Semantic Unification

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Abstract

Language and communication are about the exchange of meaning. A key feature of understanding and producing language is the construction of complex meaning from more elementary semantic building blocks. The functional characteristics of this semantic unification process are revealed by studies using event related brain potentials. These studies have found that word meaning is assembled into compound meaning in not more than 500 ms. World knowledge, information about the speaker, co-occurring visual input and discourse all have an immediate impact on semantic unification, and trigger similar electrophysiological responses as sentence-internal semantic information. Neuroimaging studies show that 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 unification.

Ultimately, language is the vehicle for the exchange of meaning between speaker and listener, between writer and reader. The unique feature of this vehicle is that it enables the assembly of complex expressions from simpler ones. The cognitive architecture necessary to realize this expressive power is tripartite in nature, with levels of form (sound, graphemes, manual gestures in sign language), syntax and meaning as the core components of our language faculty (Jackendoff, 1999, 2002; Levelt, 1999). The principle of compositionality is often invoked to characterize the expressive power of language at the level of meaning. The most strict account of compositionality states that the meaning of an expression is a function of the meanings of its parts and the way they are syntactically combined (Fodor & Lepore, 2002; Heim & Kratzer, 1998; Partee, 1984). In this account, complex meanings are assembled bottom-up from the meanings of the lexical building blocks via the combinatorial machinery of syntax. This is sometimes referred to as simple composition (Jackendoff, 1997). That this is not without problems, can be seen in adjective-noun constructions such as 'flat tyre', 'flat beer', 'flat note', etc. (Keenan, 1979). In all these cases, the meaning of 'flat' is quite different and strongly context dependent. For this and other reasons, simple composition seems not to hold across all possible expressions in the language (for a discussion of this and other issues related to compositionality, see Baggio, van Lambalgen, & Hagoort, in press). One of the challenges for a cognitive neuroscience of language is to account for the functional and neuroanatomical underpinnings of on-line meaning composition.

In linking the requirements of the language system as instantiated in the finite and real-time machinery of the human brain to the broader domain of cognitive neuroscience, three functional components are considered 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. The focus of this chapter is on the unification component.

Classically, psycholinguistic studies of unification have focused on syntactic analysis. However, as we saw above, unification operations take place not only at the syntactic processing level. Combinatoriality 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 the remainder, we will 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, as is clear from the adjective-noun examples given above. In the interaction with the preceding sentence or discourse context, the appropriate meaning is selected or constructed, so that a coherent interpretation results.

Hereafter we will first discuss the functional characteristics of semantic unification as revealed by ERP and MEG studies. Next, results from fMRI studies will be discussed to identify the neural networks of semantic unification. In the remainder we will use the terms unification and integration interchangeably. However, in the last paragraph we propose to use the terms integration and unification for two different ways of combining information.

1 Functional characteristics of semantic unification

Insights into the functional characteristics of semantic unification have been especially gained through a series of ERP studies. Most studies on semantic unification exploit the characteristics of the so-called N400 component in the ERP waveform. Kutas and Hillyard (1980) were the first to observe this negative-going potential with an onset at about 250 ms and a peak around 400 ms (hence the N400), whose amplitude was increased when the semantics of the eliciting word (i.c. *socks*) mismatched with the semantics of the sentence context, as in "He spread his warm bread with socks".

Since its original discovery in 1980, much has been learned about the processing nature of the N400 (for extensive overviews, see Kutas & Federmeier, 2000; Kutas, Van Petten & Kluender 2006; Osterhout, Kim & Kuperberg 2007). In particular, as Kutas and Hillyard (1984) and many others have observed, the N400 effect does not depend on a semantic violation. For example, subtle differences in semantic expectancy, as between *mouth* and *pocket* in the sentence context "Jenny put the sweet in her mouth/pocket after the lesson", can also modulate the N400 amplitude (Hagoort & Brown 1994). Specifically, as the degree of semantic fit between a word and its context increases, the amplitude of the N400 decreases. This general relation between individual word meanings and the semantics of the context is independent of type of context. That is, it is found for a single word context (Holcomb, 1993), a sentence context (Kutas & Hillyared, 1980, 1984), and for larger discourses (van Berkum et al., 1999). Because of such subtle modulations, the N400 is generally taken to reflect processes involved in the integration of the meaning of a word into the overall semantic representation constructed for the preceding language input (Brown & Hagoort 1993; Osterhout & Holcomb

1992). However, different views exist as to what brings about the N400 integration effect. Federmeier and Kutas (1999; Kutas & Federmeier, 2000) proposed that in addition to its sensitivity to context, the N400 is also sensitive to the ease of accessing information from semantic memory. As such, the N400 can be seen to reflect the organization of (lexical) meaning in semantic memory. According to this view, the N400 amplitude is modulated by the degree to which the context contains retrieval cues for accessing or selecting the stored representation for a particular word meaning. Recent evidence in favour of this position was obtained in a study by DeLong et al. (2005). These authors found an N400 effect to an indefinite article (*an* vs. *a*) that excluded the semantically expected continuation, such as in "the day was breezy so the boy went out to fly an ..", where *kite* would be the contextually expected noun. This result suggests a contextual pre-activation of the target word. However, other recent evidence is more compatible with a unification account. Li et al. (2008) investigated the neurophysiological response to manipulations of information structure. An important distinction at the level of semantic/conceptual structure is that between conceptual content and information structure. The latter refers to the division of the content of a sentence into information that is in the foreground or in the background (topic/focus; given/new). In many languages new information is accented, whereas old information is de-accented. Li et al. found that in Chinese the N400 to new, accented information was larger than the N400 to new, de-accented information, despite the fact that the accentuation was contextually appropriate, whereas the absence of an accent was not. The authors argue that this result is best explained by the recruitment of additional unification resources for information that is marked as more salient by accentuation.

One way to reconcile these different accounts of the N400 is by reference to a different role for the left and right hemisphere (Kutas & Federmeier, 2000, Federmeier, 2007). Federmeier and Kutas (1999) did a visual half field study in which participants read sentences such as "Every morning John makes a glass of freshly squeezed juice. He keeps his refrigerator stocked with (oranges/apples/carrots)". In this context, 'oranges' is the expected continuation, 'apples' is a violation but within the correct semantic category, and 'carrots' is a violation that crosses the category boundary. The LVF/RH results showed a smaller N400 to oranges than to both within and across category violations, but no N400 difference for the two types of violation. In contrast, for the RVF/LH not only a reduced N400 was obtained for the predicted word ('orange'), but also in part for the within category violation ('apple') (**see Figure 1**). This latter result can be explained as a consequence of a contextual prediction for the target concept. Due to the organization of semantic memory, the within-category non-target ('apple') gets activated to some degree as well, resulting in a partially reduced N400. Predictive semantic processing might thus be a left hemisphere processing mechanism, while the right hemisphere contribution is presumably strictly post-lexical in nature, only contributing to the integration of the word meaning from a lexical item that received bottom-up support on the basis of visual or acoustic input.

In recent years, the N400 and other language-relevant ERP effects have been exploited to test more specific ideas about the functional characteristics of semantic unification. These include the contribution of world knowledge, the processing of silent meaning, the integration of pragmatic information, and the syntax-semantics interface. We will discuss briefly each of these theory-driven issues.

1.1 World knowledge

At least since Frege (1892, see Seuren 1998), theories of meaning make a distinction between the semantics of an expression, and its truth-value in relation to our mental representation of the state of affairs in the world

(Jackendoff 2002). For instance, the sentence "Bill Clinton is the 43rd president of the USA" has a coherent semantic interpretation, but contains a proposition that is false in the light of our knowledge that George W. Bush is the 43rd president. The situation is different for the sentence "The presidential helicopter is divorced." Under default interpretation conditions, this sentence has no coherent semantic interpretation, since the predicate is-divorced requires an animate argument. The difference between these two sentences points to the distinction that can be made between facts of the world ('world knowledge'), and facts of the words of our language, including their meaning ('linguistic knowledge'). Hagoort et al. (2004) performed a combined EEG/fMRI study that compared the unification of linguistic knowledge with the unification of world knowledge. While participants' brain activity was recorded, they read one of three versions of a sentence such as: "The Dutch trains are *yellow/white/sour* and very crowded." (critical words are in italics). It is a well-known fact among Dutch people that Dutch trains are yellow, and therefore the first version of this sentence is correctly understood as true. However, the linguistic meaning of the alternative color term *white* applies equally well to trains as the predicate *yellow*. It is world knowledge about trains in Holland that makes the second version of this sentence false. This is different for the third version, where (under standard interpretation conditions) the core semantic features of the predicate *sour* do not fit the semantic features of its argument *trains*.

Figure 2 presents an overview of the results. As expected, the classic N400 effect was obtained for the semantic violations. For the world knowledge violations, a clear N400 effect was observed as well. Crucially, this effect was identical in onset and peak latency, and very similar in amplitude and topographic distribution to the semantic N400 effect. This finding is strong empirical evidence that lexical-semantic knowledge and general world knowledge are both integrated in the same time frame during sentence interpretation. The results of this world-knowledge experiment provide further evidence against an account of unification in which first the meaning of a sentence is determined, and only then is its meaning verified in relation to our knowledge of the world. Semantic interpretation is not separate from its integration with nonlinguistic conceptual knowledge.

Further evidence in favour of an enriched composition account comes from a study on the integration of information about the speaker. In interpreting a speaker's utterance, we not only take the preceding utterances into consideration, but also our knowledge of the speaker. For instance, we might find it odd for a man, but not for a woman of a certain age to say: "I think I am pregnant". At some point during language comprehension, the listener combines the information that is represented in the content of a sentence with the information she has about the speaker. The question is, when exactly the pragmatic information about the speaker is having its impact on the unfolding interpretation of the utterance. This question was answered in a recent ERP study by Van Berkum et al., (2008). Participants listened to sentences, some of which contained a specific word at which the message content became at odds with inferences about the speaker's sex, age, and social status, as inferred from the speaker's voice.

If voice-based inferences about the speaker are recruited by the same early unification process that combines word meanings, then speaker inconsistencies and semantic anomalies should elicit the same N400 effect. This was indeed observed. Reliable effects of speaker inconsistency were already found in the 200-300 ms latency range after word onset. The same latency effect was obtained for the straightforward semantic anomalies. These findings therefore demonstrate that sense making depends on the pragmatics of the communicative situation right from the start.

As for compositionality, the results of the studies just reviewed may mean two things, depending on one's views on the lexicon. One possibility is that the lexicon includes declarative memory in its entirety, and then simple composition seems enough to account for the similarity between the N400 effects. Alternatively, the lexicon includes invariant (i.e. linguistic) meanings only, and then enriched composition – the thesis that the lexicon is not the only source of semantic content – seems necessary to explain the observed N400 effects (Baggio et al., in press).

1.2 Event knowledge and discourse models

Unification of lexical representations ultimately results in a discourse model; that is, a representation making what is given as input true whenever possible (recall the Dutch trains examples). Events offer a vantage point for investigating the properties of discourse models, because natural languages have very sophisticated devices for characterizing time and causation. One of these devices is aspect. This is the linguistic marking of the internal profile of events. Ferretti et al. (2007) found that readers have least difficulty integrating locative nouns when the aspect of the main verb is imperfective and the denoted location is a prototypical one given the verb's semantics. In sentences with an imperfective, such as "The diver was snorkeling in the ocean/pond", a larger N400 was evoked by *pond* compared to *ocean*. This N400 effect was reduced if the aspect was perfective, as in "The diver had snorkeled in the ocean/pond". Describing an event as ongoing using the imperfective aspect, leads readers to construct a situation model in which locations and other dimensions of the action become relevant, while such dimensions are ignored if the action is viewed perfectively.

The imperfective leads also to expectations concerning the outcome of the event described. Baggio et al. (2008) investigated whether, in sentences like "The girl was writing a letter when her friend spilled coffee on the tablecloth/paper", the goal state (a complete letter) was represented on-line during the unification process. If the goal is predicted to occur whenever the imperfective is used, a difference should be observed at the word *paper* compared to *tablecloth*. Spilling coffee on the paper implies that the goal state was not attained, and forces the system to revise the earlier commitment to the event's completion (Baggio & van Lambalgen 2007). Spilling coffee on the tablecloth, however, does not have this implication. *Paper* did indeed result in a larger sustained anterior negativity (SAN) compared to *tablecloth*, and the effect was correlated with the frequency with which participants concluded that the event was not completed (**see Figure 3**). These results again suggest that semantic processing is not bound to asserted content, but can include inferences anticipating the outcome of actions and events, as well as other inferences invalidating previously drawn conclusions. In this sense, unification can be described as a defeasible process: discourse models built up incrementally at any one stage, may have to be revised when additional information becomes available, as when the word *paper* is encountered in the example above (cf. Carreiras et al. 1996; Sturt, 2007).

1.3 Fictional discourse and silent meaning

Simple composition implies that unification preserves the semantic identity of the constituent expressions. However, experimental research suggests that discourse may override even such core features of word semantics as animacy. Nieuwland and van Berkum (2006) showed that sentences which on their own make sense, like "The peanut was salted", appear anomalous if they are embedded in a context in which the inanimate subject (the peanut) is attributed animate features. In a narrative in which the peanut danced and sang, because it fell in love with an almond it had met, the final word in "The peanut was salted" resulted in a larger N400 compared to "The peanut was in love" (**see Figure 4**). This is taken to show that discourse can override seemingly context-invariant semantic features of words.

Another interesting phenomenon is that of silent meaning; that is meaning not expressed in the syntax and phonology of an expression. A number of linguistic devices are available to speakers and hearers that allow efficient communication of meaning beyond what is explicitly asserted. Among these are coercing expressions, functioning as a shorthand for lengthier definite descriptions as in the classic examples "The ham sandwich in the corner wants some more coffee", where *ham sandwich* in fact refers to the person who ordered one, and "Plato is on the top shelf next to Russell", where *Plato* and *Russell* refer to copies of the works of the two philosophers. More extreme forms of coercion are possible, as in "Fishing the edges dry", where *dry* is a condensed expression for the phrase *using a dry fly*, or in resultative constructions like "Hammering the metal flat", where *flat* denotes the final state of the metal after hammering. What all these widely-used expression types have in common is a silent semantic element, which has to be recovered (sometimes obligatorily) to make full sense of the sentence. Semantic processing might be taxed during such recovery process, and that is indeed what was found experimentally. Complement coercing sentences like "The journalist began the article", which presumably means that she began writing or typing the article, are more difficult to process than sentences in which the activity is part of the asserted content like "The journalist wrote the article". The processing costs of complement coercion have been established using reading times (Mc Elree et al., 2001), eye tracking (Traxler et al., 2002, 2005) and MEG (Pylkkänen & McElree, 2007). Pylkkänen and McElree found an MEG response that was located in ventromedial prefrontal cortex to coerced sentences, which was different from the M350, the magnetic correlate of the N400. Semantic processing beyond the single word level is therefore not restricted to processing asserted content as delivered by the input, but is crucially engaged in recovering silent meaning in presuppositions, implicatures, coercions, and so on. Crucially, recovered meanings are triggered by expressions that are given as input, but are themselves phonologically and syntactically silent, which shows that semantics is relatively independent from the two other components of the language system. This 'autonomy of semantics' is at odds with the syntax-semantics homomorphism postulated by formal semanticists (Montague 1970, Partee et al. 1990) as well as with the 'interface uniformity' upon which generative grammar is built (Culicover and Jackendoff, 2005).

1.4 Unification and the syntax-semantics interface

A language-relevant ERP effect that has been related to syntactic processing is a positivity, nowadays referred to as P600 or as P600/SPS (Coulson et al. 1998; Hagoort et al. 1999; Osterhout et al. 1997). The P600 is the syntactic equivalent of the N400 effect. One of the antecedent conditions of P600 effects is a violation of a syntactic constraint. The relation between N400 and the P600 effects might provide insights into the interplay between semantic and syntactic unification. Modulations of the P600 have been observed not only to syntactic violations, syntactic ambiguities and syntactic complexity, but also to breakdowns of normal operations at the syntax-semantics interface (for a review, see Kuperberg, 2007). For example, Kim and Osterhout (2005) reported larger P600s evoked by *devouring* in "The hearty meal was devouring …", compared to either "The hearty meal was devoured …" of "The hungry boys were devouring …"; this despite the fact that the sentence is syntactically well-formed **(see Figure 5)**. The semantics of *meal* and *devour* suggest a plausible thematic role assignment to *meal*: a Theme instead of an Agent as the syntax implies. In this case, semantic plausibility overrides syntactic constraints, and the verb *devouring* is presumably perceived as a morpho-syntactic violation indexed by the P600. Conflicts between syntactic and semantic constraints might result in N400 or P600 effects depending on whether, respectively, the semantic or the syntactic constraints are the weakest. In cases where the input is anomalous because of a conflict between semantic and syntactic cues, the *modus operandi* of the system seems to obey a 'loser takes all' principle. That is, if the semantic cues are stronger than the syntactic cues, the effect will appear at the level of syntactic unification (P600). Kuperberg (2007) argues that there are at least two neural routes subserving language comprehension: (i) a semantic, memory-based stream, which provides elementary meanings as well as conceptual, categorical and thematic relations between them; (ii) a combinatorial stream which provides analyses based on morpho-syntactic constraints and thematic roles as given in the input. The P600 reported by Kim and Osterhout (2005), for example, might be taken to suggest that semantic associations between words are the strongest constraints, for instance because in this case they are taken into account earlier than the syntactic cues.

1.5 Conclusion

In general, ERP research on semantic processing has found that word meaning is very rapidly assembled into compound meaning. This holds for individual word meanings in the context of single words, sentences or discourse. But it also holds for meaning that is extracted from pictures, co-speech gestures, or stereotypes inferred from speaker characteristics (Willems et al., 2007; Willems et al., 2008; Van Berkum et al., 2008). The effects of semantioc processing are most often observed as modulations of the N40 amplitude. The topographic distribution of the N400 differs slightly for different stimulus types. It is more evenly distributed for auditory than for the visual N400. Pictures and co-speech gestures elicit a more frontal N400 than sentences without concomitant non-linguistic information. This suggests that the set of neural generators contributing to the scalp recorded N400 is not fully overlapping for the different types of meaningful stimuli. This is consistent with the results from fMRI studies, showing both overlapping and distinct activations in connection to the various types of meaningful input (see below). Intracranial recordings and MEG studies indicate that the scalp-recorded N400 is caused by coordinated activity in a number of different brain areas, including the anterior inferotemporal cortex (McCarthy et al., 1995), the superior temporal cortex (Dale et al., 2000; Helenius et al., 1998; Halgren et al., 2002), and the left inferior frontal cortex (Halgren et al., 1994, 2002; Guillem et al., 1999). Other ERP effects (e.g., anterior negativities) have also been observed to aspects of post-lexical semantic processing. How they differ from the N400 effects in their functional characterization is an issue for further research.

2. The semantic unification network

In recent years, a series of fMRI studies aimed at identifying the semantic unification network. These studies either compared sentences containing semantic/pragmatic anomalies with their correct counterparts (Hagoort et al., 2004; Newman et al., 2001; Kuperberg et al., 2000, 2003, 2008; Ni et al., 2000; Baumgaertner et al., 2002; Kiehl et al., 2002; Friederici et al., 2003; Ruschemeyer et al., 2006), or compared sentences with and without semantic ambiguities (Hoenig & Scheef, 2005; Rodd et al., 2005; Zempleni et al., 2007; Davis 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 (see **Figure 6** for an overview), as well as left inferior parietal cortex. For instance, Rodd and colleagues 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.

In short, the semantic unification network seems to include at least LIFC, left superior/middle temporal cortex, and the (left) inferior parietal cortex. To some degree, the right hemisphere homologues of these areas are also found to be activated (see Figure 6). Below we will discuss the possible contributions of these regions to semantic unification.

2.1 The multimodal nature of semantic unification

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 et al., 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 et al., 2008 for a similar finding with pictures of objects). Interestingly, the activation of the left posterior STS 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 et al., 2007). This suggests that activation increases in left posterior temporal cortex are triggered most strongly by processes involving the retrieval of lexical-semantic 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.

2.2 Semantic unification beyond the sentence level

Recently, a few studies have set out to investigate the neural networks involved in semantic processing at the level of multi-sentence utterances, such as short stories. Besides the network that is also activated to semantic unification at the sentence level, story comprehension involves activation of dorso-medial prefrontal cortex and, presumably, right inferior frontal cortex. In a recent meta-analysis, Ferstl and colleagues report the consistent involvement of medial prefrontal cortex, left STS/MTG and LIFC when participants process coherent text as compared to sentences that do not form a coherent story or as compared to word lists (Ferstl et al., 2008). In a variant of this line of research, Kuperberg et al. (2006) presented participants with sentence quartets in which the relation of the last sentence to the previous story context was manipulated. The less related sentences required an extra causal inference in order to make sense of the story. It was found that less related sentences (which evoked more inferencing) led to stronger activations in left and right IFC, left MTG, left middle fontal gyrus and bilateral medial prefrontal cortex (Kuperberg et al., 2006) (see Hasson et al., 2007 for a related result). These and other studies (e.g. St George et al., 1999; Xu et al., 2005; Sieborger et al., 2007) suggest that LIFC and left superior/middle temporal cortex are also important for unification of information beyond the sentence level. It is interesting to note that the medial prefrontal cortex, which is found activated for discourse but not for sentence-level processing, has been implicated in so-called mentalising tasks, requiring the observer to take the perspective of someone else (Buckner, Andrews-Hanna, & Schacter, 2008; Frith and Frith, 2006). According to Mason and Just, this domain-general area is recruited in discourse processing for the sake of interpreting a protagonist's or agent's perspective (Mason and Just, 2006). In addition, right hemisphere regions are sometimes but not consistently reported in the context of discourse processing (Maguire et al., 1999; St George et al., 1999; Ferstl et al., 2008; Martin-Loeches et al., 2008) (see Ferstl et al., 2008; Mason & Just, 2006 for extensive reviews). Some studies find that the temporal poles may be related to successful integration during story comprehension (Fletcher et al., 1995; Maguire et al., 1999). The studies that report these activations are mostly done using PET. It is hard to assess the consistency of temporal pole activation during story/text comprehension because of the susceptibility to artifacts that these regions often suffer from in fMRI studies (but see Xu et al., 2005; Ferstl et al., 2008).

2.3 Controlled processing and selection accounts for LIFC

Although LIFC (including Broca's area) has traditionally been construed as a language area, there is a wealth of recent neuroimaging data suggesting that its role extends beyond the language domain. Several authors have therefore argued that LIFC function is best characterized as 'controlled retrieval' or '(semantic) selection' (Thompson-Schill et al., 1997; Wagner et al., 2001; Badre et al., 2005; Gold et al., 2005; Moss et al., 2005; Thompson-Schill et al., 2005). For instance, Thompson-Schill and colleagues showed that LIFC was more strongly activated in a verb generation task when the noun which served as the cue allowed for many different verb responses, as opposed to nouns which are reliably related to only one or a few verbs (Thompson-Schill et al., 1997). In response to the noun cue 'scissors', for example, most participants generate the verb 'to cut', whereas the noun 'wheel' triggers a more diverse set of responses. On the basis of these and other findings, it was argued that LIFC guides semantic selection among competing alternatives, with higher activation when there are more competitors.

How does the selection account of LIFC function relate to the unification account? As is discussed in more detail elsewhere, unification often implies selection (Hagoort, 2005). For instance, in the study by Rodd and colleagues described above, increased activation in LIFC is most likely due to increased selection demands in reaction to sentences with ambiguous words. Selection is often, but not always, a prerequiste for unification. Unification with or without selection is a core feature of language processing. During natural language comprehension information has to be kept in working memory for a certain period of time and incoming information has to be integrated and combined with previous information. The combinatorial nature of language necessitates that a representation is constructed on-line, without the availability of an existing representation of the utterance in long term memory. In addition, some information sources that are integrated with language do not have a stable representation in long-term memory such that they can be selected. For instance, there is no stable representation of the meaning of co-speech gestures, which are highly ambiguous outside of a language context. Still, in all these cases increased activation is observed in LIFC, such as when the integration load of information from co-speech gestures is high (Willems et al., 2007). Similarly, it is unlikely that integration of information about characteristics of the speaker as indicated by the acoustics of the voice (e.g. whether the speaker is male or female, child or adult) relies on selection. Nevertheless, increased activation levels are observed in LIFC when integrating speaker characteristics with the content of the message gets more difficult (Tesink et al., accepted). Therefore, unification is a more general account of LIFC function. It implies selection, but covers additional integration processes as well.

2.4 Integration versus unification

We have so far used the term unification to refer to the assembly of complex meaning. Although the term integration is often used as a synonym for unification, including by ourselves, we suggest that it is useful to make a functional distinction between the two. Semantic integration is at stake if different sources of information converge on a common memory representation. An example is the sound and the sight of an animal (e.g. a barking dog). The sight of a dog, the barking sound, and their combined occurrence most likely all activate a memory representation of 'dog' that has multimodal characteristics. Semantic unification, on the other hand, is always a constructive process in which a semantic representation is constructed that is not already available in memory. This distinction makes opposite predictions for the BOLD response. Semantic unification is always harder for semantic incongruities. These should result in a stronger BOLD response than semantically congruent items. In contrast, congruent input results in converging support for a pre-stored representation, which might thus be more strongly activated compared to a situation with incongruent input. Hence, in the case of integration the congruent condition will elicit a stronger BOLD response than the incongruent condition. A few studies on multimodal integration have indeed reported activation increases to matching stimulus combinations. For instance, Van Atteveldt and colleagues (2004) observed a higher activation level in left superior temporal cortex in response to a matching phoneme and letter combination (e.g. letter 'p' with phoneme [p]) as compared to a mismatching combination (e.g. letter 'k' with phoneme [p]) (see also Calvert et al., 2000 for the integration of lip movements and speech sounds). The same is true in the study by Beauchamp et al. (2004) who found higher activation in left posterior temporal cortex to the matching combination of a picture of an object and its sound versus an incongruent combination. In a recent paper, Hein et al. (2007) reported an interesting difference between inferior frontal cortex (IFC) and posterior temporal cortex. The IFC showed a stronger response to incongruent familiar animal sounds and images (e.g., a meowing dog) than to the familiar combination (a barking dog). This was however not observed in STG and pSTS. This region was found to be more strongly activated to highly familiar combinations of objects and sounds as compared to combinations of artificial objects and sounds. This result suggests a possible division of labor between inferior frontal and superior temporal areas, with a stronger contribution to integration for temporal cortex and a stronger role for the IFC in unification; i.e. in constructing a common representation that is not already available in long term memory.

However, as we have seen above, many studies on sentence processing have found increased activation in especially left superior/middle temporal cortex when the (semantic) unification load of a word increases given the preceding sentence context (e.g. Bookheimer, 2002; Friederici et al., 2003; Kuperberg et al., 2003; Hagoort et al., 2004; Rodd et al., 2005; Ruschemeyer et al., 2005; Davis et al., 2007; Willems et al., 2007; Willems et al., 2008). We propose that this results from signals from LIFC, indicating that in the service of unification lexical-semantic information needs to be maintained active longer, or needs to be reaccessed when unification load increases (cf Humphries et al., 2007). In this way, it is the dynamic interplay between LIFC and left superior/middle temporal cortex that is necessary for successful semantic unification.

3 Conclusion

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. 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 unification. In line with the MUC framework, semantic 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). A more precise account of the individual contributions of these core nodes in the unification network awaits further research.

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References

Badre, D., Poldrack, R.A., Pare-Blagoev, E.J., Insler, R.Z., and Wagner, A.D. (2005). Dissociable controlled retrieval and generalized selection mechanisms in ventrolateral prefrontal cortex. *Neuron*, *47*, 907-918.

Baggio, G., and van Lambalgen, M. (2007). The processing consequences of the imperfective paradox. *Journal of Semantics*, *24*, 307-330.

Baggio, G., Van Lambalgen, M., and Hagoort, P. (2008). Computing and recomputing discourse models: An ERP study. *Journal of Memory and Language*, *59*, 36-53.

Baggio, G., van Lambalgen, M., and Hagoort, P. (in press). The processing consequences of compositionality. In W. Hinzen, E. Machery and M. Werning (Eds.), *The Oxford handbook of compositionality*: Oxford University Press.

Baumgaertner, C., Weiller, C., and Buchel, C. (2002). Event-related fMRI reveals cortical sites involved in contextual sentence integration. *Neuroimage*, *16*, 736–745.

Beauchamp, M.S., Lee, K.E., Argall, B.D., and Martin, A. (2004). Integration of auditory and visual information about objects in superior temporal sulcus. *Neuron*, *41*, 809-823.

Bookheimer, S. (2002). Functional MRI of language: New approaches to understanding the cortical organization of semantic processing. *Annual Review of Neuroscience*, *25*, 151-188.

Brown, C., and Hagoort, P. (1993). The processing nature of the N400: evidence from masked priming. *Journal of Cognitive Neuroscience*, *5*, 34-44.

Buckner, R.L., Andrews-Hanna, J.R., & Schacter, D.L. (2008). The brain's default network: anatomy, function, and relevance to disease. *Annual New York Academy of Sciences*, *1124*, 1-38.

Calvert, G.A., Campbell, R., and Brammer, M.J. (2000). Evidence from functional magnetic resonance imaging of crossmodal binding in the human heteromodal cortex. *Current Biology*, *10*, 649-657.

Carreiras, M., Garnham, A., Oakhill, J., and Cain, K. (1996). The use of stereotypical gender information in constructing a mental model: Evidence from English and Spanish. *Quarterly Journal of Experimental Psychology*, *49A*, 639-663.

Coulson, S., King, J.W., and Kutas, M. (1998). Expect the unexpected: event-related brain response to morphosyntactic violations. *Language and Cognitive Processes*, *13*, 21-58.

Culicover, P., and Jackendoff, R. (2005). *Simpler syntax*. Oxford: Oxford University Press.

Cutler, A., and Clifton, C.E. (1999). Comprehending spoken language: A blueprint of the listener. In C.M. Brown and P. Hagoort (Eds.), *The neurocognition of language* (pp. 123-166). Oxford: Oxford University Press.

Dale, A.M., Liu, A.K., Fischl, B.R., Buckner, R.L., Belliveau, J.W., Lewine, J.D., and Halgren, E. (2000). Dynamic statistical parametric mapping: combining fMRI and MEG for high-resolution imaging of cortical activity. *Neuron*, *26*, 55-67.

Davis, M.H., Coleman, M.R., Absalom, A.R., Rodd, J.M., Johnsrude, I.S., Matta, B.F., Owen, A.M., and Menon, D.K. (2007). Dissociating speech perception and comprehension at reduced levels of awareness. *Proceedings of the National Academie of Science USA*, *104*, 16032-16037.

DeLong, K.A., Urbach, T.P., and Kutas, M. (2005). Probabilistic word pre-activation during language comprehension inferred from electrical brain activity. *Nature Neuroscience*, *8*, 1117-1121.

Federmeier, K.D., and Kutas, M. (1999). A rose by any other name: Long-term memory structure and sentence processing. *Journal of Memory and Language*, *41*, 469-495.

Federmeier, K.D. (2007). Thinking ahead: the role and roots of prediction in language comprehension. *Psychophysiology*, *44*, 491-505.

Ferretti, T.R., Kutas, M., and McRae, K. (2007). Verb aspect and the activation of event knowledge. *Journal of Experimental Psychology: Learning, Memory and Cognition*, *33*, 182-196.

Ferstl, E.C., Neumann, J., Bogler, C., and von Cramon, D.Y. (2008). The extended language network: a meta-analysis of neuroimaging studies on text comprehension. *Human Brain Mapping*, *29*, 581-593.

Fletcher, P.C., Happe, F., Frith, U., Baker, S.C., Dolan, R.J., Frackowiak, R.S., and Frith, C.D. (1995). Other minds in the brain: a functional imaging study of "theory of mind" in story comprehension. *Cognition*, *57*, 109-128.

Fodor, J., and Lepore, E. (2002). *The compositionality papers*. Oxford: Oxford University Press.

Frege, G. (1892). Uber Sinn und Bedeutung. *Zeitschrift für Philosophie und philosophische Kritik*, *100*, 25-50.

Friederici, A.D., Ruschemeyer, S.A., Hahne, A., and Fiebach, C.J. (2003). The role of left inferior frontal and superior temporal cortex in sentence comprehension: Localizing syntactic and semantic processes. *Cerebral Cortex*, *13*, 170-177.

Frith, C.D., and Frith, U. (2006). The neural basis of mentalizing. *Neuron*, *50*, 531-534.

Gold, B.T., Balota, D.A., Kirchhoff, B.A., and uckner, R.L. (2005). Common and dissociable activation patterns associated with controlled semantic and phonological processing: evidence from FMRI adaptation. *Cerebral Cortex*, *15*, 1438-1450.

Guillem, F., Rougier, A., and Claverie, B. (1999). Short- and long-delay intracranial ERP repetition effects dissociate memory systems in the human brain. *Journal of Cognitieve Neuroscience*, *11*, 437-458.

Hagoort, P., and Brown, C. (1994). Brain responses to lexical ambiguity resolution and parsing. In C. Clifton Jr., L. Frazier and K. Rayner (Eds.), *Perspectives on sentence processing* (pp. 45-81). Hillsdale, NJ: Lawrence Erlbaum Associates.

Hagoort, P., Brown, C., and Osterhout, L. (1999). The neurocognition of syntactic processing. In C.M. Brown and P. Hagoort (Eds.), *The neurocognition of language* (pp. 273-317). Oxford: Oxford University Press.

Hagoort, P., Hald, L., Bastiaansen, M., and Petersson, K.M. (2004). Integration of word meaning and world knowledge in language comprehension. *Science*, *304*, 438-441.

Hagoort , P. (2005). On Broca, brain, and binding: a new framework. *Trends in Cognitive Sciences*, *9*, 416-423.

Halgren, E., Baudena, P., Heit, G., Clarke, J.M., Marinkovic, K., and Chauvel, P. (1994). Spatio-temporal stages in face and word processing. 2. Depthrecorded potentials in the human frontal and Rolandic cortices. *Journal of Physiology Paris*, *88*, 51-80.

Halgren, E., Dhond, R.P., Christensen, N., Petten, C.v., Marinkovic, K., Lewine, J.D., and Dale, A.M. (2002). N400-like magnetoencephalography responses modulated by semantic context, word frequency, and lexical class in sentences. *Neuroimage*, *17*, 1101-1116.

Hasson, U., Nusbaum, H.C., and Small, S.L. (2007). Brain networks subserving the extraction of sentence information and its encoding to memory. *Cerebral Cortex*, *17*, 2899-2913.

Heim, I., and Kratzer, A. (1998). *Semantics in generative grammar*. NY: Blackwell.

Hein, G., Doehrmann, O., Muller, N.G., Kaiser, J., Muckli, L., and Naumer, M.J. (2007). Object familiarity and semantic congruency modulate responses in cortical audiovisual integration areas. *Journal of Neuroscience*, *27*, 7881-7887.

Helenius, P., Salmelin, R., Service, E., and Connolly, J.F. (1998). Distinct time courses of word and context comprehension in the left temporal cortex. *Brain*, *121,* 1133-1142.

Hoenig, K., and Scheef, L. (2005). Mediotemporal contributions to semantic processing: fMRI evidence from ambiguity processing during semantic context verification. *Hippocampus*, *15*, 597-609.

Holcomb, P (1993). Semantic priming and stimulus degradation: implications for he role of the N400 in language processing. *Psychophysiology, 30,* 47-61.

Humphries, C., Binder, J.R., Medler, D.A., and Liebenthal, E. (2007). Time course of semantic processes during sentence comprehension: An fMRI study. *Neuroimage*, *36*, 924-932.

Jackendoff, R. (1997). *The architecture of the language faculty*. Cambridge, MA: MIT Press.

Jackendoff, R. (1999). The representational structures of the language faculty and their interactions. In C.M. Brown and P. Hagoort (Eds.), *The neurocognition of language* (pp. 37-79). Oxford UK: Oxford University Press.

Jackendoff, R. (2002). *Foundations of language: brain, meaning, grammar, evolution*. Oxford, UK: Oxford University Press.

Keenan, E.L. (1979). On surface form and logical form. *Studies in the Linguistic Sciences*, *8*, 163-203.

Kiehl, K.A., Laurens, K.R., and Liddle, P.F. (2002). Reading anomalous sentences: an event-related fMRI study of semantic processing. *Neuroimage*, *17*, 842–850.

Kim, A., and Osterhout, L. (2005). The independence of combinatory semantic processing: Evidence from event-related potentials. *Journal of Memory and Language*, *52*, 205-225.

Kuperberg, G.R., McGuire, P.K., Bullmore, E.T., Brammer, M.J., Rabe-Hesketh, S., Wright, I.C., Lythgoe, D.J., Williams, S.C., and David, A.S. (2000). Common and distinct neural substrates for pragmatic, semantic, and syntactic processing of spoken sentences: an fMRI study. *Journal of Cognitive Neuroscience*, *12*, 321-341.

Kuperberg, G.R., Holcomb, P.J., Sitnikova, T., Greve, D., Dale, A.M., and Caplan, D. (2003). Distinct patterns of neural modulation during the processing of conceptual and syntactic anomalies. *Journal of Cognitieve Neuroscience*, *15*, 272–293.

Kuperberg, G.R., Lakshmanan, B.M., Caplan, D.N., and Holcomb, P.J. (2006). Making sense of discourse: an fMRI study of causal inferencing across sentences. *Neuroimage*, *33*, 343-361.

Kuperberg, G.R. (2007). Neural mechanisms of language comprehension: challenges to syntax. *Brain Research*, *1146*, 23-49.

Kuperberg GR, Sitnikova T, Lakshmanan BM (2008) Neuroanatomical distinctions within the semantic system during sentence comprehension: evidence from functional magnetic resonance imaging. *Neuroimage*, *40,* 367-388.

Kutas, M., and Hillyard, S.A. (1980). Reading senseless sentences: Brain potentials reflect semantic anomaly. *Science*, *207*, 203-205.

Kutas, M., and Hillyard, S.A. (1984). Brain potentials during reading reflect word expectancy and semantic association. *Nature, 307*, 161-163.

Kutas, M., and Federmeier, K.D. (2000). Electrophysiology reveals semantic memory use in language comprehension. *Trends in Cognitive Sciences*, *4*, 463-470.

Kutas, M., Van Petten, C., and Kluender, K.R. (2006). Psycholinguistics electrified II:1994-2005. In M. Traxler and M.A. Gernsbacher (Eds.), *Handbook of psycholinguistics, 2nd edition* (pp. 659-724): Elsevier.

Levelt, W.J.M. (1999). Producing spoken language: A blueprint of the speaker. In C.M. Brown and P. Hagoort (Eds.), *The neurocognition of language* (pp. 83-122). Oxford: Oxford University Press.

Li, X., Hagoort, P., and Yang, Y. (2008). Event related potential evidence on the influence on the influence of accentuation in spoken discourse comprehension in Chinese. *Journal of Cognitive Neuroscience*, *20*, 906-915.

Maguire, E.A., Frith, C.D., and Morris, R.G. (1999). The functional neuroanatomy of comprehension and memory: the importance of prior knowledge. *Brain*, *122*, 1839-1850.

Mason, R.A., and Just, M.A. (2006). Neuroimaging contributions to the understanding of discourse processes. In M. Traxler and M.A. Gernsbacher (Eds.), *Handbook of ssycholinguistics* (pp. 765-799). Amsterdam: Elsevier.

McCarthy, G., Nobre, A.C., Bentin, S., and Spencer, D.D. (1995). Language-related field potentials in the anterior-medial temporal lobe: I. Intracranial distribution and neural generators. *Journal of Neuroscience*, *15*, 1080-1089.

McElree, B., Traxler, M.J., Pickering, M.J., Seely, R.E., and Jackendoff, R. (2001). Reading time evidence for enriched composition. *Cognition*, *78*, B17-25.

Montague, R. (1970). Universal grammar. *Theoria*, *36*, 373-398.

Moss, H.E., Abdallah, S., Fletcher, P., Bright, P., Pilgrim, L., Acres, K., and Tyler, L.K. (2005). Selecting among competing alternatives: selection and retrieval in the left inferior frontal gyrus. *Cerebral Cortex*, *15*, 1723-1735.

Newman, A.J., Pancheva, R., Ozawa, K., Neville, H.J., and Ullman, M.T. (2001). An event-related fMRI study of syntactic and semantic violations. *Journal of Psycholinguistic Research*, *30*, 339–364.

Ni, W., Constable, R.T., Mencl, W.E., Pugh, K.R., Fulbright, R.K., Shaywitz, S.E., Shaywitz, B.A., and Gore, J. (2000). An event-related neuroimaging study distinguishing form and content in sentence processing. *Journal of Cognitieve Neuroscience*, *12*, 120-133.

Nieuwland, M.S., and Van Berkum, J.J.A. (2006). When peanuts fall in love: N400 evidence for the power of discourse. *Journal of Cognitive Neuroscience*, *18*, 1098-1111.

Osterhout, L., and Holcomb, P.J. (1992). Event-related brain potentials elicited by syntactic anomaly. *Journal of Memory and Language*, *31*, 785-806.

Osterhout, L., McLaughlin, J., & Bersick, M.(1997). Event-related brain potentials and human language. *Trends in Cognitive Sciences*, *1,* 203-209.

Osterhout, L., Kim, A., and Kuperberg, G.R. (2007). The neurobiology of sentence comprehension. In M. Spivey, M. Joanaisse and K. McRae (Eds.), *The Cambridge handbook of psycholinguistics*: Cambridge University Press.

Partee, B.H. (1984). Compositionality. In F. Veltman and F. Landmand (Eds.), *Varieties of formal semantics*. Dordrecht: Foris.

Partee, B.H., Ter Meulen, A., and Wall, R.E. (1990). *Mathematical methods in linguistics*: Kluwer.

Pylkkänen, L., and McElree, B. (2007). An MEG study of silent meaning. *Journal of Cognitieve Neuroscience*, *19*, 1905-1921.

Rodd, J.M., Davis, M.H., and Johnsrude, I.S. (2005). The neural mechanism of speech comprehension: fMRI studies of semantic ambiguity. *Cerebral Cortex*, *15*, 1261–1269.

Ruschemeyer, S.A., Fiebach, C.J., Kempe, V., and Friederici, A.D. (2005). Processing lexical semantic and syntactic information in first and second language: fMRI evidence from German and Russian. *Human Brain Mapping*, *25*, 266-286.

Ruschemeyer, S.A., Zysset, S., and Friederici, A.D. (2006). Native and non-native reading of sentences: an fMRI experiment. *Neuroimage*, *31*, 354-365.

Seuren, P.A.M. (1998). *Western linguistics: an historical introduction*. Oxford: Blackwell.

Sieborger, F.T., Ferstl, E.C., and von Cramon, D.Y. (2007). Making sense of nonsense: an fMRI study of task induced inference processes during discourse comprehension. *Brain Research*, *1166*, 77-91.

St George, M., Kutas, M., Martinez, A., and Sereno, M.I. (1999). Semantic integration in reading: engagement of the right hemisphere during discourse processing. *Brain*, *122*, 1317-1325.

Sturt, P. (2007). Semantic re-interpretation and garden path recovery. *Cognition*, *105*, 477-488.

Thompson-Schill, S.L., D'Esposito, M., Aguirre, G.K., and Farah, M.J. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. *Proceedings of the National Academie of Science USA*, *94*, 14792-14797.

Thompson-Schill, S.L., Bedny, M., and Goldberg, R.F. (2005). The frontal lobes and the regulation of mental activity. *Current Opinion in Neurobiology*, *15*, 219-224.

Traxler, M., Pickering, M., and McElree, B. (2002). Coercion in sentence processing: Evidence from eye movements and self-paced reading. *Journal of Memory and Language*, *47*, 530-547.

Traxler, M., McElree, B., Williams, R., and Pickering, M. (2005). Context effects in coercion: Evidence from eye movemoents. *Journal of Memory and Language*, *53*, 1-25.

Van Atteveldt N, Formisano E, Goebel R, Blomert L (2004) Integration of letters and speech sounds in the human brain. *Neuron* 43:271-282.

Van Atteveldt, N.M., Formisano, E., Blomert, L., and Goebel, R. (2007). The effect of temporal asynchrony on the multisensory integration of letters and speech sounds. *Cerebral Cortex*, *17*, 962-974.

Van Berkum, J.J.A., Van den Brink, D., Tesink, C., Kos, M., and Hagoort, P. (2008). The neural integration of speaker and message. *Journal of Cognitive Neuroscience*, *20*, 580-591.

Vigneau M, Beaucousin V, Herve PY, Duffau H, Crivello F, Houde O, Mazoyer B, Tzourio-Mazoyer N (2006) Meta-analyzing left hemisphere language areas: phonology, semantics, and sentence processing. Neuroimage 30:1414-1432.

Wagner, A.D., Pare-Blagoev, E.J., Clark, J., and Poldrack, R.A. (2001). Recovering meaning: left prefrontal cortex guides controlled semantic retrieval. *Neuron*, *31*, 329-338.

Willems, R.M., Özyürek, A., and Hagoort, P. (2007). When language meets action: The neural integration of gesture and speech. *Cerebral Cortex*, *17*, 2322 - 2333.

Willems, R.M., Özyürek, A., and Hagoort, P. (2008). Seeing and hearing meaning: event-related potential and functional magnetic resonance Imaging evidence of word versus picture integration into a sentence context. *Journal of Cognitive Neuroscience*, *20*, 1235-1249.

Xu, J., Kemeny, S., Park, G., Frattali, C., and Braun, A. (2005). Language in context: emergent features of word, sentence, and narrative comprehension. *Neuroimage*, *25*, 1002-1015.

Zempleni, M.Z., Renken, R., Hoeks, J.C., Hoogduin, J.M., and Stowe, L.A. (2007). Semantic ambiguity processing in sentence context: Evidence from event-related fMRI. *Neuroimage*, *34*, 1270-1279.

Table captions

Table 1:

Involvement of the inferior frontal cortex in fMRI studies of sentence comprehension employing semantic anomalies or semantic ambiguities. The table shows the studies that were used for the overview in Figure 6, a brief description of the contrast that was employed in each of the studies, the reported coordinates of the local maxima in inferior frontal cortex in MNI space, and a verbal description of the location of the local maxima. When necessary, Talairach coordinates were converted to MNI space using the transformation suggested by Brett (http://imaging.mrc-cbu.cam.ac.uk/imaging/MniTalairach). Note that in computing the mean coordinates the findings from Kuperberg et al., (2003), and Ni et al. (2000) were not taken into consideration, since no coordinates were reported in these studies.

Table 2:

Involvement of the temporal cortex in fMRI studies of sentence comprehension employing semantic anomalies or semantic ambiguities. The table shows the studies that were used for the overview in Figure 6, a brief description of the contrast that was employed in each of the studies, the reported coordinates of the local maxima in temporal cortex in MNI space, and a verbal description of the location of the local maxima. When necessary, Talairach coordinates were converted to MNI space using the transformation suggested by Brett (http://imaging.mrc-cbu.cam.ac.uk/imaging/MniTalairach). Note that in computing the mean coordinates the findings from Kuperberg et al., (2003), and Ni et al. (2000) were not taken into consideration, since no coordinates were reported in these studies.

Table 3:

Summary of the activations in the studies used for the overview in Figure 6. The coordinates from Table 1 and 2 were used. Table 3 specifies the mean coordinates for left and right inferior frontal and temporal cortices, the standard deviation in the x, y and z direction in mm, the mean Euclidian distance of the local maxima to the mean coordinates, the number of maxima that were reported, and the number of studies that report maxima in that region. Note that the number of maxima is higher than the number of studies, since several studies report more than one maximum. Note that the findings from Kuperberg et al., (2003), and Ni et al. (2000) were not used in computing the mean coordinates, since no coordinates were reported in these studies.

Table 1

Inferior Frontal Cortex			
Study	**Comparison**	**Coordinates**	**Region**
		x y z (MNI)	
Baumgaertner et al 2002	Sem incongruent > congruent	-51 36 -6	left IFG
Davis et al., 2007	High ambiguity > Low ambiguity	- 40 24 18	left IFG
		-48 6 34	
		-40 18 24	
		46 36 18	Right IFG
Friederici et al., 2003	Sem incongruent > congruent	no activation	-
Hagoort et al., 2004	Sem incongruent > congruent ∩ World knowledge incongruent > congruent	-44 30 8	left IFG
Hoenig & Scheef, 2005	Sem incongruent > congruent	-50 18 -14	left IFG
		-50 43 11	
Kiehl et al., 2002	Sem incongruent > congruent	-48 32 4	left IFG / Ant Temporal
		36 32 -16	right IFG / Ant Temporal
Kuperberg et al., 2000	Sem incongruent > congruent	no activation	-
	Pragm incongruent > congruent	no activation	-
Kuperberg et al., 2003	Pragm incongruent > congruent	(no coordinates)	left IFG
Kuperberg et al., 2008	Pragmatic incongruent > Congruent	-43 25 -10	left IFG
	Sem incongruent > Congruent	- 49 4 10	left IFG
		29 19 5	right IFG
Newman et al. 2001	Sem incongruent > Congruent	-50 34 5	left IFG

Ni et al. 2000	Sem incongruence detection > tone pitch discrimination	(no coordinates)	left IFG
			right IFG
	Odd-ball paradigm with semantically incongruent sentences	(no coordinates)	left IFG
		(no coordinates)	right IFG
Rodd et al., 2005	High ambiguity > Low ambiguity	-50 30 20	left IFG
		-56 16 22	left IFG
		-42 14 32	left IFS
		36 26 4	Right IFG
		50 36 16	Right IFG
Rueschemeyer et al., 2006	Sem incongruent > Synt incongruent	-50 30 15	left ant IFG
Willems et al., 2007	Sem incongruent > congruent	-43 11 27	left IFS
Willems et al., 2008	Sem incongruent > congruent	-45 14 27	left IFS
Zempleni et al., 2007	Subordinate meaning > dominant meaning	-48 26 20	left IFG
		-52 16 26	left IFG
		34 20 -10	right IFG

Table 2

Temporal Cortex			
Study	**Comparison**	**Coordinates**	**Region**
		x y z (MNI)	
Baumgaertner et al 2002	Sem incongruent > congruent	no activation	-
Davis et al., 2007	High ambiguity > Low ambiguity	-50 -44 -12	left ITG
		-54 -60 -2	
Friederici et al., 2003	Sem incongruent > congruent	-60 -42 20	left STG
		63 -40 20	right STG
		58 -24 13	right STG
Hagoort et al., 2004	Sem incongruent > congruent	no activation	-
Hoenig & Scheef, 2005	Sem incongruent > congruent	no activation	-
Kiehl et al., 2002	Sem incongruent > congruent	no activation	-
Kuperberg et al. 2000	Sem incongruent > congruent	43 -11 -7	right MTG
		49 -17 4	right STG
	Pragm incongruent > congruent	-49 -31 9	left STG
Kuperberg et al., 2003	Pragm incongruent > congruent	(no coordinates)	left STS
Kuperberg et al., 2008	Pragmatic violations > Correct sentences	-27 -28 -19	left ant. med. temporal cortex
	Sem incongruent > Congruent	-53 -20 -1	left STG
		58 -19 3	right STG
Newman et al. 2001	Sem incongruent > Congruent	70 -36 -15	right MTG
Ni et al. 2000	Sem incongruence detection > tone pitch discrimination	(no coordinates)	left STG / MTG
		(no coordinates)	right STG / MTG
	Odd-ball paradigm with semantically incongruent sentences	(no coordinates)	left pSTG

Rodd et al., 2005	High ambiguity > Low ambiguity	-52 -50 -10	left pITG
		-58 -8 -6	left STG
Rueschemeyer et al., 2006	Sem incongruent > Synt incongruent	-	-
Willems et al., 2007	Sem incongruent > congruent	-53 -52 2	left STS
Willems et al., 2008	Sem incongruent > congruent	-53 -35 -3	left STS
Zempleni et al., 2007	Subordinate meaning > dominant meaning	-50 -48 -12	left ITG/MTG
		56 -34 -16	right ITG/MTG

Table 3

Inferior frontal cortex	**Mean (x y z) (MNI)**	**SD (x y z) (mm)**	**Mean distance to mean (mm)**	**Number of studies (out of total)**
Left	-47 22 14	4.3 10.6 13.9	16.3	14 / 16
Right	39 28 3	7.9 7.7 13.6	15.0	6 / 16
Temporal cortex	**Mean (MNI)**	**SD (mm)**	**Mean distance to mean (mm)**	**number of studies**
Left	-51 -38 -3	8.6 15.4 10.9	18.0	10 / 16
Right	57 -26 0	8.8 10.9 13.7	17.2	6 / 16

Figure legends

Figure 1: Participants read the sentences as in the example in a visual-half-field presentation design. Context words were presented at central fixation, whereas sentence-final target words (e.g. oranges) were presented to the left or right of fixation. As illustrated, words presented to the left visual field travel initially to the right hemisphere and vice versa. ERPs are shown here from a representative (right medial central) site as indicated. The response to target words presented to the right visual field (left hemisphere) (shown on right), yielded the same pattern as that observed with central fixation: expected exemplars (solid line) elicited smaller N400s than did violations of either type, but within-category violations (dashed line) also elicited smaller N400s than between-category violations (dotted line). This pattern is indicative of a 'predictive' strategy, in which semantic information associated with the expected item is pre-activated in the course of processing the context information. The response to targets presented to the left visual field (right hemisphere) (shown on left), however, was qualitatively different: expected exemplars again elicited smaller N400s than violations, but the response to the two types of violations did not differ. This pattern is more consistent with a plausibility-based integrative strategy. Taken together, the results indicate that the hemispheres differ in how they use context to process semantic information in on-line language processing (Kutas & Federmeier, 2000; reprinted with permission).

Figure 2: Grand average ERPs for a representative electrode site (Cz) for correct condition (black line), world knowledge violation (blue dotted line), and semantic violation (red dashed line). ERPs are time locked to the presentation of the critical words (underlined). Spline-interpolated isovoltage maps display the topographic distributions of the mean differences from 300-

550 ms between semantic violation and control (left); and between world knowledge violation and control (right). **(B)** The common activation for semantic and world knowledge violations compared to the correct condition, based on the results of a minimum-T-field conjunction analysis. Both violations resulted in a single common activation (*P* = 0.043, corrected) in the left inferior frontal gyrus (in, or in the vicinity of Brodmann's area 45. The cross-hair indicates the voxel of maximal activation.

Figure 3: (a) Grand-average topographies displaying the mean amplitude difference between the ERPs evoked by the sentence-final verb when it terminated vs. when it did not terminate the accomplishments in the progressive. Circles represent electrodes in a significant (P<0.05) cluster. (b) Grand-average ERP waveforms from a representative site (F3) time locked to the onset (0 ms) of the verb in terminated vs. non-terminated accomplishments. Negative values are plotted upward. (c) Scatter plot displaying the correlation between the amplitude of the sustained anterior negativity elicited by terminated accomplishments and the frequency of negative responses in a button-press, probe-selection task (r=-0.415, T(22)=-2.140, P=0.043). The mean difference of negative responses between terminated and non-terminated accomplishments is plotted on the abscissa. The mean amplitude difference at fronto-polar and frontal electrodes between terminated and non-terminated accomplishments in the 500-700 ms interval following the onset of the sentence-final verb is plotted on the ordinate.

Figure 4: N400 effects triggered by a correct predicate (*salted*) that is, however, contextually disfavored in comparison to an incorrect predicate (*in love*). Waveforms are presented for representative electrode sites, time locked to the onset of the critical inanimate/animate predicate in the fifth sentence (after Nieuwland & Van Berkum 2006).

Figure 5: At the interface between syntax and semantics. Grand-average ERPs recorded at three midline sites and six medial-lateral sites. All sentences are syntactically correct. (A) ERPs to passive control verbs (solid line) and thematic violation verbs (dashed line). (B) ERPs to active control verbs (solid line) and thematic violation verbs (dashed line). In both cases the inconsistency between grammatical roles and thematic role biases resulted in robust P600 effects. Onset of the critical verbs is indicated by the vertical bar. Each has mark represents 100 ms. Positive voltage is plotted down (Kim and Osterhout, 2005; reprinted with permission).

Figure 6: Overview of local maxima in inferior frontal cortex and in temporal cortex in neuroimaging studies employing sentences with semantic anomalies or semantic ambiguities. The local maxima (in MNI space) of each study were overlaid on a rendering of a brain in MNI space. For local maxima see Table 1 and 2, for a summary of the results see Table 3. Rendering was made using MRIcroN. Please note that the local maxima of the Ni et al., 2000 and the Kuperberg et al., 2003 studies are displayed, but that these are not based on coordinates, since no coordinates were provided. The local maxima are drawn by hand based upon the figures in the respective papers.

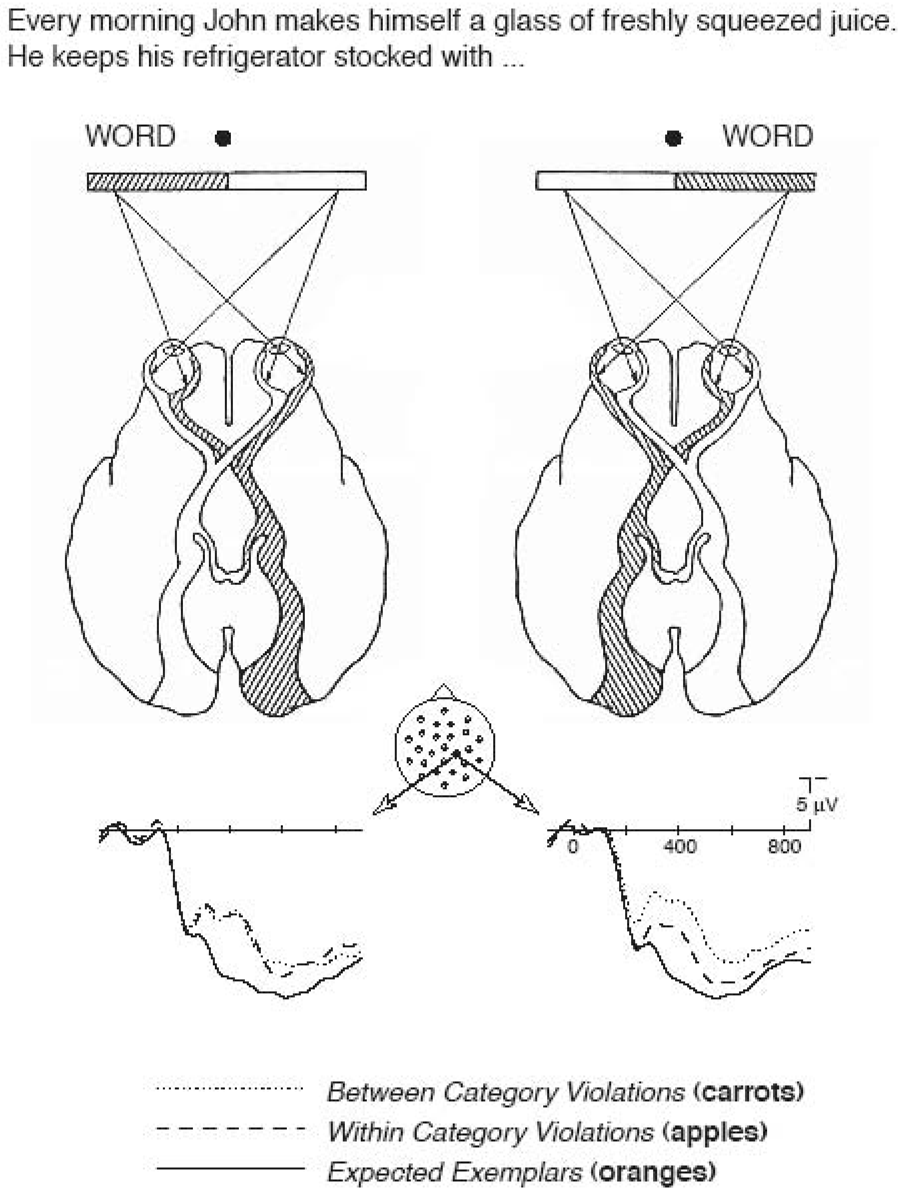
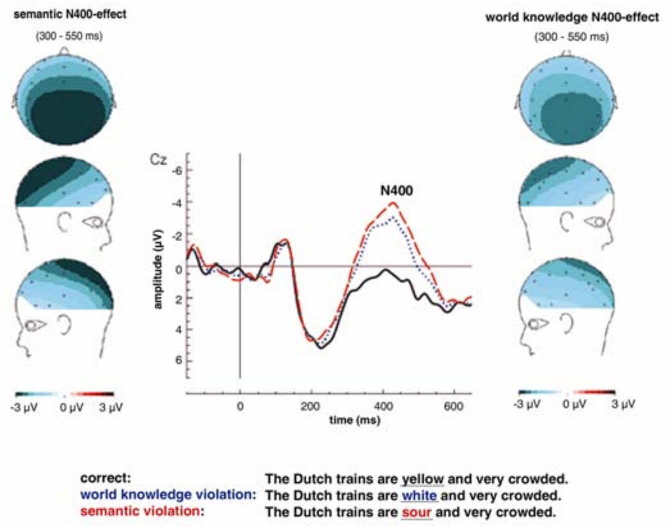

Every morning John makes himself a glass of freshly squeezed juice.
He keeps his refrigerator stocked with ...
WORD
WORD
5 µV
0
400
800
Between Category Violations (carrots)
Within Category Violations (apples)
Expected Exemplars (oranges)

Figure 1


semantic N400-effect
(300 - 550 ms)
world knowledge N400-effect
(300 - 550 ms)
Cz
N400
amplitude (μV)
time (ms)
-3 μV
0 μV
3 μV
correct: The Dutch trains are yellow and very crowded.
world knowledge violation: The Dutch trains are white and very crowded.
semantic violation: The Dutch trains are sour and very crowded.

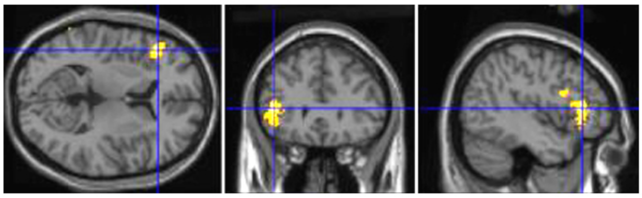
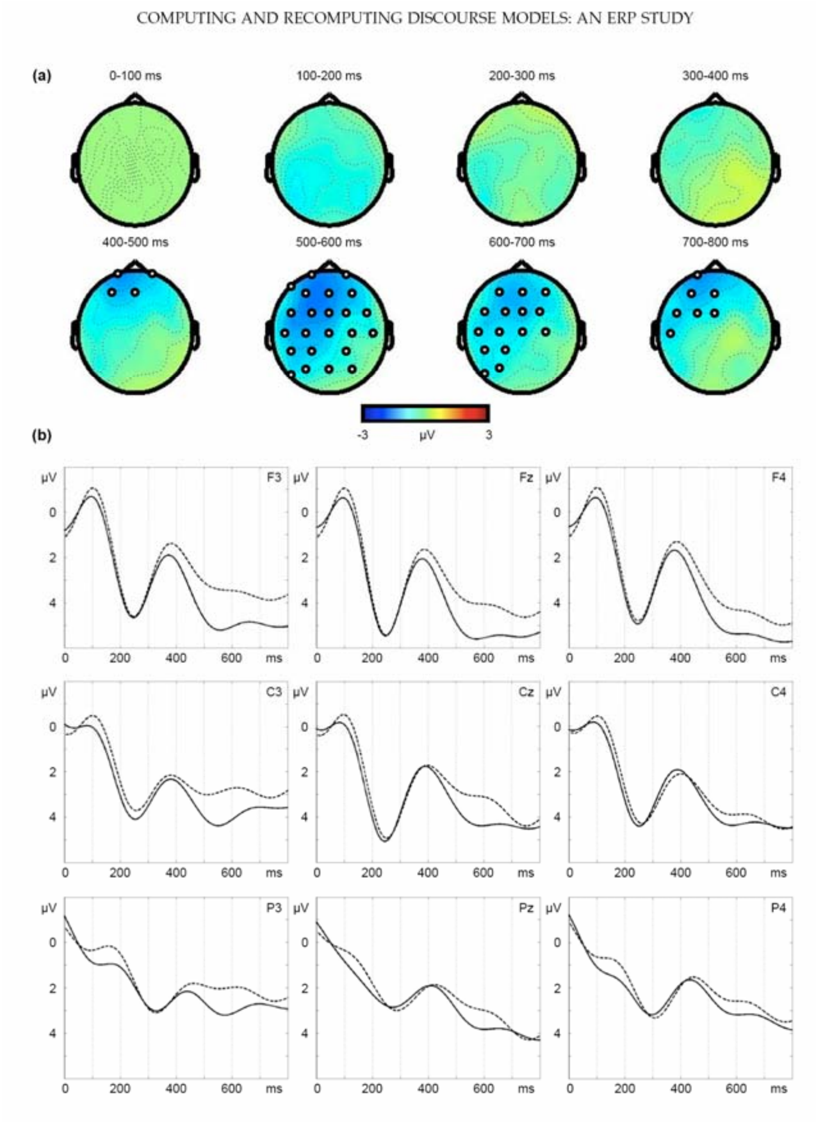


Figure 2


COMPUTING AND RECOMPUTING DISCOURSE MODELS: AN ERP STUDY
(a)
0-100 ms
100-200 ms
200-300 ms
300-400 ms
400-500 ms
500-600 ms
600-700 ms
700-800 ms
-3
μV
3
(b)
F3
Fz
F4
C3
Cz
C4
P3
Pz
P4
μV
ms

(c)

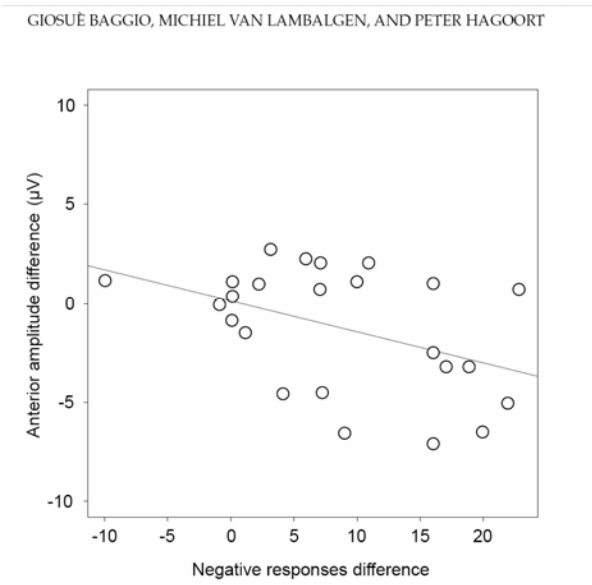

GIOSUÈ BAGGIO, MICHIEL VAN LAMBALGEN, AND PETER HAGOORT
Anterior amplitude difference (μV)
Negative responses difference

Figure 3

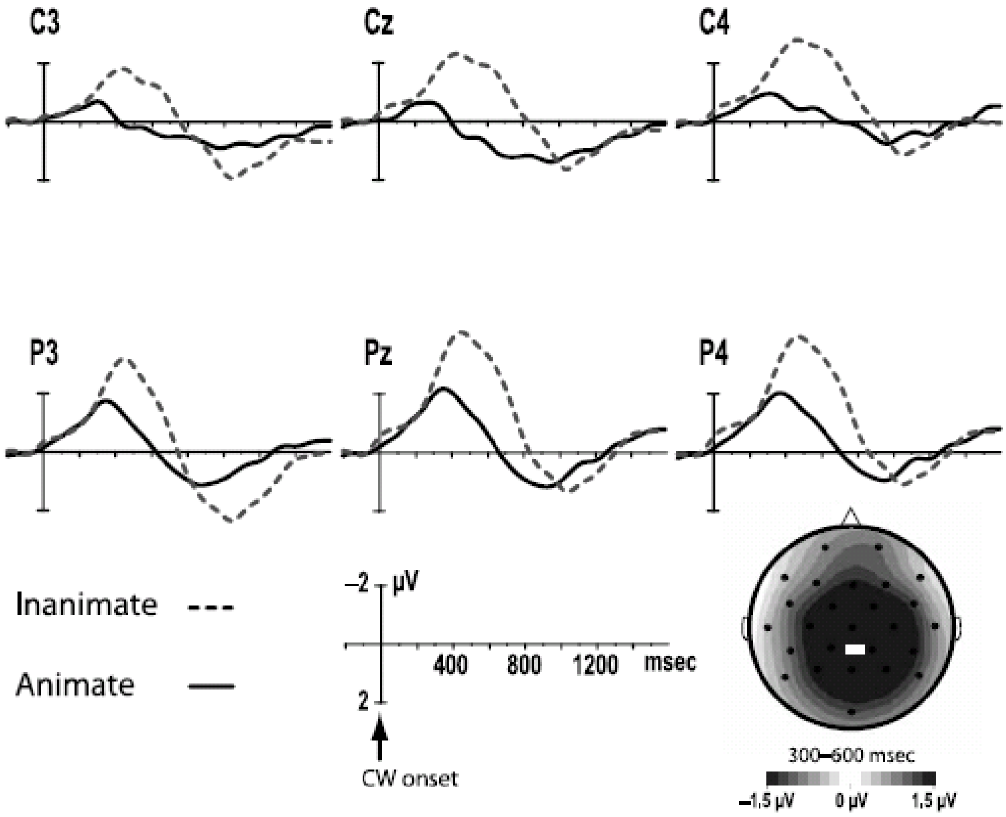

C3
Cz
C4
P3
Pz
P4
Inanimate
Animate
–2
μV
2
400
800
1200
msec
CW onset
300–600 msec
–1.5 μV
0 μV
1.5 μV

Figure 4

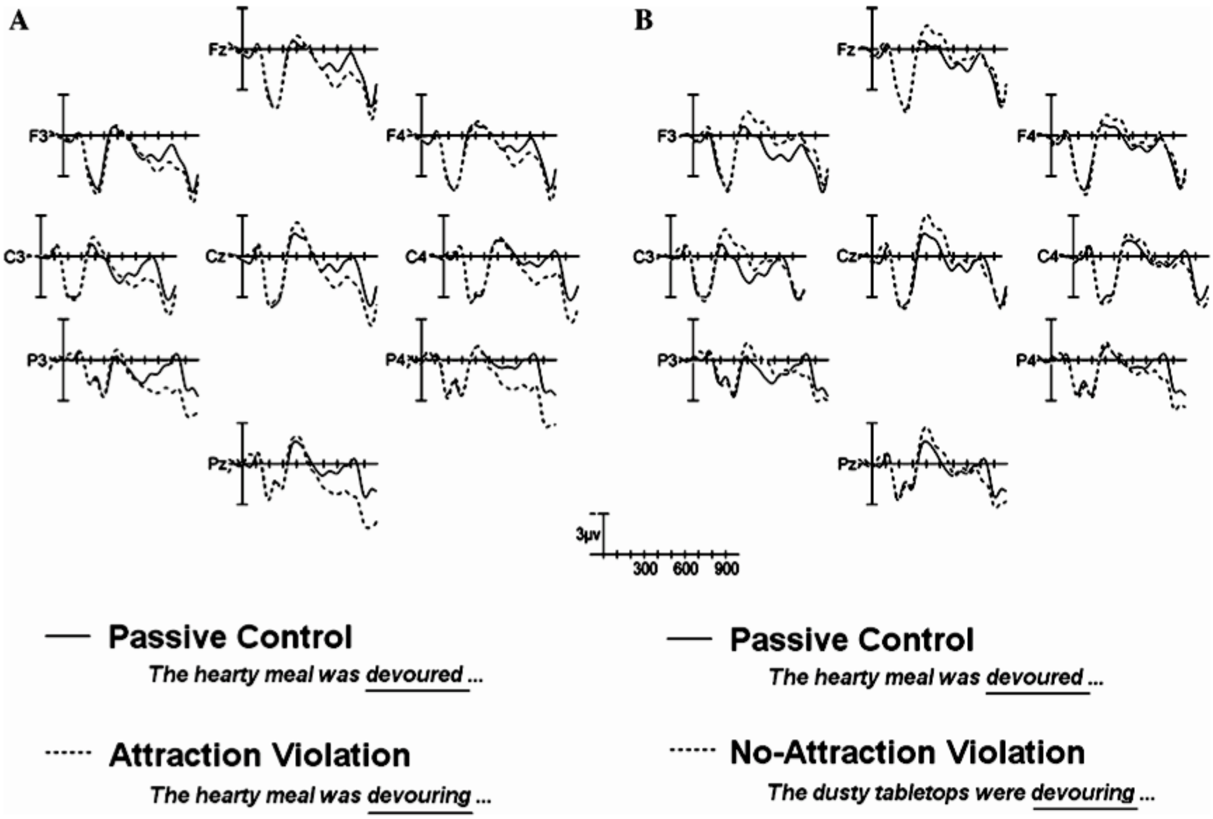

A
B
Fz
F3
F4
C3
Cz
C4
P3
P4
Pz
3μv
300
600
900
Passive Control
The hearty meal was devoured ...
Attraction Violation
The hearty meal was devouring ...
Passive Control
The hearty meal was devoured ...
No-Attraction Violation
The dusty tabletops were devouring ...

Figure 5

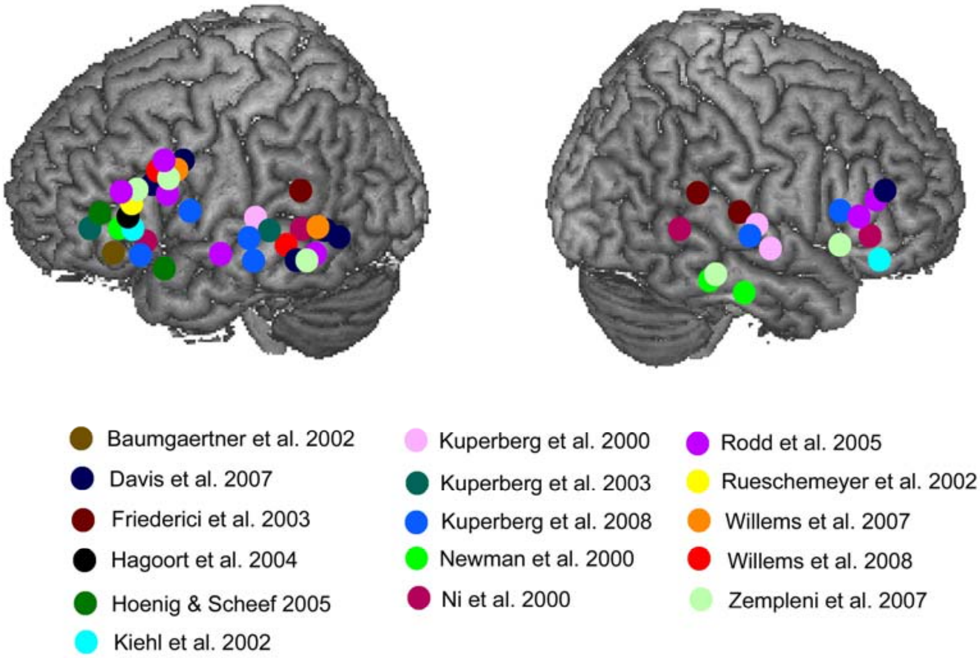

Baumgaertner et al. 2002
Davis et al. 2007
Friederici et al. 2003
Hagoort et al. 2004
Hoenig & Scheef 2005
Kiehl et al. 2002
Kuperberg et al. 2000
Kuperberg et al. 2003
Kuperberg et al. 2008
Newman et al. 2000
Ni et al. 2000
Rodd et al. 2005
Rueschemeyer et al. 2002
Willems et al. 2007
Willems et al. 2008
Zempleni et al. 2007

Figure 6