

FEATURE ARTICLE

Retrieval and Unification of Syntactic Structure in Sentence Comprehension: an fMRI Study Using Word-Category Ambiguity

Sentence comprehension requires the retrieval of single word information from long-term memory, and the integration of this information into multiword representations. The current functional magnetic resonance imaging study explored the hypothesis that the left posterior temporal gyrus supports the retrieval of lexical-syntactic information, whereas left inferior frontal gyrus (LIFG) contributes to syntactic unification. Twenty-eight subjects read sentences and word sequences containing word-category (noun-verb) ambiguous words at critical positions. Regions contributing to the syntactic unification process should show enhanced activation for sentences compared to words, and only within sentences display a larger signal for ambiguous than unambiguous conditions. The posterior LIFG showed exactly this predicted pattern, confirming our hypothesis that LIFG contributes to syntactic unification. The left posterior middle temporal gyrus was activated more for ambiguous than unambiguous conditions (main effect over both sentences and word sequences), as predicted for regions subserving the retrieval of lexical-syntactic information from memory. We conclude that understanding language involves the dynamic interplay between left inferior frontal and left posterior temporal regions.

Keywords: integration, left inferior frontal gyrus, lemma retrieval, parsing, temporal lobe

Introduction

We hear and see thousands of words each day, and effortlessly interpret them in their context. To achieve this, several intricate processes are engaged by the brain. Whatever model of language comprehension one adheres to, all make the general distinction between retrieval and integration processes. Retrieval entails selecting the lexical representation of a word from memory. Information we have learned about single words has been laid down in long-term memory, in what psycholinguists usually call the “mental lexicon” (e.g., Levelt 1992). This information includes a word’s form, its syntactic properties (e.g., word class, gender), and the meaning of a lexical item. In order to understand single words we have to map the input signal onto word form representations in the mental lexicon (access) and select the corresponding lexical representation (Marslen-Wilson 1987). In this way the information associated with the word form is retrieved. However, what makes language useful and creative is that words occur in all sorts of different contexts, with the varying combinations of words allowing for an infinite number of higher-level representations (von Humboldt 1836). This process of combining the retrieved single word information into higher-level representations, has been called “integration” or “unification” (Marslen-Wilson 1987;

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Hagoort et al. 1999; Sag and Wasow 1999; Kempen and Harbusch 2002). Both memory and unification processes occur in parallel at the semantic (conceptual) and at the syntactic (structural) level (Jackendoff 2002). The current functional magnetic resonance imaging (fMRI) study focuses on the *syntactic* level. We aim to disentangle the syntactic retrieval and unification processes and identify their respective neural correlates.

Computational Model

Recently, in linguistic theories the separation between lexical items and traditional rules of grammar is fading. Increasing support has been found for lexicalist parsing models (Macdonald et al. 1994; Joshi and Schabes 1997; Jackendoff 2002). In lexicalist models syntactic properties of words needed for integration are retrieved from the lexicon (from memory), and the only remaining “rule” is unification (Jackendoff 2002).

A lexicalist model that is computationally explicit is the Unification Space Model of parsing by Vosse and Kempen (2000). This model accounts for a large series of empirical findings in the parsing literature and in the neuropsychological literature on aphasia. According to the Unification Space Model, every incoming word retrieves one or more lexical frames from the “mental lexicon” These lexical frames are elementary syntactic trees, specifying the possible structural environment of the particular input word. See Figure 1 for examples of lexical frames for a noun (“flights”) and a verb (“flee”). This parsing account is “lexicalist” in the sense that all syntactic information associated with a lexical item is retrieved from the mental lexicon rather than being supplied by grammatical rules (Vosse and Kempen 2000; for a similar account, see Culicover and Jackendoff 2005).

Lexical frames that are retrieved from memory will enter the Unification Space in a sequential fashion, as new words arrive as input. Then, in Unification Space binding operations between lexical frames are performed, resulting in an incremental structural interpretation of the sentence. During the unification process lexical frames are linked, and agreement features (number, gender, person, etc.) and word order constraints are applied. Unification links are dynamic, that is, the strength of the unification links varies over time until one stable phrasal configuration results. As language is intrinsically ambiguous, often several different unification possibilities exist. In the Unification Space model, selection among alternative unification links occurs via lateral inhibition (Vosse and Kempen 2000; see Thompson-Schill 2005 on selection).

Brain Regions

With the Unification Space Model as our theoretical framework, can we identify distinct neural systems subserving

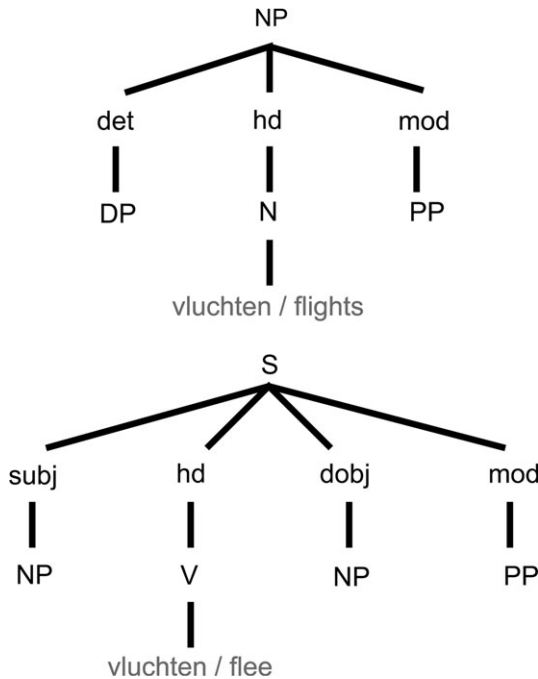


Figure 1. Lexical frames for the noun *vluchten* “flights” and the verb *vluchten* “flee.” When encountering the word *vluchten*, the lexical frame of both the noun and the verb will be retrieved. In the Vosse and Kempen model, lexical frames consist of 3-tiered treelets. The top-layer of a frame consists of a single phrasal node (e.g., NP). This “root”-node is connected to one or more functional nodes in the second layer (e.g., subject, head, direct object, modifier). Every functional node is linked to again a phrasal node in the third layer. Each lexical frame is attached to one lexical item (situated under the “head” node).

lexical-syntactic retrieval and syntactic unification? Large areas within left frontal and temporoparietal cortex are involved in language processing (e.g., Ojemann 1991; Vigneau et al. 2006). Within the perisylvian cortex there is some evidence for a distribution of labor between lexical retrieval and unification operations over temporal and inferior frontal regions respectively (Hagoort 2005b). The left temporal cortex plays a central role in the storage and retrieval of information about single words, information that has been encoded during language acquisition and stored in long-term memory. Information about the meaning of words is probably distributed over a number of brain regions, but there are indications that different parts of the left middle and inferior temporal gyri are most important for lexical-semantic processing (see e.g., Damasio et al. 1996; Saffran and Sholl 1999; Hickok and Poeppel 2000, 2004; Keller et al. 2001; Indefrey and Cutler 2005). Apart from extensive literature investigating the differential processing of nouns and verbs (see e.g., Caramazza and Hillis 1991; Damasio and Tranel 1993; Pulvermuller et al. 1999; Shapiro et al. 2006; Longe et al. 2007; Vigliocco et al. 2008), hardly anything is known about the brain regions involved in the lexical retrieval of a word’s syntactic properties (grammatical gender, syntactic frames, etc.). Based on a meta-analysis of syntactic processing (Indefrey 2004), Hagoort (2003, 2005) hypothesized that left posterior temporal cortex might be involved in the retrieval of lexical-syntactic information, including the lexical-syntactic frames that form the building blocks for syntactic unification.

The left inferior frontal gyrus (LIFG) of the human brain might be particularly suitable for performing unification

operations. The lateral prefrontal cortex—of which the LIFG is a part—plays a fundamental role in integration, in particular the integration of information in the temporal domain (Fuster et al. 2000; Fuster 2001, 2002). The prefrontal cortex is capable of actively maintaining representations of various forms of information, through recurrent circuits between prefrontal cortex and posterior cortex (Durstewitz et al. 2000; Fuster 2001; Miller and Cohen 2001). Furthermore, in lateral prefrontal cortex these representations can be manipulated and flexibly updated. For instance, the left inferior frontal cortex is involved in selection among competing sources of information (Thompson-Schill et al. 1999, 2005). The properties of LIFG (the ability to maintain information online, manipulate, select and temporally integrate this information) make it an ideal candidate for a brain region contributing to combinatorial (unification) operations in language (Hagoort 2005a, 2005b).

Thus, the hypothesis is that the left posterior temporal cortex and the LIFG are involved in the retrieval of lexical-syntactic information and the unification of this information, respectively (Hagoort 2003, 2005b). However, the evidence for this hypothesis is limited and indirect, coming from studies with widely varying design and stimulus materials. No study systematically manipulated both lexical-syntactic retrieval and syntactic unification. Here we set out to disentangle the retrieval and unification processes in sentence structure comprehension within one study, using the computationally explicit model by Vosse and Kempen (2000) as our starting point.

Ambiguity Processing in Sentences

In order to achieve this goal we exploited word-category (noun-verb) ambiguous words. These words can be interpreted as a noun or as a verb, such as the words “bike” or “trains.” Behavioral and electroencephalogram studies have shown that multiple meanings of ambiguous words are transiently activated, even in a strongly disambiguating context (see e.g., Swinney 1979; Seidenberg et al. 1982; Duffy et al. 1988; Federmeier et al. 2000; Van Petten 2002; Swaab et al. 2003). Relatively few neuroimaging studies have addressed the processing of lexical ambiguities within sentence comprehension (Stowe et al. 1994; Stowe et al. 1998; Rodd et al. 2005; Zempleni et al. 2007).

In an early positron emission tomography study, Stowe and colleagues presented subjects with sentences containing a noun-verb ambiguous word in a neutral context. The sentence remained ambiguous for at least 3 words, and then was disambiguated into the least frequent (subordinate) meaning of the ambiguous word. The ambiguous sentences elicited more activity in the LIFG than the unambiguous sentences (Stowe et al. 1994, 1998).

More recently, Rodd and colleagues compared “high-ambiguity” sentences that included several ambiguous words (e.g., “*the shell was fired towards the tank*”) with “low-ambiguity” sentences (“*her secrets were written in her diary*”). Besides noun-noun ambiguities their materials included noun-verb ambiguities as well (e.g., *lock, beam*). Rodd and colleagues found increased activation for high-ambiguity relative to low-ambiguity sentences in left posterior inferior temporal cortex and bilateral inferior frontal gyri (Rodd et al. 2005).

Zempleni and colleagues showed participants sentences that contained noun-noun ambiguities of which one meaning was more frequent than the other (i.e., they were unbalanced). The final words of the sentence disambiguated the meaning to the dominant (most frequent), or the subordinate (less frequent)

interpretation of the homograph. The sentences to a subordinate interpretation showed enhanced blood oxygenation level-dependent (BOLD) activation compared to sentences with a dominant interpretation in the left posterior and right anterior inferior frontal gyri and left posterior and right mid inferior/middle temporal gyri. Only the LIFG showed, in addition, more activity for the sentences with a dominant interpretation than for unambiguous sentences (Zemleni et al. 2007).

The above-mentioned studies cannot yet unravel the relative contributions of the lexical retrieval and unification processes as part of ambiguity resolution. Sentences containing lexical ambiguities tax both retrieval and unification processes stronger than unambiguous sentences (see below). Thus, although these previous studies do indicate that LIFG and left temporal gyrus (LTG) are involved in retrieval and unification, they do not disentangle the 2 processes, nor do they target specifically the retrieval and unification of syntactic information. This is what we set out to do in the current study.

Design and Predictions

To disentangle the lexical retrieval and unification processes related to syntactic information we presented subjects with (Dutch) sentences and with matched scrambled word sequences. In both sentences and word sequences the critical word was either word-class (noun/verb) ambiguous or unambiguous (see Table 1). The noun-verb ambiguous words were “balanced” in the sense that the noun and verb meaning had similar frequencies. The context preceding the ambiguous word was always neutral. For example, in the Dutch sentence beginning with *Beide vluchten...*, the word *vluchten* can be either a noun (*flights*) or a verb (*flee*), resulting in continu-

ations such as for example: *Beide vluchten werden geannuleerd* (“both flights were cancelled”; disambiguation toward the noun reading for *vluchten*) or *Beide vluchten het behekste huis uit* (“both flee the bewitched house”; disambiguation toward the verb reading). The logic of this design, formalized in terms of the computational model of Vosse and Kempen, is as follows.

Ambiguity Effect: Retrieval from Mental Lexicon

In a neutral context both noun and verb reading of a noun-verb ambiguous word are activated (Seidenberg et al. 1982; Duffy et al. 1988). That is, presentation of a noun-verb ambiguous word triggers the retrieval of both the noun and the verb version of the ambiguous word. As 2 lexical frames are retrieved instead of one (see Fig. 1), ambiguous words tax the lexical-syntactic retrieval process more heavily than unambiguous words. This ambiguity effect should occur in sentences as well as word sequences.

Grammaticality Effect: Unification Process

Whereas the factor Ambiguity manipulates the retrieval process, the Grammaticality factor is hypothesized to affect the unification process. When we compare sentences and word sequences, the sentences will require unification of the words into an overall sentence structure, whereas the word sequences do not. Thus, sentences will induce a higher Unification load.

Interaction: Unification Process

Given that the Grammaticality effect is not specific to syntactic unification (as there will be general semantic and phonological differences between sentences and word sequences as well), the crucial effect in our design is the interaction between Grammaticality and Ambiguity. In the sentence condition the 2 retrieved lexical frames (noun and verb) will compete for unification via lateral inhibition (the selection mechanism in our account). In the word condition no unification occurs, and the ambiguous words do not impose a higher unification load than their unambiguous counterparts. Thus, crucially, unification load will only be affected by ambiguity in the sentence condition, and not in the “random” word condition.

Because we hypothesize LIFG to be contributing to the unification process, we expect that LIFG will be activated more for sentences than for word sequences, and within the sentences more for ambiguous than for unambiguous words. We predict the lexical-syntactic retrieval processes to occur in the left posterior temporal cortex. The ambiguous words will induce a higher lexical retrieval load than the unambiguous words in both word sequences and sentences. Hence, we expect the Ambiguity effect to identify the temporal area as subserving the retrieval of lexical frames.

Materials and Methods

Participants

Twenty-eight right-handed healthy volunteers (14 females, aged 18–35) participated in the experiment after having given written informed consent. Subjects were paid for their participation. All participants were native speakers of Dutch, without any history of neurological illness or head injury. Six additional subjects were scanned but excluded from analysis because of excessive movement in the MR scanner (2 subjects) or poor task performance (4 subjects, see below).

Table 1

Example of the experimental materials, with the critical word *bewijzen* (evidence/to prove)

SAn: sentence ambiguous (noun context)

Zodra jullie bewijzen_(n/v) leveren kunnen we beginnen.
As-soon-as you evidence_(n/v) provide can we start.
(As soon as you provide evidence_(n/v) we can start.)

SUn: sentence unambiguous (noun context)

Zodra jullie kopij_(n) leveren kunnen we beginnen.
As-soon-as you copy_(n) provide can we start.
(As soon as you provide copy_(n) we can start.)

SAv: sentence ambiguous (verb context)

Zodra jullie bewijzen_(n/v) dat hij erbij betrokken is arresteren we hem.
As-soon-as you prove_(n/v) that he in-it involved is arrest we him.
(As soon as you prove_(n/v) that he is involved we will arrest him.)

SUV: sentence unambiguous (verb context)

Zodra jullie beweren_(v) dat hij erbij betrokken is arresteren we hem.
As-soon-as you claim_(v) that he in-it involved is arrest we him.
(As soon as you claim_(v) that he is involved we will arrest him.)

WAn: words ambiguous (derived from SAn)

Genoemd tegen bewijzen_(n/v) uit helaas gezeten jullie
Named against proof/prove_(n/v) from alas seated you

WUn: words unambiguous (derived from SUn)

Genoemd tegen kopij_(n) uit helaas gezeten jullie
Named against copy_(n) from alas seated you

WAv: words ambiguous (derived from SAV)

In nogal bewijzen_(n/v) meestal maar dit in struikelen hem verschil opeens
In quite proof/prove_(n/v) mostly but this in stumble him difference suddenly

WUV: words unambiguous (derived from SUV)

In nogal beweren_(v) meestal maar dit in struikelen hem verschil opeens
In quite claim_(v) mostly but this in stumble him difference suddenly

Stimulus Material

The stimulus material consisted of 68 (Dutch) sentences (S) and 68 matched scrambled sequences of Dutch words (W). Both the Sentences and the Word sequences contained a critical word that was either word-class (noun/verb) ambiguous (A) or unambiguous (U). The critical word in the sentences was disambiguated by the continuation of the sentence into either a noun (n) or a verb (v) reading. In total, this resulted in 8 possible conditions: SAn, SAV, SUn, SUv, WAn, WAv, WUn, WUv (see e.g., Table 1). For the full set of experimental materials, see the Supplementary Appendix.

Ambiguous Critical Words

Word-class ambiguous words were selected from the Dutch lexical databases CELEX (Baayen et al. 1993) and CLEF (Beek et al. 2001). Selected words had to be both a noun and a verb (and should not belong to any other word category). To ensure that both noun and verb meaning would be initially activated, all selected ambiguous words had a noun-ratio (noun frequency/summed frequency) between 0.25 and 0.75. We required that the 2 databases (CELEX and CLEF) agree on all criteria. In this way we got a highly reliable indication of frequency and noun-ratio. The average noun-ratio of the single ambiguous critical words was 0.51.

Ambiguous Sentences

The ambiguous sentences were constructed such that both categories of the critical word fitted syntactically as well as semantically with the initial part of the sentences (up to and including the critical word); the sentences were disambiguated by the subsequent part of the sentence (after the ambiguous word; see Table 1 for an example). A pretest was conducted in order to assess the noun-ratio of the words in the sentence context. In this pretest, subjects ($n = 38$) had to complete sentences (e.g., “Beide vluchten. . .”). For all items the “pretest noun-ratio” was defined as the percentage of subjects that completed the sentence in accordance with a noun interpretation of the ambiguous word. Only critical items with a “pretest noun-ratio” between 0.2 and 0.8 were selected. Based on the pretest selection procedure, 68 suitable ambiguous sentence-beginnings were selected, with an average noun-ratio of 0.46.

For every ambiguous item a noun and a verb sentence ending was constructed, with the same neutral sentence context preceding the critical word (SAn and SAV, see an example in Table 1). Noun and verb sentences were matched for average length. The sentences consisted of 6–12 words, with an average of 8.5 words per sentence. The critical word occurred on the second (34 sentences), third (27 sentences), or fourth (7 sentences) position of the sentence. None of the noncritical words in the sentences were balanced noun-verb ambiguous words.

Unambiguous Sentences

For every ambiguous sentence item we constructed 2 suitable, unambiguous alternatives for the ambiguous critical word (a noun and a verb; see example SUn and SUv in Table 1) that fitted the remaining part of the sentence equally well as the ambiguous word. We selected part of the alternative words from the CLEF-corpus based on distributional similarity (Plas and Bouma 2004). Words that are distributionally similar are words that share a large number of lexical-syntactic contexts, that is, they form grammatical dependency relations with the same words (e.g., *lemon* and *orange* can both be the direct object of *squeeze*). If for a critical word no such alternative could be found in the corpus, it was constructed by hand. Ambiguous and unambiguous words were matched for average length and (summed) word form frequency.

Word Sequences

Word sequences were constructed from the sentences (WAn, WUn, WAv, WUv). For each sentence, every word (except the critical word) was substituted by a different corpus word belonging to the same syntactic category (noun, verb, adjective, rest), and with a similar length and frequency (the resulting average length for both sentences and word sequences was 42 characters, and the average CLEF/CELEX log frequency was 3.7 for sentences compared with 4.2 for word sequences). Subsequently the order of all words in the sequence (except the critical word) was randomized, with the constraint that 2 words could not be succeeding each other in the same way as in the original sentence. Sequences were checked on local grammaticality and were scrambled

again if 3 or more consecutive words formed a coherent sentence fragment. We again made sure that none of the noncritical words in the sequence were balanced noun-verb ambiguous words.

Experimental Lists

The stimuli were distributed over 4 lists. For every item, one of the following combinations occurred in each list: SAn+WUn; SAV+WUv; SUn+WAn; SUv+WAv; hence, no subject encountered the same critical word twice. This resulted in 34 items per subject per condition (SA, SU, WA, WU). The pretest noun-ratios, sentence lengths, and position and frequency of the critical words were all matched across the 4 lists. In addition, each list contained the same 28 sentence and 28 word sequence fillers, 36 of which (18 for each condition) contained a consonant string (e.g., *grpsd*) at various positions in the sentence/sequence (see Procedure).

Procedure

Stimuli were presented visually in serial presentation mode (word by word in the middle of the screen) using the Presentation software (Version 9.13, www.neuro-bs.com). Every word remained on the screen for 300 ms, with a 200-ms interword interval. Between sentences a visual fixation cross was presented for 5–8 s (low-level baseline). The participants were instructed to read each sentence/sequence carefully and attentively, and were told that after the experiment some questions concerning the experiment would have to be answered. The participants' task was spotting the consonant-strings (e.g., *cdsnf*), that were presented in 36 of the fillers. This simple control task was added to check whether subjects were paying attention. Subjects were defined as poor task performers if they made more than 5 errors (missing hits and false alarms) on the task, suggesting that these subjects did not pay enough attention to the stimuli.

Every subject saw 68 sentences and 68 word sequences (ambiguous/unambiguous; in noun/verb version), intermingled with 56 fillers (28 sentences and 28 sequences). Stimuli were presented in mini-blocks of 3 to 4 sentences or word sequences. All mini-blocks were shorter than 40 s. Before each block the label “Zinnen:” (“Sentences:”) or “Woorden:” (“Words:”) appeared on the screen (for 1.5 s) to indicate the condition of the following mini-block, which started after a fixation cross of 1–3 s. We expected the labels to encourage (“Sentences”) or discourage (“Words”) attempts to syntactically/semantically integrate the stimulus items in the upcoming mini-block. The ambiguous/unambiguous and verb/noun conditions were intertwined within the mini-blocks in a pseudo-randomized presentation order.

fMRI Data Acquisition

During the sentence/sequence presentation we acquired T_2^* -weighted EPI-BOLD fMRI data with a SIEMENS Trio 3T MR scanner using an ascending slice acquisition sequence (volume time repetition = 2 s, time echo [TE] = 35 ms, 90° flip-angle, 29 slices, slice-matrix size = 64 × 64, slice thickness = 3 mm, slice gap = 0.5 mm, field of view = 224 mm, isotropic voxel size = 3.5 × 3.5 × 3.5 mm³). At the end of the scanning session, a structural MR image volume was acquired for which a high-resolution T_1 -weighted 3D MP-RAGE sequence was used (TE = 3.93 ms, 8° flip-angle, 192 sagittal slices, slice thickness = 1.0 mm, voxel size = 1 × 1 × 1 mm³).

Data Analysis

Image preprocessing and statistical analysis were performed using Statistical Parametric Mapping (SPM2; www.fil.ion.ucl.ac.uk/spm). The first 5 image volumes were discarded in order to avoid transient non-saturation effects. The functional EPI-BOLD images were realigned, slice-time corrected, and the subject-mean functional MR images were coregistered with the corresponding structural MR images using mutual information optimization. Subsequently, images were normalized onto a Montreal Neurological Institute (MNI)-aligned echo planar imaging template (based on 28 male brains acquired on the Siemens Trio at the F. C. Donders Centre) and resampled to an isotropic voxel size of 2 mm. Finally, the normalized images were spatially filtered by convolving the functional images with an isotropic 3D Gaussian kernel (10 mm full width at half maximum).

The fMRI data were proportionally scaled to account for various global effects, and analyzed statistically using the general linear model and statistical parametric mapping (Friston et al. 1995) in a 2-step mixed design procedure. At the first-level, single-subject fixed effect analyses were conducted. The linear model included mini-block regressors to model the sentence/sequence presentation from the onset of the critical word to the offset of the sentence/sequence-final word. The beginnings of sentences/sequences and filler items were modeled together as a regressor of no interest (other words, OW), and the presentation of the fixation cross (FIX) was modeled as explicit baseline. We temporally convolved the explanatory variables with the canonical hemodynamic response function provided by SPM2. We included the realignment parameters for movement artifact correction and a temporal high-pass filter (cut-off 128 s) to account for various low-frequency effects as effects of no interest. Temporal autocorrelation was modeled as a first-order plus white noise autoregressive process.

ROI Analysis

A meta-analysis (Bookheimer 2002) suggests that activations related to syntactic processing in LIFG are centered in a 13-mm sphere around MNI coordinates [-44, 19, 14] (Pettersson et al. 2004). This sphere was taken as the region of interest (ROI) of the relevant subpart of the LIFG (which henceforth we will simply refer to as LIFG). An average time course was calculated for LIFG (for every participant separately) using Marsbar (<http://marsbar.sourceforge.net/>). Although we had a strong *a priori* hypothesis regarding the part of LIFG involved in syntactic unification, we did not have such a specifically defined region for the part of left posterior temporal cortex involved in lexical-syntactic retrieval. Thus, we specified a region of interest only for LIFG, and did not use an ROI for LTG. For the ROI analysis at the second level a repeated measure ANOVA with the factors Grammaticality (S,W), Ambiguity (A,U), and Word class (n,v) was carried out on the subject contrast values using the SPSS software (SPSS Inc., Chicago, IL).

Whole-Brain Analysis

For the second-level whole-brain analysis, we generated single-subject contrast images for the SAn, WAn, SUn, WUn, SA_v, WA_v, SU_v, and WU_v items relative to the baseline FIX, and used these in a one-way random effects repeated measures ANOVA (including the factors: condition [8] and subject [28]). To correct for multiple comparisons, statistical inference was based on the cluster-size statistics from the relevant second-level SPM[T] volumes (Forman et al. 1995; Friston et al. 1996). SPMs were thresholded at $P < 0.002$ (uncorrected at the voxel level). To protect against false-positive results, only clusters of a size of 50 voxels or more are reported (unless otherwise specified). In this way SPM[T] volumes were generated to investigate the effect of grammaticality (i.e., sentences > words; words > sentences; Fig. 3A; Tables 2 and 3) and the effects of ambiguity (ambiguous > unambiguous; unambiguous > ambiguous, Fig. 3B, Table 4). Additionally, an SPM[T] volume was created for the effect of ambiguity within sentences only (SA > SU, Fig. 3C, Table 5).

Anatomical Inference

All local maxima are reported as MNI coordinates (Evans et al. 1993). Relevant anatomical landmarks were identified and Brodmann areas were defined using the Atlas of the Human Brain (Mai et al. 2004) and the Talairach Daemon (Lancaster et al. 2000).

Results

Control Task

All 28 included participants made ≤ 3 errors (mean: 0.18 misses, 0.5 false alarms). Subjects that made more than 5 errors were excluded from analysis (4 subjects, see participants).

ROI Analysis

For the syntactic processing in the LIFG we had a very specific region of interest (see Data Analysis). Figure 2 shows the ROI, and the mean contrast estimates of LIFG for SA, SU,

Table 2
Sentences versus word sequences

Region	BA	Cluster size	Voxel T^{189} value	x	y	z
Sentences > words						
<i>L temporal gyrus, L IFG</i>						
		13 262				
L temporal pole	38		24.21	-54	18	-30
L anterior MTG	21		22.01	-56	-6	-16
L posterior MTG	21		18.77	-62	-44	-2
L IFG	47		17.13	-52	34	-8
L posterior STG	22		15.12	-58	-56	12
L IFG	45		15.04	-58	22	12
L posterior STG	39		14.22	-44	-58	18
L amygdala			10.66	-26	-6	-20
L ITG	20		9.56	-44	-16	-30
L culmen (cerebellum)			8.61	-26	-36	-26
L putamen			8.28	-18	2	4
<i>R temporal gyrus</i>						
		3138				
R temporal pole	38		16.22	54	20	-32
R anterior MTG	21		13.39	56	8	-26
R middle MTG	21		10.24	52	-14	-16
R posterior MTG	21		6.96	62	-42	0
<i>R IFG</i>						
		370				
R anterior IFG	47		8.85	56	36	-10
R IFG	45		6.5	60	34	4
R posterior IFG	45		5.94	62	28	10
L SFG/mOrbG	11	328	10.85	-4	54	-20
L anterior SFG	9	227	13.01	-8	60	28
L MFG	6	208	7.55	-38	-2	-50
L Lingual gyrus		79	5.35	-6	-62	2
L posterior cingulate gyrus		78	6.88	-12	-46	34
R Culmen (cerebellum)		62	6.01	30	-32	-32

Note: Significant activation peaks >8 mm apart ($P < 0.05$ FWE corrected, cluster extent threshold 20 voxels). Multiple peaks within a single activation cluster are shown indented. BA = Brodmann's area; T^{189} value = T value for 189 degrees of freedom; x,y,z = the original SPM x,y,z coordinates in millimeters of the MNI space; STG = superior temporal gyrus; MTG = middle temporal gyrus; ITG = inferior temporal gyrus; MFG = middle frontal gyrus; IFG = inferior frontal gyrus; mOrbG = medial Orbital Gyrus.

Table 3
Word sequences versus sentences

Region	BA	Cluster size	Voxel T^{189} value	x	y	z
Words > sentences						
<i>Bilateral M/SFG, CG</i>						
		12 144				
R anterior MFG	11		11.21	36	58	-12
R CG/med SFG	32		11.15	4	36	30
R posterior MFG	9		10.88	40	26	42
L anterior MFG	10		10.61	-38	58	4
R anterior I/MFG	46		10.31	48	44	16
L MFG	9		10.25	-40	34	32
R frontopolar G	10		10.25	24	64	4
L anterior M/SFG	10		9.24	-30	56	-4
R AC/rostral G	32		8.43	8	46	-4
R anterior SFG	9		8.20	28	44	36
L AC/rostral G	32		6.94	-8	40	0
R middle CG	23	1704	13.64	0	-24	30
R SMG	40	1280	12.25	58	-50	36
L sup parietal lob	7	772	9.76	-10	-72	30
R precuneus	7		9.07	-12	-62	34
<i>L angular G /SMG</i>						
		125				
L angular gyrus	40		7.19	-36	-50	36
L SMG	40		6.06	-44	-44	38
L SMG	40		5.24	-60	-38	40
Planum polare/orbital G		82	6.69	32	22	-20
L posterior ITG		31	6.23	-58	-54	-20

Note: Significant activation peaks > 8 mm apart ($P < 0.05$ FWE corrected, cluster extent threshold 20 voxels). Multiple peaks within a single activation cluster are shown indented. AC = anterior cingulate; SMG = supramarginal gyrus; CG = cingulate gyrus; Sup Parietal Lob = superior parietal lobule; for additional abbreviations see Table 2.

WA, and WU. LIFG was activated more strongly for sentences than for words ($F_{1,27} = 31.2$, $P < 0.001$), whereas only within sentences there was an effect of ambiguity (ambiguity \times

Table 4
Ambiguous versus unambiguous conditions

Region	BA	Cluster size	Voxel T^{189} value	x	y	z
Ambiguous > unambiguous						
<i>R striatum</i>		502				
R putamen			3.96	24	0	8
R caudate body			3.94	14	8	16
R putamen			3.83	26	-10	8
<i>L posterior I/MTG</i>		109				
L post-MTG / ITS	37		3.82	-52	-50	-8
L posterior ITG	37		3.27	-46	-46	-14
L post-MTG / ITS	37		3.11	-46	-54	-4
<i>R MTG</i>	37	72	3.57	48	-44	-6
<i>WM/PCL/CG</i>		56	3.61	-22	-38	34
<i>R parahippocampal gyrus</i>		50				
R para-HCG	36		3.28	22	-42	-6
R para-HCG/occipital G			3.19	28	-48	-2
Unambiguous > ambiguous: no significant activations						

Note: Significant activation peaks > 8 mm apart ($P < 0.002$ uncorrected, cluster extent threshold 50 voxels). Multiple peaks within a single activation cluster are shown indented. ITS = inferior temporal sulcus; WM = white matter; PCL = paracentral lobule; CG = cingulate gyrus; paraHCG = parahippocampal gyrus; for additional abbreviations see Table 2.

Table 5
Ambiguous versus unambiguous, separately for sentence and word sequence conditions

Region	BA	Cluster size	Voxel T^{189} value	x	y	z
SA > SU						
<i>L posterior I/MTG</i>		290				
L post-MTG/ITS	37		4.48	-52	-50	-8
L post-MTG	21		3.42	-60	-44	-4
L post-MTG/ITS	37		3.37	-46	-54	-4
<i>L mid-ITG</i>		73				
L mid-ITG	20		4.02	-50	-20	-28
L fusiform gyrus	20		3.80	-42	-24	-28
L mid-ITG	20		3.18	-46	-30	-22
<i>R MTG</i>		65				
R ITS			3.54	48	-34	-14
R posterior MTG	37		3.31	50	-44	-4
<i>L IFG/PrG</i>	9	62	3.49	-44	0	22
<i>R IFG</i>		51				
R IFG	45		3.35	46	28	6
R IFG	44/45		3.24	44	18	14
R IFG	44/45		2.99	54	18	12
SU > SA; WA > WU; WU > WA: no significant activations						

Note: Significant activation peaks > 8 mm apart ($P < 0.002$ uncorrected, cluster extent threshold 50 voxels). Multiple peaks within a single activation cluster are shown indented. SA = sentence ambiguous; SU = sentence unambiguous; WA = word sequence ambiguous; WU = word-sequence unambiguous; ITS = inferior temporal sulcus; PrG = precentral gyrus; for additional abbreviations see Table 2.

grammaticality: $F_{1,27} = 5.6$, $P = 0.025$; SA > SU: $T(27) = 2.75$, $P = 0.005$). This activation pattern corresponds to the activation predicted for the Unification Space, supporting the hypothesis that the LIFG plays a role in syntactic unification operations during language comprehension.

As mentioned in the Data Analysis section, we did not have an *a priori* specifically defined region of interest within the left posterior temporal cortex, so we used the whole-brain analysis (ambiguity effect) to identify the part of the LTG involved in the retrieval of lexical-syntactic information.

Whole-Brain Analysis

Grammaticality Effect

For the whole-brain comparison between sentences and word sequences a voxel-level threshold of 0.05 corrected for

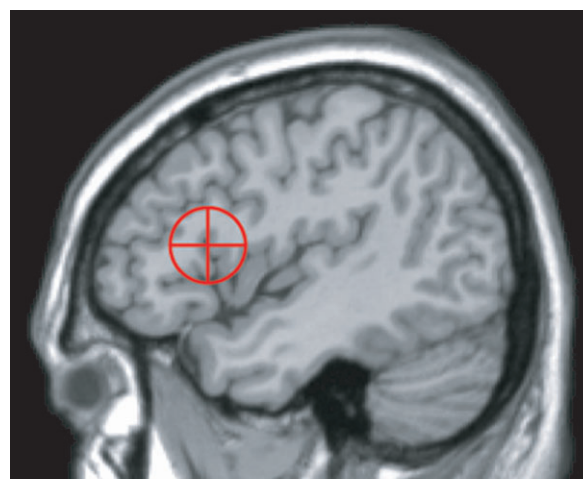


Figure 2. ROI results. Mean contrast estimates for LIFG for SA, SU, WA, and WU. The ROI used is shown on top (13 mm sphere around coordinates $[-44,19,14]$).

multiple comparisons based on random field theory (Worsley et al. 1996), and a cluster-size threshold of 20 voxels were used (Fig. 3A, Tables 2 and 3). As shown in Figure 3A, sentences caused increased activation in comparison with word sequences in a large area in the perisylvian network, including LIFG, left middle temporal gyrus (LMTG) and both temporal poles (see Table 2 for a complete list). This is the network that we would indeed expect to see activated in sentence comprehension (e.g., Bavelier et al. 1997; Friederici 2002; Indefrey and Cutler 2005; Vigneau et al. 2006). For word sequences there was enhanced activation in the bilateral middle/superior frontal gyrus (M/SFG), the cingulate cortex, and supramarginal/angular gyrus (see Table 3, Fig. 3A). This network of areas is reminiscent of the “default mode” network described by Raichle et al. (2001). Indeed, inspection of the beta weights showed that both word sequences and sentences deactivate these areas compared to low-level baseline, but sentences gave rise to a larger deactivation than word sequences.

Ambiguity Effect

Ambiguous words are expected to induce a larger load on the mental lexicon for both sentences and word sequences, as 2 lexical frames have to be retrieved from memory. We hypothesized these retrieval operations to take place in the left posterior temporal cortex. Indeed, we see an increased signal for the ambiguous compared to the unambiguous items

in the left posterior middle temporal gyrus (LpMTG, see Fig. 3B). Furthermore, enhanced activation for ambiguous items was seen in the striatum (Fig. 3B), right posterior middle temporal gyrus and the right parahippocampal gyrus (see Table 4). There were no areas that showed larger activation for the unambiguous than for the ambiguous items. Figure 4 shows the mean contrast estimates for the activated cluster in LpMTG and the striatum (computed with Marsbar, <http://marsbar.sourceforge.net/>). It can be seen that the ambiguity effect in LpMTG was larger in the sentences than in the word sequences. An ANOVA on the mean contrast estimates in LpMTG showed a significant interaction between grammaticality and ambiguity, with the WA > WU comparison being marginally significant ($F_{\text{gram} \times \text{amb}}(1,27) = 6.98, P = 0.014$; SA > SU: $T(27) = 4.72, P < 0.001$; WA > WU: $T(27) = 1.40, P = 0.086$, see Fig. 4). The effect of ambiguity in the striatum (the largest effect for this comparison, see Table 4) did not differ for sentences and word sequences ($F < 1$; see Fig. 4).

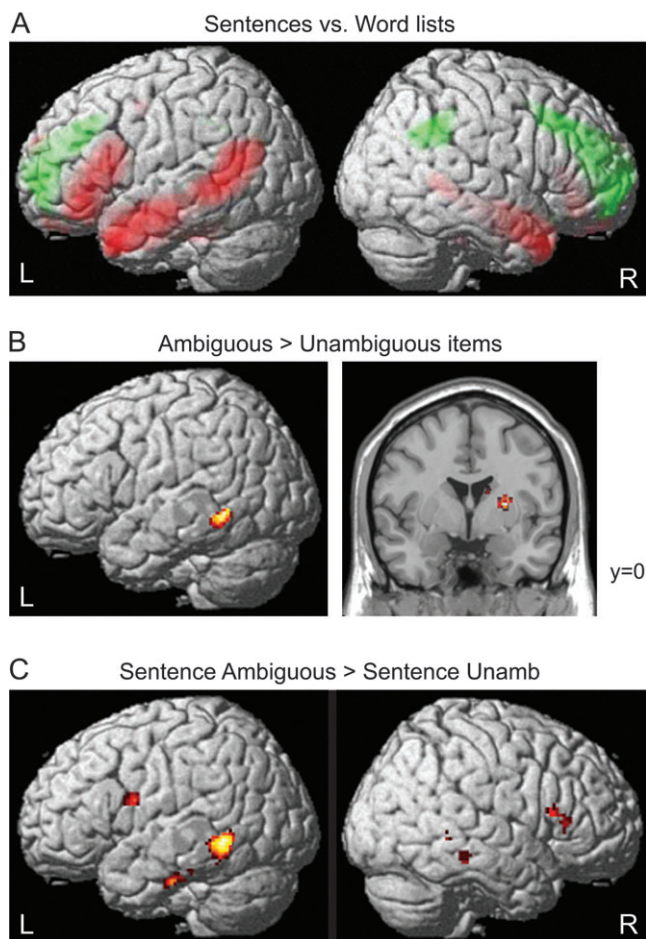


Figure 3. Whole-brain analysis. Significant activations projected onto a rendered template brain surface in MNI stereotactic space. (A) Effect of grammaticality. Enhanced activity within sentences is shown in red, increased signal for words is shown in green. (Activations shown at voxel-level $P_{\text{FWE}} < 0.05$, cluster-size threshold 20 voxels.) (B) Effect of ambiguity: enhanced activity for ambiguous as compared to unambiguous conditions. The right panel shows a coronal view of the brain at $y = 0$, displaying the ambiguity effect in the right striatum. (Activations shown at voxel-level $P_{\text{uncorr}} < 0.002$, cluster-size threshold 50 voxels.) (C) Effect of ambiguity within sentences: enhanced activity for ambiguous sentences as compared to unambiguous sentences. (Activations shown at voxel-level $P_{\text{uncorr}} < 0.002$, cluster-size threshold 50 voxels.)

Ambiguity Effect in Sentences

Additionally, we explored the effect of ambiguity within sentences only (SA > SU). The ambiguous sentences showed enhanced activation in the bilateral posterior MTG and the bilateral posterior IFG compared to the unambiguous sentences (see Table 5, Fig. 3C). This is the same network of areas that was found previously in studies of lexical ambiguity in sentence processing (Rodd et al. 2005; Zempleni et al. 2007). The left inferior frontal region we identified in this contrast (SA > SU) is overlapping with, but slightly posterior to, our region of interest. To explore whether other areas within LIFG (besides our ROI) might be involved, we show the whole-brain sentence ambiguity effect at lower thresholds in Figure 5 (frontal cortex). In Figure 5B this SA > SU activation is masked by the Grammaticality effect (Sentences > Words), as this is the pattern we were looking for in our ROI (unification). Although there is some activation in the anterior LIFG at a low threshold, most of the activation for SA > SU is situated posterior of $[-44 \ 19 \ 14]$ (the center of our ROI). For the masked activation, we see activation only in posterior LIFG (Fig. 5B).

Post Hoc Analysis on Context-Irrelevant Associates

It is the case that word-category ambiguous words are semantically ambiguous as well. Therefore, we conducted a post-test to investigate the semantic consequences of the ambiguity. The issue at hand is whether our results can be explained by a different amount of selection/inhibition of semantic information evoked by ambiguous and unambiguous

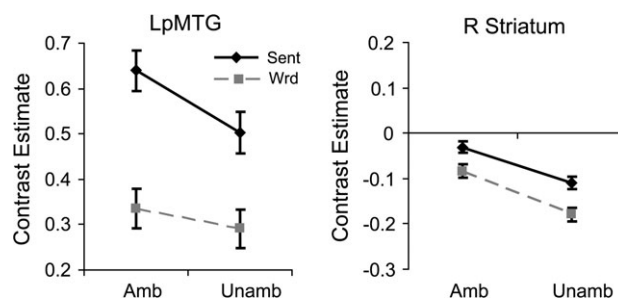


Figure 4. Mean contrast estimates for LpMTG and the right striatum (clusters identified by the whole-brain ambiguity effect) for SA, SU, WA, and WU.

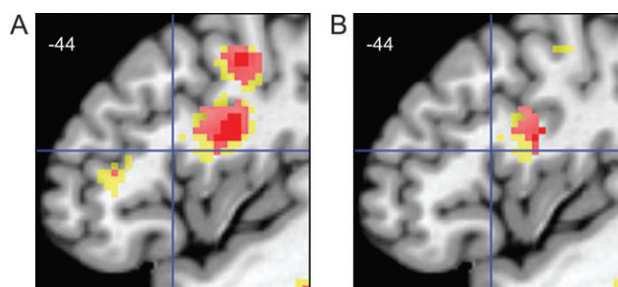


Figure 5. LIFG effect: comparison of ROI and whole-brain analysis (exploratory thresholds). Activations from the whole-brain analysis are displayed on a template (frontal cortex, sagittal view). Voxel-level P_{uncorr} : yellow $P < 0.01$; pink $P < 0.005$; red $P < 0.001$. Crosshair at $[-44 \ 19 \ 14]$ (ROI). (A) Effect of ambiguity within sentences (SA > SU). (B) Effect of ambiguity within sentences (SA > SU), masked (inclusively) with the effect of grammaticality (sentences > words) at $P_{\text{FWE}} < 0.05$. Regions contributing to the syntactic unification process should show this pattern of activation.

words. A full description of the methods and results can be found in the supplementary materials. First, in a normative study we determined the semantic associates of the sentence onsets (e.g., *Beide vluchten*). Of these associates we identified the ones that were context-irrelevant (i.e., inhibited in the remainder of the sentence). Then we compared the number of context-irrelevant semantic associates for ambiguous and unambiguous conditions. Statistical analysis indicated that there were more context-irrelevant associates for ambiguous than unambiguous items ($F_{1,43} = 46.16, P < 0.001$). To investigate whether this difference in context-irrelevance could explain our fMRI results, we included the context-irrelevance score for each sentence item as a covariate in the fMRI analysis (see Supplementary Materials). Context-irrelevance showed no effect in LIFG or LpMTG and the effect of word-category ambiguity was very similar, irrespective of whether the context-irrelevance regressor was included as a covariate in the statistical analysis or not. This shows that the difference in the amount of context-irrelevant information evoked by ambiguous and unambiguous items cannot explain our fMRI results.

Discussion

Starting point of this study was the general distinction between retrieval and unification (integration) processes in language (Hagoort 2005b; Vosse and Kempen 2000). We explored the hypothesis that LIFG contributes to syntactic unification operations, whereas the left posterior temporal gyrus subserves the retrieval of lexical-syntactic information. To do this, we exploited word-category ambiguities in sentence and word sequence contexts. First, we predicted that the syntactic unification load should be larger for the sentence than for the word sequence condition, and larger for ambiguous than unambiguous items only within the sentences. This is exactly the activation pattern we found in the LIFG, supporting the hypothesis that LIFG is involved in the unification process. Second, we expected retrieval of lexical-syntactic frames to be more demanding in the ambiguous than in the unambiguous condition in both sentences and word sequences. Indeed, LpMTG showed a main effect of ambiguity, suggesting that LpMTG subserves the retrieval of lexical-syntactic information from the mental lexicon. Thus, our study could confirm the role of posterior LIFG and LpMTG in syntactic unification and lexical-syntactic retrieval processes, respectively. (The effect of ambiguity in sentences that we find could be an effect occurring at the ambiguous word [2 lexical frames enter Unification Space and are competing] as well as an effect at the disambiguating word [one lexical frame wins and is selected]. The low temporal resolution of fMRI does not permit us to distinguish between these 2 possibilities. We are currently running an MEG study using the same materials to look into this issue.)

LIFG as the Unification Space for Language

Evidence on the involvement of LIFG in unification/integration processes in language comprehension is accumulating (Hagoort 2005b; Willems et al. 2007). Our study confirms the contribution of the posterior LIFG to the syntactic part of the unification process. However, we do not claim that the processing role of LIFG is restricted to syntax or even to language in general (see e.g., Decety et al. 1997; Hamzei et al.

2003; Kaan and Swaab 2002; Patel 2003). Nor do we claim that unification is the only function of the LIFG. A different but related proposal is that LIFG is associated with selection of information among competing alternatives (Thompson-Schill et al. 2005). This is compatible with our results, as the outcome of the unification process is dependent on a selection mechanism that chooses between different unification options (Hagoort 2005a; Vosse and Kempen 2000). We prefer the term “unification” over “selection”, as we think “unification” is both a more general account of LIFG functioning and a computationally explicit process. For example, unification in LIFG occurs also for information that has no stable representation in long-term memory, and thus cannot be selected (such as co-speech gestures, see Willems and others 2007). Specific brain regions (such as LIFG) probably participate in a wide range of tasks, with specialized function emerging from the unique cooperation of a network of brain areas subserving domain-general mechanisms (Mesulam 1998; Fuster 2001; Marcus et al. 2003). Even if the processing role of LIFG as a whole is domain-general, due to the interplay with content specific areas there might emerge some specialization for unification “content,” with anterior LIFG being involved with semantic operations, and posterior LIFG with syntactic operations (see Hagoort 2005b). In our case, syntactic unification might be the result of posterior LIFG working together with representational areas in the posterior temporal lobe.

Retrieval in LpMTG: Sustained Activation in Dynamic Interplay with LIFG

We found the LpMTG (on the border of the inferior temporal sulcus) to be activated more strongly for ambiguous than unambiguous conditions. This ambiguity effect is what we predicted for retrieval of lexical-syntactic information from the mental lexicon. However, in LpMTG there was more activation for sentences than for words, and the ambiguity effect in LpMTG was larger in sentences than in word sequences (see Fig. 4). Moreover, the ambiguity effect in the word sequences was only marginally significant. One possible interpretation of this pattern of results is that LpMTG plays a role in unification that is similar to that of LIFG. However, we favor an alternative interpretation: Sentence processing requires *sustained activation* of lexical frame information. During sentence comprehension, the lexical information has to be available for longer time intervals than during the processing of random word sequences. The lexical-syntactic information is most likely not “copied” from the area necessary for its retrieval (mental lexicon) to the area necessary for unification (Unification Space). Instead, the sustained activation of lexical frame information could be triggered by feedback from the Unification Space to the mental lexicon (as implemented—for independent theoretical modeling reasons—in the recently revised Unification Space model, see Vosse and Kempen 2008). The amount and/or duration of lexical frame activation is a function of the unification load imposed by the combinatorial operations necessary for unification. This explains why the lexical activation of the noun and verb frames has to be maintained longer in sentences as the unification load increases due to a word-class ambiguity.

How could the above-mentioned sustained activation and feedback be implemented neurally? LIFG has the neural machinery to provide feedback signals to other areas in the brain (Miller and Cohen 2001). Research has shown that the

sustained activation of representations in posterior cortices is under dynamic frontal top-down control (Tomita et al. 1999; Fuster 2001; Curtis and D'Esposito 2003; Miller and D'Esposito 2005; Fiebach et al. 2006). For the present experiment, our interpretation is that the syntactic unification process requires the dynamic interplay between posterior LIFG and LpMTG. A similar reasoning can be found in Keller et al. (2001), who manipulated lexical and syntactic factors (word frequency and syntactic complexity) and found a similar interaction pattern for both temporal and frontal regions. This interpretation is also in line with a recent fMRI study suggesting context-dependent interactions or feedback mechanism between LIFG and LpMTG (Gennari et al. 2007).

Our findings with regard to ambiguity resolution are consistent with earlier neuroimaging studies. The activation in LIFG is roughly comparable, but slightly more posterior, to the region that was identified in the studies by Rodd and Zemleni (Rodd et al. 2005; Zemleni et al. 2007). Striking is the fact that in these studies the coordinates for the activation peak in LpMTG for sentence ambiguous compared to sentence unambiguous conditions are very similar (this study: [-52 -50 -8], Rodd et al. [-52 -50 -10], Zemleni et al. [-50 -48 -12]; Rodd et al. 2005; Zemleni et al. 2007). Although Rodd also included noun-verb ambiguities in her study, the focus of both these other studies was on noun-noun ambiguities. Thus, LpMTG might be involved in the retrieval of both semantic and syntactic properties of words. The more posterior locus of our LIFG activation fits well with the idea that there might be some specialization within subregions of LIFG for unification content, with the posterior LIFG contributing to syntactic unification, whereas semantic unification is subserved by a more anterior portion of LIFG (Hagoort 2005b).

Other Perspectives

An alternative interpretation of the interaction effects in LIFG and LpMTG might be a general attentional difference between the processing of sentences and word sequences, resulting in larger ambiguity effects for sentences. Sentences evoked more activation in perisylvian areas than word sequences. However, it is not the case that the ambiguity effect is larger in the sentences for all brain areas involved in ambiguity processing (see e.g., the activity in the striatum in Fig. 4). Moreover, the fact that our participants were highly accurate in the control task (for both sentences and word sequences) argues against an attention interpretation.

A second alternative interpretation relates to semantic ambiguity. Word-category ambiguous words are intrinsically also ambiguous semantically. Thus, besides syntactic retrieval and unification differences, our ambiguity manipulation will also lead to semantic retrieval and unification differences. With our current experiment we cannot entirely rule out the possibility that our fMRI results reflect semantic rather than syntactic processes. In order to address this issue we conducted a post-test to investigate the semantic consequences of the ambiguity. Each meaning of the ambiguous word can potentially activate a distinct set of semantic associates. The post-test showed that for the word-category ambiguous condition more associates were "context-irrelevant" in that they had to be inhibited as a consequence of the ambiguity resolution. The left inferior prefrontal cortex is sensitive to difficulty in the selection of semantic information (e.g., Thompson-Schill et al. 2005). Thus, selection/inhibition of this

semantic information during sentence processing might potentially drive the observed LIFG ambiguity effects, and possibly the observed LpMTG ambiguity effects as well. However, when we included the context-irrelevance score for each sentence item as a covariate in the fMRI analysis, this did not alter the results, suggesting that the difference in the amount of context-irrelevant information evoked by ambiguous and unambiguous items cannot explain our fMRI results. More importantly, when looking at the effect of context-irrelevance itself, there was absolutely no activation in LIFG or LpMTG, not even at very low threshold levels. In other words, the post-test strongly suggests that our fMRI results are not due to the diffuse semantic consequences (more context-irrelevant associates for ambiguous words) of the word-category ambiguity. Thus, the sentence ambiguity effect in LIFG is most likely due to the increased unification demands (competition between alternatives and/or selection of the correct syntactic structure, see note 1) resulting from our syntactic manipulation (word-category ambiguity).

Additionally Involved Brain Regions

A striking effect that we did not expect beforehand is that, in addition to LpMTG, also the right striatum showed a large effect of ambiguity. The striatum is known to be involved in selection of behaviorally relevant stimuli and inhibition of competing alternatives (e.g., Cools et al. 2004, 2006). The left striatum has been found to be modulated by syntactic variables (e.g., Moro et al. 2001; Friederici and Kotz 2003). Copland and colleagues have demonstrated the importance of the striatum in ambiguity processing, using semantic priming paradigms in patients with damage to the basal ganglia. Typically striatal dysfunction spares automatic activation of multiple meanings of ambiguous words, but disrupts later language processes that require inhibition of competing alternatives (Copland et al. 2000, 2001; Copland 2003, 2006). Our study again stresses the importance of the striatum in ambiguity processing. The ambiguity effect we find in the striatum in both sentences and word sequences might reflect the selection of one meaning/lemma of the ambiguous word and/or the inhibition of the competing alternative.

Interestingly, when processing ambiguities in sentences, not only LIFG and LpMTG are activated, but also their right-hemisphere homologue areas (see Table 5 and Fig. 3C). The involvement of the right hemisphere in language processing is more and more acknowledged, especially for the processing of complex, natural language (Faust and Chiarello 1998; Kircher et al. 2001; Jung-Beeman 2005). Our study again emphasizes the involvement of right perisylvian areas in language comprehension in ambiguous contexts. However, our results do not clarify whether the right-hemisphere areas really contribute functionally to unification processes in language, or whether the activations we find simply reflect interhemispheric connections between homologous areas (see also Rodd et al. 2005). The precise role of the striatum, RIFG, and RpMTG in language processing remains an issue for future research.

Conclusion

In conclusion, using the computational model of syntactic parsing by Vosse and Kempen (2000) as a starting point, this study disentangled syntactic unification and lexical-syntactic retrieval processes. Posterior LIFG plays a role in the unification of words into a sentence structure, whereas LpMTG is involved

in the retrieval of lexical-syntactic information from memory. Although their specific contributions to the process may differ, syntactic unification in language requires the dynamic interplay between both brain regions.

Supplementary Material

Supplementary material can be found at: <http://www.cercor.oxfordjournals.org/>.

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