

Language Comprehension: The Interplay between Form and Content

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Abstract

In a 2x2 event-related fMRI study we find support for the idea that the inferior frontal cortex, centered on Broca's region and its homologue, is involved in constructive unification operations during the structure-building process in parsing for comprehension. Tentatively, we provide evidence for a role of the dorsolateral prefrontal cortex centered on BA 9/46 in the control component of the language system. Finally, the left temporo-parietal cortex, in the vicinity of Wernicke's region, supports the interaction between the syntax of gender agreement and sentence-level semantics.

Keywords: fMRI; syntax; semantics; language comprehension; Broca's region; Wernicke's region; inferior parietal region

Introduction

Humans encounter many new and unexpected sentences in everyday life and typically interpret them without cognitive effort. This ability is grounded in a peculiar biological system, part of the human brain, called the faculty of language. Most current models of language processing agree that different types of constraints are rapidly utilized in on-line sentence processing (Hagoort, 2005). Constraints on how words can be structurally combined operate interactively and in parallel with qualitatively distinct constraints on the combination of word meanings, the grouping of words into phonological phrases, and their referential binding in discourse models (Jackendoff, 2007). Most models make a distinction between retrieval and combinatorial/compositional processes, implying that sentences have internal structure. Retrieval entails lexical selection from the mental lexicon, a specific long-term memory store. Lexical representations include knowledge about lexical form, syntactic properties (e.g., constituent class, syntactic gender etc.), and lexical meaning. The creative aspect of language is in part captured by its generative structure-building processes which create sentence-internal structure that represents for example who did what to whom and how.

A recent trend in theoretical linguistics suggests that the separation between lexical items and traditional rules of grammar is fading and increasing support for these so-called *lexicalized models* have accumulated. In lexicalized models

of parsing, the properties of words needed for sentence level integration are retrieved from the mental lexicon in the form of structured primitive representations (e.g., treelet) and only relatively generic structure building operations like *unification* (Vosse & Kempen, 2000), *unify-pieces* (Culicover & Jackendoff, 2005), or *merge* (Chomsky, 2005) are necessary to complete the on-line combinatorial integration process. Vosse and Kempen (2000) proposed a computationally explicit lexicalist *unification space model* that accounts for a large range of empirical findings in the parsing- and neuropsychological aphasia literature. According to this unification space model, every incoming word retrieves lexical frames (elementary syntactic trees) that specify possible structural environments for input words. When retrieved, these lexical frames enter the unification space in a sequential fashion and are integrated interactively and in parallel in a unification process in which lexical frames are dynamically linked and various constraints, like agreement and linear order constraints, are applied (Kempen & Harbusch, 2002).

A key question in our understanding of language is whether and where in the human brain the different levels are localized and processed as well as whether and where they interact. Understanding where, how, and when the linguistic subcomponents are interacting in order to provide a coherent interpretation is a fundamental challenge in the neurobiological study of the language faculty (Chomsky, 2005). It is well-accepted that large regions within the frontal, temporal, and temporo-parietal cortices are involved in language processing. The temporal and temporo-parietal cortices play a central role in both short-term verbal memory (e.g., Petersson et al., 2009), storage and retrieval of lexical information, that has been encoded during language acquisition (Indefrey & Cutler, 2005). Based on a meta-analysis of syntactic processing (Indefrey, 2004), Hagoort (2005) suggested that the left posterior temporal cortex is involved in the retrieval of lexical frames that form the building blocks for syntactic unification, which he argued, is supported by the left inferior frontal cortex (LIFC). Functional magnetic resonance imaging (fMRI) evidence support the role of the LIFC in the unification operations that are performed at the structural/syntactic (Petersson et al., 2004; Snijders et al., 2008) and

conceptual/semantic levels (Hagoort et al., 2004; Menenti et al., 2008; Tesink et al., 2008). While these studies tackle the unification operations within each linguistic component, in the current study we investigated the interplay between sentence-level semantics and syntax.

In the present event-related fMRI study we adapted a well characterized language comprehension paradigm used in a previous EEG study (Hagoort, 2003). The experimental design constituted a 2x2 factorial experiment including the factors syntax and semantics. Each factor included two levels, correct/anomalous, yielding 4 conditions: correct (CR), syntactic (SY), semantic (SE), and combined (CB) anomalies. The ERP results reported by Hagoort (2003) showed typical P600 and N400 effects related to syntactic and semantic anomalies, while their combined effect revealed an interaction expressed in the N400 component ($[CB-SE] - [SY-CR] > 0$). Although the N400 component was similar in the correct and syntactic conditions ($SY \sim CR$), the combined effect was significantly larger than the effect of semantic anomaly alone ($CB > SE$). In contrast, the size of the P600 effect was not affected by an additional semantic violation, suggesting an asymmetry between semantic and syntactic processing. Our primary objective in the current fMRI study was to characterize this asymmetry as well as the neural correlates of sentence-level syntactic and semantic interaction.

Methods

Participants

Thirty two right-handed (16 females, mean age \pm SD = 22 \pm 3 years; mean years of education \pm SD = 16 \pm 2), healthy Dutch university students volunteered to participate in the study. They were all pre-screened and none of the subjects used any medication, had a history of drug abuse, head trauma, neurological or psychiatric illness, or a family history of neurological or psychiatric illness. All subjects had normal or corrected-to-normal vision. Written informed consent was obtained from all participants according to the Declaration of Helsinki and the local medical ethics committee approved the study. One subject was excluded from further analysis because he did not indicate that any of the sentences including a semantic anomaly were unacceptable.

Stimulus Material

The stimulus material consisted of 160 sentences from Hagoort (2003). The material consisted of sentence frames with a critical word position. There were four versions of sentence, one for each factor level combination (Table 1): (1) syntactically and semantically well-formed, correct sentences (CR); (2) semantically correct sentences with a gender agreement violation between the definite article and the noun (SY); (3) syntactically correct sentences including a lexical semantic anomaly that consisted of a semantically unacceptable combination of the adjective and the following noun (SE); and (4) a combination of the syntactic and semantic anomalies (CB) described in (2) and (3). In the semantically correct and anomalous conditions, different

adjectives preceded the nouns in the critical word (CW) position. These adjectives were matched in length and frequency. Critically, the violation of the gender agreement and the violation of the semantic constraint became clear at the same noun in critical word position. Thus, lexical differences do not interfere with the experimentally manipulated factors.

Table 1. Example sentences. The critical noun is italicized, incorrect articles and anomalous adjectives are in bold.

De kapotte <i>paraplu</i> staat in de garage.	(CR)
Het kapotte <i>paraplu</i> staat in de garage.	(SY)
De eerlijke <i>paraplu</i> staat in de garage.	(SE)
Het eerlijke <i>paraplu</i> staat in de garage.	(CB)
The _{com} / The _{neut} broken/ honest <i>umbrella</i> _{com} is in the garage.	

The sentence materials were constructed so that 50% of the sentences contained a syntactic and 50% a semantic anomaly. To make sure that the violations of gender agreement did occur with equal probability after a common and neuter gender article, 160 filler sentences were added. In this way, violations of gender agreement could not be predicted on the basis of probability or sentence context. The materials were distributed among four versions of the experiment such that no subject saw more than one version of a sentence quartet, but across subjects, the critical items were distributed equally over conditions. In addition to experimental and filler items, the materials included 20 practice items and 15 start up items. The sentences had a mean length of 8 words (SD = 1 word). Words were never longer than 12 letters, with nouns in the CW position having a maximal length of 10 letters. All sentences were simple active or passive sentences. In the semantically correct/anomalous conditions, different adjectives preceded the nouns in the critical word position. These adjectives were matched in length and frequency.

Experimental Procedure

The subjects were informed that they were to participate in a natural language experiment. They were instructed to read the sentences carefully and attentively for full comprehension and to indicate for each sentence whether or not it was acceptable. fMRI data were acquired during sentence comprehension. All items in the experiment were presented visually in Presentation (nbs.neuro-bs.com). The stimulus items were presented via an LCD-projector outside the scanner room, projecting the computer display onto a semi-transparent screen that the subject comfortably viewed through a mirror device mounted on the head-coil. Sentences were presented word by word at the centre of a computer screen. Each word was presented for 300ms, followed by a blank screen for another 300ms, after which the next word of the sentence appeared. The final sentence word ended with a period. After a variable delay (1-2s) from sentence offset, an asterisk appeared on the screen signaling to the subjects that they had to push one of two response buttons indicating whether the sentence was acceptable or not. The asterisk remained on the screen for a period of 2s, followed by a blank screen for a period of 2-5s preceding

the next sentence. Before the fMRI experiment started, each subject practiced on practice sentences to familiarize with the experimental procedure. The experimental sentences were presented in 4 blocks of approximately 10 minutes each, with a short break between each block. Each block started with 2 start-up filler sentences. The response hand was balanced over subjects and over experimental blocks.

Data Procedures

Behavioral data analysis

Repeated measures ANOVAs were used for the analysis of the data, unless otherwise stated (SPSS 15). A significance level of $P < .05$ was used throughout.

MR data acquisition

Whole head T2*-weighted functional echo planar blood oxygenation level dependent (EPI-BOLD) fMRI data were acquired with a SIEMENS Avanto 1.5T scanner using an ascending slice acquisition sequence (volume TR = 2.6s, TE = 40 ms, 90 degree flip-angle, 33 axial slices, slice-matrix size = 64x64, slice thickness = 3 mm, slice gap = 0.5 mm, FOV = 224 mm, isotropic voxel size = 3.5x3.5x3.5 mm³) in a randomized event related fashion. For the structural MR image volume a high-resolution T1-weighted magnetization prepared rapid gradient-echo pulse sequence was used (MP-RAGE; volume TR = 2250 ms, TE = 3.93 ms, 15 degree flip-angle, 176 axial slices, slice-matrix size = 256x256, slice thickness = 1 mm, field of view = 256 mm, isotropic voxel-size = 1.0x1.0x1.0 mm³).

MR image preprocessing and statistical analysis

We used the SPM5 software (www.fil.ion.ucl.ac.uk/spm) for image preprocessing and statistical analysis. The critical word position was manipulated independently in a 2x2 factorial design and the fMRI data analysis was time-locked on the onset of the critical word position. The EPI-BOLD contrast volumes were realigned to correct for individual subject movement and acquisition-time corrected. The subject-mean EPI-BOLD images were subsequently spatially normalized to the functional EPI template provided by SPM5. The normalization transformations thus generated were applied to the corresponding functional volumes and transformed into an approximate Talairach space (Talairach and Tournoux 1988) defined by the SPM5 template. Finally, the anatomically normalized image volumes were spatially filtered with an isotropic 3D Gaussian filter kernel (FWHM = 10mm). The fMRI data were analyzed statistically using the general linear model framework and statistical parametric mapping (Friston et al., 2007) in a two-step mixed-effects summary-statistics procedure (Friston et al., 2007). At the first-level, single-subject fixed effect analyses were conducted. The linear model included explanatory regressors modeling the string presentation period from the critical word onset for the CR, SY, SE, and CB conditions separated on correct and incorrect responses. The initial part of the sentences was modeled separately as were the filler items and the inter-sentence interval. Effects related to sentence endings were modeled by a separate regressor. We

temporally convolved the explanatory variables with the canonical hemodynamic response function provided by SPM5. We included the realignment parameters for movement artifact correction and a temporal high-pass filter (cycle cut-off = 128s) to account for various low-frequency effects. For the second-level analysis, we generated single-subject contrast images for the correctly classified CR, SY, SE, and CB sentences from the critical word onset until the sentence final word relative the pre-critical sentence part in a one-way subject-separated random effects repeated measures ANOVA with unequal variance between conditions and non-sphericity correction. Because of the high behavioral performance we did not further analyze the few incorrectly classified sentences. Statistical inference was based on the suprathreshold cluster-size statistic from the relevant second-level SPM[F] and SPM[T] (thresholded at $P = .001$ uncorrected). Only clusters significant at $P < 0.05$ family-wise error (FWE) corrected (for multiple non-independent comparisons based on smooth 3D random field theory; Friston et al., 2007) are described. In the following, we use the terms activation and deactivation as synonyms for a relative increase and decrease in BOLD signal, respectively.

Results

Acceptability judgments

Participants classified 94% of the correct sentences as acceptable and for the sentences that contained syntactic or semantic anomalies the results were as follows: For sentences with a syntactic violation, 98% was rated as unacceptable, for semantic anomalous sentences, 81% was rated as unacceptable, and the sentences with combined violations, 99% were rated as unacceptable. One sample t-tests, comparing classification performance to 100% for each sentence type were all non-significant.



Figure 1. Sentence comprehension versus visual fixation.

MRI Results

Comparing sentence processing (Figure 1) to the low-level visual fixation baseline revealed a highly significant ($P < .001$, FWE), bilaterally symmetric pattern of typical language related activations, including most of the inferior frontal, anterior cingulate, middle and superior temporal, inferior parietal, and lateral occipital and occipito temporal regions, as well as the basal ganglia (thalamus, caudate and lentiform nuclei). Descriptively, the left hemispheric activations were more prominent compared to the right; in

particular, in the angular/supramarginal region of the left inferior parietal region.

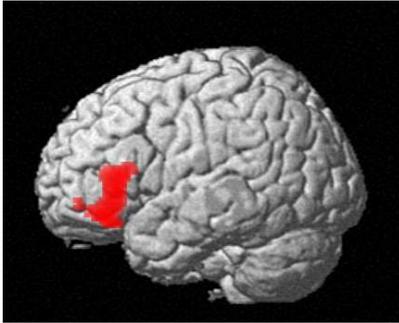


Figure 2. The main effect of semantic anomaly.

Consistent with several previous studies (Hagoort et al., 2004; Menenti et al., 2008; Tesink et al., 2008), the main effect of semantic anomaly ($[CB+SE] > [SY+CR]$; Figure 2) yielded significantly greater activation in the anterior left inferior frontal region (BA 45/47; $P < .038$, FWE). The opposite contrast revealed a deactivation pattern sharing significant overlap with the typical default mode network (Raichle et al., 2001).

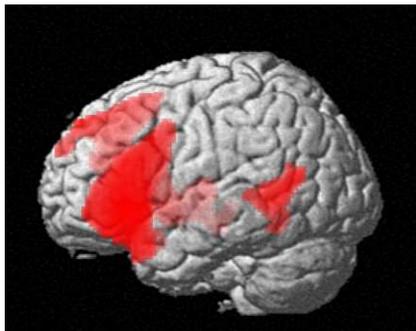


Figure 3. The main effect of syntactically correct sentences.

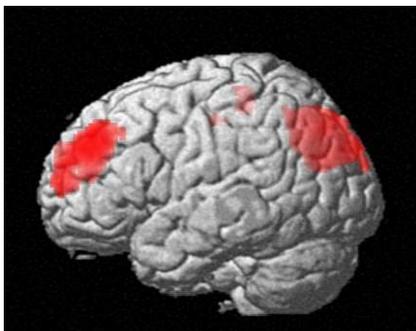


Figure 4. The main effect of syntactic anomaly.

The main effect of syntactically correct sentences ($[SE+CR] > [CB+SY]$; Figure 3), showed significant activation in the inferior frontal cortex (BA 6/44/45/47; $P < .001$, FWE; left > right), including the mid-anterior insula extending into the

superior temporal poles (BA 22/38). In addition, significant effects were observed in medial prefrontal/anterior cingulate cortex (BA 6/8/32; $P < .001$, FWE), posterior middle and superior temporal regions (BA 21/22; $P < .001$, FWE), and the basal ganglia (caudate and lentiform nuclei). In the reverse contrast (Figure 4) we observed significant activations in the middle frontal region bilaterally (BA 9/46; $P < .001$, FWE), the right inferior parietal region (BA 39/40; $P < .001$, FWE), precuneus bilaterally (BA 7; $P = .001$, FWE) and the left posterior cingulate region (BA 23/31; $P = .001$, FWE).

The only region that showed a significant interaction ($[CB-SE] - [SY-CR] > 0$; Figure 5) between the factors semantics and syntax was the left temporo-parietal region (BA 22/40; $P = .003$, FWE). This interaction was mainly due to the fact that $CB > SE$ ($P = .025$, FWE), while there was no significant difference between SY and CR ($P = 1.00$).

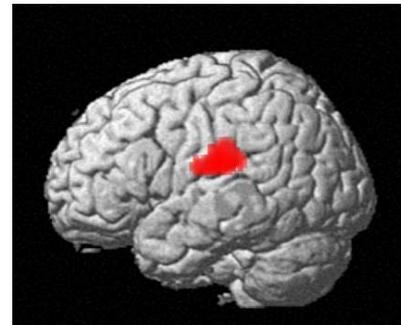


Figure 5. The interaction between semantics and syntax.

Discussion

The present study investigated the neural correlates of sentence level syntactic and semantic processing using a well-characterized stimulus material from a previous EEG study (Hagoort, 2003). So far, the only functional neuroimaging studies that have investigated whether semantic parameters have an influence on the structure building process (and vice versa) are ERP studies; (Hagoort, 2003; Friederici, Steinhauer, & Frisch, 1999; Osterhout & Nicol, 1999) with the exception of the fMRI study of Kuperberg et al. (2003).

The sentence processing vs. low-level baseline and the main effect of semantic anomalies are in line with previous findings (Hagoort et al., 2004; Kuperberg et al., 2003; Menenti et al., 2008; Tesink et al., 2008). The effect of syntactically correct sentences (Figure 3) included significant activation of the inferior frontal region, extending into the mid-anterior insula, as well as the posterior middle and superior temporal regions, in general agreement with the findings of Snijders et al. (2008). The gender agreement violations yielded significant activation of the middle frontal region bilaterally (Figure 4).

This set of syntax related results is interesting for several reasons. First, they show that the inferior frontal cortex (IFC), centered on Broca's region, is not only responding to syntactic violations per se. On the contrary, the memory, unification, and control model proposed by Hagoort (2005)

predicts that a complete unification failure, as is the case of gender agreement violations, should engage the LIFC less than when unification is possible and succeeds. Here we note that the syntactic processing seems unaffected by the semantic context when the incremental build-up of structure on the basis of the incoming word input is deterministic. This is different from the case of structural ambiguity, where at specific moments in the structural assignment process more than one syntactic structure can be assigned (cf., Hagoort, 2003). Second, the right Broca's homologue was also significantly engaged by syntactically correct compared to anomalous sentences, although the left sided activation was more pronounced. Third, gender agreement violations, which induce complete unification failure, activated the dorsolateral prefrontal cortex (BA 9/46) bilaterally. The cortex centered on BA 9/46 has been related to attention control processes and other, albeit ill-defined, control aspects of working memory (e.g., Hagoort, 2005; Petersson et al., 2006). Several researchers have raised the issue of working memory in the context of sentence processing (e.g., Cooke et al., 2006; MacLeod et al., 1998). Activation of BA 9/46 has also been observed in verbal fluency tasks (e.g., Abrahams et al., 2003). Hagoort (2005) argued that the control component accounts for the fact that the language system operates in the context of communicative intentions (and actions). Language control has for example been investigated in the context of Stroop tasks, suggesting an involvement of the dorsolateral prefrontal (BA 9/46) and the anterior cingulate cortices (Hagoort, 2005). In the study by Kuperberg et al. (2003), syntactic violations elicited an increased response in the medial and lateral parietal regions bilaterally and also in the right middle frontal gyrus (BA 9/46). Several fMRI studies have investigated syntactic gender processing (for a review see Heim 2008) in metalinguistic (Longoni et al., 2005) and automatic on-line processing tasks (Hammer et al., 2006). Hammer et al. (2006) found activation of Broca's region and also an involvement of the supramarginal gyrus. In comparison, the semantic anomalies did not evoke an activation of the control region. Semantic integration is a more graded process and there is no clear boundary between what can be, is difficult or impossible to semantically integrate (Hagoort, 2003).

Finally, the only region that showed a significant interaction between the semantic and syntactic factor was the left temporo-parietal region (BA 22/40; Figure 5). At a general level, this interaction effect patterned with the corresponding EEG findings of Hagoort (2003). More specifically, the ERP results showed classical P600 and N400 effects related to syntactic and semantic anomalies, respectively, while their combined effect revealed an interaction expressed in the N400 component ($[CB-SE] - [SY-CR] > 0$). More specifically, the N400 component was similar in the correct and syntactic conditions ($SY \sim CR$), while the combined effect was significantly larger than the effect of semantic anomaly alone ($CB > SE$). It is worth noting that we do not know whether the different language processing events are directly or only indirectly reflected to the ERP effects. This complication has its parallel in fMRI where it is unknown whether a region of an increased

hemodynamic response is the source of the cognitive operation or the site where it has its effect. However, the observation of an interaction between syntax and semantics suggests that the language parsing processes that feed into the generator ensembles of the N400 and P600 components are interacting at some level. The fMRI results suggest that the left temporo-parietal region is one region where this interaction takes place.

Although, intuitively, the semantic interpretation of the sentences are not particularly affected by the gender mismatch between the definite article and the noun, both the acceptability judgments and the brain responses showed a significant sensitivity of the language processing system to violations of gender agreement. Interestingly, the behavioral control study of Hagoort (2003) showed that subjects took longer to evaluate semantic acceptability compared to the syntactic acceptability of sentences. Taken together, these results suggested an asymmetry between semantic and syntactic processing: syntactic processing was unaffected by semantic integration problems. Intuitively, the assigning structure to a Jabberwocky sentence is as easy as assigning structure to a meaningful sentence; semantic integration is, however, harder in the presence of a syntactic processing problem. On this account, the processing consequences of complicated unification process might influence semantic integration before the unification process comes to a halt (Hagoort, 2003). There is clear evidence from both behavioral and EEG data that lexical context and discourse context immediately influence the assignment of structure when there are different structural options. Thus, Hagoort (2003) argued that syntactic constraints conspire with semantic constraints if the latter are necessary for determining structure, but semantics is ignored by syntax if its contribution is not needed.

Conclusion

In this study we show that the brain honors the distinction between syntax and semantics, not only in terms of ERP components, but also in terms of brain regions. The results show that the IFC (BA 6/44/45/47) is involved in constructive unification operations during the structure-building process in parsing for comprehension. The effect of semantic anomaly and its implied unification load engages the anterior IFC (BA 45/47) while the effect of syntactic anomaly and its implied unification failure engages MFC (BA 9/46). Tentatively, we provide evidence that the dorsolateral prefrontal cortex centered on BA 9/46 subserves aspects of the control component of the language system, albeit ill-defined. In addition, the fMRI results suggest that the syntax of gender agreement interacts with sentence-level semantics in the left temporo-parietal region.

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