

# The Neurobiology of Language Beyond Single Words

Peter Hagoort<sup>1,2</sup> and Peter Indefrey<sup>2,3</sup>

<sup>1</sup>Max Planck Institute for Psycholinguistics, 6525 XD Nijmegen, The Netherlands; email: peter.hagoort@donders.ru.nl

<sup>2</sup>Donders Institute for Brain, Cognition and Behaviour, Radboud University Nijmegen, 6525 EN Nijmegen, The Netherlands

<sup>3</sup>Heinrich Heine University, 40225 Düsseldorf, Germany; email: indefrey@phil.hhu.de

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## Keywords

syntactic processing, semantic processing, neuropragmatics, Broca's area, Wernicke's area, meta-analysis

## Abstract

A hallmark of human language is that we combine lexical building blocks retrieved from memory in endless new ways. This combinatorial aspect of language is referred to as unification. Here we focus on the neurobiological infrastructure for syntactic and semantic unification. Unification is characterized by a high-speed temporal profile including both prediction and integration of retrieved lexical elements. A meta-analysis of numerous neuroimaging studies reveals a clear dorsal/ventral gradient in both left inferior frontal cortex and left posterior temporal cortex, with dorsal foci for syntactic processing and ventral foci for semantic processing. In addition to core areas for unification, further networks need to be recruited to realize language-driven communication to its full extent. One example is the theory of mind network, which allows listeners and readers to infer the intended message (speaker meaning) from the coded meaning of the linguistic utterance. This indicates that sensorimotor simulation cannot handle all of language processing.

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## INTRODUCTION

Language processing is more than memory retrieval and more than the simple concatenation of retrieved lexical items. The expressive power of human language is based on the ability to combine elements from memory in novel ways. This notion led the linguist Wilhelm von Humboldt (1829) to his famous claim that language “makes infinite use of finite means.” This central feature of the human language system is, however, not represented in the classical Wernicke-Lichtheim-Geschwind (WLG) model of the neural architecture of language. This model did not go beyond the single word level (Hagoort 2013, Levelt 2013). Even today a large proportion of neuroimaging research on language focuses on processing at or below this level. For example, one of the most influential recent models of the neurobiology of language, that of Hickok & Poeppel (2007), focuses mainly on speech processing at lexical and sublexical levels. Our focus here is instead on processes beyond the retrieval of lexical information. Clearly, retrieval of the lexical building blocks for language (e.g., phonological, morphological, syntactic building blocks) is a crucial component of human language processing (Hagoort 2005, 2013). But equally important is the process of deriving new and complex meaning from the lexical building blocks. This process is referred to in different ways. Here we use the term unification to indicate the real-time assembly of the pieces retrieved from memory into larger structures, with contributions from context. Classic psycholinguistic studies of unification had a strong focus on syntactic analysis (parsing). Unification operations take place at the syntactic processing level, but not only there (cf. Jackendoff 2002, 2007). At the semantic and phonological levels, too, conceptual and lexical elements are combined and integrated into larger structures. It is therefore useful to distinguish between syntactic, semantic, and phonological unification (Hagoort 2005, 2013). Before discussing the neurobiological infrastructure for unification in more detail, we discuss the temporal dynamics of the operations supported by this infrastructure.

### Unification and Prediction

One of the most remarkable characteristics of speaking and listening is the speed at which it occurs. Speakers produce easily between 2 and 5 words per second, information that must be decoded by the listener within roughly the same time frame. Given the rate of typical speech we can deduce that word recognition is extremely fast and efficient, taking no more than 200–300 ms. Language processing is highly incremental, with a continuous interaction between the preceding context and the ongoing lexical retrieval operations (Zwitserslood 1989). Here prediction and postlexical

integration might work together (cf. Kutas et al. 2015). Electrophysiological data from event-related brain potential (ERP) studies on language provide relevant insights about the time course of the incremental updating of the input representation.

Considering that the acoustic duration of many words is on the order of a few hundred milliseconds, the immediacy of the electrophysiological language-related effects is remarkable. For instance, the early left anterior negativity (ELAN), a syntax-related effect (Friederici et al. 2003), starts at ~100–150 ms after onset of the acoustic word (but see Steinhauer & Drury 2012 for a critical discussion of the ELAN). The onset of the N400 is at ~250 ms, and another language-relevant ERP, the so-called P600, usually starts at ~500 ms. Thus some of these effects occur well before the end of a spoken word. Classifying visual input (e.g., a picture) as depicting an animate or inanimate entity takes the brain ~150 ms (Thorpe et al. 1996). Roughly the same amount of time is needed to classify orthographic input as a letter (Grainger et al. 2008). If we take this time estimate as our reference point, the early appearance of electrophysiological responses to a spoken word is a salient feature of word processing. In physiological terms, the earliness of some of these brain responses suggests that they are not influenced by long-range recurrent feedback to the primary and secondary auditory cortices involved in first-pass acoustic and phonological analysis. Recent modeling work suggests that early ERP effects are best explained by a model with feedforward connections only. Backward connections become essential only after 220 ms (Garrido et al. 2007). The effects of backward connections are, therefore, not manifest in the latency range of early ERP effects such as the ELAN because not enough time has passed for return activity from higher levels to auditory cortex. In the case of speech, the N400 follows the word recognition points closely in time, which suggests that what occurs on-line (that is, in real time) in language comprehension is presumably based partly on predictive processing. Under many circumstances, there is simply not enough time for top-down feedback to exert control over a preceding bottom-up analysis. Very likely, lexical, semantic, and syntactic cues conspire to predict sometimes very detailed characteristics of the next anticipated word, including its syntactic and semantic makeup. A mismatch between contextual prediction and the output of bottom-up analysis results in an immediate brain response recruiting additional processing resources to salvage the on-line interpretation process. Recent ERP studies have provided evidence that context can indeed result in predictions about the syntactic features (i.e., grammatical gender; Van Berkum et al. 2005) and word form (DeLong et al. 2005) of the next word. Lau et al. (2006) showed that the ELAN elicited by a word category violation was modulated by the strength of the expectation for a particular word category in the relevant syntactic slot. More general event knowledge or semantic domains seem to assist with prediction of upcoming information (see Metusalem et al. 2012, Szewczyk & Schriefers 2013, Kutas et al. 2015 for a review of the relevant literature). Whereas the evidence for prediction is strong in the case of language comprehension, the role of prediction in language production (speaking) is less clear. The listener can, at best, guess (predict) what the speaker will say next, but the speaker herself knows where her speech is headed. Hence, in this case, planning an utterance seems to coincide with prediction (Meyer & Hagoort 2013).

Unification refers to the ongoing combinatorial operations in language, which include both context-driven predictions and integration of the lexical information into a representation that spans the whole utterance. The difference is that predictions work forward in time, whereas integration works backward in time; in the latter case, information is integrated into a context that preceded the currently processed lexical item.

Unification is not restricted to linguistic building blocks. ERP studies have shown that non-linguistic information also contributes to unification. Here one can think of information about the speaker (Van Berkum et al. 2008), co-speech gestures (Willems et al. 2007), or world knowledge (Hagoort et al. 2004). These studies found the same effects for nonlinguistic compared with

linguistic information on the amplitude and latency of ERPs such as the N400. These data suggest that both linguistic and nonlinguistic contexts have an immediate impact on the interpretation of an utterance (Hagoort & van Berkum 2007).

### Shared Circuitry for Comprehension and Production

The WLG model strictly divided between areas involved in language production (Broca's area) and language comprehension (Wernicke's area). It has become clear that this division is incorrect. Lesions in Broca's area impair not only language production but also language comprehension (Caramazza & Zurif 1976), whereas lesions in Wernicke's area also affect language production. More recent neuroimaging studies provided further evidence that the classical view on the role of these regions is no longer tenable. Central aspects of language production and comprehension are subserved by shared neural circuitry (Menenti et al. 2011, Segaert et al. 2012). For instance, Segaert et al. (2012) investigated whether the neurobiological substrate for coding and processing syntactic representations is shared between speaking and listening. To ensure that not just the same brain regions but in fact the same neuronal populations within these regions are involved in both modalities, these investigators used a repetition suppression design (Grill-Spector et al. 2006). For repeated syntactic structures (e.g., actives, passives) within and between modalities (i.e., speaking and listening), they found the same suppression effects for within- and for between-modality repetitions. These effects were localized in the left middle temporal gyrus (MTG), the left inferior frontal gyrus (IFG), and the left supplementary motor area (see **Supplemental Figure 1**. Follow the **Supplemental Material link** from the Annual Reviews home page at <http://www.annualreviews.org>).

Given that speaking and listening have different processing requirements, the same areas may not be recruited to the same degree in these two cases (Indefrey et al. 2004). This difference between speaking and listening, however, does not detract from the finding that when needed, the same areas subserve unification operations in language production and language comprehension.


Even less clear is the degree of separation between networks for syntactic and semantic unification. Separation of these networks is nontrivial because syntactic differences are not without semantic consequences. For instance, sentences containing an object-relative clause (e.g., "The reporter who the senator attacked admitted the error") are found to be more difficult to understand than sentences with a subject-relative clause (e.g., "The reporter who attacked the senator admitted the error"). This increased difficulty is usually attributed to the difference in the syntactic structure of object and subject relative clauses. Chen and coworkers (2006), however, showed that increases in activation of Broca's area for object compared with subject relative clauses are observed only when the subject of the relative clause is inanimate and the subject of the main clause is animate (e.g., "The golfer that the lightning struck") and not for the syntactically identical sentences with animate relative clause subjects (e.g., "The wood that the man chopped heated the cabin"). Chen et al. argue that this finding rules out hypotheses based on syntactic structure complexity and rather suggests that activation of Broca's area reflects the relative difficulty of thematic role assignment; inanimate referents were dispreferred agents of an action and animate referents dispreferred undergoers of action (see also Kuperberg et al. 2008). A difference in syntactic structure clearly has immediate consequences for mapping grammatical roles (subject, object) onto thematic roles (agent, undergoer) and hence for the event structure depicted in these sentences. The event structure is part of the conceptual/semantic representation of the sentence. Despite the intertwined nature of syntactic and semantic unification, for this review we attempt to segregate these two types of unification as much as possible using data from a new meta-analysis of numerous functional imaging studies.

## SYNTACTIC VERSUS SEMANTIC UNIFICATION: A META-ANALYSIS

So far, the available information is most clear for the areas involved in syntactic analysis. In a recent meta-analysis of more than 80 neuroimaging studies on sentence processing, Indefrey (2012) identified consistent activations in a comparison of sentences that were syntactically more demanding and control sentences that were syntactically less demanding (e.g., object-relative versus subject-relative sentences). Two regions were systematically more strongly activated when participants were reading or listening to syntactically demanding sentences. The one region is Broca's area in the left inferior frontal gyrus (LIFG), more specifically the pars opercularis [Brodmann area (BA) 44] and the pars triangularis (BA 45). The other region includes the posterior parts of the left superior and middle temporal gyri. These results are remarkably consistent with those from the syntactic adaptation study by Segaert et al. (2012), with the outcome of a representational similarity analysis of magnetoencephalography (MEG) data (Tyler et al. 2013), and with a recent analysis of lesion data in patients with a syntactic comprehension deficit (Tyler et al. 2011). Although the specific contributions of these areas to syntactic analysis is a matter of debate, the involvement of the LIFG and left posterior MTG cannot be denied.

Hereafter we present a new meta-analysis of neuroimaging studies on sentence processing to establish, among other things, the degree to which the network for semantic unification can be segregated from the network for syntactic unification. We analyzed 151 hemodynamic studies on sentence processing that reported activated brain regions with Talairach coordinates or Montreal Neurological Institute (MNI) coordinates (see **Supplemental Table 1**). A subset of 85 studies contrasting sentence-level processing with lower-level control conditions, or syntactically more demanding sentences with less demanding sentences, were taken from previous meta-analyses, such as the one discussed above (Indefrey 2011, 2012). To identify additional studies on sentence-level semantic processing, we conducted a search in Thomson Reuters Web of Knowledge with the search term “fMRI OR functional magnetic resonance imaging OR PET OR Positron Emission Tomography AND semantic AND sentence.” This search yielded 409 studies, of which 66 reported contrasts between semantically more demanding and less demanding sentences, contrasts between syntactically more-demanding and less-demanding sentences, or contrasts between sentences and nonsentential control conditions. All these studies tested healthy participants. The activation foci and the spatial extent of 198 contrasts were coded in an anatomical reference system of 112 regions on the basis of the stereotaxic atlas of Talairach & Tournoux (1988) (for details, see caption to **Supplemental Table 2** and Indefrey & Levelt 2000, 2004).

For any particular region the reliability of its activation was assessed using the following estimate: The average number of activated regions reported per experiment divided by the number of regions (112) corresponds to the probability for any particular region to be reported in an experiment, if reports were randomly distributed over regions. Assuming this probability, the chance level for a region to be reported as activated in a certain number of experiments is given by a binomial distribution. The possibility that the agreement of reports about a certain region was coincidental was rejected if the chance level was below 5% (uncorrected for the number of regions). Regions with a chance level below 0.0004 survived a Bonferroni correction for 112 regions and are reported as 0.05 (corrected). This estimate takes into account that not all studies covered the whole brain owing to the heterogeneity of techniques and analysis procedures (for example, analyzing only regions of interest). The procedure also controls for the fact that the average number of activated regions per study differs between contrasts. In contrasts comparing sentences to low-level control conditions, the number of activated regions is typically higher than in contrasts comparing syntactically demanding to less demanding sentences; thus the chances of

 [Supplemental Material](#)

coincidental agreements between studies are also higher. **Supplemental Tables 2, 3, and 4** show the summary data for all 112 regions and all comparisons reported here.

## Results

The contrasts we analyzed fall into two main categories: About one-third of the contrasts compared sentences to nonsentential stimuli, ranging from word lists to cross-hair fixation or rest conditions. The resulting brain activations can be expected to include whichever brain regions are involved in sentence-level syntactic and semantic processing. However, many other regions subserving lower-level processes, such as lexical retrieval, may also show up. About two-thirds of the contrasts compared syntactically or semantically demanding sentences to less demanding sentences. The latter studies controlled much more tightly for lower-level (e.g., lexical) differences between stimuli so that the resulting activations could be considered specific to syntactic or semantic unification. Note, however, that these studies not only may have missed neural correlates of sentence-level processing that were shared between demanding and less demanding sentences, but also may have induced processes related to higher general cognitive demands, such as attention or error-related processes.

The main manipulations for increasing syntactic demands are the use of sentences containing syntactic violations or word-class ambiguities (e.g., “watch” as noun or verb) and the use of structurally more complex sentences, such as those containing center-embedded object-relative clauses. Manipulations for increasing semantic demands are semantic violations (“The trains were very sour . . .”) and lexical-semantic ambiguities (e.g., “bank”) that did not affect the syntactic structure in comparing with the correct control sentences. In addition, as instances of higher semantic demands, we also considered experimental manipulations that complicated the listener’s ability to assign an overall meaning without inducing a syntactic difference. These instances include sentences with a metaphoric meaning, sentences inducing semantic operations such as coercion, metonymy, and sentences making connections to the previous discourse context. These instances also include sentences requiring listeners to assess speakers’ intentions (irony, indirect replies, or requests; see also the section on neuropragmatics).

**Sentences compared with control conditions below sentence level.** Compared with control conditions below sentence level, the comprehension of sentences reliably activates the temporal lobes and the posterior IFG bilaterally (**Figure 1a**, **Supplemental Figure 2**, **Supplemental Table 2**), albeit with a clear left hemisphere dominance. Not activated in any of the 53 studies were large parts of the right parietal and right inferior temporal cortices. These areas are thus reliably not involved during sentence comprehension. As shown in **Supplemental Figure 3**, some differences can be seen among the regions involved in processing written and spoken sentences. Some right hemisphere temporal regions are not reliably found in reading, and posterior frontal regions are less frequently found in listening. Of particular interest are the results for a subset of studies that used the most natural kind of sentence processing: The participants just listened or read

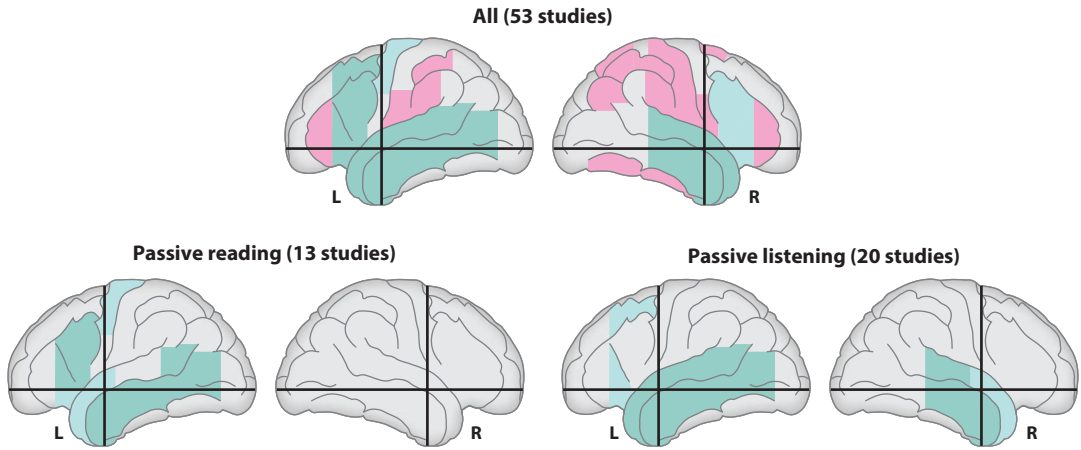
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### Figure 1

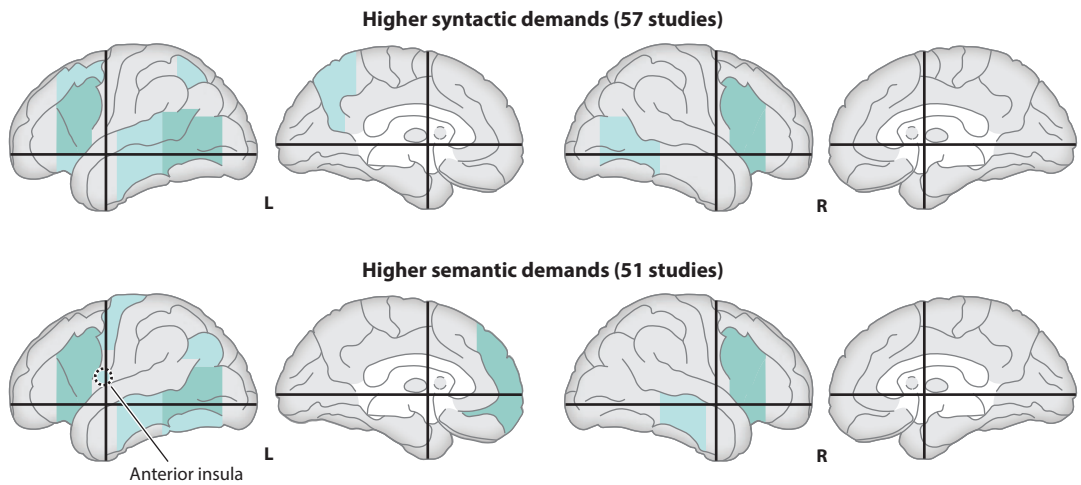
Schematic representation of the brain showing regions with reliably reported activations for sentences compared with nonsentential stimuli (*a*) and sentences with high syntactic or semantic processing demands compared with simpler sentences (*b,c*). The left posterior inferior frontal gyrus is further subdivided into Brodmann areas (BA) 44 (*above black line*), BA 45 (*below black line, above AC-PC line*) and BA 47 (*below AC-PC line*). Green regions indicate a reliable number of reports. Pink regions indicate no reports in 53 studies. For details, see **Supplemental Tables 2, 3, and 4** (follow the **Supplemental Material link** from the Annual Reviews home page at <http://www.annualreviews.org>). Abbreviations: AC, anterior commissure; PC, posterior commissure).



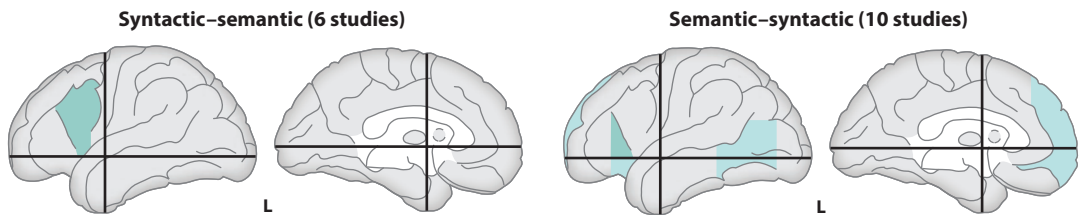
**a** Sentences compared with control conditions below sentence level



**b** Sentences with higher compared with sentences with lower processing demands



**c** Direct comparisons between sentences with high syntactic and high semantic demands



● Reliably activated  $p < 0.05$ , corrected    ● Reliably activated  $p < 0.05$ , uncorrected    ● Reliably not activated  $p < 0.05$ , uncorrected

for comprehension without performing any additional tasks (**Figure 1a**, **Supplemental Figure 4**). Irrespective of the input modality, passive sentence comprehension activates the left MTG, the superior temporal gyrus (STG), and the orbital (BA 47) and triangular (BA 45) parts of LIFG. The most dorsal part of the IFG (pars opercularis, BA 44), however, is not reliably activated during passive listening to (simple) sentences. The same holds when sentence processing is compared with the processing of word lists (see **Supplemental Figure 2**). This result suggests that either BA 44 is not involved in any sentence-level unification process or this unification process is not necessarily active for passive listening, for instance because a good-enough processing strategy (Ferreira et al. 2002) does not require a full compositional analysis.

**Sentences with higher demands on syntactic or semantic processing.** So far, we have identified a set of candidate regions that may be involved in sentence-level processing. However, the contrast of sentences compared with nonsentential stimuli neither excludes the involvement of these regions in lexical processes nor allows for a distinction between semantic and syntactic unification. This limitation is not present for studies comparing syntactically or semantically more demanding sentences with simpler sentences. In these studies, the words used in both conditions are typically well-matched. A contribution of word-level differences to the resulting brain activation can hence be excluded. Despite that syntactic complexity may always have repercussions for the construction of sentence meaning, semantic and syntactic processes can, in principle, be independently taxed in this type of design. **Figure 1b** shows the results of 57 studies comparing syntactically demanding sentences with less-demanding control sentences and 51 studies comparing semantically demanding sentences with less-demanding control sentences. Higher syntactic processing demands most reliably activate the more dorsal parts of posterior LIFG (BA 44/45), the right posterior IFG and the left posterior STG and MTG. In addition, the left precuneus, the left inferior parietal lobule, and the right posterior MTG all activated reliably. Higher semantic processing demands most reliably activate all parts of posterior LIFG (but BA 45/47 are reported twice as often as is BA 44; see **Supplemental Figure 5**, **Supplemental Table 4**), the right posterior IFG, and the left middle and posterior MTG. In addition, the data indicate a reliable activation of the medial prefrontal cortex that is not seen for higher syntactic processing demands and demonstrate activations of the left anterior insula, angular gyrus, and the posterior ITG.

The results of 16 studies directly comparing sentences with high syntactic and high semantic processing demands (**Figure 1c**, **Supplemental Figure 6**) confirm that the medial prefrontal cortex is important for processing sentences with high semantic processing demands. Direct comparisons also demonstrate a syntactic/semantic gradient in the LIFG: a reliably stronger activation of BA 44 is seen for syntactically, compared with semantically, demanding sentences; a reliably stronger activation of BA 45/47 is observed for semantically, compared with syntactically, demanding sentences.

In sum, compared with studies contrasting relatively undemanding sentences with nonsentential control conditions, studies contrasting higher with lower demands on syntactic or semantic sentence-level processing have found that IFG and some additional regions activate reliably. However, they have found no reliable activation of the anterior temporal lobe, despite some claims that it might be involved in semantic and syntactic combinatorial processing (Hickok & Poeppel 2007, Friederici 2012). We now consider the different kinds of experimental manipulations that induced increased processing demands to determine in which way they contributed to the observed overall results.

**Violations, ambiguity, and complexity.** Studies comparing sentences with syntactic violations (mostly agreement violations and phrase-structure/word-category violations) with correct



sentences have most reliably found BA 44/45 activation (**Supplemental Figure 7**). Studies comparing sentences containing semantic violations with correct sentences have most reliably found activation of all parts of the left posterior IFG; activation of BA 45/47 was again reported more often than was activation of BA 44. Both semantic and syntactic violations generally activate the posterior temporal cortex less frequently than do demanding sentences. Within semantic violations, we also compared violations of semantic selection restrictions (e.g., “Dutch trains are sour”/“My mother ironed a kiss”) with violations of world knowledge (e.g., “Dutch trains are white”/“The woman painted the insect”; examples taken from Hagoort et al. 2004 and Kuperberg et al. 2000). Both types of semantic violation activate BA 45/47 (**Supplemental Figure 8**). World knowledge violations also seem to activate widespread medial brain structures.

**Supplemental Figure 9** shows the reliably activated regions for sentences containing local syntactic ambiguities (mostly word-class ambiguities, e.g., “He noticed that landing planes frightens some new pilots”) or semantic ambiguities (“The reporter commented that modern compounds react unpredictably”; examples from Rodd et al. 2010). Both types of ambiguities activate the posterior IFG bilaterally and the left posterior MTG. For syntactic ambiguities, activation in the left posterior IFG is confined to BA 44. Semantic ambiguities activate the left posterior inferior medial temporal lobe.

Sixty-three studies increased the degree of syntactic or semantic complexity using means other than violations or ambiguities. The majority of studies on syntactic complexity compared sentences containing complex relative clauses with simpler relative clauses. The main manipulation in the remaining studies was the use of noncanonical word order. Our criterion for studies inducing semantic complexity was a comparison of a condition in which understanding the meaning of the sentence required some additional effort compared with that required for syntactically identical control sentences. In most of the studies this goal was achieved by comparing sentences containing a metaphoric meaning (e.g., “A sailboat is a floating leaf”; example from Diaz & Hogstrom 2011) with sentences containing a literal meaning. Whereas a metaphor can be understood without knowing the context of the utterance or the speaker, the same is not true for a different kind of nonliteral sentence. To understand that ironic/sarcastic sentences or indirect replies/requests go beyond a literal interpretation of the sentence requires that a listener assesses the situation and the speaker’s intention (see below).

Both syntactic and semantic complexity reliably induce stronger activation of the posterior IFG bilaterally and the left mid and posterior MTG (see **Supplemental Figure 10**). Left posterior IFG activation again shows a gradient with activation of BA 44 for syntactic but not semantic complexity and shows activation of BA 47 for semantic but not syntactic complexity. The posterior STG may selectively be recruited for syntactic complexity. Conversely, semantic complexity induces medial prefrontal activations that are not reliably seen for syntactic complexity manipulations.

Separate analyses of the two main kinds of syntactic complexity studied by investigators (**Supplemental Figure 11**) yielded results that were similar to the overall activation patterns induced by syntactic complexity; therefore, the mechanism that drives these activations seems to be shared by noncanonical word orders and relative clause complexity. Separate analyses of different kinds of semantic complexity, however, yielded differential activation patterns (**Supplemental Figure 12**). Sentences with metaphoric meaning contributed most to the overall activation of BA 45/47 and left posterior MTG. This result replicates the findings of a recent voxel-based meta-analysis on metaphor processing (Bohrn et al. 2012; see contrast “metaphor > literal” in their table 3). A few studies also reported activations of BA 47 and left MTG by comparing literal sentences inducing additional semantic operations (metonymy, coercion, establishment of a causal relationship with preceding context) with literal sentences without such operations. By contrast, sentences that required the listener to assess the speaker’s intentions did not reliably

activate BA 45 or the left posterior temporal lobe. These kinds of sentences most frequently activated the medial prefrontal cortex (also reliably reported for metaphoric sentences but in a relatively smaller number of studies) and also the right temporoparietal cortex (mainly observed in studies using indirect utterances).

## Summary and Discussion

Our meta-analysis comparing reliable activations for the processing of various syntactically and semantically demanding sentences yielded several important results. The most robust result is a distinctive activation pattern in the posterior LIFG; syntactic demands activated more dorsal parts (BA 44/45) and semantic demands activated more ventral parts (BA 45/47) across all kinds of increased processing demands (violations, ambiguity, complexity) and in studies performing direct comparisons of high syntactic and semantic processing demands (see **Figure 2a**). This result indicates that syntactic unification cannot simply be reduced to semantic unification. In particular, BA 44 activation is clearly driven more strongly by syntactic than by semantic demands, suggesting that this region contains neuronal populations involved in syntactic operations as such or that the semantic consequences of syntactic demands (difficulty of thematic role assignment) are processed by neuronal populations that differ from those processing other kinds of semantic unification.

A novel observation is that the dorsal/ventral gradient observed in the left posterior IFG seems to be mirrored in the left posterior temporal lobe. Higher syntactic demands reliably activate the STG and MTG, and higher semantic demands reliably activate the MTG and ITG.

To confirm these gradients, we conducted a spatially more fine-grained analysis on a subset of 28 studies reporting Talairach or MNI coordinates of activation foci in the left posterior temporal cortex. Whereas the mean locations of the activations reported for syntactically (mean  $y = -45.0$ ,  $SD = 7.7$ ) and semantically (mean  $y = -46.5$ ,  $SD = 5.9$ ) demanding sentences did not differ significantly in the rostral/caudal dimension, the mean location of activation foci for semantically demanding sentences was significantly more ventral (middle temporal gyrus, mean  $z = 0.9$ ,  $SD = 8.6$ ) than the mean location of activation foci for syntactically demanding sentences (superior temporal sulcus, mean  $z = 10.2$ ,  $SD = 5.7$ ; see **Figure 2b** and **Supplemental Figure 13**). Activations in the left posterior inferior frontal gyrus reported for the same contrasts in this set of studies confirmed a significantly more ventral and rostral mean location of activation foci for semantically demanding sentences (BA 45, mean  $y = 22.2$ ,  $SD y = 6.3$ , mean  $z = 4.2$ ,  $SD z = 10.8$ ) as compared with syntactically demanding sentences (BA 44, mean  $y = 14.8$ ,  $SD y = 8.0$ , mean  $z = 15.0$ ,  $SD z = 5.6$ ).

These corresponding gradients in posterior frontal and temporal regions are remarkably consistent with a functional connectivity pattern found by Xiang et al. (2010), which links seed regions in BA 44, BA 45, and BA 45/47 to left posterior STG, MTG, and ITG, respectively. This finding

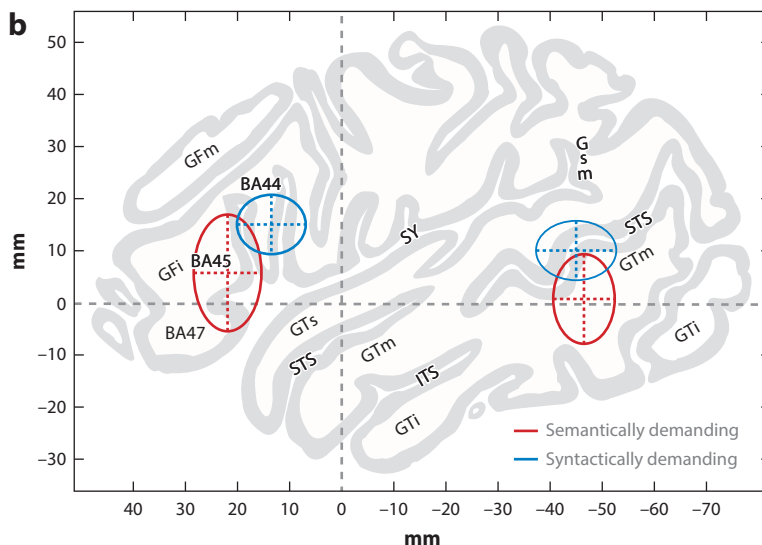
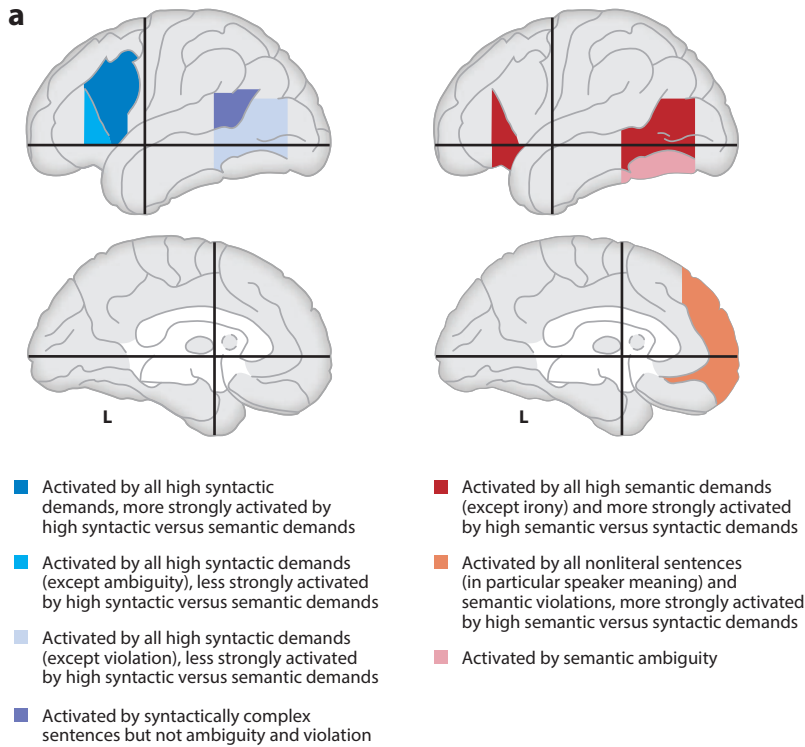
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### Figure 2

(a) Summary of activation patterns for sentences with high syntactic or semantic processing demands compared with simpler sentences. (b) Syntactic/semantic gradients in left inferior frontal and posterior temporal cortex based on 28 studies reporting posterior temporal cortex activation for syntactically demanding or semantically demanding sentences compared with less demanding sentences (see **Supplemental Figure 13** for details). The centers represent the mean coordinates of the local maxima, and the radii represent the standard deviations of the distance between the local maxima and their means. Abbreviations: GFm, GF<sub>i</sub>, middle and inferior frontal gyri; BA, Brodmann area; GTs, GT<sub>m</sub>, GT<sub>i</sub>, superior, middle, and inferior temporal gyri; STS, ITS, superior and inferior temporal sulci; Gsm, supramarginal gyrus.

clearly supports the idea that sentence-level unification relies on the coactivation of neuronal populations in a network of posterior frontal and temporal regions, with a similar functional gradient in both parts of the brain.

Another important observation is the degree to which posterior temporal lobe activation differs between violations and other kinds of higher processing demands. Syntactic violations do



not seem to elicit posterior temporal lobe activations reliably, and reports about such activations are relatively infrequent for semantic violations. A plausible account for this dissociation may be based on a distinction between Broca's area subserving sentence-level compositional processes and the posterior temporal lobe subserving the retrieval of lexical syntactic and semantic information (Hagoort 2005). Violation paradigms may tap relatively specifically into a unification stage, whereas ambiguities and complexity manipulations typically also require lexical syntactic and semantic specifications to be retrieved. In sentences with unambiguous violations ("The blouse was on ironed"/"The thunderstorm was ironed"; examples from Friederici et al. 2003), no alternative lexical specifications can be constructed to help remedy the problem; however, not only for ambiguities ("he noticed that landing planes frightens some new pilots"/"the reporter commented that modern compounds react unpredictably"), but also for many kinds of syntactic and semantic complexities, alternative lexical specifications may solve the comprehension problem.

Finally, our results suggest that the neuronal substrate underlying the processing of ironic and indirect utterances differs from that activated in other kinds of high-demand sentences. Such utterances do not seem to induce reliable activation of Broca's area (BA 44/45) and Wernicke's area but, instead, show the most reliable activation in the medial prefrontal cortex and the right temporoparietal cortex. The difficulty in processing these sentences does not seem to be in decoding the meaning of the sentence but in a different aspect of comprehension to which we now turn in more detail.

## BEYOND CORE AREAS FOR LANGUAGE: THE CASE OF NEUROPRAGMATICS

In many instances, linguistic expressions are underdetermined with respect to the meaning they convey. What is said and what is understood are often not the same. Communication goes further than the exchange of explicit propositions. In essence, the goal of the speaker is either to change the listener's mind or to commit the addressee to the execution of certain actions, such as closing the window in reply to the statement, "It is cold here." A theory of speech acts is needed to understand how we move from coded meaning to inferred speaker meaning (cf. Grice 1989, Levinson 2013, Hagoort & Levinson 2015). The steps required to progress from coded meaning to speaker meaning involve additional neuronal systems, as recent studies have shown.

In a study on conversational implicatures and indirect requests, for example, Bašnáková and coworkers (2013) contrasted direct and indirect replies, two classes of utterances whose speaker meanings are either very similar to, or markedly different from, their coded meaning. In this study, participants listened to natural spoken dialogue in which the final utterance, e.g., "It is hard to give a good presentation," had different meanings depending on the dialogue context and the immediately preceding question. This final utterance either served as a direct reply (to the question "How hard is it to give a good presentation?") or as an indirect reply (to "Did you like my presentation?"). In the indirect reply condition, activations were observed in the medial prefrontal cortex (mPFC) extending into the right anterior part of the supplementary motor area (SMA), and in the right temporoparietal junction (TPJ). The data thus demonstrated a pattern typical for tasks that involve mentalizing based on a theory of mind (ToM) (Amodio & Frith 2006, Mitchell et al. 2006, Saxe et al. 2006). Although the exact role of all the individual ToM regions is not yet clearly established, both mPFC and right TPJ constitute core regions in ToM tasks (Carrington & Bailey 2009). The most specific hypothesis about the role of the posterior part of right TPJ (Mars et al. 2012) in the mentalizing network is that it is implicated in mental state reasoning, i.e., thinking about other people's beliefs, emotions, and desires (Saxe 2010).

mPFC activation in the Bašnáková et al. study (2013) was found in parts of the mPFC associated with complex sociocognitive processes such as mentalizing or thinking about the intentions of others (such as communicative intentions, right anterior mPFC) or about oneself (right posterior mPFC). The involvement of these regions is also consistently observed in discourse comprehension (e.g., Mason & Just 2009, Mar 2011). This finding might come as no surprise because the motivations, goals, and desires of fictional characters are likely accessed in a manner similar to that of real-life protagonists (Mar & Oatley 2008). In fact, an influential model from the discourse-processing literature (Mason & Just 2009) ascribes to the dorsomedial part of the frontal cortex and the right TPJ a functional role as a protagonist perspective network, which generates expectations about how the protagonists of stories will act on the basis of understanding their intentions.

Although the literature on the neuropragmatics of language is still limited, studies have, with remarkable consistency, demonstrated that understanding the communicative intent of an utterance requires mentalizing. Because the linguistic code underdetermines speaker meaning, the ToM network needs to be invoked to progress from coded meaning to speaker meaning. Despite the popular view that the mirror neuron system (MNS) is sufficient for action understanding (Rizzolatti & Sinigaglia 2010), the MNS does not provide the crucial neural infrastructure for inferring speaker meaning. In addition to core areas for retrieving lexical information from memory and unifying the lexical building blocks to produce and understand multiword utterances, other brain networks are needed to realize language-driven communication to its full extent (for a more extended review of studies on neuropragmatics, see Hagoort & Levinson 2015).

## CONCLUSION

We have outlined the contours of the neurobiological infrastructure that supports language processing beyond the comprehension or production of single words. In this context, research has established substantial deviations of the classical WLG model, with its focus on single-word processing. Three major deviations are worth highlighting: (a) Although not discussed in detail here (for more extended discussions, see Hagoort 2013, Amunts & Catani 2015) the connectivity of the language cortex in left perisylvian regions is much more extended than was proposed in the classical model and is certainly not restricted to the arcuate fasciculus; (b) the distribution of labor between the core regions in left perisylvian cortex is fundamentally different than that proposed in the classical model (in contrast to the claims of the WGL model, there is strong evidence for shared circuitry for core aspects of sentence-level language production and comprehension); and (c) the operation of language to its full extent requires a much more extended network than what the classical model assumed. The basic principle of brain organization for higher cognitive functions proposes that these functions are based on the interaction between numerous neuronal circuits and brain regions that support the various contributing functional components. These circuits are not necessarily specialized for language but nevertheless need to be recruited for the sake of successful language processing. One example is the ToM network, which seems critical for speakers to construct utterances with knowledge of the listener in mind and for listeners to progress from coded meaning to speaker meaning. As described above in the section on the temporal profile of unification, the network of language areas in the brain is highly dynamic despite the static nature suggested by pictures of the neuronal infrastructure for language. The specific contribution that any area makes to information processing depends on the input it receives at a certain time step, which itself depends on the computational environment in which it is embedded. Moreover, a large meta-analysis has at last confirmed a clear division of labor in both frontal and temporal areas for syntactic and semantic unification.

## DISCLOSURE STATEMENT

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