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Neural segregation in left inferior frontal gyrus of semantic processes at different levels of syntactic hierarchy

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ABSTRACT

Humans are unique in their ability to parse hierarchical structures of sentences. Previous studies demonstrated that syntactic processes at different hierarchies are subserved by distinct subregions in left inferior frontal gyrus (LIFG), in which BA45 is mainly involved in processing lower-level syntactic structures and BA44 is mainly involved in processing higher-level syntactic structures. However, little is known about whether semantic processes at different syntactic hierarchies show similar dissociations in LIFG. In the present fMRI experiment, participants read sentences with the structure "subject noun + verb + numeral + classifier + object noun", in which the object noun is constrained by the classifier at the lower-level and by the verb at the higher-level. The object noun was manipulated to be either semantically congruent or incongruent with the classifier at the lower-level and/or with the verb at the higher-level. Both the whole brain contrasts and the region of interest (ROI) analyses showed that, in LIFG, the semantic process of integrating the object noun with the classifier induced stronger activation in BA45 whereas the semantic process of integrating the object noun with the verb induced stronger activation in BA44. This dissociation demonstrates a neural segregation for semantic processes at different syntactic hierarchies, with the lower-level process relying more on neural substrates for general semantic processes and the higher-level process relying more on neural substrates for processing structural hierarchies.

1. Introduction

The ability to parse a hierarchical syntactic structure is proposed to be crucial and unique to human beings (Chomsky, 1956; Fitch and Hauser, 2004; Friederici, 2017a, 2017b). The syntactic hierarchy is created by embedding a sentence constituent within a local phrase structure (to form a local dependency) or by embedding a constituent within a more complex structure (to form a long-distance dependency).

Previous researches have demonstrated neural segregations for syntactic processes at different levels of syntactic hierarchy (Friederici et al., 2006; Makuuchi et al., 2009; Opitz and Friederici, 2007; Zaccarella et al., 2017a,b). For example, functional magnetic resonance imaging (fMRI) studies using artificial language stimuli showed that, relative to simpler syntactic relations, cognitive processing of more complex syntactic relations involves posterior left inferior fontal gyrus (LIFG) (Friederici et al., 2006; Opitz and Friederici, 2007). Studies using natural language stimuli also revealed neural segregations in the frontal regions (Makuuchi et al., 2009). For example, Makuuchi et al. (2009) created a hierarchical dependency between the subject and the auxiliary verb by embedding a relative clause or a linear dependency by simply lengthening the linear distance between these words. Compared with the activation peak locus in LIFG induced by long-vs. short-distance regardless of the nature of the dependency between words, a more posterior peak locus in LIFG was induced by hierarchical vs. linear dependency. These functional segregations in LIFG are consistent with the anatomical parcellation of Jülich Histological Atlas, which divides LIFG into BA44 and the more anterior BA45 (Amunts et al., 1999). By applying the anatomical atlas of these LIFG divisions to define regions of interest, researchers demonstrated the dominant role of BA44 in processing hierarchical structure in fMRI studies both with artificial

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language (Chen et al., 2021) and with natural language (e.g., Japanese, Iwabuchi et al., 2019).

Words in a sentence are not only organized by syntactic rules but also associated by their semantic properties. A question then arises: do semantic processes at different syntactic hierarchies also have differential neural substrates, similar to the neural segregation for syntactic processes? Establishing semantic relations between words in a sentence depend to a certain extent on the syntactic relations between these words (Jackendoff and Pinker, 2005). A word in a sentence can be constrained, both syntactically and semantically, by multiple constituents in the prior sentential representation, including lower-level constraints characterized by local dependency and higher-level constraints characterized by long-distance dependency. For instance, in a sentence "he ate a delicious apple", the object noun "apple" is constrained syntactically and semantically by the adjective "delicious" at the local phrase level and by the verb "ate" at the higher-level.

Studies directly addressing the potential neural segregation for semantic processes at different syntactic levels are very limited. Previous researches typically manipulated the semantic congruency between sentential constituents either at the lower-level or at the higher-level independently without contrasting them in the same study. Nevertheless, a careful examination of the locus of peak activations across studies showed that semantic processes at different syntactic hierarchies indeed have differential neural substrates in LIFG. Table 1 and Table 2 [2] summarize respectively fMRI studies examining processes of local dependencies (Table 1) and fMRI studies examining semantic processes involving more complex hierarchies (Table 2).

As can be seen in Table 1, semantic processes occurring at local dependencies commonly have peak activations in BA45, for comparisons between conditions demanding more and less costly semantic processes. For example, Mason and Just (2007) found that the ambiguous words (e.g., "pen") locally constrained by verbs in sentences (e.g., "Last year the *pen* was abandoned because it was too dirty for the animals to live in") had increased activation in BA45 of LIFG as compared with the matched unambiguous words (e.g., "zoo"). A study manipulating the semantic expectancy of the object noun constrained by a local verb (e.g., "睡觉前他调了闹钟/灯光/月亮 …" for high expectancy, low expectancy, and semantic violation condition respectively; English translation: *before he went to bed he set* ***alarm clock/light/moon*** …) revealed increased peak activation in BA45 of LIFG as the semantic expectancy toward the target noun decreased (Zhu et al., 2012). The activation in left BA45 was also be stronger with the increasing severity of semantic violation (Hagoort et al., 2004; Schulz et al., 2008; Zhu et al., 2009), the reduction of contextual constraints (Kuperberg et al., 2006), and the decreasing pragmatic plausibility (Kuperberg et al., 2008).

In contrast, studies examining semantic processes involving more complex sentence structures (Table 2) commonly showed peak activations in BA44 for comparisons between costly semantic processes and easier semantic processes. These studies manipulated the difficulty in assigning the syntactic/thematic roles or the semantic congruency between constituents at different syntactic hierarchies of sentences. They analyzed comparisons which reflect whether the processes demanded the reassignment of syntactic/thematic roles or the building of semantic relations in a hierarchical structure. For example, as compared with the preferred German subject-initial structure (e.g., "dass | der Junge | den Lehrern | hilft", English translation: *that the boy helps the teachers*), the unpreferred object-initial structure (e.g., "dass | dem Jungen | die Lehrer | helfen", English translation: *that the teachers help the boy*) had enhanced peak activation in BA44 of LIFG (Bornkessel et al., 2005). Relative to the subject-initial sentence, processing the object-initial sentence involved an additional operation of reassigning syntactic/thematic roles to constituents in an initially built structural/thematic relation. Hence, this result demonstrated that BA44 is involved in the process of building a semantic relation across hierarchical levels. Another fMRI study showed that animacy, as a semantic feature, modulated the effect of subject-object order of German passivized ditransitive structure on activations in BA44 of LIFG. Activations in BA44 of LIFG were enhanced for subject-initial structure relative to object-initial structure when the subject was inanimate but not when the subject was animate (Grewe et al., 2006). In manipulating semantic expectancy towards nouns constrained by distant sentential constituents in Dutch (e.g., "*That illness can be treated with the new* ***medicine/device/moment*** …" for high expectancy, low expectancy, and semantic violation condition respectively), Zhu et al. (2019) found that activations in both BA44 and BA45 of LIFG were enhanced as the semantic expectancy decreased. These results are consistent with the view emphasizing the role of BA44 in processing syntactic hierarchy (Friederici, 2011; Friederici et al., 2017; Zaccarella et al., 2017a,b).

Contrasting the MNI peaks of neural responses reported in Tables 1 and 2, it is clear that semantic processes for local dependencies activated more anterior portions of LIFG than semantic processes involving complex hierarchies, probably because the latter processes rely more on syntactic operations to build complete linguistic representations (Grewe et al., 2006, 2007; Hagoort et al., 2004; Schulz et al., 2008).

The neural segregation of semantic processes is consistent with the Memory, Unification, and Control (MUC) model (Hagoort, 2005, 2014, 2017, 2019), which proposes that language comprehension is an orchestration of memory retrieval of linguistic items, unification of these items, and cognitive control of selecting relevant information among multiple sources. The MUC model emphasizes a general role of LIFG in unification, which integrates phonological, semantic, and syntactic information with the context to form a whole representation. The level of information integrated demands different portions of LIFG. A meta-analysis of neuroimaging studies on sentence processing showed that the semantic unification is related to a mean activation location in BA45 of LIFG, whereas the syntactic unification is related to a mean activation location in BA44 of LIFG (Hagoort and Indefrey, 2014). We thus hypothesize that, during comprehending sentential meanings, semantic unification between constituents constrained by the higher-level dependency, on the one hand, is dominated by syntactic operations to form a hierarchical structure consisting of these constituents (Zaccarella et al., 2017a,b) and likely involves BA44; semantic unification for locally dependent constituents, which requires little syntactic operations, on the other hand, is dominated by semantic processes and likely involves BA45.

To directly compare neural correlates of semantic processes at different hierarchical levels, it is advantageous to use materials forming hierarchical semantic relations in an integral structure. Nam and Hong (2016) manipulated semantic congruencies at different levels using verb-final declarative sentences in Korean with a structure "subject noun + adjective + object noun + adverb + verb" (e.g., "진수가 [Jinsu] 달콤한 [sweet] 수프-를 [soup] 빨리 [quickly] 끓였다 [cook]", English translation: *Jinsu cooked a sweet soup quickly*) with the object noun constrained by the adjective at the lower-level and the verb constrained by the object noun at the higher-level. Their ERP results showed that, the semantic incongruence at the lower-level elicited enhanced N400 relative to the congruent condition on the object noun, whereas the semantic incongruence at the higher-level elicited enhanced N400, followed by a larger P600, than the semantic congruence on the verbs. This pattern suggested dissociable neural correlates of semantic congruency effect at different levels of syntactic hierarchy. However, a potential problem in Nam and Hong (2016) is that the observed dissociation of ERPs could be simply due to the difference in the words being read (e.g., nouns vs. verbs) rather than due to the hierarchical levels that the words were in.

In an earlier ERP study without such a concern, Zhou et al. (2010) used Chinese sentences with a hierarchical structure "subject noun + verb + numeral + classifier + object noun" (e.g., "小赵 [Zhao] 修理

[2] In the tables, all coordinates originally reported in the Talairach system were converted into the MNI system using the Talairach to MNI converter of the BrainImage Suite (https://bioimagesuiteweb.github.io/webapp/mni2tal.html).

Table 1
The activation in LIFG for studies on semantic processes within local structures, covering authors, reported years, tasks involved, statistical comparisons, stimulus modality, the peak in MNI (Montreal Neurological Institute) coordinate and reported Brodmann Areas.

Authors (year)	Task	Comparison	Stimulus modality	Peak in MNI coordinate	Brodmann area
Hagoort et al. (2004)	Reading without overt response	Semantic/world knowledge violated vs. correct sentences	Visual	[-45 32 6]	BA45
Zhu et al. (2012)	Reading without overt response/semantic congruency or font size judgement	Negative correlation with semantic expectancies	Visual	[-50 38 4]	BA45/47
Zhu et al. (2009)	Semantic acceptability judgment	Positive correlation with the degree of semantic violation	Visual	[-52 19 14]	BA45
Kuperberg et al. (2006)	Causal coherence judgment	Intermediately vs. highly contextual constraint sentences	Visual	[-44 42–10]	BA45/47
Mason & Just (2007)	Yes-no comprehension question	Ambiguous vs. unambiguous sentences	Visual	[-52 26 12]	BA45
Schulz et al. (2008)	Occasional meaningfulness judgement	Semantic incongruent vs. congruent sentences	Visual	[-55 18 2]	BA45
Kuperberg et al. (2008)	Sentence acceptability judgement	Pragmatic violated vs. normal sentences	Visual	[-44 30–15]	BA 47
Vitello et al. (2014)	Semantic relatedness judgement	Ambiguous vs. unambiguous sentences	Auditory	[-45 32 4]	BA45

Table 2
The activation in LIFG for studies on semantic processes across different syntactic hierarchies, covering author and reported years, tasks involved, statistical comparisons, stimulus modality, the peak in MNI coordinate and reported Brodmann Areas.

Authors (year)	Task	Comparison	Stimulus modality	Peak in MNI coordinate	Brodmann area
Bornkessel et al. (2005)	Comprehension task	Object-initial vs. subject-initial sentences with active verbs	Visual	[-45 16 18]	BA44
Bornkessel et al. (2005)	Comprehension task	Subject-initial vs. object-initial sentences with object–experiencer verbs	Visual	[-45 16 18]	BA44
Grewe et al. (2006)	Sentence acceptability judgement	Sentences with an inanimate subject preceding an animate object vs. with an animate object preceding an inanimate subject	Visual	[-56 8 21]	BA44
Grewe et al. (2007)	Sentence acceptability judgement	Object- vs. subject-initial sentences	Visual	[-57 12 14]	BA44
Bornkessel-Schlesewsky et al. (2009)	Sentence acceptability judgement	Object- vs. subject-initial sentences	Visual	[-56 14 2]	BA44
Zhu et al. (2019)	Reading without overt response	Positive correlation with the degree of semantic violation	Visual	[-48 12 30]	BA44/45

[repaired] 一 [one] 张 [*zhang*, classifier] 长椅 [chair]", English translation: *Zhao repaired a chair*) and focused on the same object nouns in different conditions. In this structure, the classifier (e.g., 张 *zhang*) functions to specify semantic features of the following object noun, such as shape, size, rigidity, animacy, or type, and therefore imposes local selectional restrictions on the scope of the noun (Jiang and Zhou, 2009, 2012; Saalbach and Imai, 2007). Hence, the object noun is simultaneously constrained by the classifier at the lower-level and by the verb at the higher-level. By manipulating these constraints, the authors found that, on the object noun, the semantic incongruence between the classifier and the noun (at the lower-level) elicited increased N400 responses while the semantic incongruence between the verb and the noun (at the higher-level) elicited a biphasic pattern of N400 plus late positivity. Taken together, the ERP results in the studies of Zhou et al. (2010; see also Jiang and Zhou, 2009) and Nam and Hong (2016) suggest that there were indeed differential neural correlates for semantic processes at different hierarchical levels although these results did not point directly to the potential neuroanatomical segmentation in LIFG.

By using fMRI, the present study aimed to examine the potential neural segregation in LIFG between semantic processes at different hierarchical levels during the comprehension of sentences with the same structure used in Zhou et al.'s study (2010; see Table 3). Participants were instructed to read sentences for comprehension. Importantly, we minimized task demands by instructing participants to make semantic

Table 3
Experimental conditions and exemplar sentences with the structure of "subject + verb + numeral + classifier + noun". The constraint of the classifier is noted in the brackets. The semantic congruence or incongruence at the lower (classifier-noun) or higher (verb-noun) level of syntactic hierarchy is marked in the right columns, with "√" indicating congruence and "×" indicating incongruence.

Condition	Exemplar sentence						Higher-level congruence	Lower-level congruence
Correct (COR)	赵庆	修好	一	张	长椅	。	✓	✓
	Zhaoqing	repaired	one	zhang (classifying chairs or papers)	chair	.		
	Zhaoqing repaired a chair.							
Classifier-noun mismatch (CNM)	赵庆	修好	一	台	长椅	。	✓	×
	Zhaoqing	repaired	one	tai (classifying electric appliance)	chair	.		
	Zhaoqing repaired a chair.							
Verb-noun mismatch (VNM)	赵庆	修好	一	张	布告	。	×	✓
	Zhaoqing	repaired	one	zhang	notice	.		
	Zhaoqing repaired a piece of notice.							
Double- mismatch (DM)	赵庆	修好	一	台	布告	。	×	×
	Zhaoqing	repaired	one	tai	notice			
	Zhaoqing repaired a piece of notice.							

plausibility judgments for only a small portion of (filler) sentences. This procedure aimed to avoid potential confounds on brain activation caused by cognitive control if an explicit task was carried out on the critical sentences. According to the MUC model, a task could tax the control system when processing difficulty caused by semantic anomaly or ambiguity is encountered (Hagoort and Indefrey, 2014; Mason and Just, 2007; Schulz et al., 2008; Zhu et al., 2012, 2019). Thus, neural activations in LIFG could be triggered by cognitive control rather than semantic or syntactic processes *per se* (Fedorenko and Blank, 2020; January et al., 2009; Miller and Cohen, 2001; Novick et al., 2005; Ye and Zhou, 2009a,b). Moreover, the current design with minimal task demands shares more resemblance to human's daily language understanding than more popular designs with explicit tasks, as we normally do not make semantic judgments during communications (Erickson and Mattson, 1981). Given that previous fMRI experiments on reading with minimal task demands showed stronger activations in LIFG for congruent semantics than for either incongruent semantics (Ilg et al., 2007) or senseless sentences (Matchin et al., 2017) and given that, with minimal task demand, EEG responses related to semantic/syntactic unification were shown to increase for semantic congruence relative to incongruence (Bastiaansen and Hagoort, 2015), we predicted that the BOLD signals would exhibit in a similar way in the current experiment.

2. Methods

2.1. Participants

Twenty students from Beijing Normal University, with a mean age of 21.4 years (range: [18, 24]), participated in the fMRI experiment. They were right-handed, had normal or corrected-to-normal vision, and had no known history of neurological or psychiatric disorders. Informed consents were obtained from all participants. This study was approved by the Institutional Review Board of Beijing Normal University Imaging Center for Brain Research.

2.2. Design and materials

Two hundred quadruplets of critical sentences in Chinese with the hierarchical structure "subject noun + verb + numeral + classifier + object noun" were inherited from Zhou et al.'s study (2010). In this structure, the object noun was semantically constrained by the classifier at the lower-level, and by the verb at the higher-level (Table 3). The semantic congruencies at the lower-level and at the higher-level were manipulated by using different object nouns and classifiers, forming a 2 × 2 factorial design shown in Table 3. The four conditions within each quadruplet were (1) correct sentence (COR) with semantic congruencies at both the lower-level (classifier-noun match) and the higher-level (verb-noun match); (2) the sentence with semantic incongruence at the lower-level only (classifier-noun mismatch, CNM); (3) the sentence with semantic incongruence at the higher-level only (verb-noun mismatch, VNM); and (4) the sentence with semantic incongruences at both the lower-level and the higher-level (double mismatches, DM).

In each quadruplet, the COR and the VNM sentences shared a classifier and the CNM and the DM sentences shared another classifier, while the COR and the CNM sentences shared an object noun and the VNM and DM sentences shared another object noun. The object nouns in the COR and VNM sentences were matched in word frequencies, $t_{(49)} = 0.24$, $p > 0.1$ (Cai and Brysbaert, 2010), while the classifiers in the COR were of slightly higher character frequencies than the classifiers in the CNM sentences, $t_{(49)} = 2.13$, $p = 0.038$ (Cai and Brysbaert, 2010). The classifiers and the object nouns were matched across conditions in visual complexity, as indexed by the number of strokes, classifiers: $t_{(49)} = -0.39$, $p > 0.1$; object nouns: $t_{(49)} = -1.0$, $p > 0.1$. The numeral preceding the classifier was always the same character "一" ("one"). All the subject nouns were two- or three-character animate words denoting human names and/or their occupations and all the object nouns were inanimate. Another 40 filler sentences with the same structure, 10 for each corresponding condition, were presented as filler trials (see *2.4 Procedure* for details).

2.3. Pretests

2.3.1. Sentence acceptability rating

The aim of sentence acceptability rating was to check the validity of the manipulation of conditions. Two groups of 16 native Chinese speakers who did not participate in the fMRI experiment rated acceptability of the local phrase embedded in all critical sentences ("numeral + classifier + noun") and the whole critical sentences of all conditions, respectively, on 5-point Likert scale. The results, as shown in Table 4, indicated that the sentences with incongruences were much less acceptable than the correct sentences.

For the local phrase acceptability rating, the local phrases in the COR and VNM sentences were rated more acceptable than either the CNM sentences, COR: $t_{(49)} = 43.35$, $p < 0.001$; VNM: $t_{(49)} = 47.37$, $p < 0.001$, or the DM sentences, COR: $t_{(49)} = 49.08$, $p < 0.001$; VNM: $t_{(49)} = 47.85$, $p < 0.001$. The acceptability of the local phrases in the COR and that in the VNM sentences were comparable, $p > 0.6$, as the classifier-object pairs in these local phrases were both semantically congruent. For the whole sentence acceptability rating, the COR sentences were rated more acceptable than the CNM, VNM, and DM sentences, CNM: $t_{(49)} = 29.69$, $p < 0.001$; VNM: $t_{(49)} = 28.99$, $p < 0.001$; DM: $t_{(49)} = 57.58$, $p < 0.001$. Both the CNM and VNM sentences were rated more acceptable than the DM sentences, CNM: $t_{(49)} = 9.05$, $p < 0.001$; VNM: $t_{(49)} = 6.72$, $p < 0.001$.

2.3.2. Cloze probability

To check whether the predictability of the object noun differed between conditions, we asked 40 native Chinese speakers who did not participate in the fMRI experiment to complete the sentence fragment (i.e., without the final object noun) of the COR sentences and the CNM sentences. Note, sentences without the final object nouns were the same for the COR and the VNM conditions and for the CNM and the DM conditions. As shown in Table 4, the average cloze probability for the actually used object nouns was 10.4% in the COR sentences and was 0% in the CNM sentences, although the average cloze probability for the most frequently produced (but not used in the experimental stimuli) words was 33.7% for sentence fragments in the COR condition and 47.5% in the CNM condition.

2.4. Procedure

Sentences were presented on a projection screen which was viewed by participants through a mirror attached to the head coil. Each trial began with a fixation cross presented for 600 ms, followed by a blank screen for 400 ms. Sentences were presented word by word for 400 ms

Table 4
Mean scores and standard deviations (SD) in the three pretests. The local phrase acceptability and the sentence acceptability rating used 5-point Likert scales, with 5 representing "totally acceptable" and 1 representing "totally unacceptable". The listed scores for the cloze probability test are for the target nouns actually used in the correct sentences.

Experimental condition	Local phrase acceptability		Sentence acceptability		Cloze probability of the target noun (%)	
	Mean	SD	Mean	SD	Mean	SD
Correct (COR)	4.72	0.33	4.73	0.3	10.4	14.5
Classifier-noun mismatch (CNM)	1.5	0.39	2.07	0.55	0	0
Verb-noun mismatch (VNM)	4.74	0.35	1.93	0.69	0	0
Double-mismatch (DM)	1.38	0.31	1.35	0.28	0	0

each, followed by a 400 ms interval blank screen. Participants were instructed to read each sentence for comprehension. To minimize the task demand while ensuring participants to read sentences carefully and to reduce the potential artifact in BOLD signals to critical sentences, participants were only instructed to explicitly respond to the 40 filler sentences (17% of all stimulus sentences). For each filler sentence, a response cue "?????" was presented for 500 ms at the end of the sentence. Participants were asked to respond as accurately as possible by pressing a button with the index or middle finger of their right-hand whether the sentence was acceptable. The assignment of fingers to "yes" and "no" responses was counter-balanced across participants. In addition, 50 null trials were interspersed in the test sequence to improve estimation efficiency (Miezin et al., 2000). In the null trials, a fixation cross was presented for 600 ms followed by a blank screen for 3600 ms. The inter-trial interval was jittered with a variable duration of 0, 500, 1000 or 1500 ms.

In total, 240 sentences (200 critical sentences and 40 filler sentences) were presented to each participant. The order of presentations was pseudo-randomized, with the constraints that (a) sentences in each condition were preceded by an equal number of sentences in other conditions; (b) repetitions of the same verb were separated by at least 30 intervening trials; (c) sentences close to each other used different classifiers; and (d) no more than 3 consecutive trials came from the same condition (see also Hahne and Friederici, 2002; Ye and Zhou, 2009a).

The whole experimental sequence was broken into 5 blocks, one for a formal fMRI session, each of which lasted for about 10 min. A practice session with 12 sentences, which were not presented in the fMRI sessions, was administered to each participant before the fMRI scanning outside the scanner. In the instruction to participants, an emphasis was placed on the understanding of sentence meaning and the accuracy of judgments.

2.5. FMRI data acquisition

A 3 T Siemens Trio system with a standard head coil at the MRI Center for Brain Research at Beijing Normal University was used to obtain T1-weighted structural images ($1 \times 1 \times 1.3$ mm^3 voxel size) and functional images. The functional images were T2*-weighted echo-planar images (EPI) with blood oxygenation level-dependent (BOLD) contrast, with 2,000 ms repetition time, 30 ms echo time, and 90° flip angle. Each functional image consisted of 28 axial slices, obtained in interleaved ascending order and covering the whole brain. Slice thickness of the functional images was 4 mm, with a 200×200 mm^2 field of view, 64×64 matrix, and $3.1 \times 3.1 \times 4$ mm^3 voxel size.

2.6. FMRI data analysis

2.6.1. Preprocessing

The preprocessing was performed using the FMRIB Software Library (FSL Version 6.00, http://www.fmrib.ox.ac.uk/fsl/) package (Woolrich et al., 2001). All images were transformed from DICOM to nifti-format, and the first five volumes of each functional session were discarded to avoid the effect of any start-up magnetization transients in the data. Non-brain tissues of images were removed using BET based on the T1-weighted structural images (Smith, 2002). The images were preprocessed in the following procedure: motion correction using MCFLIRT (Jenkinson et al., 2002); slice-timing using Fourier-space time-series phase-shifting; spatial smoothing using a Gaussian kernel of FWHM 5 mm; and registrations to spatially normalize images to the MNI152 standard template (2 mm isotropic resolution) for group-level analysis using FLIRT (Jenkinson et al., 2002; Jenkinson and Smith, 2001). Hence, all coordinates reported below are in the MNI (Montreal Neurological Institute) system. To remove low-frequency drift in the temporal signal, we applied a high-pass temporal filtering (Gaussian-weighted least-squares straight line fitting, with sigma = 50 s).

2.6.2. Whole-brain analyses

General linear models (GLMs) of fMRI data were fitted at three levels using FEAT (FMRI Expert Analysis Tool) in FSL.

At the first level, GLMs were fitted for each session and each participant with 16 regressors: critical sentence presentations (2.8 s), each of which was consisted of four words (1.6 s) interleaved with three blank screens (1.2 s), for the four conditions (COR, CNM, VNM and DM) separately and their temporal derivatives, filler sentence presentations (2.8 s), responses to the filler sentences fitted as pulses (regardless of participants' judgments), and six head motion parameters.

We conducted planned contrasts to examine effects of experimental conditions. First, to examine neural responses to each condition, we conducted four contrasts for the conditions (i.e., COR, CNM, VNM, and DM) respectively. To compare each condition with zero baseline, each contrast had the regressor of critical sentence representations in one condition coded as 1 and other regressors coded as 0.

Second, to examine the main congruency effects at the two hierarchical levels, two contrasts were defined for "Congruence vs. Incongruence", (a) at the lower-level, "(COR + VNM) – (CNM + DM)", and (b) at the higher-level, "(COR + CNM) – (VNM + DM)" (see *Supplementary Information* for the contrasts of reversed directions).

Third, we conducted a contrast for an interaction, "(COR - CNM) – (VNM - DM)" since the previous ERP study using the stimuli with the same structure showed the interaction between a higher-level congruency and a lower-level congruency (Zhou et al., 2010).

For the second level GLM, a fixed-effect model with all five sessions assigned equal weights was fitted to compute parameter estimates of the planned contrasts for each participant. For the third level GLM, a mixed effect model with all participants assigned equal weights was fitted to compute group-level parameter estimates of the planned contrasts. Z-statistic maps of the parameter estimates were applied with a voxel-level Gaussian random field (GRF) based maximum height threshold of $z > 2.3$ and a cluster-level GRF based significance threshold of $p < 0.05$ (reference to https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FEAT/UserGuide#Post-Stats:_Contrasts.2C_Thresholding.2C_Rendering).

2.6.3. Region of interest (ROI) analyses

To examine potential neural segregations in LIFG for semantic congruency effects (Congruence vs. Incongruence) at the lower-level and the higher-level, independent region of interest (ROI) analyses were conducted. To limit the ROI analyses within BA44 and BA45 of LIFG, we first created left BA44 mask and left BA45 mask based on the probability maps of Jülich Histological Atlas (Amunts et al., 1999). Voxels were assigned to either left BA44 or left BA45 according to their maximum probability in the probability maps, resulting in a left BA44 mask with a volume of 39,576 mm^3 and a left BA45 mask with a volume of 26,408 mm^3.

We defined four sphere ROIs with a radius of 10 mm based on the conjunction of these anatomical masks and the activations in previous meta-analyses, which reported activation coordinates in BA44 for syntactic processes and that in BA45 for semantic processes. The center of two sphere ROIs were defined based on the meta-analytical results of neuroimaging studies on sentence reading (Hagoort and Indefrey, 2014). One of these ROIs had center coordinates in left BA44 ([−56, 16, 15]), and the other had center coordinates in left BA45 ([−52, 25, 3]).[3] The center of another two sphere ROIs were defined based on the meta-analytical results of neuroimaging studies on content/function

[3] Hagoort and Indefrey (2014) originally reported the coordinates in the Talaraich system. Here we converted the original coordinates into the MNI system using the Talairach to MNI converter of the BrainImage Suite. Because Hagoort and Indefrey did not report x-coordinate, we assigned x-coordinate of the voxel with highest probability in either the left BA 44 mask or the left BA45 mask from Jülich Histological Atlas as the center x-coordinate in either of the two sphere ROIs.

words processing (Zaccarella et al., 2017b). One of these ROIs had center coordinates in left BA44 ([−60, 14, 12]), and the other had center coordinates in left BA45 ([−52, 28, 10]).

Average *z*-transformed parameter estimates of the planned contrasts of the lower-level congruency effect (Congruence vs. Incongruence) and the higher-level congruency effect (Congruence vs. Incongruence) were extracted in each ROI for each participant's second-level GLM. A 2 (contrast types: lower-level vs. higher-level) × 2 (ROI types: BA44 vs. BA45) repeated-measures analysis of variance (ANOVA) was performed for ROIs based on either Hagoort and Indefrey (2014) or Zaccarella et al. (2017b) using *aov* function in R environment.

2.6.4. Analyses of y-coordinates of individuals' peaks in LIFG

The analyses of y-coordinates aimed to investigate the separation of peak activation coordinates in LIFG between the higher-level congruency effect and the lower-level congruency effect along the anterior-posterior axis. This separation, which is reflected by the y-coordinate in the MNI system, is consistent with the parcellation between BA44 and BA45 of LIFG (Rodd et al., 2015). We defined four y-coordinates of interest, including the y-coordinates in BA44 (16) and BA45 (25) from the meta-analysis of Hagoort and Indefrey (2014) and the y-coordinates in BA44 (14) and BA45 (28) from the meta-analysis of Zaccarella et al. (2017b).

To limit the analyses of y-coordinates in LIFG, an LIFG mask was created by combining the left BA44 mask and the left BA45 mask. For each participant, with voxel-level threshold of $z > 1.5$ and cluster-based significance threshold of $p < 0.05$, we extracted the largest significant cluster in the intersection between the LIFG mask and the thresholded *z*-statistic maps of the contrasts of the lower-level congruency effect (Congruence vs. Incongruence) and the higher-level congruency effect (Congruence vs. Incongruence) respectively. The peak in this largest significant cluster was defined as an individual's peak of congruency effect in LIFG.

By using Bayesian one-sample *t*-tests, which were performed with the *BayesFactor* package (Andraszewicz et al., 2015; Rouder et al., 2012) in R environment, we compared y-coordinates of individuals' peaks with the y-coordinates of interest from the meta-analyses. Each test had a null hypothesis (H_0): mean y-coordinate of individuals' peaks is drawn from the population with a mean of either y-coordinates of interest. Bayes factor BF_{01} was computed to indicate the preference of H_0 to alternative hypothesis (H_1) given the data (i.e., y-coordinates of individuals' peaks). In these tests, individuals' peak y-coordinates of the lower-level congruency effect were compared with y-coordinates of interest in BA45, 25 and 28 from Hagoort and Indefrey (2014) and Zaccarella et al. (2017b), respectively; individual peak y-coordinates of the higher-level congruency effect were compared with y-coordinates of interest in BA44, 16 and 14 from Hagoort and Indefrey (2014) and Zaccarella et al. (2017b), respectively. Bayes factors BF_{01} were reported and interpreted in *Results* based on Andraszewicz et al.'s (2014) suggestion.

3. Results

As average head motion replacements of each fMRI session for all participants were less than 3 mm, all fMRI data were included in the analyses.

The contrast of the interaction between higher-level congruency and lower-level congruency showed no significant voxel. Hence, the statistics of this contrast were not reported in this section.

3.1. Behavioral results

The average accuracy in responding to the 40 filler sentences was 92.78% ($SD = 5.3\%$), indicating that participants read the sentences carefully.

3.2. Neural activation in each condition

Planned contrasts between experimental conditions and zero baseline (Fig. 1) showed increased activations in both BA44 and BA45 of LIFG, extending to premotor region, as well as in occipital region and hippocampus subiculum.

3.3. The lower-level congruency effect

As shown in Fig. 2 (left) and Table 5, the results for the lower-level congruency effect showed that, relative to the incongruent condition, the congruent condition had enhanced activation in BA45 of LIFG.

3.4. The higher-level congruency effect

As shown in Fig. 2 (right) and Table 5, the results for the higher-level congruency effect showed that, relative to the incongruent condition, the congruent condition had enhanced activation in BA44 of LIFG extending to orbitofrontal cortex, and in other frontal regions including left superior frontal gyrus, paracingulate cortex, and supplementary motor area.

3.5. ROI analyses

3.5.1. ROIs from Hagoort and Indefrey (2014)

The repeated-measures ANOVA showed that (Fig. 3A), the interaction between contrast types and ROI types was significant, $F_{(1,19)} = 6.07$, $p = 0.024$, $\eta_p^2 = 0.24$. Further tests indicated that, in BA45 of LIFG, the lower-level congruency effect was numerically larger than the higher-level congruency effect, 0.45 vs. 0.39, but did not reach statistical significance, $p = 0.735$; in BA44 of LIFG, the higher-level congruency effect was significantly larger than the lower-level congruency effect, 0.63 vs. 0.25, $t_{(19)} = 2.68$, $p = 0.015$, *Cohen's* $d = 0.6$.

3.5.2. ROIs from Zaccarella et al. (2017b)

ANOVA showed that (Fig. 3B), the interaction between contrast types and ROI types was significant, $F_{(1,19)} = 4.62$, $p = 0.045$, $\eta_p^2 = 0.2$. Further tests indicated that, in BA45 of LIFG, the lower-level congruency effect was numerically larger than the higher-level congruency effect, 0.28 vs. 0.25, but did not reach statistical significance, $p = 0.87$; in BA44 of LIFG, the higher-level congruency effect was significantly larger than the lower-level congruency effect, 0.51 vs. 0.12, $t_{(19)} = 2.68$, $p = 0.015$, *Cohen's* $d = 0.53$.

3.6. Analyses of y-coordinates of the individuals' peaks in LIFG

For the contrast of the lower-level congruency effect (Fig. 4), y-coordinates of individuals' peaks in LIFG ($mean = 22.5$) were compared with 25 (Hagoort and Indefrey, 2014) and 28 (Zaccarella et al., 2017b) by Bayesian one-sample *t*-tests respectively. The results showed $BF_{01} = 3.64$ for the comparison with 25, suggesting moderate evidence to support the null hypothesis[4] that the individuals' peak y-coordinates for the lower-level congruency effect were drawn from a population with a mean of 25; and $BF_{01} = 1.97$ for the comparison with 28, suggesting anecdotal evidence to support the null hypothesis that the individuals' peak y-coordinates for the lower-level congruency effect were drawn from a population with a mean of 28.

For the contrast of the higher-level congruency effect (Fig. 4), y-coordinates of the individuals' peaks in LIFG ($mean = 14.6$) were

[4] According to Andraszewicz and colleagues' suggestion (2015, see Table 1 in their article), a BF_{01} between 3 and 10 indicates moderate evidence for null hypothesis, and a BF_{01} between 1 and 3 indicates anecdotal evidence for null hypothesis.

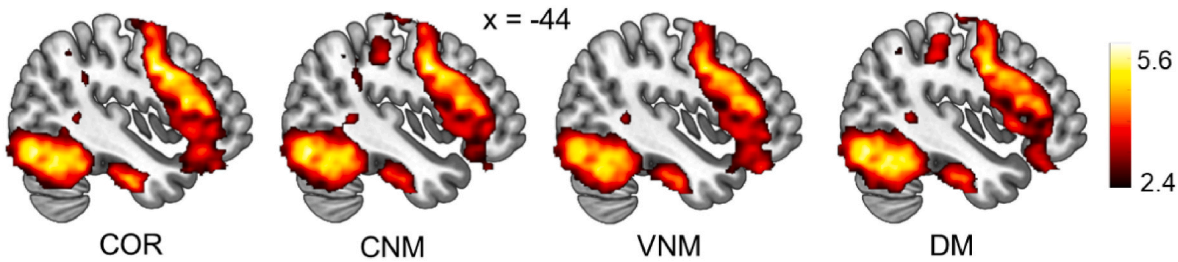

Fig. 1. Results of planned contrasts for each experimental condition with zero baseline in the whole brain analysis. COR: Correct sentences; CNM: Classifier-noun mismatch; VNM: Verb-noun mismatch; DM: Double-mismatch.

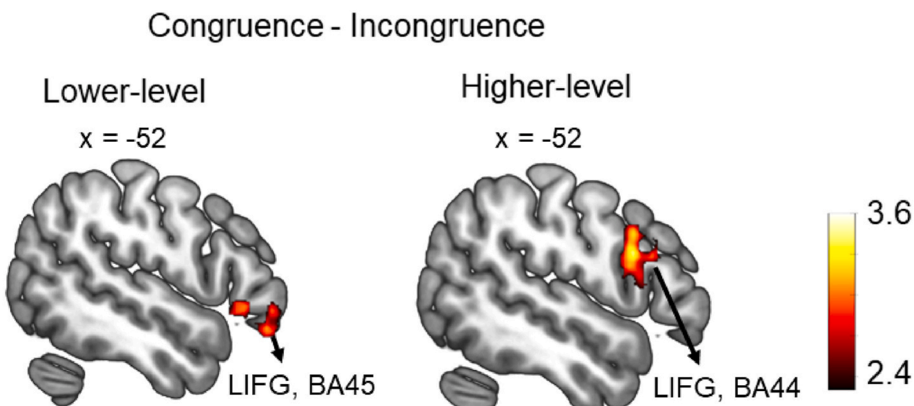

Fig. 2. Results of the whole brain analysis for congruency effects. (Left) the main effect of semantic congruence vs. incongruence at lower-level [(COR + VNM) – (CNM + DM)]. (Right) the main effect of semantic congruence vs. incongruence at higher-level [(COR + CNM) – (VNM + DM)]. COR: Correct sentences; CNM: classifier-noun mismatch; VNM: verb-noun mismatch; DM: double-mismatch.

Table 5
MNI-coordinates corresponding to brain regions that showed significant clusters with greater activations for semantic congruence than incongruence at either the lower-level or the higher-level. Displayed are the coordinates of the maximally activated voxel (in bold) and relevant local maxima within the cluster (in italics). Definitions of regions were referenced to Harvard-Oxford Cortical Structural Atlas and Jülich Histological Atlas.

Region	Hemisphere	Peak in MNI			Z-score	Size (mm^3)
		x	y	z		
Lower-level: Congruence > Incongruence						
Inferior frontal gyrus, BA45	**L**	**−42**	**34**	**−16**	**3.34**	**3304**
	L	*−52*	*26*	*−4*	*3.06*	
	L	*−50*	*38*	*−6*	*3.03*	
Higher-level: Congruence > Incongruence						
Orbitofrontal cortex	**L**	**−28**	**22**	**−6**	**4.21**	**10,616**
Inferior frontal gyrus, BA44	*L*	*−52*	*12*	*24*	*3.48*	
	L	*−50*	*8*	*16*	*3.22*	
	L	*−52*	*12*	*32*	*3.28*	
	L	*−40*	*6*	*34*	*3.22*	
	L	*−58*	*20*	*20*	*3.21*	
Superior frontal gyrus	**L**	**−2**	**18**	**54**	**3.78**	**6936**
Paracingulate gyrus	*L*	*−2*	*26*	*46*	*3.6*	
	R	*8*	*26*	*40*	*3.28*	
	L	*−4*	*12*	*46*	*3,15*	
Supplementary motor area	*L*	*−2*	*2*	*60*	*3.2*	

Note. L: left; R: right.

compared with 16 (Hagoort and Indefrey, 2014) and 14 (Zaccarella et al., 2017b) by Bayesian one-sample *t*-tests respectively. The results showed $BF_{01} = 3.82$ for the comparison with 16, and $BF_{01} = 4.21$ for the comparison with 14, suggesting moderate evidence to support the null hypothesis that the individuals' peak y-coordinates for the higher-level congruency effect were drawn from a population with a mean of either 16 or 14.

4. Discussion

The aim of the present study was to investigate the neural segregation in LIFG for semantic processes at different syntactic hierarchies. Participants were asked to read sentences for comprehension with a minimal task demand during fMRI scanning. Both the whole brain analysis and the ROI analyses of fMRI data showed that, at the lower-level, the semantic process for a congruent semantic relation between the local classifier and the object noun activated BA45 as compared with the semantic process for an incongruent semantic relation; whereas, at the higher-level, the semantic process for a congruent semantic relation between the verb and the object noun activated BA44 as compared with the semantic process for an incongruent semantic relation. These findings are in line with the cross-study comparison (Tables 1 and 2), which demonstrated the role of BA45 in processing semantic relations of local-dependencies (Hagoort et al., 2004; Kuperberg et al., 2006) and the role of BA44 in processing semantic relations in more complex structures (Bornkessel et al., 2005; Grewe et al., 2006, 2007). Moreover, the present fMRI results showed increased activations in parieto-occipital regions for semantic incongruence relative to congruence (see *Supplementary Information*). These activations are consistent with the increased N400-late positivity effect in the previous ERP study using the stimuli with the same structure as the present ones (Zhou et al., 2010). These results probably reflect the increased effort in detecting and resolving the conflict in linguistic information, which is less relevant to our current purpose.

The segregation between BA45 for the lower-level congruency effect and BA44 for the higher-level congruency effect was clearly revealed by the whole brain analysis. Similarly, the ROI analyses based on two meta-

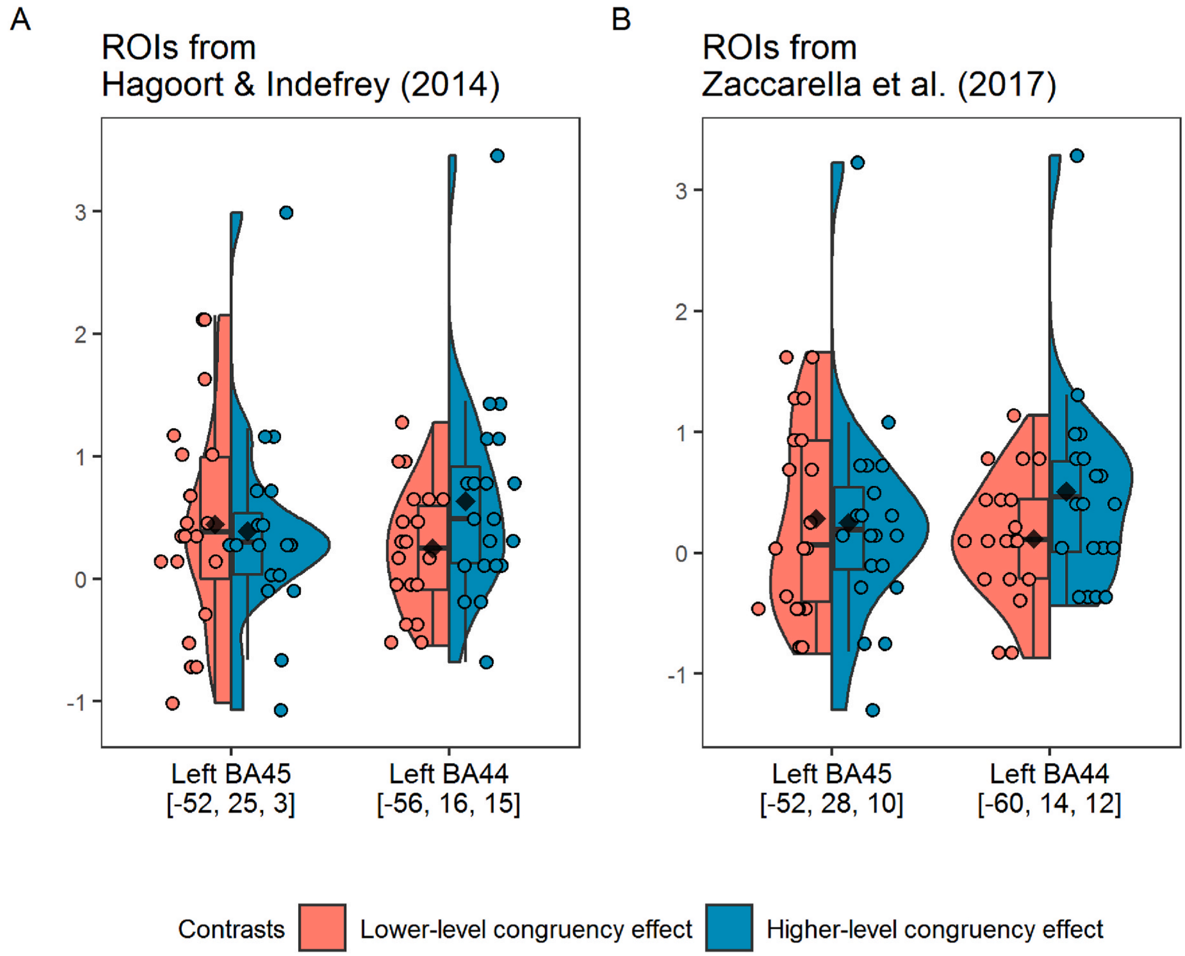

Fig. 3. Violin plots for ROI analyses. Red part denotes planned contrast for the lower-level congruency effect [(COR + VNM) – (CNM + DM)], whereas turquoise part denotes planned contrast for the higher-level congruency effect [(COR + CNM) – (VNM + DM)]. The x-axes specify the two ROIs: (A) sphere ROIs with center coordinates derived from the meta-analysis of Hagoort and Indefrey (2014), with center coordinates of [-52, 25, 3] in left BA45 and [-56, 16, 15] in left BA44; (B) sphere ROIs with center coordinates derived from the meta-analysis of Zaccarella et al. (2017b), with center coordinates of [-52, 28, 10] in left BA45 and [-60, 14, 12] in left BA44.

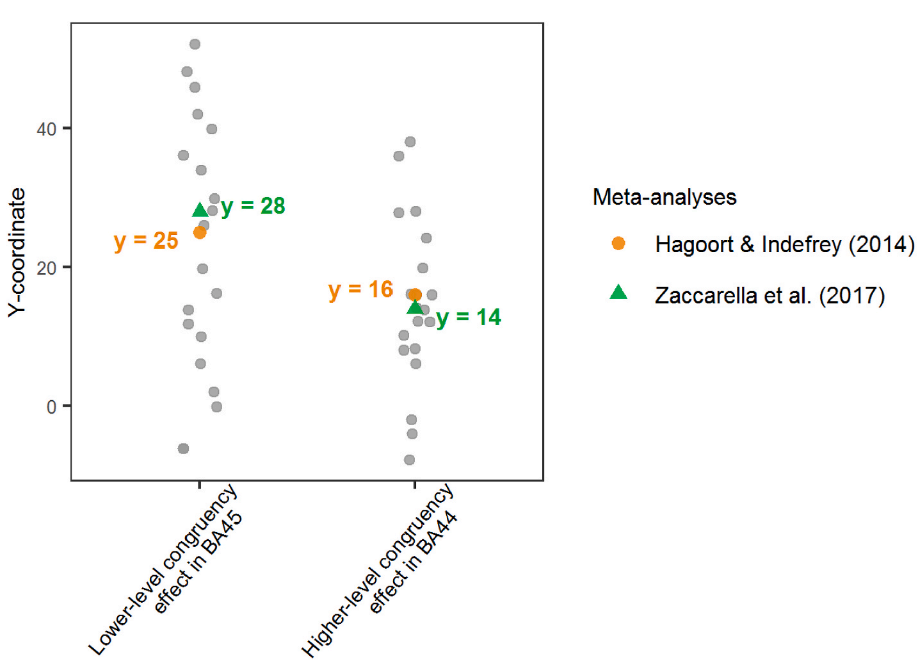

Fig. 4. Visualization of y-coordinate analyses. The gray dots denote y-coordinates of individual peaks for the lower-level congruency effect and the higher-level congruency effect. The orange circles with texts in orange denote y-coordinate (25) in left BA45 and y-coordinate (16) in left BA44 from the meta-analysis of Hagoort and Indefrey (2014). The green triangles with texts in green denote y-coordinate (28) in left BA45 and y-coordinate (14) in left BA44 from the meta-analysis of Zaccarella et al. (2017b).

analyses showed numerically enhanced activations in BA45 of LIFG for lower-level semantic congruence (vs. incongruence) and significantly enhanced activations in BA44 of LIFG for higher-level semantic congruence (vs. incongruence). Moreover, along the anterior-posterior axis of the brain, across participants, the parcellation of peak activations in LIFG between lower- and higher-level semantic congruency effects is consistent with the results of the above ROI analyses, with the distribution of individuals' peak locations for the lower-level congruency effect centralized around the location in BA45 previously identified to be involved in semantic processes and the distribution of individuals' peak locations for the higher-level congruency effect centralized around the location in BA44 previously identified to be involved in syntactic processes.

To interpret the function of LIFG when reading sentences, our experimental design with a minimal task demand allowed the dissociation of the semantic processes from cognitive control although LIFG could be a neural correlate for either semantic processes or cognitive control processes (Fedorenko and Blank, 2020; Ye and Zhou, 2009a,b). Because the present task minimally taxed the cognitive system to make explicit responses, the activation in LIFG was less likely to reflect the cognitive control processes. In contrast, most of the previous studies with explicit tasks (Tables 1 and 2) could have confounded semantic processes with cognitive control when interpreting their results.

One might concern that our fMRI results of LIFG dissociation between different levels of hierarchy are potentially confounded with either linear distances between sentential constituents or phrase categories of them since the increased level of hierarchy was seemingly associated with the lengthening of linear distance and the variation of phrase categories in our critical sentences. The manipulations of the structural hierarchy in previous studies on syntactic process were typically correlated with the lengthening or shortening of linear distance between sentential constituents (e.g., Nam and Hong, 2016; Opitz and Friederici, 2007; Zhang et al., 2011) given that linguistic relations have to be expressed in a linear sequence (Jackendoff and Pinker, 2005). However, neither linear dependency nor phrase categories seem to explain the differential neural responses in LIFG underlying our semantic manipulations. The activation in left BA45 is expected to be enhanced for longer linear distance relative to shorter distance (Makuuchi et al., 2009) and more anterior LIFG activation is expected to be enhanced for Chinese verbs relative to nouns (Li et al., 2004). However, the present results showed more posterior BA44 activation for the higher-level dependency (with longer distance and verb phrase) relative to the lower-level dependency (with shorter distance and noun phrase). Therefore, the current correspondence between areas of LIFG and hierarchical semantic processes cannot be explained by linear distances or phrase categories.

There could be two hypotheses regarding how BA44 and BA45 are involved in hierarchical semantic processes. First, BA44 and BA45 are both involved in either lower- or higher-level semantic process, with different degrees of involvement for processing at different hierarchical levels. Second, BA44 is uniquely involved in higher-level semantic processes while BA45 is uniquely involved in lower-level semantic processes. In the whole brain analysis, the results of planned contrasts between each condition with zero baseline showed that both left BA45 and left BA44 were activated in all the four conditions (i.e., COR, CNM, VNM, and DM). These results reject the second hypothesis and favor the first one, suggesting that both BA45 and BA44 contribute to the lower- or higher-level semantic processes.

Moreover, the observed segregation in LIFG is not only consistent with previous studies on semantic processes (see Tables 1 and 2), but is reminiscent of neural segregation between syntactic and semantic processes (Friederici, 2011, 2017a; Hagoort and Indefrey, 2014). The present observations suggested that the spatial segregation in LIFG for semantic processes at different levels of syntactic hierarchy is derived from the relative dependency of semantic processes on syntactic processes: the lower-level semantic process relies on the neural substrates in BA45 for the general semantic processes while the higher-level semantic process relies more on the neural substrates in BA44 for the corresponding syntactic process to guide the semantic combination of sentential constituents in the hierarchical structure. In other words, some of the semantic processes are not independent from the syntactic processes and the syntactic hierarchy plays differential roles in the semantic combination of sentential constituents at different syntactic levels.

The MUC model (Hagoort, 2005, 2014, 2017, 2019) suggests that BA45 of LIFG subserves semantic unification, which refers to the process of building semantic relations between sentence constituents based on their linguistic representations in the cognitive system, while the more posterior BA44 of LIFG subserves syntactic unification, which refers to the process of binding sentential constituents with different grammatical functions to construct a complete hierarchical structure. Findings in the present study extend these proposals by showing that the higher-level unification in BA44 includes not only the syntactic process constructing grammatical relations between sentential constituents in a simple structure but also the semantic process relying on the syntactic hierarchy.

To conclude, the present study investigated the neural segregation in LIFG between lower- and higher-level semantic processes. Several lines of fMRI data analyses provided convergent evidence for the stronger involvement of BA45 for the lower-level semantic process and stronger involvement of BA44 for the higher-level semantic process.

Author contributions

X.J. and X.Z. conceived of this topic and conducted the experiment. X.L., X.J., and W.C. conducted the literature search, analyzed the data, and wrote the manuscript. X.L., X.J., W.C., Y.T., and X.Z. revised the work. X.L., X.J., W.C., Y.T., and X.Z. edited the manuscript.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuropsychologia.2022.108254.

References

Amunts, K., Schleicher, A., Bürgel, U., Mohlberg, H., Uylings, H.B., Zilles, K., 1999. Broca's region revisited: cytoarchitecture and intersubject variability. J. Comp. Neurol. 412 (2), 319–341.

Andraszewicz, S., Scheibehenne, B., Rieskamp, J., Grasman, R., Verhagen, J., Wagenmakers, E.-J., 2015. An introduction to Bayesian hypothesis testing for management Research. J. Manag. 41 (2), 521–543. https://doi.org/10.1177/0149206314560412.

Bastiaansen, M., Hagoort, P., 2015. Frequency-based segregation of syntactic and semantic unification during online sentence level language comprehension. J. Cognit. Neurosci. 27 (11), 2095–2107. https://doi.org/10.1162/jocn_a_00829.

Bornkessel-Schlesewsky, I., Schlesewsky, M., von Cramon, D.Y., 2009. Word order and Broca's region: evidence for a supra-syntactic perspective. Brain Lang. 111 (3), 125–139. https://doi.org/10.1016/j.bandl.2009.09.004.

Bornkessel, I., Zysset, S., Friederici, A.D., von Cramon, D.Y., Schlesewsky, M., 2005. Who did what to whom? The neural basis of argument hierarchies during language comprehension. Neuroimage 26 (1), 221–233. https://doi.org/10.1016/j.neuroimage.2005.01.032.

Cai, Q., Brysbaert, M., 2010. SUBTLEX-CH: Chinese word and character frequencies based on film subtitles. PLoS One 5 (6), e10729.

Chen, L., Goucha, T., Männel, C., Friederici, A.D., Zaccarella, E., 2021. Hierarchical syntactic processing is beyond mere associating: functional magnetic resonance imaging evidence from a novel artificial grammar. Hum. Brain Mapp. 42 (10), 3253–3268. https://doi.org/10.1002/hbm.25432.

Chomsky, N., 1956. Three models for the description of language. IEEE Trans. Inf. Theor. 2 (3), 113–124. https://doi.org/10.1109/tit.1956.1056813.

Erickson, T.D., Mattson, M.E., 1981. From words to meaning: a semantic illusion. J. Verb. Learn. Verb. Behav. 20 (5), 540–551.

Fedorenko, E., Blank, I.A., 2020. Broca's area is not a natural kind. Trends Cognit. Sci. 24 (4), 270–284.

Fitch, W.T., Hauser, M.D., 2004. Computational constraints on syntactic processing in a nonhuman primate. Science 303 (5656), 377–380. https://doi.org/10.1126/science.1089401.

Friederici, A.D., 2011. The brain basis of language processing: from structure to function. Physiol. Rev. 91 (4), 1357–1392. https://doi.org/10.1152/physrev.00006.2011.

Friederici, A.D., 2017a. Evolution of the neural language network. Psychon. Bull. Rev. 24 (1), 41–47. https://doi.org/10.3758/s13423-016-1090-x.

Friederici, A.D., 2017b. Neurobiology of syntax as the core of human language. Biolinguistics 11, 325–337.

Friederici, A.D., Bahlmann, J., Heim, S., Schubotz, R.I., Anwander, A., 2006. The brain differentiates human and non-human grammars: functional localization and structural connectivity. Proc. Natl. Acad. Sci. U. S. A. 103 (7), 2458–2463. https://doi.org/10.1073/pnas.0509389103.

Friederici, A.D., Chomsky, N., Berwick, R.C., Moro, A., Bolhuis, J.J., 2017. Language, mind and brain. Nat. Human Behav. 1 (10), 713–722.

Grewe, T., Bornkessel-Schlesewsky, I., Zysset, S., Wiese, R., von Cramon, D.Y., Schlesewsky, M., 2007. The role of the posterior superior temporal sulcus in the processing of unmarked transitivity. Neuroimage 35 (1), 343–352. https://doi.org/10.1016/j.neuroimage.2006.11.045.

Grewe, T., Bornkessel, I., Zysset, S., Wiese, R., von Cramon, D.Y., Schlesewsky, M., 2006. Linguistic prominence and Broca's area: the influence of animacy as a linearization principle. Neuroimage 32 (3), 1395–1402. https://doi.org/10.1016/j.neuroimage.2006.04.213.

Hagoort, P., 2005. On Broca, brain, and binding: a new framework. Trends Cognit. Sci. 9 (9), 416–423. https://doi.org/10.1016/j.tics.2005.07.004.

Hagoort, P., 2014. Nodes and networks in the neural architecture for language: Broca's region and beyond. Curr. Opin. Neurobiol. 28, 136–141.

Hagoort, P., 2017. The core and beyond in the language-ready brain. Neurosci. Biobehav. Rev. 81, 194–204.

Hagoort, P., 2019. The neurobiology of language beyond single-word processing. Science 366 (6461), 55–58.

Hagoort, P., Hald, L., Bastiaansen, M., Petersson, K.M., 2004. Integration of word meaning and world knowledge in language comprehension. Science 304 (5669), 438–441. https://doi.org/10.1126/science.1095455.

Hagoort, P., Indefrey, P., 2014. The neurobiology of language beyond single words. Annu. Rev. Neurosci. 37 (1), 347–362. https://doi.org/10.1146/annurev-neuro-071013-013847.

Hahne, A., Friederici, A.D., 2002. Differential task effects on semantic and syntactic processes as revealed by ERPs. Cognit. Brain Res. 13 (3), 339–356. https://doi.org/10.1016/s0926-6410(01)00127-6.

Ilg, R., Vogeley, K., Goschke, T., Bolte, A., Shah, J.N., Poppel, E., Fink, G.R., 2007. Neural processes underlying intuitive coherence judgments as revealed by fMRI on a semantic judgment task. Neuroimage 38 (1), 228–238. https://doi.org/10.1016/j.neuroimage.2007.07.014.

Iwabuchi, T., Nakajima, Y., Makuuchi, M., 2019. Neural architecture of human language: hierarchical structure building is independent from working memory. Neuropsychologia 132, 107137. https://doi.org/10.1016/j.neuropsychologia.2019.107137.

Jackendoff, R., Pinker, S., 2005. The nature of the language faculty and its implications for evolution of language (Reply to Fitch, Hauser, and Chomsky). Cognition 97 (2), 211–225. https://doi.org/10.1016/j.cognition.2005.04.006.

January, D., Trueswell, J.C., Thompson-Schill, S.L., 2009. Co-localization of stroop and syntactic ambiguity resolution in Broca's area: implications for the neural basis of sentence processing. J. Cognit. Neurosci. 21 (12), 2434–2444. https://doi.org/10.1162/jocn.2008.21179.

Jenkinson, M., Bannister, P., Brady, M., Smith, S., 2002. Improved optimization for the robust and accurate linear registration and motion correction of brain images. Neuroimage 17 (2), 825–841. https://doi.org/10.1016/s1053-8119(02)91132-8.

Jenkinson, M., Smith, S., 2001. A global optimisation method for robust affine registration of brain images. Med. Image Anal. 5 (2), 143–156. https://doi.org/10.1016/s1361-8415(01)00036-6.

Jiang, X., Zhou, X., 2009. Processing different levels of syntactic hierarchy: an ERP study on Chinese. Neuropsychologia 47 (5), 1282–1293. https://doi.org/10.1016/j.neuropsychologia.2009.01.013.

Jiang, X., Zhou, X., 2012. Multiple semantic processes at different levels of syntactic hierarchy: does the higher-level process proceed in face of a lower-level failure? Neuropsychologia 50 (8), 1918–1928. https://doi.org/10.1016/j.neuropsychologia.2012.04.016.

Kuperberg, G.R., Lakshmanan, B.M., Caplan, D.N., Holcomb, P.J., 2006. Making sense of discourse: an fMRI study of causal inferencing across sentences. Neuroimage 33 (1), 343–361. https://doi.org/10.1016/j.neuroimage.2006.06.001.

Kuperberg, G.R., Sitnikova, T., Lakshmanan, B.M., 2008. Neuroanatomical distinctions within the semantic system during sentence comprehension: evidence from functional magnetic resonance imaging. Neuroimage 40 (1), 367–388. https://doi.org/10.1016/j.neuroimage.2007.10.009.

Li, P., Jin, Z., Tan, L.H., 2004. Neural representations of nouns and verbs in Chinese: an fMRI study. Neuroimage 21 (4), 1533–1541. https://doi.org/10.1016/j.neuroimage.2003.10.044.

Makuuchi, M., Bahlmann, J., Anwander, A., Friederici, A.D., 2009. Segregating the core computational faculty of human language from working memory. Proc. Natl. Acad. Sci. Unit. States Am. 106 (20), 8362–8367. https://doi.org/10.1073/pnas.0810928106.

Mason, R.A., Just, M.A., 2007. Lexical ambiguity in sentence comprehension. Brain Res. 1146, 115–127. https://doi.org/10.1016/j.brainres.2007.02.076.

Matchin, W., Hammerly, C., Lau, E., 2017. The role of the IFG and pSTS in syntactic prediction: evidence from a parametric study of hierarchical structure in fMRI. Cortex 88, 106–123. https://doi.org/10.1016/j.cortex.2016.12.010.

Miezin, F.M., Maccotta, L., Ollinger, J.M., Petersen, S.E., Buckner, R.L., 2000. Characterizing the hemodynamic response: effects of presentation rate, sampling procedure, and the possibility of ordering brain activity based on relative timing. Neuroimage 11 (6), 735–759. https://doi.org/10.1006/nimg.2000.0568.

Miller, E.K., Cohen, J.D., 2001. An integrative theory of prefrontal cortex function. Annu. Rev. Neurosci. 24 (1), 167–202. https://doi.org/10.1146/annurev.neuro.24.1.167.

Nam, Y., Hong, U., 2016. Local and global semantic integration in an argument structure: ERP evidence from Korean. Brain Res. 1642, 590–602. https://doi.org/10.1016/j.brainres.2016.04.037.

Novick, J.M., Trueswell, J.C., Thompson-Schill, S.L., 2005. Cognitive control and parsing: reexamining the role of Broca's area in sentence comprehension. Cognit. Affect Behav. Neurosci. 5 (3), 263–281. https://doi.org/10.3758/cabn.5.3.263.

Opitz, B., Friederici, A.D., 2007. Neural basis of processing sequential and hierarchical syntactic structures. Hum. Brain Mapp. 28 (7), 585–592. https://doi.org/10.1002/hbm.20287.

Rodd, J.M., Vitello, S., Woollams, A.M., Adank, P., 2015. Localising semantic and syntactic processing in spoken and written language comprehension: an Activation Likelihood Estimation meta-analysis. Brain Lang. 141, 89–102. https://doi.org/10.1016/j.bandl.2014.11.012.

Rouder, J.N., Morey, R.D., Speckman, P.L., Province, J.M., 2012. Default Bayes factors for ANOVA designs. J. Math. Psychol. 56 (5), 356–374.

Saalbach, H., Imai, M., 2007. Scope of linguistic influence: does a classifier system alter object concepts? J. Exp. Psychol. Gen. 136 (3), 485–501. https://doi.org/10.1037/0096-3445.136.3.485.

Schulz, E., Maurer, U., van der Mark, S., Bucher, K., Brem, S., Martin, E., Brandeis, D., 2008. Impaired semantic processing during sentence reading in children with dyslexia: combined fMRI and ERP evidence. Neuroimage 41 (1), 153–168. https://doi.org/10.1016/j.neuroimage.2008.02.012.

Smith, S.M., 2002. Fast robust automated brain extraction. Hum. Brain Mapp. 17 (3), 143–155. https://doi.org/10.1002/hbm.10062.

Vitello, S., Warren, J.E., Devlin, J.T., Rodd, J.M., 2014. Roles of frontal and temporal regions in reinterpreting semantically ambiguous sentences. Front. Hum. Neurosci. 8 (530), 530. https://doi.org/10.3389/fnhum.2014.00530.

Woolrich, M.W., Ripley, B.D., Brady, M., Smith, S.M., 2001. Temporal autocorrelation in univariate linear modeling of FMRI data. Neuroimage 14 (6), 1370–1386. https://doi.org/10.1006/nimg.2001.0931.

Ye, Z., Zhou, X., 2009a. Conflict control during sentence comprehension: fMRI evidence. Neuroimage 48 (1), 280–290. https://doi.org/10.1016/j.neuroimage.2009.06.032.

Ye, Z., Zhou, X., 2009b. Executive control in language processing. Neurosci. Biobehav. Rev. 33 (8), 1168–1177. https://doi.org/10.1016/j.neubiorev.2009.03.003.

Zaccarella, E., Meyer, L., Makuuchi, M., Friederici, A.D., 2017a. Building by syntax: the neural basis of minimal linguistic structures. Cerebr. Cortex 27 (1), 411–421.

Zaccarella, E., Schell, M., Friederici, A.D., 2017b. Reviewing the functional basis of the syntactic Merge mechanism for language: a coordinate-based activation likelihood estimation meta-analysis. Neurosci. Biobehav. Rev. 80, 646–656.

Zhang, Y., Jiang, X., Saalbach, H., Zhou, X., 2011. Multiple constraints on semantic integration in a hierarchical structure: ERP evidence from German. Brain Res. 1410, 89–100. https://doi.org/10.1016/j.brainres.2011.06.061.

Zhou, X., Jiang, X., Ye, Z., Zhang, Y., Lou, K., Zhan, W., 2010. Semantic integration processes at different levels of syntactic hierarchy during sentence comprehension: an ERP study. Neuropsychologia 48 (6), 1551–1562. https://doi.org/10.1016/j.neuropsychologia.2010.02.001.

Zhu, Z., Bastiaansen, M., Hakun, J.G., Petersson, K.M., Wang, S., Hagoort, P., 2019. Semantic unification modulates N400 and BOLD signal change in the brain: a simultaneous EEG-fMRI study. J. Neurolinguistics 52, 100855. https://doi.org/10.1016/j.jneuroling.2019.100855.

Zhu, Z., Hagoort, P., Zhang, J.X., Feng, G., Chen, H.C., Bastiaansen, M., Wang, S., 2012. The anterior left inferior frontal gyrus contributes to semantic unification. Neuroimage 60 (4), 2230–2237. https://doi.org/10.1016/j.neuroimage.2012.02.036.

Zhu, Z., Zhang, J.X., Wang, S., Xiao, Z., Huang, J., Chen, H.C., 2009. Involvement of left inferior frontal gyrus in sentence-level semantic integration. Neuroimage 47 (2), 756–763. https://doi.org/10.1016/j.neuroimage.2009.04.086.