subject of "will arrive." However, although "conspiracy" provides a less good fit semantically to "will arrive" than does "ambassador," there are semantic features of "conspiracy" (such as the fact that a conspiracy implies a group of people) which provide some degree of match to the required semantic features of "will arrive" (i.e., the subject would prototypically be concrete persons or objects). Also, non-concrete subjects often appear with movement verbs when used in a metaphorical sense (e.g., "New Year's will arrive with a bang"). Because of the greater subtleties in determining fit on semantic grounds, the buildup of conflict between the target and distractor on semantic grounds may take a longer time, with the resolution of conflict (and the involvement of the LIFG) coming on line later than is the case in resolving syntactic conflict. Thus, even though such semantic processing may begin immediately upon access to the semantic cues associated with the main verb, conflict resolution processes may not be sufficiently strong to be detectable neurally until a later time point for semantic than syntactic features. It is therefore possible that the semantic interference effect will not appear until after the sentence itself was read, making the observation of this effect during questions unrelated to processing the question itself.

Alternatively, our finding of semantic interference at question answering may suggest that it was only when participant's attention was focused on their error that they invoked processes necessary for distinguishing the target subject from the distractor. This would be consistent with the idea that participants were truly fooled by the semantic distractor, not even noticing the concomitant syntactic anomaly because they have settled on a seemingly plausible interpretation. This would be the outcome of a "Good-Enough" parsing strategy (Christianson, Hollingworth, Halliwell, & Ferreira, 2001; Ferreira & Patson, 2007) where participants adopt a low threshold for enforcing syntactic well-formedness during online processing in favor of attainting a semantically plausible interpretation. In this case, the semantic interference effect observed here will be related to a controlled process in which previously processed information is retrieved during offline reanalysis of the incorrect interpretation.

4.2. Neuroimaging results: the left inferior frontal gyrus

Regions in the LIFG were identified in contrasts of both types of interference, with syntactic interference invoking responses centered in BA45 and extending into BA44 and semantic interference invoking responses in BA45 and BA47. The association of BA44 and BA45 and syntactic interference is in line with other findings pointing to a syntactic role for these regions. Although the LIFG (especially Broca's area) has long been considered to be a critical region for syntactic processing (Caplan & Futter, 1986; Caramazza & Zurif, 1976; Schwartz, Saffran, & Marin, 1980), recent insights from neuropsychological and neuroimaging research have led to alternative interpretations of its function (e.g., Badre & Wagner, 2005; Caplan, Hildebrandt, & Makris, 1996; Jonides, Smith, Marshuetz, & Koeppe, 1998; Kan & Thompson-Schill, 2004a; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997). In response to these findings, some researchers have argued that the LIFG is not an area involved in syntactic processing per se, but rather is recruited when the demand for working memory is high in comprehension tasks (Caplan & Waters, 1999; Fiebach, Schlesewsk, Lohmann, Cramon, & Friederici, 2005; Waters & Caplan, 2005). However, the current results suggest that the role of the LIFG in sentence comprehension cannot be related simply to storing unintegrated information in working memory because the high and low semantic interference conditions in the present study have the same syntactic structure and the same number of unintegrated noun phrases. Thus, demands for working memory capacity should be equated in these conditions. Consequently, our findings would argue against the claim that involvement of the LIFG in sentence processing necessarily results from working memory demands (Fiebach et al., 2005; Makuuchi, Bahlmann, Anwander, & Friederici, 2009).

Rather, our results are more consistent with those who emphasize the role of LIFG in cognitive control (Hagoort, 2005, 2009; Novick et al., 2005, 2009; Ye & Zhou, 2008, 2009a, 2009b), as our syntactic and semantic manipulations served to increase the number of distractors for identifying the desired subject noun along each dimension. Accordingly, our conjunction analysis revealed that a common area restricted to BA45 was associated with both types of interference. This result is consistent with the view that this area in particular is involved in post-retrieval selection among representations retrieved via automatic cue-based associative retrieval (Badre & Wagner, 2007; Badre et al., 2005; Kan & Thompson-Schill, 2004a; Moss et al., 2005; Thompson-Schill et al., 1997; Thothathiri, Kim, Trueswell, & Thompson-Schill, 2012).

Our observation that a region in BA47 was involved only in semantic interference during questions is consistent with the idea that there may be somewhat different regions within the LIFG specific to semantic and syntactic interference. However interpretation of function underlying this result is confounded by the uncertainty discussed above, related to whether the semantic interference effect appears online during reading, or offline during question answering. If this is an online effect, then our results may be consistent with the unification model of Hagoort and colleagues (Hagoort, 2005, 2009; Snijders et al., 2008), who suggested that BA47 and BA45 are involved in semantic processing, while BA45 and BA44 are involved in syntactic processing. Additionally, in a study examining sentence sequencing, Bornkessel-Schlesewsky, Grewe, and Schlesewsky (2012) proposed a similar idea that the anterior–superior portion of LIFG contributed to linking the semantic/pragmatic information of the current sentence with the broader discourse, whereas the posterior-inferior LIFG is involved in processing argument prominence.

Alternatively, if our semantic interference effect is associated with an offline process, then our results are consistent with the view of Badre and colleagues (Badre & Wagner, 2007; Badre et al., 2005; Wagner, Paré-Blagoev, Clark, & Poldrack, 2001), who argued that BA47 in particular is associated with a controlled retrieval process which interacts with the stored semantic knowledge in lateral temporal cortex and is distinct from the selection process associated with BA45. We prefer this interpretation on purely theoretical grounds, due to specifics of the cue-based parsing model, which differ from the unification approach. Specifically, the Hagoort model suggests that the LIFG is important for unification because of its role in maintaining representations retrieved from posterior temporal regions. In contrast, the cue-based parsing approach deemphasizes the need for maintaining active representations, in favor of a fast cue-based retrieval mechanism that restores representations into the focus of attention as needed (Lewis et al., 2006). On this view, the inappropriate activation of similar distractors is inevitable when cues provide partial matches to non-target information, making the selection aspect of cognitive control, and not the maintenance aspect, more relevant for explaining interference effects. In terms of the Badre model, the conflict produced by the semantic distractors would produce the activations in the putative post-retrieval selection region (BA45) observed here, while the need to deliberately revise an incorrect semantic interpretation would produce activations in the region that supports controlled retrieval (BA47) such as those observed here.

4.3. The left mid-STG

In addition to the regions in the LIFG, a small portion of the left mid-STG was also activated in both syntactic and semantic interference contrasts, with the activation associated with the semantic interference effect extending to a more posterior area. These findings are in line with a number of other reports of the involvement of regions of the superior temporal gyrus in semantic and syntactic processing (Caplan, Alpert, & Waters, 1998; Caplan, Stanczak, & Waters, 2008; Fiebach et al., 2004; Friederici et al., 2003; Just et al., 1996; Rodd et al., 2010). In particular, Friederici et al. (2003) found that the mid and posterior portion of the STG was more activated for sentences with semantic violations than for correct sentences. In contrast, the anterior portion of the STG was more engaged for sentences with syntactic violations than correct sentences. The dissociated neural basis of semantic and syntactic processing is consistent with the activation pattern observed in the present study with the semantic region posterior to the syntactic region. Interestingly, however, our results show that these regions are involved in the processing of sentences which do not contain violations but instead differ in their degree of semantic or syntactic interference.

The association of the these regions with our syntactic and semantic interference effects suggests that, contrary to the view of Hagoort (2005) which argues that retrieval is the only role of the posterior superior temporal gyrus, integration of syntactic and semantic information occurs in posterior temporal cortex. As discussed in the introduction, retrieval interference occurs as a side effect of a global matching process, guided by a retrieval probe derived from syntactic and semantic cues associated with particular lexical items and the current state of the parse. Hence, a pre-requisite for interference effects is the integration of syntactic and semantic cues to create the retrieval probe. Friederici (2012) suggested that this integration occurs in the posterior temporal cortex (Bornkessel et al., 2005; Friederici, 2011; Newman, Ikuta, & Burns, 2010), though she was not referring to the integration of semantic and syntactic *retrieval cues*, per se, but rather to different types of linguistic knowledge.

Positioning feature integration in STG regions is also consistent with findings that suggest syntactic and semantic integration can occur without involvement of the LIFG when conflict is not present. For instance, patients with LIFG damage can show good comprehension of sentences with low conflict (Novick et al., 2009) and agrammatic aphasic patients (who are assumed to have LIFG damage) tend to do well on grammaticality judgments (Linebarger, Schwartz, & Saffran, 1983). Moreover, some fMRI studies have shown an absence of activation in frontal regions for the comprehension of coherent passages where conflict between representations is presumably minimized (e.g., Brennan et al., 2012). Thus, we would suggest that the retrieval of semantic and syntactic features of words, the generation of retrieval cues, and the integration of representations based on a match between retrieval cues and features of encoding representations may all occur without involvement of the LIFG. Greater activation in the STG in the high interference conditions may result because more representations are retrieved due to the partial match with retrieval cues. The LIFG comes on line when there is a need to resolve this interference generated by similar competitors in the linguistic context.

4.4. Other regions

The superior frontal region (BA9/10) was activated in both interference contrasts following the onset of comprehension questions, but not identified in the contrasts following the onset of sentences (although it showed greater deactivation in high vs. low interference conditions during sentence processing). This area may be involved in the post-interpretive processing proposed by Caplan and Waters (1999), in which readers use propositional content of the sentences to accomplish additional tasks, such as answering the comprehension questions in this study. Moreover, there were regions in the medial frontal, superior frontal, prefrontal and precuneus exhibiting enhanced deactivations for high vs. low interference conditions following the onset of sentences and comprehension questions. These regions have often been considered part of a ‘‘default mode network’’ that shows greater deactivation when more cognitive resources are occupied by the ongoing task (e.g., Bluhm et al., 2010; Buckner & Vincent, 2007; Mason et al., 2007).

4.5. Inclusion of inaccurate trials

We included both accurate and inaccurate trials in the neuroimaging analyses because we assumed that subjects attempted to resolve interference on inaccurate trials but were unsuccessful in doing so[3]. In understanding this approach, it is necessary to realize that our comprehension questions were unlike those employed in most experiments, in which the question is present primarily to prevent attention lapses, and often appears on only a subset of trials. In these studies, the content of the question is usually incidental to the critical manipulation, querying general aspects of the read material so that they are easy to answer correctly. Due to this, accuracy levels are typically near 100% and do not raise an issue for data analysis (e.g., Bornkessel et al., 2005; Makuuchi et al., 2009; Mason et al., 2003; Thothathiri et al., 2012). In the present experiment, the comprehension questions were designed specifically to assess individuals' identification of the subject of the critical verb (i.e., the manipulated dependency) and could therefore reveal susceptibility to interference from the distracting noun. This made the comprehension questions critical data in their own right, with the theoretically motivated prediction that significantly lower accuracy levels will be found in conditions with high interference precisely because the incorrect noun phrase is retrieved. This is both a direct and necessary consequence of a cue-based retrieval mechanism that utilizes global matching processes. Therefore, the greater activations we found in the LIFG and the mid-STG regions for high interference conditions than low interference conditions are more likely due to the influence of the distractor, and not to simple lapses in attention. Moreover, the inclusion of comprehension questions on every trial, regardless of the amount of interference, discouraged attention lapses in general, and meant that any incidental lapses would likely be evenly distributed across conditions, rather than focused on any particular condition in the experiment.

A possible criticism of this approach is that the inclusion of incorrect trials may increase noise in our dataset because of possible error detection processes. We note, however, that the region responsible for error detection has been found to be the anterior cingulate cortex (e.g., Carter, Braver, Barch, Botvinick, & Cohen, 1998; Van Veen & Carter, 2002; Yeung, Botvinich, & Cohen, 2004), and not the regions we identified in the study.

5. Conclusion

The present study replicated behavioral findings pointing to a cue-based retrieval mechanism as the means for creating dependencies between non-adjacent linguistic constituents. With regard to the neural basis of these processes, regions in the LIFG were activated during interference with BA44 and 45 showing greater activation in the presence of increased syntactic interference and BA45 and 47 showing greater activation in the presence of increased semantic interference. A conjunction analysis of activations in both types of interference revealed a region centered in BA45 and extending into BA44 which was associated with both syntactic and semantic interference. The region of semantic interference in BA47, however, did not overlap with any region of syntactic interference. Thus, there appear to be overlapping but distinct regions within the LIFG that mediate semantic and syntactic interference. Importantly, the behavioral and imaging results could not be attributed to greater working memory capacity demands for the high versus low interference conditions. The results instead support a direct role for these regions in resolving retrieval interference, with the region in BA45 associated with post-retrieval selection and the region in BA47 associated with controlled retrieval of semantic information.

[3] This assumption is supported by the findings that participants spent longer time in responding to high semantic interference sentences than low semantic interference sentences regardless of whether inaccurate trials were included in the analyses.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.bandl.2013.06.006.

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