

The neuronal infrastructure for unification at multiple levels

Peter Hagoort

In a series of elegant patient and fMRI studies on inflectional morphology, William Marslen-Wilson (WMW) and colleagues have found convincing evidence for the crucial contribution of left inferior frontal cortex (LIFC), especially Brodmann area (BA) 45 to morphological decomposition. Recent intracranial recordings in BA 45 from epileptic patients during presurgical preparation indicate that the same brain area is also involved in the generation of inflected forms during language production. (Hagoort and Levelt 2009; Sahin et al. 2009).

The important contribution of this area in LIFC, has led WMW and colleagues to propose a general model about the neural infrastructure for language processing. In this model, the perisylvian cortices in both left and right hemisphere contribute to language comprehension through general purpose processing mechanisms involved in perception, competition and selection. In addition, specific nodes in the left perisylvian network of brain areas instantiate the core decompositional (and compositional) machinery that is specifically linguistic in nature. These domain-specific areas are LIFC and STG/MTG. The evidence for this account of language processing comes mainly from patient and fMRI studies in which the words with regular inflectional morphemes, which require decomposition, are compared to monomorphemic words with different levels of perceptual complexity. For spoken words, the trigger for decomposition is the inflectional rhyme pattern (IRP), which is a phonological pattern signaling the potential presence of an affix.

Although the model entails claims about bi-hemispheric foundations of language comprehension, a cautionary note is warranted. The evidence for the model is largely based on single word processing. Clearly, language comprehension goes well beyond recognizing and decomposing individual word forms. In the remainder I will focus on the neural architecture beyond single word processing. At the end, I will attempt to bring the different strands of evidence together.

1. Unification beyond the single word level

The requirements of the language system are instantiated in the finite and real-time machinery of the human brain, and presumably shared to a large extent with other functional domains. I consider three functional components to be the core of language processing (Hagoort 2005). The first one is the *Memory* component, which refers to the different types of language information stored in long term memory (the mental lexicon), and to how this information is retrieved (lexical access). The *Unification* component refers to the integration of lexically retrieved information into a representation of multi-word utterances, as well as the integration of meaning extracted from non-linguistic modalities; this component is at the heart of the combinatorial nature of language. Finally, the *Control* component relates language to action, and is invoked, for instance, when the correct target language has to be selected (in the case of bilingualism), or for handling turn taking during conversation. In principle, this MUC (Memory, Unification, Control) framework applies to both language production and language comprehension, although details of their functional anatomy within each component will be different. No claims are made about language-specificity. It is an empirical issue to what extent the neural infrastructure for language-relevant components is shared with other domains of cognition (e.g. the perception of music).

Classically, psycholinguistic studies of unification have focused on syntactic analysis. However, unification operations take place not only at the syntactic processing level. Combinatorality is a hallmark of language across representational domains (cf. Jackendoff 2002). Thus, also at the semantic and phonological levels, lexical elements are combined and integrated into larger structures (cf Hagoort 2005). In this context, I will first discuss semantic unification. Semantic unification refers to the integration of word meaning into an unfolding representation of the preceding context. This is more than the concatenation of individual word meanings. In the interaction with the preceding sentence or discourse context, the appropriate meaning is selected or constructed, so that a coherent interpretation results.

In recent years, several fMRI studies have been conducted with the aim of identifying the semantic unification network. These studies either compared sentences containing semantic/pragmatic anomalies with their correct counterparts (Baumgaertner, Weiller, and Büchel 2002; Friederici et al. 2003; Hagoort et al. 2004; Kiehl, Laurens, and Liddle 2002; Kuperberg et al. 2000, 2003, Kuperberg, Sitnikova, and Lakshmanan 2008; Newman et al. 2001; Ni et al. 2000; Ruschemeyer, Zysset, and Friederici 2006), or

compared sentences with and without semantic ambiguities (Davis et al. 2007; Hoenig and Scheef 2005; Rodd, David, and Johnsrude 2005; Rodd et al 2010; Zempleni et al. 2007). The most consistent finding across all of these studies is the activation of the left inferior frontal cortex (LIFC), more in particular BA 47 and BA 45. In addition, the left superior and middle temporal cortex is often found to be activated, as well as left inferior parietal cortex (see Hagoort, Baggio, and Willems 2009) For instance, Rodd and colleagues (2005) had subjects listen to English sentences such as “There were dates and pears in the fruit bowl” and compared the BOLD response of these sentences to the BOLD response of sentences such as “There was beer and cider on the kitchen shelf”. The crucial difference between these sentences is that the former contains two homophones, i.e. ‘dates’ and ‘pears’, which, when presented auditorily, have more than one meaning. This is not the case for the words in the second sentence. The sentences with the lexical ambiguities led to increased activations in LIFC and in the left posterior middle/inferior temporal gyrus. In this experiment all materials were well-formed English sentences in which the ambiguity usually goes unnoticed. Nevertheless, very similar results were obtained as in experiments that used semantic anomalies. Areas involved in semantic unification were found to be sensitive to the increase in semantic unification load due to the ambiguous words.

An indication for the respective functional roles of the left frontal and temporal cortices in semantic unification comes from a few studies investigating semantic unification of multimodal information with language. Using fMRI, Willems and colleagues assessed the neural integration of semantic information from spoken words and from co-speech gestures into a preceding sentence context (Willems, Özyürek, and Hagoort 2007). Spoken sentences were presented in which a critical word was accompanied by a co-speech gesture. Either the word or the gesture could be semantically incongruous with respect to the previous sentence context. Both an incongruous word as well as an incongruous gesture led to increased activation in LIFC as compared to congruous words and gestures (see Willems, Özyürek, and Hagoort 2008 for a similar finding with pictures of objects). Interestingly, the activation of the left posterior temporal cortex was increased by an incongruous spoken word, but not by an incongruous hand gesture. The latter resulted in a specific increase in dorsal premotor cortex (Willems, Özyürek, and Hagoort 2007). This suggests that activation increases in left posterior temporal cortex are triggered most strongly by processes involving the retrieval of lexical information. LIFC, on the other hand, is a key node in the semantic unification network, unifying semantic information from different modalities

From these findings it seems that semantic unification is realized in a dynamic interplay between LIFC as a multimodal unification site on the one hand, and modality specific areas on the other hand. This general contribution of LIFC is further corroborated by empirical evidence from neuroimaging studies on syntactic processing.

Next to semantic unification at the level of sentence processing, syntactic information has to be unified as well. In a meta-analysis of 70 neuroimaging studies, Indefrey (in press) found two areas that were critical for syntactic processing, independent of the input modality (visual in reading, auditory in speech). These two supramodal areas for syntactic processing were the left posterior superior and middle temporal gyrus and the left prefrontal cortex, in particular BA 44 and BA 45 (see Figure 1). I have hypothesized (Hagoort 2005) that LIFC (Broca's area) is involved in syntactic unification operations, whereas left posterior temporal cortex is important for the retrieval of lexical-syntactic information. This information includes syntactic frames that specify the local syntactic environment of different word types (Vosse and Kempen 2000).

Empirical support for this distribution of labour between LIFC and temporal cortex was recently found in a study of Snijders et al. (2009). These authors carried out an fMRI study in which participants 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 with words, and only within a sentence context, but not within a word list, display a larger signal for ambiguous than unambiguous conditions. The reason is that only sentences require syntactic unification. In the context of sentence processing, the retrieval of both a VP and an NP frame for lexical-syntactic ambiguities will increase the unification load, due to the requirement to select and integrate the contextually appropriate frame and to reduce the activation of the alternative frame. The posterior LIFC showed exactly this predicted pattern, confirming the hypothesis that LIFC contributes to syntactic unification (see Figure 2). The left posterior middle temporal gyrus was activated more for ambiguous than unambiguous conditions, as predicted for regions subserving the retrieval of lexical-syntactic information from memory (see Snijders et al. 2009, for further details).

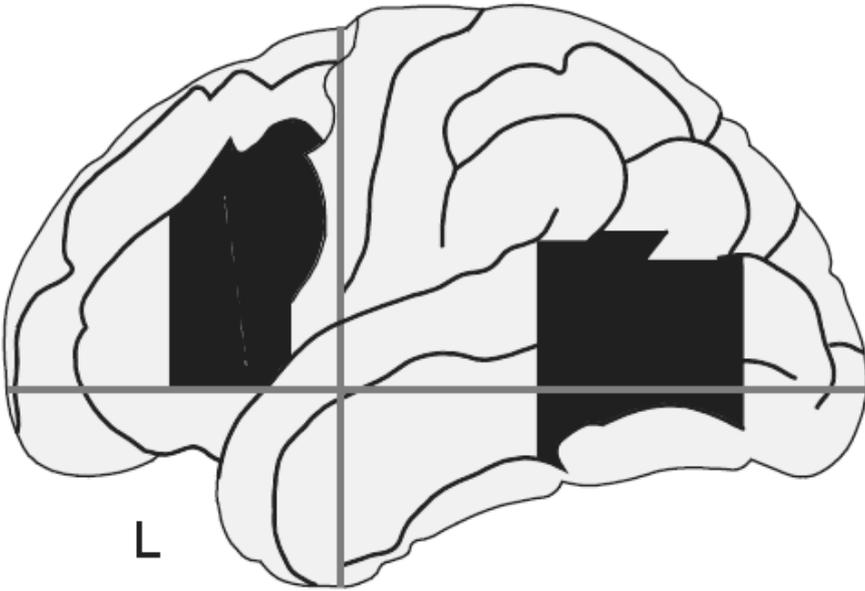


Figure 1. Reliable activation for reading or listening to structurally complex sentences compared to simpler sentences (22 studies). After Indefrey (in press). This figure is based on a subset of the 70 studies in the meta-analysis, which included other manipulations, such as syntactic violations.

In conclusion, not only morpho-syntactic processing of single words recruits the contribution of left inferior frontal cortex in connection with temporal cortex areas, this also holds for the processing of multi-word utterances. Especially for aspects of syntactic processing at the word and sentence level, there is a clearly much stronger involvement of the left perisylvian cortex than of the homologue areas in the right hemisphere. This raises the question whether left perisylvian cortex has network characteristics that make it especially suited for language processing.

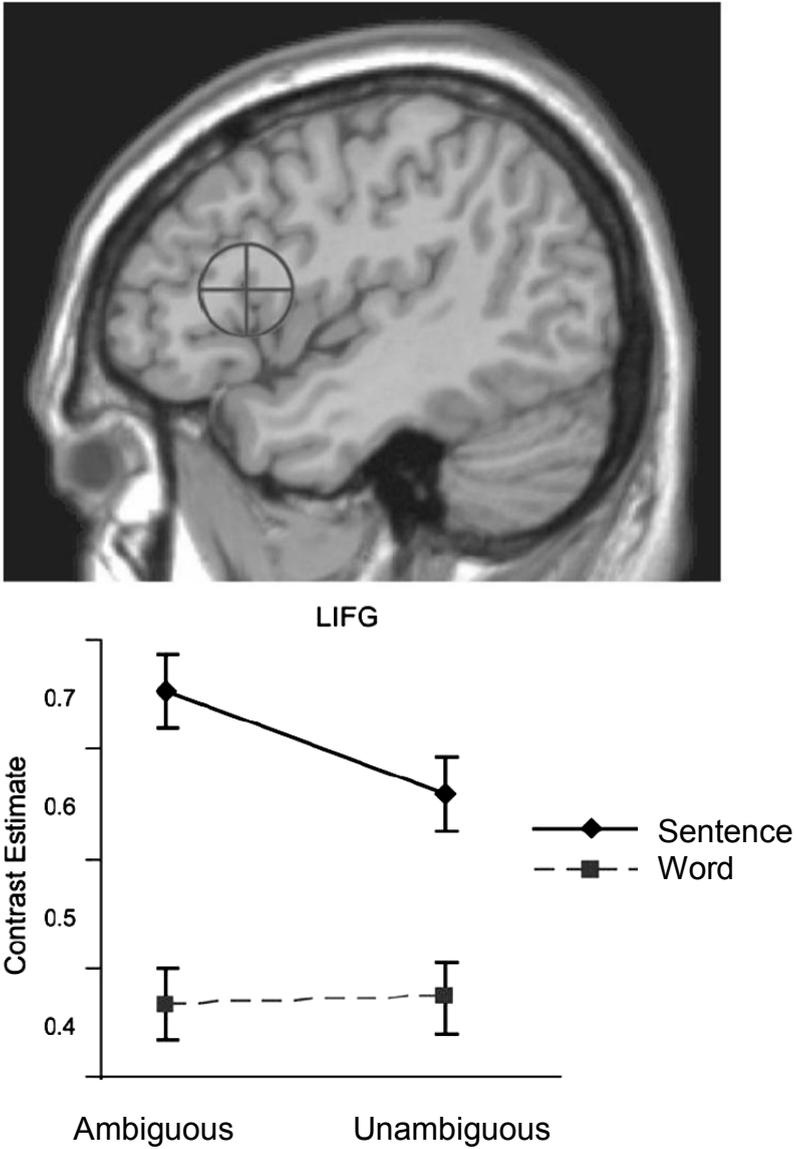


Figure 2. Mean contrast estimated for LIFC for sentences and word sequences, with and without noun-verb ambiguities. On top the Region Of Interest (ROI; 13 mm sphere around coordinates [-44, 19, 14]) is shown. This ROI includes both BA 44 and parts of BA 45 (Snijders et al. 2009).

Recent research has found clear asymmetries in connectivity between inferior frontal and temporal cortex regions (cf. Tyler and Marslen-Wilson 2008). Using Diffusion Tensor Imaging, Catani et al. (2007) found that the large majority of subjects had a direct connection between Broca's and Wernicke's territories through the articulate fasciculus exclusively or most strongly in the left hemisphere. Further evidence for clear hemispheric asymmetries in the network organization of language relevant cortex was found in a recent study by Xiang et al. (2010). These authors performed a resting state functional connectivity study to investigate directly the functional correlations within the perisylvian language networks by seeding from three subregions of Broca's complex (pars opercularis, pars triangularis and pars orbitalis) and their right hemisphere homologues. A clear topographical connectivity pattern in the left middle frontal, parietal and temporal areas was revealed for the three left seeds in Broca's complex. These results demonstrate that a functional connectivity topology can be observed in the perisylvian language areas in the left hemisphere, in which different parts of Broca's area and adjacent cortex show a differential pattern of connectivity. This pattern is only seen in the left hemisphere and seems to be organized according to information type: semantic, syntactic, phonological (see Figure 3).

2. Conclusions

Over and above the retrieval of individual word meanings, sentence and discourse processing requires combinatorial operations that result in a coherent interpretation of multi-word utterances. These operations do not adhere to a simple principle of compositionality. World knowledge, information about the speaker, co-occurring visual input and discourse information all trigger similar electrophysiological responses as sentence-internal semantic information (Hagoort, Baggio, and Willems 2009). A network of brain areas, including the left inferior frontal gyrus, the left superior/middle temporal cortex, the left inferior parietal cortex and, to a lesser extent, their right hemisphere homologues are recruited to perform semantic and syntactic unification. In line with the MUC framework, these unification operations are under top-down control of left, and in the case of discourse, also right inferior frontal cortex.. This contribution modulates activations of lexical information in memory as represented by the left superior and middle temporal cortex, with presumably additional support for unification operations in left inferior parietal areas (e.g., angular gyrus).

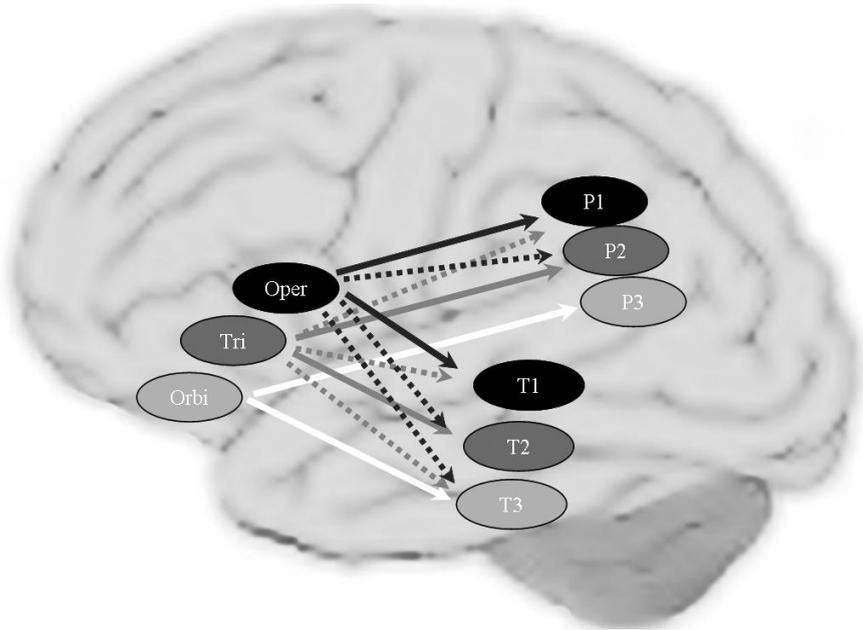


Figure 3. The topographical connectivity pattern between frontal and temporal/parietal cortex in the perisylvian language networks. Connections to the left pars opercularis (oper), pars triangularis (tri) and pars orbitalis (orbi) are shown in black, dark grey and white arrows respectively. The solid arrows represent the main (most significant) correlations and the dashed arrows represent the extending (overlapping) connections. Brain areas assumed to be mainly involved in phonological, syntactic and semantic processing are shown in black, dark grey and light grey circles, respectively. P1: Supramarginal gyrus; P3: AG: Angular gyrus; P2: the area between SMG and AG in the superior/inferior parietal lobule; T1: posterior superior temporal gyrus; T2: posterior middle temporal gyrus; P3: posterior inferior temporal gyrus.

Both fMRI and lesion studies have shown that LIFC is also involved in processing inflectional morphology during comprehension (Tyler and Marslen-Wilson 2008). In combination with the Sahin et al. (2009) findings, showing involvement of the same area in inflectional composition during production, this strongly suggests that LIFC is recruited during both language production and language comprehension.

Proposals have been made that LIFC (Broca's area) has a more specialized role in language processing, to do with linguistically motivated operations of syntactic movement (Grodzinsky and Santi 2008), and the processing of hierarchical structures (Friederici et al. 2006). The results of the research by WMW and colleagues on morphological processing indicate that the role of LIFC is not limited to such operations, but should be characterized in more general terms. The speculative suggestion that I like to put forward is that LIFC is most likely involved in unification operations at the word and sentence level, in connection with temporal regions that are crucial for memory retrieval (Hagoort 2005). Compositional and decompositional operations occur at multiple levels and at multiple time slices in the language processing system. Any time lexical and other building blocks enter into the process of utterance interpretation or construction, and any time the input string requires decomposition (maybe through analysis-by-synthesis) in order to contact the right lexical representations, LIFC is recruited. The content-specifics of the recruitment are determined by the recruiting areas and the recruiting time slices. As is known for neurons in visual cortex (Lamme and Roelfsema 2000), the specific contribution of LIFC may well vary with time, as a consequence of the different dynamic cortical networks in which it is embedded at different time slices. This fits well with the finding that Broca's area is not language-specific, but also recruited in the service of other cognitive domains, such as music (Patel 2003) and action (Hamzei et al. 2003), and with the finding that its contribution crosses the boundaries of semantics, syntax, and phonology (Hagoort and Levelt 2009).

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