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Research Report

Neural mechanisms of language comprehension: Challenges to syntax

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ARTICLE INFO

Article history:
Accepted 19 December 2006
Available online 23 December 2006

Keywords:
Language
N400
P600
ERP
Semantic
Syntax
Thematic role

ABSTRACT

In 1980, the N400 event-related potential was described in association with semantic anomalies within sentences. When, in 1992, a second waveform, the P600, was reported in association with syntactic anomalies and ambiguities, the story appeared to be complete: the brain respected a distinction between semantic and syntactic representation and processes. Subsequent studies showed that the P600 to syntactic anomalies and ambiguities was modulated by lexical and discourse factors. Most surprisingly, more than a decade after the P600 was first described, a series of studies reported that semantic verb–argument violations, in the absence of any violations or ambiguities of syntax can evoke robust P600 effects and no N400 effects. These observations have raised fundamental questions about the relationship between semantic and syntactic processing in the brain. This paper provides a comprehensive review of the recent studies that have demonstrated P600s to semantic violations in light of several proposed triggers: semantic–thematic attraction, semantic associative relationships, animacy and semantic-thematic violations, plausibility, task, and context. I then discuss these findings in relation to a unifying theory that attempts to bring some of these factors together and to link the P600 produced by semantic verb–argument violations with the P600 evoked by unambiguous syntactic violations and syntactic ambiguities. I suggest that normal language comprehension proceeds along at least two competing neural processing streams: a semantic memory-based mechanism, and a combinatorial mechanism (or mechanisms) that assigns structure to a sentence primarily on the basis of morphosyntactic rules, but also on the basis of certain semantic–thematic constraints. I suggest that conflicts between the different representations that are output by these distinct but interactive streams lead to a continued combinatorial analysis that is reflected by the P600 effect. I discuss some of the implications of this non-syntactocentric, dynamic model of language processing for understanding individual differences, language processing disorders and the neuroanatomical circuitry engaged during language comprehension. Finally, I suggest that that these two processing streams may generalize beyond the language system to real-world visual event comprehension.

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0006-8993/$ – see front matter © 2007 Published by Elsevier B.V.
doi:10.1016/j.brainres.2006.12.063

1. Introduction

As language unfolds in real time, the meaning of individual words and the syntactic structure of a sentence must be combined to build up a representation of whole meaning. Most current models of how this occurs have taken their cue from linguistic theory where it has traditionally been assumed that meaning is read off from syntactic structure and is dependent on the syntax for its combinatorial properties (Chomsky, 1965; Chomsky, 1981; see Jackendoff, 2007-this issue, for discussion). The analogous assumption in psycholinguistics has been that the overall meaning of a proposition is extracted by slotting the meaning of individual words into syntactic structure as it is built up word by word, although it is debated whether this occurs in two separable stages (Ferreira and Clifton, 1986; Frazier and Rayner, 1982) or during a single stage of processing (Boland and Tanenhaus, 1991; MacDonald et al., 1994; Marslen-Wilson et al., 1988; Tanenhaus and Carlson, 1989; Trueswell and Tanenhaus, 1994; Tyler, 1992). It is usually assumed that any meaning derived purely from the semantic features of words (e.g. semantic associations or semantic–thematic relationships) will challenge the syntax and lead to processing costs only when the syntax is ambiguous.

Studies examining the neural basis of language processing have generally made the same assumption. Following the behavioral psycholinguistic literature, such studies have attempted to address the debate about whether semantic and syntactic neural processes come together in a single stage of processing (Fiebach et al., 2002; Kaan et al., 2000) or after an initial phase of structure building (Ferreira and Clifton, 1986; Friederici, 1995; see Friederici and Weissenbor, 2007-this issue, for discussion). However, few have entertained the idea that a semantic combination of words can even temporarily challenge an unambiguous and simple, canonical syntax in building up higher-order meaning during online neural processing.

The current paper reviews a series of event-related potential (ERP) studies that call this assumption into question. Taken together, they point to a processing system that is more dynamic than has often been supposed, and in which semantic factors such as semantic associations and semantic–thematic relationships (such as those determined by animacy constraints) can, under some circumstances, temporarily challenge the unambiguous morphosyntactic assignment of thematic roles, even in simple, canonical sentences, and can lead to later neural processing costs.

In Section 2, I present a brief overview of the two ERP components on which this review focuses—the N400 and the P600, and outline evidence for the traditional associations of these components with semantic and syntactic variables respectively. In Section 3, I describe a series of studies from our lab and other groups that have demonstrated P600 effects, and sometimes attenuated or absent N400 effects, to unambiguous semantic verb–argument violations within sentences. These studies suggest that there is no one single trigger for the P600, but that a number of factors interact to produce this effect.

In Section 4, I attempt to bring these findings together. I will suggest that normal language comprehension of simple events proceeds along distinct but interactive neural processing streams. The first, reflected in part by the N400, is a semantic memory-based mechanism that computes associative and categorical relationships between verbs and arguments (and other content words), comparing them with lexical semantic relationships that are stored within semantic memory. The second is a combinatorial mechanism (or mechanisms) that assigns thematic roles to arguments within sentences primarily through the application of morphosyntactic rules, but that also appears to be influenced directly by certain semantic–thematic constraints such as animacy. I will suggest that the P600 effect reflects prolonged processing within this combinatorial stream (or streams) that is triggered and/or enhanced when it initially fails altogether and/or when its output contradicts a coherent representation that is output by the semantic memory-based stream. In section 5, I consider the implications of this model for understanding the brain mechanisms of abnormal language processing and, more broadly, for understanding the neural basis of comprehension in general.

2. The N400 and the P600

It is now well established that the amplitude of the N400 – a negative-going ERP component that peaks at around 400 ms after the onset of a content word – is sensitive to semantic congruity. The N400 was first described at the sentence level: in 1980, Kutas and Hillyard (1980) demonstrated a more negative N400 to words that were semantically anomalous *versus* congruous with their preceding sentence contexts, such as to the word *"socks"*, in the sentence, *"He spread the warm bread with socks."* (Fig. 1A). This difference in N400 amplitude between semantically congruous and incongruous words became known as the N400 effect. The amplitude of the N400 was subsequently shown to be modulated by a variety of factors other than frank semantic anomaly. Within sentences, words that are congruous but unpredictable, such as *"thought"* in the sentence *"He mailed the letter without a thought."* elicit a more negative N400 than more expected words such as *"stamp"* (Kutas and Hillyard, 1984), and words that violate real-world expectations such as *"white"* in sentences such as, *"The Dutch trains are white…"* elicit a more negative N400 than words that are consistent with such expectations such as *"yellow"* (Dutch comprehenders know that Dutch trains are, in fact, yellow) (Hagoort et al., 2004). And, across sentences, van Berkum, Hagoort and Brown (1999) demonstrated that words that are acceptable within a sentence, but incongruous with their global discourse context, also evoke an N400 effect.

In parallel with the work demonstrating the sensitivity of the N400 to preceding semantic context at the sentence and discourse levels, a literature has cumulated that documents the sensitivity of the N400 to the organization of lexical items stored within semantic memory. When word pairs or word triplets are presented in isolation, the amplitude of the N400 is modulated by close semantic associations (Bentin et al., 1985; Rugg, 1985), by more subtle semantic associations of the kind that occur in scripts (Chwilla and Kolk, 2005) and that are captured using measures such as a Latent Semantic Analysis (Landauer and Dumais, 1997; Landauer et al., 1998), by indirect semantic relationships in which words are linked through an unseen mediating word (Chwilla and Kolk, 2002; Chwilla et al., 2000;

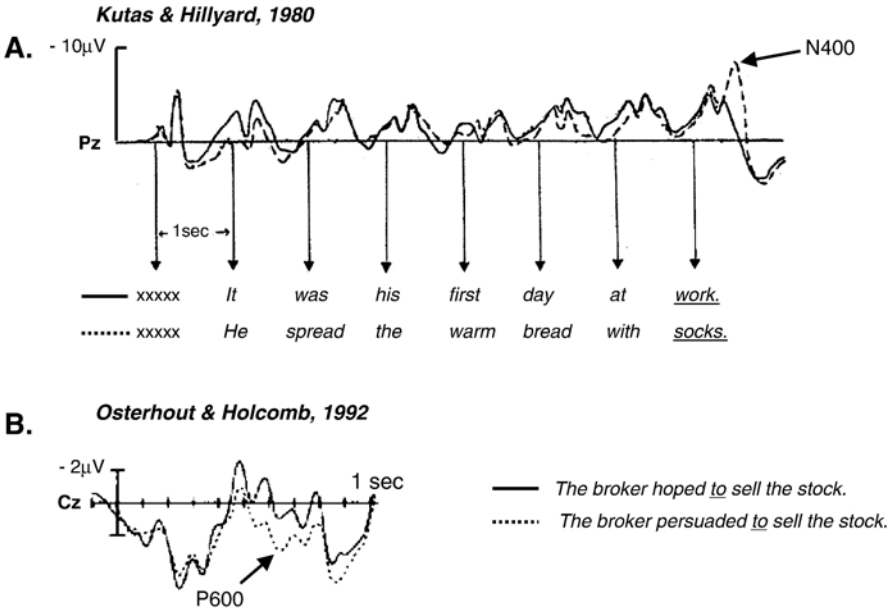

Fig. 1 – The N400 and the P600 effects.

Kreher et al., 2006), and by semantic categorical relationships (Deacon et al., 2004; Grose-Fifer and Deacon, 2004).

Attempts to bring together the sentence/discourse-level findings with the semantic memory findings at the level of single words have yielded some evidence that the N400s produced under both circumstances interact. Van Petten (1993) showed that, regardless of the overall congruity of a sentence, the N400 is also modulated by semantic associations between its individual words. And, in a pivotal study, Federmeier and Kutas (1999) demonstrated that words that are incongruous with their preceding context but that share semantic features with the expected word produce a smaller N400 than incongruous unrelated words.

In 1992, Osterhout and Holcomb (1992) reported a large positive waveform peaking at approximately 600 ms after the onset of critical words that were incongruous with the expected syntactic structure in garden path sentences (e.g. *"The broker persuaded to sell the stock was sent to jail."*) (Fig. 1B). At around the same time, Hagoort, Brown, and Groothusen (1993) demonstrated a similar Late Positivity to outright syntactic agreement violations (e.g. *"The spoiled child throw the toys on the floor."*) and word order violations (e.g. *"the expensive very tulip"*). Subsequent studies confirmed that this so-called P600 effect was evoked by many other types of syntactic violations including those of phrase structure (Friederici et al., 1996; Neville et al., 1991) and subcategorization (Osterhout, 1997; Osterhout et al., 1994).

Several studies also suggested that the amplitude of the P600 evoked by both syntactic ambiguities and violations could be modulated by both lexical and semantic contextual variables. For example, Osterhout et al. (1994) reported a smaller P600 to disambiguating words such as *"was"* in sentences such as *"The doctor believed the patient was lying"* than in sentences such as *"The doctor charged the patient was lying"*, suggesting that the subcategorization bias of the verb had an immediate impact on the degree to which participants were garden-pathed towards the direct-object rather than the relative clause reading of these sentences (*"believe"* is more often used intransitively than *"charge"*) (Fig. 2A). And Gunter, Friederici and Schriefers (2000) showed that the amplitude of the P600 evoked by nouns violating gender agreement was more positive when the violated nouns were highly semantically expected (e.g. *"Sie bereist den Land auf einem kraftigen Kamel/She travels the$_{masc.}$ land$_{neuter}$ on a strong Camel"*) than when they were less expected in the sentence context (e.g. *"Sie befährt den Land mit einem alten Wartburg/She drives the$_{masc.}$ land$_{neuter}$ with an old Wartburg car"*) (Fig. 2B). These sorts of findings were interpreted as suggesting that both lexical information held within a verb as well as semantic expectancy across a whole sentence could influence the word-by-word build-up of syntactic structure within a sentence. The P600 was interpreted as reflecting a syntactic process that was sensitive to lexical and semantic contextual influences. In serial models of language processing, this process was thought to reflect a reanalysis and revision of a syntactic structure that had initially been established during a first stage of processing on the basis of minimal constraints such as major syntactic category information (Ferreira and Clifton, 1986; Frazier, 1987; Friederici, 1995). In constraint-based models (MacDonald et al., 1994; Tanenhaus et al., 1995), the P600 was considered to reflect the difficulty of syntactic integration once syntactic frames had already been activated and modulated by multiple sources of information during a single stage of parsing (Fiebach et al., 2002; Kaan et al., 2000).

3. Sometimes a P600 effect and not an N400 effect is evoked by unambiguous semantic violations

In 2003, we published a study that aimed to determine whether the brain distinguished between processing two

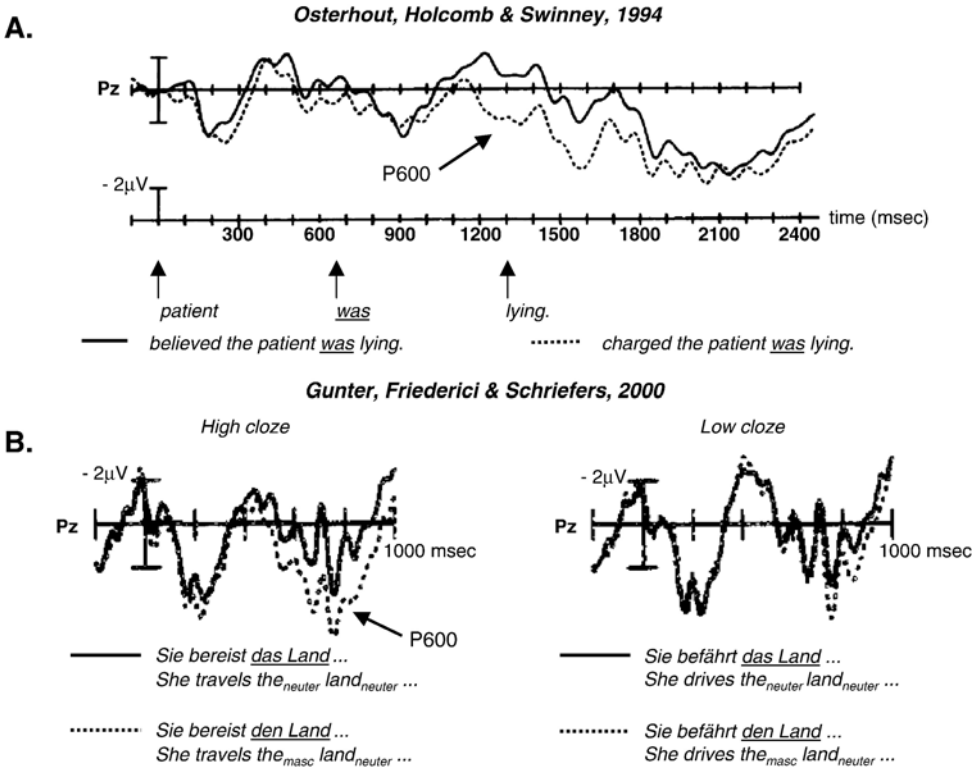

Fig. 2 – Modulation of the P600 by lexical and semantic contextual variables.

different types of semantic violation in unambiguous, simple English sentences (Kuperberg et al., 2003b). We contrasted sentences that violated the semantic–thematic relationships between critical verbs and their preceding subject inanimate NP arguments (e.g. *"Every morning at breakfast the eggs would eat…"*; *"eggs"*, being inanimate, do not have the semantic properties to be able to eat) with sentences in which there were no violations between the verbs and their arguments but in which the verbs were incongruous with respect to their entire preceding contexts (e.g. *"Every morning at breakfast the boys would plant…"*; boys can certainly plant but it is unlikely for them to do so at breakfast time). We indeed found marked neurophysiological distinctions. As expected, we saw a robust N400 effect to contextually violated verbs such as *"plant"*. But the pattern of ERPs evoked by verbs such as *"eat"* – the thematic violations (for definition, see Table 2) – were unexpected and were at odds with the literature at that time in two striking ways: first, these unambiguous semantic violations failed to evoke an N400 effect—the ERP effect that had traditionally been associated with semantic violations; second, despite the absence of any syntactic violation or ambiguity, they produced a robust P600 effect—the ERP effect that had been closely associated with violations of syntax (Fig. 3A).

We were not the only group to be seeing such surprising effects to semantic verb–argument violations in sentences. In English, Kim and Osterhout (2005) reported a P600 effect and no N400 effect to verbs such as *"devouring"* in even simpler active sentences such as *"The meal was devouring…"* (Fig. 3B). And, in Dutch, two groups were reporting similar findings: First, Kolk, van Herten, Chwilla and colleagues (2003) documented a significant P600 effect but no N400 effect to verbs such *"fled"* in semantically reversible sentences such as *"The cat that from the mice fled ran across the room"/"De kat die voor de muizen vluchtte rende door de kamer"* (see also van Herten et al., 2005) (Fig. 3C). Second, Hoeks, Stowe and Doedens (2004) demonstrated that verbs such as *"thrown"/"geworpen"* in sentences such as *"The javelin has thrown the athletes"/"De speer heeft de atleten geworpen"* evoked a clear P600 effect but, once again, an attenuated N400 effect (Fig. 3D). This set of initial studies, together with these example sentences, are listed in Table 1 (left, middle). Note once again that, in all these sentences, the violation was semantic in nature and that there were no syntactic violations or ambiguities.

These studies raised fundamental questions. How did these semantic anomalies evoking a P600 effect differ from semantic anomalies evoking an N400 effect? And what did the P600 evoked by these types of semantic anomalies have in common with the P600 evoked by syntactic anomalies and ambiguities? Below I review these studies as well as subsequent follow-up studies in more detail. I discuss six factors that have been considered critical to influencing when a P600 effect, and sometimes an attenuated N400 effect, is evoked by semantic verb–argument violations in unambiguous sentences. Because the terms used to refer to different types of semantic and thematic relationships have been used differently by different groups, depending on their theoretical perspectives, Table 2 gives definitions of key terms used throughout this review. Further discussion of the different types of semantic relationships considered and their relationships with morphosyntax, as well as a discussion of what neurocognitive process(es) the N400 and P600 ERPs might index is delayed until Section 4.

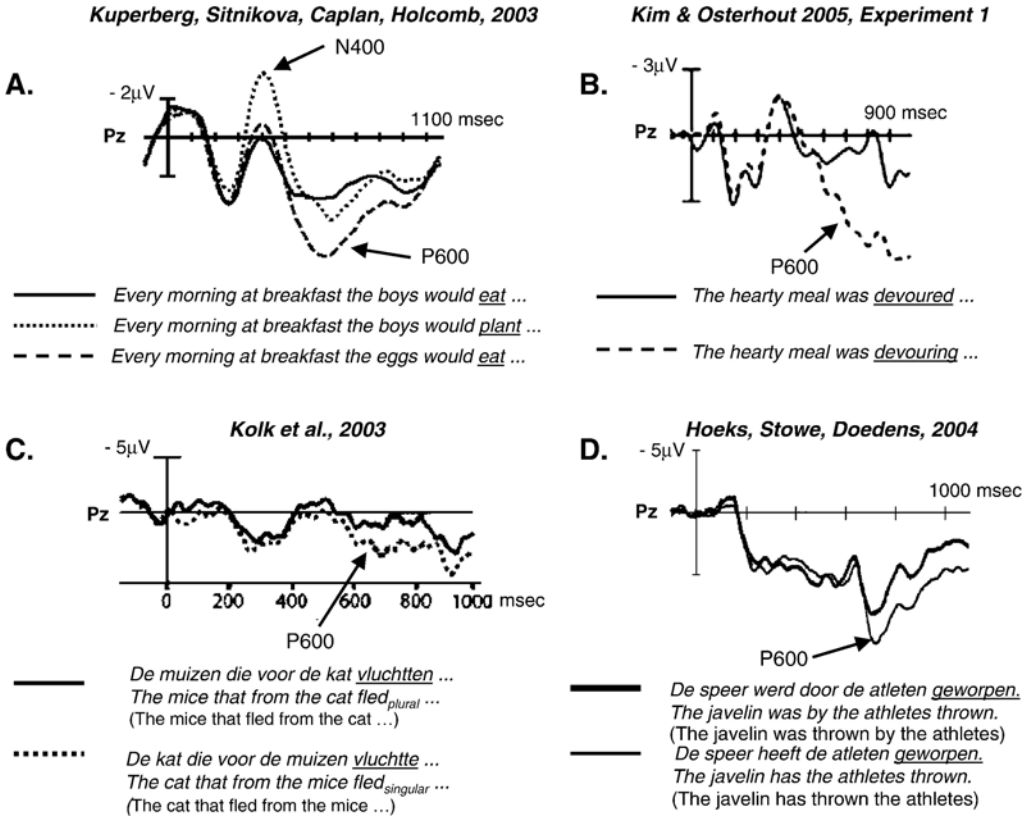

Fig. 3 – Examples of P600 effects but no N400 effects evoked by semantic violations.

3.1. *Semantic–thematic fit, attraction and reparability*

Perhaps the most obvious commonality between the types of semantic anomalies that evoked a P600 rather than an N400 effect in the studies listed in Table 1 is that they were verb–argument semantic violations in which the argument(s) could have plausibly occupied alternative thematic role(s) around the critical verb, had the syntax allowed. Simply put, many of these semantically incongruous sentences appeared to be repairable by ignoring the syntax and changing the thematic roles of the critical verb's arguments. So, for example, in our own experiments, sentences such as *"Every morning at breakfast the eggs would eat…"*, would make sense if the role of *"eggs"* was changed so that it was no longer an Agent, but rather a

Table 1 – Initial set of studies demonstrating P600 effects and absent (or attenuated) N400 effects to semantic verb–argument violations

Reference	Example of verb–argument semantic violation evoking a P600 effect and an attenuated N400 effect	Thematically restructured sentence
Kuperberg et al., 2003b. See also: Kuperberg et al., 2006a and Kuperberg et al., 2007b	Every morning at breakfast the eggs would eat…	Every morning at breakfast the eggs would be eaten…
Kim and Osterhout, 2005 Experiment 1	The hearty meal was devouring…	The hearty meal was devoured…
Kolk et al., 2003 See also van Herten et al. (2005)	De kat die voor de muizen vluchtte… The cat that from the mice fled… [a] The cat that fled from the mice… [b]	De muizen die voor de kat vluchtten… The mice that fled from the cat…
Hoeks et al. (2004)	De speer heeft de atleten geworpen. The javelin has the athletes thrown. [a] The javelin has thrown the athletes. [b]	De speer werd door de atleten geworpen. The javelin was thrown by the athletes.

[a] Literal word-by-word translation.
[b] Paraphrased translation.

Table 2 – Terminology

Term used in this review	Definition	Example and explanation
Semantic–thematic fit or attraction or reparability.	The likelihood that a particular noun plays a particular thematic role around a particular verb (regardless of a sentence's syntax).	In all the sentences listed in Table 1, the arguments can be said to be semantically–thematically attracted to the critical verbs and, as illustrated in Table 1 right, these sentences are all repairable. In Kuperberg et al. (2006a), *"cameras"* and *"interview"* are not thematically–semantically attracted: *"cameras"* is an unlikely theme of *"interview"*. In Kim and Osterhout Experiment 2 (Kim and Osterhout, 2005), *"tabletops"* and *"devouring"* are not thematically–semantically attracted: *"tabletops"* is an unlikely theme of *"devouring"*.
Lexico-semantic association	The likelihood that groups of content words have been previously encountered together in text or speech. While free association norms will often pick up closely associated words, measures such as a *Latent Semantic Analysis* (Landauer and Dumais, 1997; Landauer et al., 1998) can derive more subtle measures of semantic association. These are based not only on lexical co-occurrence but also on context information extracted from a large text corpus.	The content words within all the examples listed in Table 1 are, as a group, semantically associated.
Thematic by violation	A violation of the thematic *structure* of a predicate, i.e. of the number or types of arguments taken by that predicate. It is closely related to the syntax but can often be derived from the meaning of verbs and their arguments. Verbs can be grouped into classes with broadly similar meanings and the same thematic–semantic structures and syntactic behaviors (Levin, 1993). Note that violations of thematic structure will include semantic verb–argument violations that may be semantically–thematically attracted, non-attracted, semantically associated or not associated.	All the sentences listed in Table 1 except those of Kolk et al. (2003), can be considered thematic violations: the inherent thematic structure of the critical verb is violated by one or more of its arguments.
Animacy violation	A violation of thematic structure that arises because of the animacy constraint imposed by a verb on its argument is violated by the animacy of that argument.	All the examples given in Table 1 except for Kolk et al. (2003), are animacy violations. For example, in the studies by Kuperberg et al. *"eat"* is a verb that assigns its subject NP the role of Agent. The thematic structure of "eat" is such that this NP must be animate in nature for the proposition to make sense. *"eggs"* is inanimate in nature and does not have the semantic properties to be able to eat.
Contextual violation	All the above violations can be considered violations of context. However, in this review we use the term contextual violation specifically to refer to incongruities are not violations of the thematic structure of a verb. The incongruity arises at the level of relating the thematic role assigned by the syntax to the entire preceding context.	In Kuperberg et al. (2003a,b) and (2006a): *"Every morning at breakfast the boys would plant…"* Note that, in these previous papers, we have referred to these violations as pragmatic non-thematic-role violations.

Theme, such as in the passive sentence, *"Every morning at breakfast the eggs would be eaten…"*. This potential (but syntactically unlicensed) semantic–thematic relationship between a particular verb and a particular argument has been termed by Kim and Osterhout a semantic–thematic 'attraction' (Kim and Osterhout, 2005) and by us, a potential semantic–thematic 'fit' (Kuperberg et al., 2006a) (Table 2). Thematically repaired versions of each of the example sentences listed in the middle column of Table 1 are illustrated in the right column of Table 1.

In a first follow-up to our original report, we addressed the question of whether the key factor triggering a P600 to semantic verb–argument violations was indeed a semantic–thematic fit or attraction between the critical verb and its preceding argument (Kuperberg et al., 2006a). In this study, we took a closer look at whether the sentences evoking a P600 effect (and no N400 effect) were semantically–thematically repairable. We did this by changing the thematic roles of our original active sentences by constructing passive versions of sentences, and then asking volunteers to rate these passive sentences for plausibility. The passive versions of many of our sentences were plausible. So, for example, the original sentence, *"Every morning at breakfast the eggs would eat…"*, became *"Every morning at breakfast the eggs would be eaten…"*, and this passive sentence was generally rated as highly plausible: *"eggs"* is an unlikely

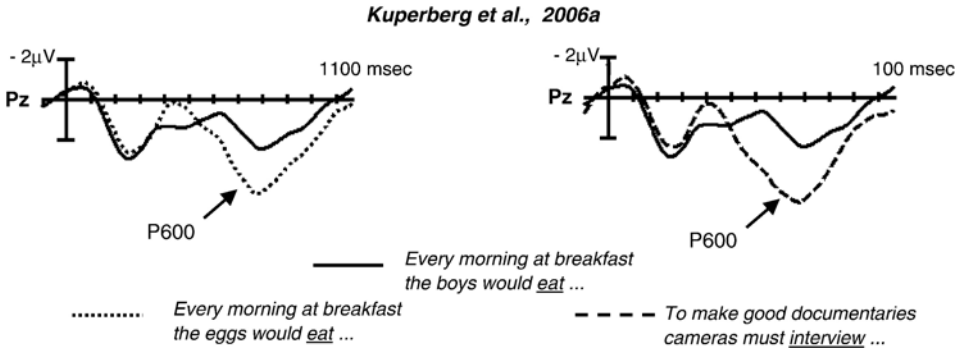

Fig. 4 – A P600 effect is evoked by critical verbs in both semantically-thematically repairable and non-repairable sentences.

Agent but a likely Theme for *"eat"*. However, in other sentences, the NP could not have plausibly occupied an alternative thematic role around the verb. For example, the original sentence *"To make good documentaries cameras must interview…"* became *"To make good documentaries cameras must be interviewed…"* and this was generally rated as implausible: *"cameras"* is not only an unlikely Agent but also an unlikely Theme of *"interview"*.

We then conducted an ERP study with our original active sentences and examined the ERPs evoked by the critical verbs in relation to the plausibility ratings of the passive versions of the sentences. Our logic was that, if the only factor driving the P600 was the presence of an alternative thematic role for the critical verb, i.e. if the P600 was only evoked by semantic violations in highly-attracted, repairable sentences, then violations such as *"interview"* in sentences such as *"To make good documentaries cameras must interview…"*, should not evoke a robust P600 effect. What we in fact found was that verbs such as *"interview"* in such sentences did evoke a robust P600 that, if anything, was slightly more positive in amplitude than the P600 evoked by verbs in the semantically–thematically repairable sentences[1] (Fig. 4). Thus, semantic–thematic reparability alone could not explain the P600 effects evoked by these semantic verb–argument violations.

3.2. *Semantic associations between verbs and arguments*

The study described above suggests that a close semantic–thematic fit or attraction between particular verbs and their preceding arguments is not an essential trigger for a P600 to semantic verb–argument violations. I next consider the possibility that a trigger of a P600 to semantic verb–argument violations is *any* type of semantic associative relationship between a verb and its argument(s). As outlined in Table 2, row 2, I am using the term semantic association not only to refer to the types of close associations produced on word association tasks, but also to the types of semantic associations between words within story scripts that can be captured using measures such as a Latent Semantic Analysis (Landauer and Dumais, 1997; Landauer et al., 1998). Note that the degree to which a verb and its argument are semantically associated does not necessarily translate on to the degree to which they are semantically–thematically attracted (or repairable), although these are often related. So, for example, in our study described above (Kuperberg et al., 2006a), an independent rating study established that the degree of semantic association between verbs and arguments that were semantically–thematically attracted (e.g. *"eggs"* and *"eat"*) was the same as between verbs and arguments that were not semantically–thematically attracted (e.g. *"cameras"* and *"interview"*).

In all the studies listed in Table 1, the critical verb that evoked the P600 effect (and the attenuated N400 effect) was, often, to some degree, semantically associated with its preceding NP argument(s): for example, *"eggs"; "eat"* in our studies (Kuperberg et al., 2006a; Kuperberg et al., in press; Kuperberg et al., 2003b); *"meal"; "devouring"* in Kim and Osterhout (Kim and Osterhout, 2005), *"fled"; "cat"; "mice"* in the studies by Kolk, van Herten, Chwilla and colleagues (Kolk et al., 2003; van Herten et al., 2005), and *"javelin"; "athletes"; "thrown"* in the study by Hoeks, Stowe and Doedens (Hoeks et al., 2004). In addition, there are two other reports by Kolk and colleagues that also describe a P600 effect to critical verbs that were, at least to some degree, semantically associated with their arguments. In Kolk's original study (Kolk et al., 2003), when participants made acceptability judgments (Experiment 1), a P600 effect was evoked by critical verbs such as *"played"* in sentences such as *"The trees that in the park played…"*. And, in a more recent study by van Herten et al., (2006, Experiment 1), a P600 effect was also evoked by verbs such as *"climbed"* in sentences such as *"The apple that in the tree climbed…"*. Unlike the studies listed in Table 1, in both these studies the P600 effect was accompanied by an N400 effect in response to the critical verbs. Taken together, these findings suggest that some degree of semantic association between a verb and its argument(s) may trigger a P600 effect. When these semantic associations are particularly close (as in the studies listed in Table 1), they may also semantically prime the critical verb,

[1] In the same study (Kuperberg et al., 2006a), we also looked at another measure that indexed how easily repairable these sentences were: the subcategorization properties of the critical verbs. We showed that intransitive verbs that would not be able to take the original Agent NPs as direct object Themes, rendering these sentences less easily repairable, evoked a robust P600 that was slightly more positive than the P600 evoked by transitive verbs.

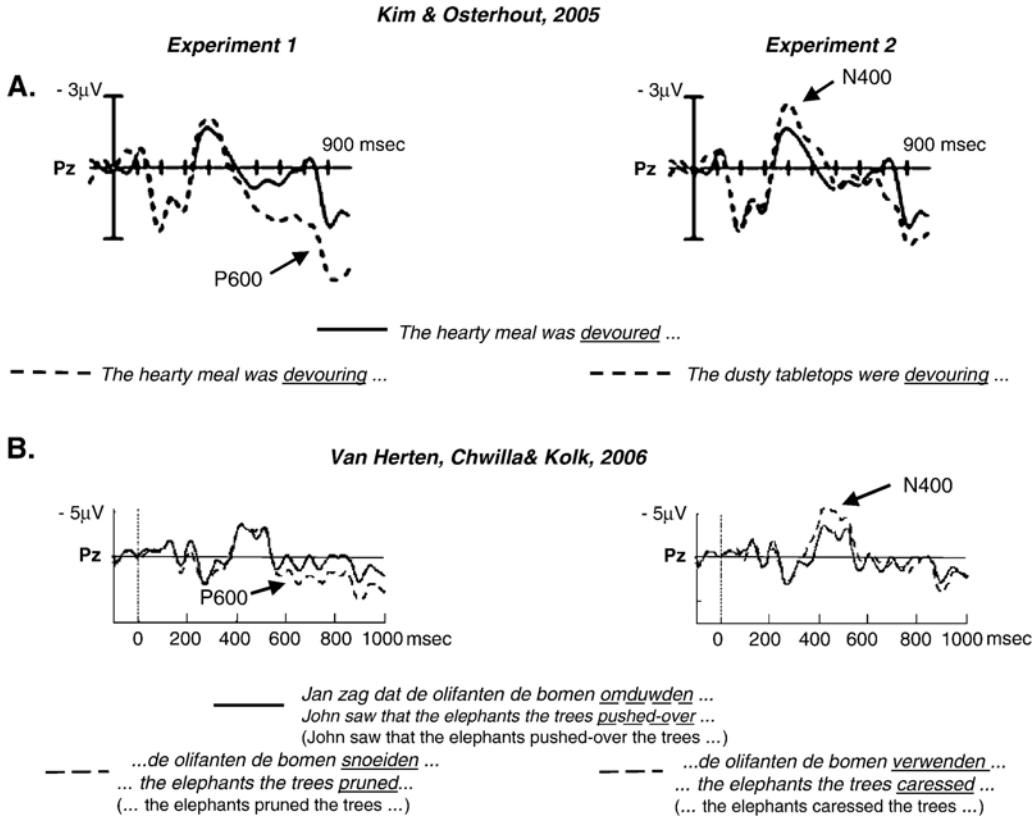

Fig. 5 – The effect of semantic associations between a verb and its argument(s) on the ERPs evoked by that verb.

leading to an attenuation of the N400—a temporary neural 'semantic illusion'.[2]

There is less consistency amongst studies that have examined whether a P600 can be evoked by semantic verb–argument violations in the absence of any semantic association between the verb and its argument(s). Some studies have reported that non-associated semantic verb–argument violations fail to evoke a P600 effect. Recall that, in their Experiment 1, Kim and Osterhout (2005) demonstrated a significant P600 effect to verbs such as *"devouring"* in sentences such as *"The hearty meals were devouring"* (Fig. 5A, left). In a follow-up experiment (Kim and Osterhout, 2005: Experiment 2), they presented participants with sentences of exactly the same structure as in Experiment 1, but this time with no semantic association (or, indeed, no semantic–thematic attraction) between the critical verbs and their preceding arguments (e.g. *"The dusty tabletops were devouring…"*). In these sentences, verbs such as *"devouring"* evoked an N400 effect rather than a P600 effect relative to non-violated verbs (Fig. 5A, right). Also in a follow-up experiment, van Herten, Chwilla and Kolk (2006, Experiment 2) systematically manipulated the degree of semantic association between the critical verb and one of its arguments (quantified using a Latent Semantic Analysis). They demonstrated that, in sentences such as *"John saw that the elephants the trees pruned…"*, verbs such as *"pruned"* (semantically associated with one of its arguments, *"trees"*) evoked a P600 effect (Fig. 5B, left). But, in sentences such as *"John saw that the elephants the trees caressed…"*, verbs such as *"caressed"* (that were not semantically associated with any of their arguments) failed to evoke a P600 effect and only evoked an N400 effect (Fig. 5B, right). Together, these two studies suggested that a P600 is not evoked by semantic verb–argument violations in the absence of any semantic associative relationships between the verb and any of its arguments.

On the other hand, other investigators have reported significant P600 effects to non-associated verb–argument semantic violations. For example, Friederici and Frisch (2000) reported that, in sentences such as *Anna weiß, dass der Kommissar (NOM) den Banker (ACC) abbeizte (V) und wegging./ Anna knows that the inspector (NOM) the banker (ACC) stained (V) and left.",* verbs such as *"abbeizte/stained"* that were not semantically associated with their preceding arguments, *"Kommissar/inspector"* and *"Banker/banker"*, evoked a P600 effect (as well as an N400 effect) (Fig. 6A). Similarly, in their original study, Hoeks et al. (2004) demonstrated that in sentences such as, *"De speer heeft de atleten opgesomd/The javelin has the athletes*

[2] The term 'semantic illusion' has been used to refer to an absent (or attenuated) N400 effect to semantically incongruous or anomalous words in sentences (Hoeks et al., 2004; Nieuwland and Van Berkum, 2005). This has been conceptually linked with phenomena such as the Moses illusion — the failure to register the incongruity in questions such as "How many animals of each kind did Moses take on the ark?" (Erikson and Binder, 1986; Kamas et al., 1996). However, in many of these cases where the N400 to semantic incongruities or anomalies is absent or attenuated, the comprehender does come to the correct conclusion that the sentence is semantically anomalous and, as discussed throughout this review, there is an online cost in processing such semantic anomalies that is reflected by the later P600 effect. I therefore refer to the attenuation of the N400 effect to semantically incongruous words within sentences or discourse more conservatively as a temporary neural semantic illusion.

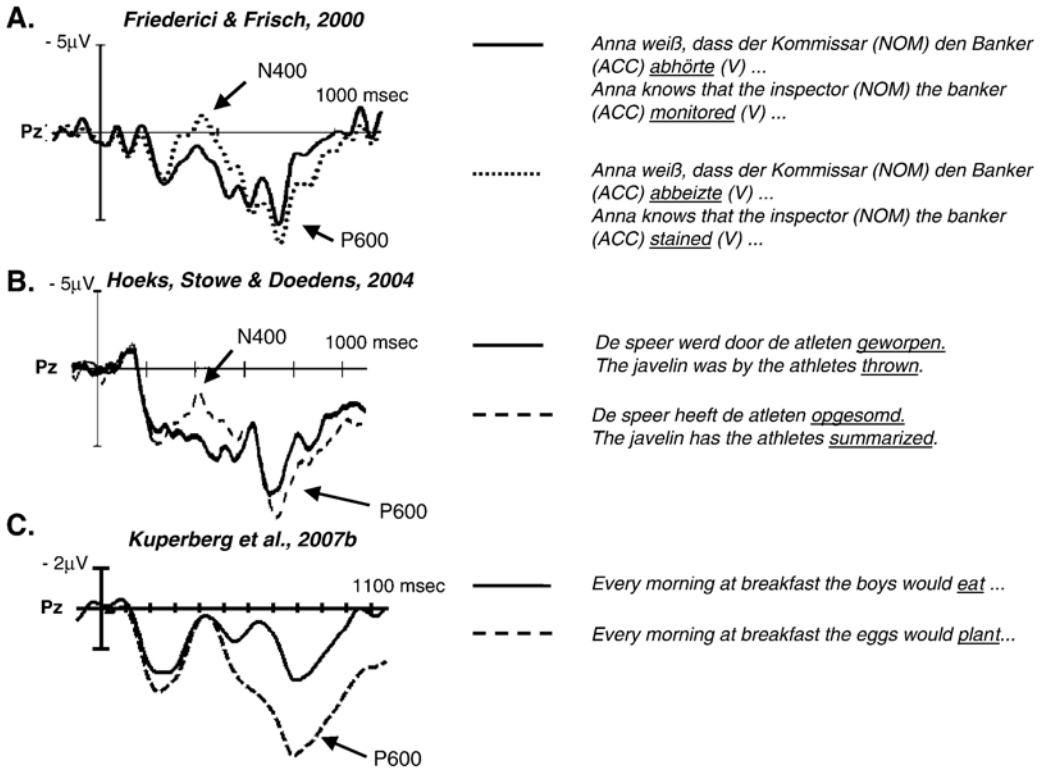

Fig. 6 – P600 effects evoked by semantic verb-argument violations in absence of associations between critical verbs and their arguments.

summarized", verbs such as "*opgesomd/summarized*" that were also not associated with their arguments, "*speer/javelin*" and "*atleten/athletes*", also evoked a robust P600 effect (as well as an N400 effect) (Fig. 6B). Finally, in a second follow-up study conducted in our lab (Kuperberg et al., in press), we presented participants with our original semantic verb–argument violations in which there were often some semantic associations between the critical verbs and their preceding arguments (e.g. "*Every morning at breakfast the eggs would eat…*"), as well as with sentences in which there were no semantic associations between the critical verbs and their preceding arguments (or, indeed, between the critical verbs and any other content words in the introductory clause, see Section 3.6), e.g. "*Every morning at breakfast the eggs would plant…*". We showed that the non-associated semantically violated verbs in these sentences still evoked a robust P600 effect[3] (Fig. 6C).

[3] Interestingly, unlike the non-associated semantic verb-argument violations presented by Hoeks et al. (2004) and Friederici and Frisch (2000) that evoked fairly robust N400 effects in addition to P600 effects, the non-associated semantic verb-argument violations in this study only evoked a very small N400 effect at some electrode sites that was no larger than the N400 effect evoked by the associated semantic verb-argument violations. This led us to infer that, under some circumstances, the attenuation of the N400–temporary 'neural semantic illusion'–may have been related to the generation of the P600 itself: either the neurocognitive process underlying the P600 may have 'switched off' the underlying process generating the N400, or the P600 may have temporally overlapped with the N400, leading to cancellation of the N400 on the scalp surface.

I will discuss possible reasons for these inconsistencies between findings in Sections 3.6 and 3.7. For now, note that, although a P600 effect to semantic verb–argument violations is more commonly evoked when there is at least some semantic association between the verb and its argument(s), it is still possible, under some circumstances, to evoke a P600 to semantic verb–argument violations without these verbs and arguments being semantically associated.

3.3. *Violating a verb's thematic structure: the role of animacy*

In surveying the studies that have reported a P600 effect to semantic verb–argument violations, another commonality emerges. In many of these studies (although, notably, not in the two studies by Kolk and colleagues; Kolk et al., 2003; van Herten et al., 2005), the semantically violated critical verbs that evoked the P600 effect were preceded by inanimate subject NP arguments, even though, in many cases, these verbs could only plausibly assign the role of Agent to a subject NP that was animate in nature (Jackendoff, 1978). Thus, regardless of whether these verbs were semantically–thematically attracted or not to their specific preceding inanimate NPs, the inherent thematic structures (for definition, see Table 2) of these so-called Agent-Theme or Experiencer-Theme verbs were violated by the inanimate nature of the Agent NP. We suggested that, in our studies, these types of animacy violations were critical to evoking the P600 effect.

We have recently collected additional data suggesting that violations of animacy constraints can play a key role in evoking

a P600 (Paczynski et al., 2006). We constructed passive sentences beginning with stems such as, *"At long last the man's pain was understood by the…"*. As in our previous studies, we manipulated the animacy of the Agent NP but, in this study, we fully crossed animacy with the semantic associative relationship between the critical NP and its preceding verb and context. Also, unlike our previous studies, we measured our ERPs on the Agent NP rather than on the verb. We contrasted ERPs evoked by congruous animate nouns (e.g. *"doctor…"*) with incongruous animate nouns that were semantically associated (e.g. *"hypochondriac…"*) or not associated (e.g. *"violinist…"*) with the preceding context, as well as with animacy violated inanimate nouns that were associated (e.g. *"medicine…"*) or not associated (e.g. *"pens…"*) with the preceding context. Only the animacy violations, regardless of semantic association, evoked a significant P600 effect (although, unlike our previous studies on verbs, both types of animacy violation also evoked a significant N400 effect). Although the amplitude of the N400 evoked by the contextually incongruous animate nouns was attenuated by semantic associations between the critical noun and preceding content words (the N400 to *"violinist"* was larger than to *"hypochondriac"*), neither the N400 nor the P600 evoked by the animacy violated inanimate nouns were modulated by semantic association (there were no differences in the amplitude of the N400 or P600 between *"medicine"* and *"pens"*) (Fig. 7).

This set of findings has two implications. First, it suggests that a P600 effect is not only evoked by verbs whose thematic structure is violated by their preceding inanimate NPs, but that it can also be evoked by nouns that violate the thematic structures of their preceding verbs. Second, it is consistent with the idea that the brain may recognize animacy as a 'special' semantic feature that has particular implications for determining thematic relationships between verbs and arguments. From a theoretical perspective, animacy is closely bound up with thematic–syntactic structure (Jackendoff, 1978). In some languages, different levels of animacy (human, animal, inanimate) are evident in the grammar, with certain nouns taking specific verb forms according to their rank in this animacy hierarchy (Frishberg, 1972; Young and Morgan, 1987). And, in other languages (split-ergatives), animacy can condition case markings such that more animate entities (more likely to be Agents than Patients) are unmarked in the Agent role but are marked in the Patient role (Blake, 1994; Dixon, 1994; Silverstein, 1976).

A special role of animacy in influencing online neural processing is also consistent with other ERP evidence. Weckerly and Kutas (1999) demonstrated larger P600 effects (not N400 effects) on verbs such as *"inspired"* in object-relative sentences such as *"The novelist that the movie inspired…"* relative to verbs such *"praised"* in object-relative sentences such as *"The movie that the novelist praised…"*. Although both these sentences are grammatically correct, in the former, the verb *"inspired"* assigns a thematic role of Agent to the inanimate NP *"movie"* and the role of Theme to the animate NP, *"novelist"*. This conflicts with the roles of Agent and Theme that are more commonly taken by animate and inanimate NPs respectively. There was no such conflict on *"praised"*. Similar processing costs associated with contrasting these types of sentences have been observed in first-pass eye movements (Traxler et al., 2002) and in fMRI studies using hemodynamic measures (Caplan and Chen, 2006; Chen et al., 2006).

While animacy appears to be an important factor in influencing whether a P600 effect will be evoked by semantic verb–argument violations, there is no one-to-one relationship between animacy violations and the P600. All animacy violations do not lead to P600 effects. As we have seen, in the follow-up Experiment 2 by Kim and Osterhout (2005), verbs such as *"devouring"* in sentences such as *"The dusty tabletops were devouring thoroughly"* failed to evoke a P600 effect but rather produced an N400 effect (Fig. 5A, right). And, in an earlier experiment, Rösler et al. (1993) showed that verbs appearing in their past participle form and violating the animacy constraints of their preceding object NPs, such as *"murdered"* in sentences such as *"the honey is being murdered"*, also failed to evoke a P600 effect but rather produced an N400 effect. Moreover, as is evident from the studies by Kolk, van Herten, Chwilla and colleagues (Kolk et al., 2003; van Herten et al., 2005) using contextually incongruous semantically reversible sentences and from the example given above from the study by Friederici and Frisch (2000), it is possible for a verb-argument semantic violation to evoke a P600 effect without violating animacy constraints.

3.4. *Plausibility*

So far, we have seen that it is possible for the P600 effect to be evoked by animacy violations, even in the absence of close semantic associative relationships or close semantic–thematic attractions between critical verbs and their arguments.

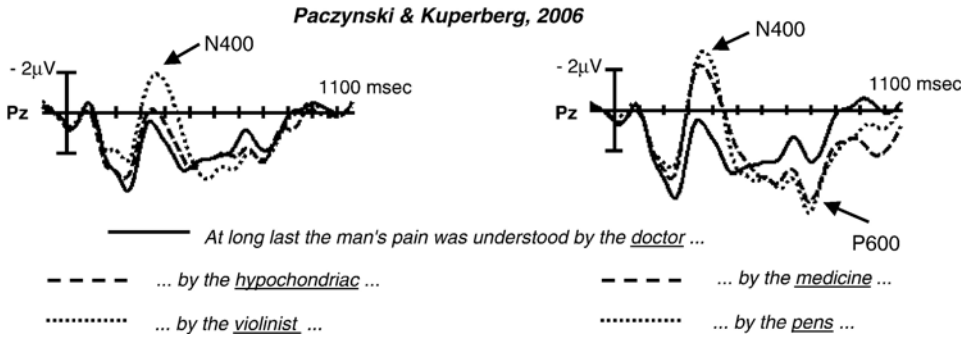

Fig. 7 – Animacy violated Agent nouns evoked a P600 effect, regardless of semantic association.

However, we have also seen that a P600 effect seems more likely to be evoked by semantic verb–argument violations (including those that do not violate animacy constraints; Kolk et al., 2003; van Herten et al., 2005) when there is some degree of semantic association between the verbs and their arguments. One way of understanding these observations is in terms of plausibility. Specifically, one trigger for the P600 might be the syntactic assignment of thematic roles that lead to completely impossible interpretations. Indeed, this may be the reason why a P600 is evoked by animacy violations which always lead to impossible interpretations (e.g. *"Every morning at breakfast the eggs would eat…"*: an egg simply does not have the semantic properties to carry out the action of eating) as opposed to pragmatic/semantic violations that lead to possible but implausible interpretations (e.g. *"Every morning at breakfast the boys would plant…"*: boys can plant; it is just unlikely for them to do so at breakfast). As discussed in Section 4.4, such an account assumes a system in which real-world plausibility is assessed online as propositional meaning is built up, word by word.

We have recently conducted a study in which we systematically investigated the effects of plausibility, determined using independent plausibility ratings, on ERPs evoked by semantic violations between verbs and object NPs in very simple sentences (Geyer et al., 2006). We found that, when participants made plausibility judgments, object nouns such as *"birthday"* in relatively implausible sentences such as *"Tyler canceled the birthday…"* evoked only an N400 effect (relative to nouns such as *"subscription"* in highly plausible sentences, such as *"Tyler canceled the subscription…"*). However, nouns such as *"tongue"* in sentences that were rated as impossible, e.g. *"Tyler canceled the tongue…"* evoked not only an N400 effect (of the same amplitude), but also a P600 effect (Fig. 8). These observations are consistent with the idea the P600 produced by semantic verb–argument violations may be related to the perceived *impossibility* of these violations, and further suggest that selection restrictions other than animacy can influence this perceived impossibility.

3.5. *What participants are asked to do*

We have seen that whether a P600 effect and/or an N400 effect will be evoked by semantic verb–argument violations can be influenced by more than one factor including animacy and semantic association. This picture is further complicated by interactions between these factors and the task participants are asked to perform as they process sentences. In most of the studies reviewed above, participants made explicit acceptability or plausibility judgments about the sentences. It has long been recognized that this task tends to evoke late positivities on sentence-final words (Friedman et al., 1975). Note, however, that in almost all of these studies, the critical word was encountered before the end of the sentence and that the acceptability decision was delayed until after the sentence-final word. Moreover, despite the task being held constant throughout the experiments, P600s were only observed on some types of semantic violations and not on others.

The effect of task in many of the paradigms described above has not been carefully explored, but there is some evidence that an acceptability judgment makes it more likely that certain types of verb–argument semantic violations will evoke a P600. For example, in Kolk et al. (2003), critical animacy violated verbs such as *"played"* in the sentence, *"The trees that in the park played…"* evoked a P600 effect (and no N400 effect) when participants made explicit sentence acceptability judgments about these sentences (Fig. 9A, left), but when participants simply read the sentences for comprehension (in an Experiment 2), the same critical words evoked an N400 effect and no P600 effect (Fig. 9A, right). And, in our study examining the effects of plausibility (described above in Section 3.4), impossible violations evoked a P600 effect (and an N400 effect) when participants made plausibility judgments (Fig. 9B, left) but when we repeated the same experiment without this requirement, the impossible violations such as *"Tyler canceled the tongue…"* failed to evoke a P600 effect (Geyer et al., 2006) (Fig. 9B, right).

In the past, task-specific modulations of late positivities evoked by semantic or syntactic violations have sometimes been used to dismiss the theoretical relevance of these late positivities to understanding language processing. Three arguments have been raised. First, some have taken it as evidence that the P600 evoked by linguistic violations is part of the P300 family of waveforms elicited by task-relevant, rare (oddball) stimuli outside the language domain (Coulson et al., 1998). A second point, often raised in this context, is that, if the P600 is not specific to language processing, it does not give helpful information about how language is processed. The third point is that, because acceptability or plausibility judgment are tasks that are artificially imposed by an experimenter in the laboratory, any modulation of the P600 by such tasks tells us little of importance about how language is processed in the real world. Although these three points have often been raised in consort, my own view is that they are orthogonal issues.

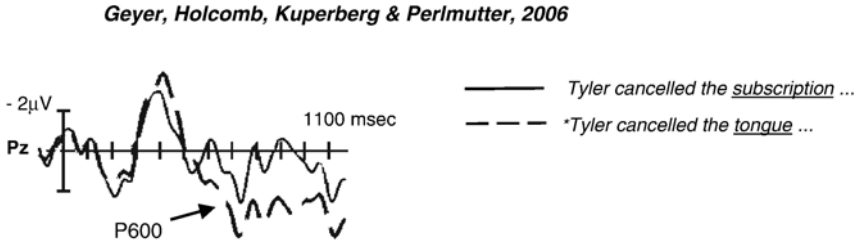

Fig. 8 – A P600 effect can be evoked by violations that lead to impossible interpretations when participants carry out a plausibility judgment task.

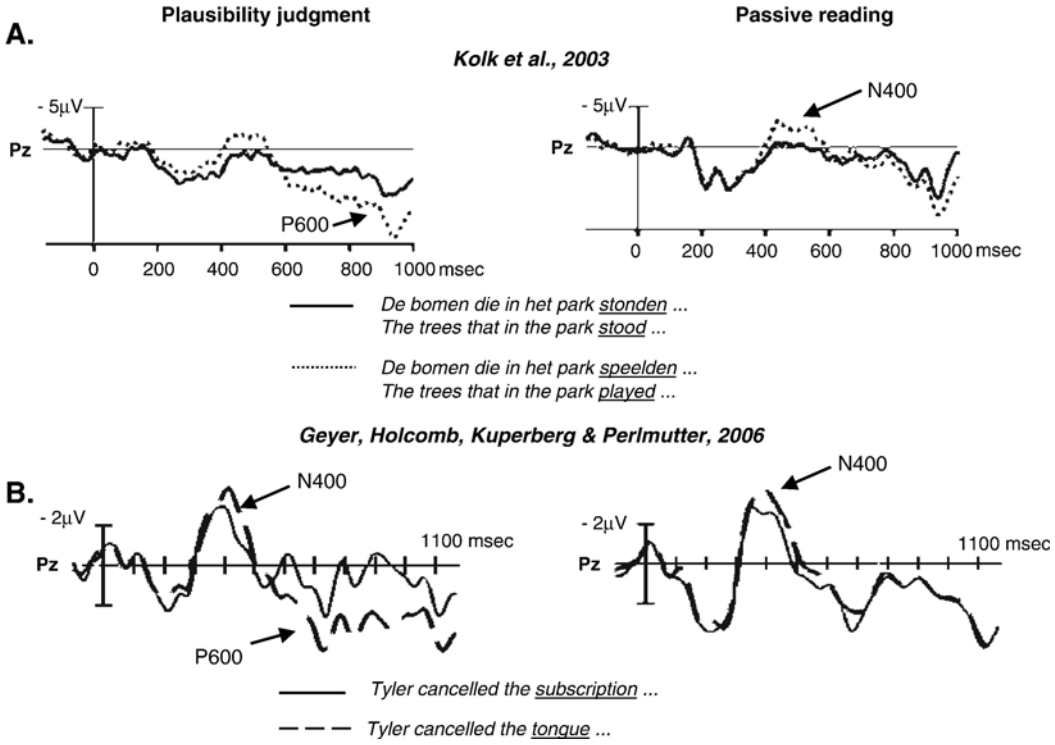

Fig. 9 – The effect of task in determining whether certain types of semantic violation evoke a P600 effect.

First, the question of whether a P600 evoked by semantic (or syntactic) violations is part of the P300 family of waveforms remains open: there is currently empirical evidence for (Coulson et al., 1998) and against (Osterhout and Hagoort, 1999; Osterhout et al., 1996) this view. Determining whether its underlying neural sources are identical or shared with those underlying the P300 in simpler, non-linguistic paradigms will ultimately come from using ERPs in combination with other techniques such as fMRI and MEG.

Second, if the P600 does share neural sources and/or common cognitive processes with the P300 that is evoked by task-relevant rare stimuli, this would not negate its theoretical importance. Specifically, one would need to explain why some types of semantic violations were more relevant to a plausibility judgment task than others, bringing us back to the more language-specific explanations discussed in this review. Moreover, commonalities between the P600 and the P300 might also tell us something about commonalities between neurocognitive processes underlying aspects of language comprehension and those that mediate information processing in other domains (see Osterhout et al., 2007 and Sections 4.1 and 4.4 for further discussion).

Finally, it seems unlikely that a P600 evoked by certain types of violation in association with a judgment task would have no relevance to normal language processing. This is because, in real life, we are constantly called upon to make decisions on the basis of what we have read or been told, and the degree to which we attend to a sentence's meaning varies according to situation and instruction. Understanding how task instructions and decision requirements modulate the neural dynamics of language comprehension must surely have implications for understanding real-world communication.

3.6. *The role of context*

There is increasing evidence for a role of context in influencing whether a semantic violation between a verb and its argument(s) will evoke a P600 and/or an N400 effect. Perhaps the most striking example of contextual effects comes from a study by Nieuwland and Van Berkum (2005) in which participants listened to stories about a particular topic and ERPs were recorded to object nouns that were related to the overall topic but that violated the animacy constraints of their preceding verbs (e.g. a story about traveling that led up to a woman talking to a *suitcase*). A large P600 effect but no N400 effect was observed on the animacy violated critical word (*"suitcase"*). Yet, without the preceding discourse context, an N400 effect but no P600 effect was observed on these violated nouns (Fig. 10).

In that study, the discourse set up an extensive context, but there is some evidence that even small amounts of context within sentences can influence how the brain will process a semantic violation. Consider again the discrepancy between the findings of our study that revealed a robust P600 effect (but only a small N400 effect) to non-associated animacy violated verbs such as to *"plant"* in sentences such as, *"Every morning at breakfast the eggs would plant…"* (Kuperberg et al., 2007b, Fig. 6C), and the findings of Experiment 2 by Kim and Osterhout (2005) who demonstrated that an N400 effect but no P600 effect to non-associated animacy violated verbs such *"devouring"* in sentences such as *"The dusty tabletops were devouring…"* (Fig. 5A, right). It is possible that the differences in these findings were attributable to the small amount of preceding context used in our sentences (in the above example: *"Every morning at breakfast…"*) as opposed to the

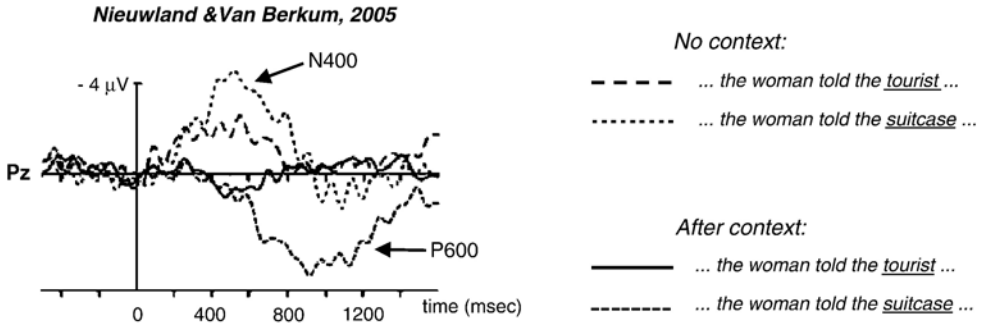

Fig. 10 – The effect of discourse context on determining whether a P600 or an N400 effect is evoked by animacy violations.

sentences used by Kim and Osterhout. Supporting this idea is some preliminary data from our lab suggesting that, if the lead-in context is removed from our non-associated animacy violated sentences, no P600 effect is evoked by the critical verbs.

3.7. Summary and discussion of the necessary and sufficient triggers for a P600 effect to be evoked by verb–argument semantic violations

I have thus far reviewed evidence that, under certain circumstances, semantic violations between verbs and their arguments evoke a P600 effect. This P600 effect can be evoked in the absence of an N400 effect or in addition to an N400 effect. In most of these cases, the P600 is evoked by critical verbs that follow their NP argument(s), but in some cases it can be evoked by the NP arguments themselves.

The simplest account of why a P600 effect is evoked in all these situations is that there is some clue that a later or more prolonged analysis, beyond that which occurs between 300 and 500 ms (the N400 time-window), is necessary or worthwhile. Below I summarize and discuss four factors that, in some combination, appear to influence whether this extra analysis to semantic verb–argument violations is likely to occur.

(1) The syntactic assignment of thematic roles by a verb to its NP argument(s) that violate the animacy constraints, and possibly other selection restriction constraints, of that verb.
(2) The presence of semantic associations between a verb and any of its argument(s).
(3) The performance of an explicit acceptability judgment task.
(4) The presence of a coherent surrounding sentence or discourse context.

Factor (1) is often associated with a P600 effect, but is not always sufficient. It is unclear what exactly it is about animacy violations that can bias towards a P600 effect being evoked. One possibility is that animacy and other thematic constraints are recognized by the processing system as being *syntactic* in nature; a second possibility is that the P600 is triggered by the impossibility of the animacy (and other selection restriction) violations; a third possibility is that the P600 is triggered by a *conflict* between syntactically-driven and semantically-driven competing assignment of thematic roles. These explanations and their implications are discussed in further detail in the next section.

Factor (2) – the presence of semantic associations between verbs and arguments – is once again not always necessary for a P600 to be evoked by semantic verb–argument violations. However, the presence of such associations does appear to increase the likelihood that a P600 will be evoked. In other words, a trigger of the P600 effect appears to be a conflict between the violated thematic roles that are syntactically assigned by a verb to its argument(s) and coherent semantic associations between the verb and its argument(s). Again, it is unclear what exactly it is about such semantic associations that can challenge the syntactic assignment of thematic roles: it may be simply be that these associations match information that is pre-stored within semantic memory, or it may be that such associations are asyntactically combined to form a potentially more *plausible* proposition that challenges the meaning of the highly unlikely proposition that is dictated by the syntactic assignment of thematic roles.

Factors (3) and (4) once again do not act in isolation, but appear to increase the likelihood that a P600 effect will be evoked in the presence of factors (1) and (2). Below I suggest several mechanisms by which acceptability judgments and context might exert their effects. These explanations and any relationships between them remain speculative, but they do suggest future experiments that might explore their roles more systematically.

An acceptability judgment may increase the likelihood of a P600 being evoked by certain types of semantic violation by increasing the comprehender's attention to plausibility. First, an acceptability judgment may bias readers towards paying particular attention to the plausibility of the syntactic assignment of thematic roles. If, as discussed above and in Section 3.4, the resulting interpretation is impossible with respect to our real-world knowledge, then this may be more likely to trigger a P600 effect than if the interpretation is implausible (but possible) with respect to our real-world knowledge. Second, an acceptability judgment may bias readers or listeners towards paying particular attention towards any potential plausibility driven by semantic associative relationships as discussed above. This might, in turn, enhance the conflict between such coherent associative relationships and the violated thematic roles actually assigned by the syntax, once again evoking a P600 effect.

There are a few possible mechanisms by which a congruous context might increase the likelihood of a P600 effect being evoked by semantic verb–argument violations. First, if the content of the context is semantically associated with the anomalous word, this could increases the likelihood that the language processing system detects any coherent semantic associations between the verb and its argument(s), challenging the syntactic assignment of thematic roles as discussed above. This might explain the findings of Nieuwland and Van Berkum (2005) where, in the example discussed in Section 3.6 and shown in Fig. 10, the context described a traveling scenario that was semantically associated with the critical word, *"suitcase"*. A second possibility is that context can introduce syntactic complexity, biasing participants away from assigning thematic roles on the basis of syntactic rules and towards paying relatively more attention to coherent semantic associative relationships or semantic–thematic relationships (for consistent evidence, see findings in syntactically complex, non-canonical sentences Ferreira, 2003). This could again increase the likelihood of a conflict between different representations, triggering a P600 effect. These two explanations, however, would not easily account for why, in the presence of a small preceding context, a P600 effect was evoked by semantically violated verbs (Kuperberg et al., in press) and nouns (Paczynski et al., 2006) that were not semantically associated with any content words in their preceding contexts. It is possible that the very presence of a context that is plausible and that makes sense in its own right motivates participants to try to make sense of anomalies that are initially perceived as impossible (such as animacy violations), in much in the same way as plausibility judgments can modulate the way such anomalies are processed.

What is clear from the discussion above is that factors (1) through (4) do not influence language processing in an all-or-nothing fashion. Rather, the P600 to semantic verb–argument violations appears to be triggered at a particular threshold that can be influenced by some or all of these factors acting in consort. So, for example, in the semantically reversible sentences presented by Kolk and colleagues (*"The cat that from the mice fled ran across the room"*), although the syntax assigns thematic roles that are implausible rather than impossible (it is implausible but not impossible that a mouse could chase a cat), the large discrepancy between this implausible interpretation and the semantic associations between *"mouse"*, *"cat"* and *"chased"* appeared to have been sufficient to evoke a significant P600 effect, even when participants did not perform explicit acceptability judgments, and even in the absence of a biasing context. But, in the same study, sentences such as *"The trees that in the park played…"*, in which the thematic roles that were assigned were impossible, but the semantic associative relationships between *"trees"*, *"park"* and *"played"* were weaker, an acceptability judgment appears to have been necessary to trigger the P600 effect. In Kim and Osterhout's Experiment 2 (Kim and Osterhout, 2005), no P600 effect was evoked by semantic violations between verbs and arguments that were not semantically associated in sentences such as *"The dusty tabletops were devouring…"*, despite the fact that the inanimate noun arguments in these sentences violated the animacy constraints of many of the critical verbs, and despite the acceptability judgments made by participants. But, in our second follow-up study (Kuperberg et al., in press) that also introduced non-associated semantic verb–argument violations in sentences such as *"Every morning at breakfast the eggs would plant…"*, the additional presence of a small amount of preceding context may have been what tipped the processing system past the threshold for extra analysis to occur.

4. At least two neural routes towards language comprehension

I have presented evidence that the precise relationships between a verb and its argument(s) within a sentence influence the degree and timing of online neural activity. Throughout this review, I have referred to the influence of three types of relationships:[4] (1) lexical semantic memory-based relationships—those that relate words in the lexicon through semantic association and through other semantic relationships that are stored within semantic memory (such as categorical relationships or shared semantic properties) without syntactic structure, (2) morphosyntactic relationships—the rules or patterned relationships that govern the way words combine to form sentences, and (3) lexical thematic relationships—the gray zone that lies at the interface between lexical semantic memory and morphosyntax and that describe those aspects of meaning of a verb and its arguments (a subset of all their meanings) that have a direct bearing on the number and types of morphosyntactic arguments assigned by a verb. Thematic relationships can be characterized as being both semantic and syntactic in nature, with different weights being placed on the semantics and the syntax depending on the theoretical linguistic model assumed. In the paragraphs below, I will argue that the processing system computes all three types of relationship online, and, at least partially, in parallel. I will suggest that the current evidence points to the presence of at least two processing streams or routes to comprehending verb–argument relationships within sentences.

The first 'semantic memory-based' stream appears to compute the semantic features, associative relationships and other types of semantic relationships between content words (including verbs and arguments) within a sentence, and to compare these relationships with those that are pre-stored within lexical semantic memory. I will suggest that the N400 event-related potential, is, in part, sensitive to these computations.

This semantic memory-based stream can be contrasted with a second processing stream (or set of streams) that appears to be sensitive to multiple linguistic constraints. At this stage I will use the term 'combinatorial' to describe this stream (or set of streams) to emphasize that it involves the

[4] Note that these three types of relationships are not the only factors that can modulate the N400 and P600 event-related potentials. Although not the focus of the current view, there is also increasing evidence that both these ERP components can be modulated by discourse-level factors such as causality. Also, as discussed later in the review, a late positivity effect can be evoked by violations other than those of syntax or semantics.

combination of words through algorithmic mechanisms[5] to build up higher-order meaning. I will focus on the sensitivity of this stream (or streams) to morphosyntactic constraints as well as to certain types of semantic–thematic constraints such as animacy. I will argue (a) that the combinatorial processing stream operates at least partly in parallel with the semantic memory-based processing stream, and (b) that the P600 reflects a continued analysis within the combinatorial stream that occurs when its first-pass output is unlicensed or anomalous, and that this continued analysis is most likely to occur when this first-pass output contradicts a more coherent semantic representation that is output by the semantic memory-based stream. I will suggest that the operation of such distinct but interactive neural processing streams paints a picture of language comprehension that is less syntacto-centric and more dynamic than has often been assumed.

4.1. *The semantic memory-based stream and its relationship with the N400*

As reviewed in Section 2, the N400 is sensitive to associative and categorical relationships between individual words and, even at the sentence and discourse levels of processing, its amplitude is modulated by such associative and categorical semantic relationships. Kutas and Federmeier (Federmeier and Kutas, 1999; Kutas and Federmeier, 2000) have suggested that there exists a route or stream towards language comprehension that continuously evaluates the meaning of content words and their semantic relationships against lexico-semantic information and relationships stored and structured within semantic memory. In the case of verbs and their arguments, I suggest that such relationships are computed, regardless of their implications for syntactic stucture, between 300 and 500 ms.

Exactly how this semantic memory-based processing operates is unclear. One possibility is that there is a continuous comparison between the semantic relationships between incoming content words and those relationships that are stored within semantic memory, to determine whether or not there is a match or a mismatch. Another possibility is that the meanings of the verb, argument(s) and other content words are first combined through pragmatic or inferential heuristic mechanisms into tentative propositions (a 'quick and dirty' means of deriving the gist of a proposition) and that it is the *plausibility* of this proposition as a whole that is then evaluated against real-world knowledge that is stored within semantic memory.

This view is not to say that the N400 is *entirely* modulated by semantic associations between individual content words and that it only reflects the operation of this semantic memory-based processing. The fact that the N400 can also be modulated by both sentence (Hoeks et al., 2004) and discourse (van Berkum et al., 1999) level contexts, regardless of semantic association, suggests that that the N400 can be influenced by the outcome of syntactically-driven combinatorial processing that determines the build-up of such propositional content within sentences (discussed further below). There is also some evidence that the amplitude of the N400 evoked by semantic violations can be increased by certain types of syntactic violations (Hagoort, 2003). However, the fact that the N400 can be modulated by semantic associative relationships and by semantic memory structure, even at the sentence and discourse levels, suggests that semantic memory structure plays an immediate role in comprehension.

The immediate influence of semantic associative relationships on sentence and discourse processing has consequences for how the N400 is interpreted. It suggests that in cases when coherent semantic relationships contradict or conflict with a syntactically-determined propositional meaning, the amplitude of the N400 may not necessarily reflect the difficulty of semantically integrating a word into the final product of comprehension. More specifically, it suggests that, in cases of such conflict, the N400 can be attenuated, even when the overall sentential meaning is semantically anomalous. This is what appears to happen in all the studies illustrated in Table 1 where, despite the overall implausibility or impossibility of the sentences, there was no significant N400 effect, introducing a temporary neural semantic illusion. As I will discuss further below, this conflict between the output of the semantic memory-based stream (manifest as the temporary neural semantic illusion) and the syntactically-determined assignment of thematic roles that are output by the combinatorial stream, will lead to continued combinatorial analysis, reflected by a P600 effect. It is also possible that a temporary neural semantic illusion may, in some cases, arise if this continued analysis begins within the N400 time-window and 'switches off' the underlying neural semantic integration process that is reflected by the N400 (see footnote 3).

4.2. *The combinatorial stream(s) and the P600*

The second mechanism or set of mechanisms combines words to build up propositional meaning on the basis of multiple constraints. For now, I focus on two types of constraints: morphosyntactic constraints, and certain types of semantic-thematic constraints (such as those determined by animacy) that describe those aspects of meaning of a verb and its arguments that have a direct bearing on the combination of words to build up sentence structure, and that have morpho-syntactic implications. Note that the semantic features that influence these thematic relationships form only a *subset* of all types of semantic features and relationships stored within semantic memory. I suggest that both syntactically-driven and semantic-thematically-driven combinatory processing operate at least partially in parallel with the semantic memory-based mechanism: such combinatory processing may begin within the N400 time window and its outcome may modulate the amplitude of the N400 component itself. However, under certain circumstances, it will continue after the N400 time window is over in which case it is reflected by the P600 component, i.e. the P600 reflects a continued combinatory analysis.[6] Moreover, I

[5] The processing mechanisms can be considered 'algorithmic' in that they may involve the operation of sets of principles and rules. However, I have avoided this term to describe the stream itself because it implies that such rules are instantiated in a step-by-step linear fashion which may not necessarily be the case.

[6] In this review I refer to the P600 broadly as reflecting a continued analysis rather than referring specifically to a reanalysis. This is because the term 'reanalysis' has been used by different researchers in different ways and what 'counts' as reanalysis can vary depending on the processing model assumed.

suggest that understanding the precise circumstances under which this continued combinatorial analysis occurs can give us important information about its very nature as well as its interactions.

As discussed in Section 2, the P600 is classically associated with outright syntactic violations or with the recovery of a non-preferred reading in syntactically ambiguous sentences. As also discussed, the amplitude of the P600 evoked by syntactic violations can be modulated by semantic expectancy as assessed by close probability (Gunter et al., 2000). In other words, even in cases of unambiguous syntactic violations, the P600 appears to be sensitive to a conflict between the output of a failed morphosyntactic parse (the violation of morphosyntactic constraints) and the coherent semantic representation that is output by semantic memory-based processing. This suggests that the interaction between the semantic memory-based stream and the combinatorial stream(s) is not one-way: in just the same way as the amplitude of the N400 can be modulated by the output of the combinatorial stream as outlined above, a coherent output of a semantic memory-based analysis appears to interact with morphosyntactic processing and determine whether it should continue. Indeed, there is some evidence, at least in written sentence comprehension, that a P600 will not be evoked at all if the full meaning of individual words is not accessed; Munte et al. (1997) demonstrated that agreement violations within pseudoword Jabberwocky sentences failed to evoke any P600 effect, even in the presence of other ERP effects to these violations (although note that this is not necessarily the case when Jabberwocky sentences are presented in the auditory domain; (Hahne and Jescheniak, 2001)).

The current review has focused on the situations in which a P600 is evoked by verb–argument structures that violate semantic–thematic constraints such as animacy. What we have seen is that, like the P600 evoked by unambiguous syntactic violations and syntactic ambiguities, the P600 evoked by semantic verb–argument violations is more likely to be evoked in the presence of close semantic associations. Once again, this suggests that the outcome of semantic memory-based processing interacts directly with the output of the combinatorial stream that recognizes the violation of such semantic verb–argument structures and that, in the face of this conflict in representations, continued combinatorial processing again takes place. This explains why such a prolonged combinatorial analysis reflected by the P600 effect is often accompanied by the temporary neural semantic illusion referred to above (as in all the examples given in Table 1).[7]

This review has also focused on the important question of why certain types of semantic–thematic verb–argument violations should be recognized as violations by this combinatorial processing stream or streams, rather than by the semantic memory-based stream, and what they have in common with morphosyntactic violations. The first possibility is that certain semantic features such as animacy are unique and lexically marked in such a way that they are recognized by the same combinatorial processing stream that computes morphosyntax (see Section 3.3). On this account, when these animacy constraints between a verb and its argument(s) are violated, such violations are recognized by the processing system as being *syntactic*, not semantic, in nature. Supporting this hypothesis is a study in which we directly compared the P600 evoked by semantic verb–argument violations such as *"…the eggs would eat…"* (animacy violations) and the P600 evoked by morphosyntactic violations such as *"…the boys would eats…"* and showed that they shared similar time courses, morphologies and scalp distributions (Kuperberg et al., 2006a). This argument could be extended to encompass not only the recognition of animacy violations, but all types of semantic–thematic violations that have implications for determining syntactic structure.

A second possibility is that animacy or thematic structure is not recognized as being syntactic at all, but rather that the propositional output of the syntactically-driven combinatorial parse (its assignment of thematic roles) is passed on to semantic memory during online processing and evaluated as being impossible (and not simply implausible) with respect to real world knowledge (Section 3.4). On this account, the conflict that triggers the continued combinatorial analysis, reflected by the P600 effect, is not between a failure of *syntactic*–thematic combinatorial processing and a coherent semantic memory-based output, but rather, between the impossible propositional meaning that the syntactically-driven combinatorial processing outputs and the plausible propositional meaning that the semantic memory-based stream outputs (see also discussion by Kolk, van Herten, Chwilla and colleagues; Kolk et al., 2003; van Herten et al., 2006; van Herten et al., 2005).

Note that the explanations discussed above place the burden of evaluating the output of a thematic–semantic verb–argument parse on syntax (explanation 1) or on semantic memory (explanation 2). A third possibility is that the combinatorial stream recognizes the *semantic* nature of the thematic violation. This is not quite the same as claiming that animacy violations and certain other types of semantic violations are recognized as being syntactic in nature. Rather, the suggestion is that the combinatorial processing stream is divisible such that, independently of computing sentence structure on the basis of morphosyntactic constraints, some sentence structure is built up on the basis of primitive semantic features (such as animacy) that are relevant to verb meaning but that form only a subset of all those features recognized by the semantic memory-based stream. On this account, another trigger for the P600 is the conflict between the output of such a semantically-driven combinatorial stream and the output of a morphosyntactically-driven combinatorial stream, each biasing towards different thematic assignments. This hypothesis makes the testable prediction that the P600 might act as a marker of processing cost in the many situations in which there is no 1:1 correspondence between the structure

[7] It is, however, important to recognize that an attenuated N400 effect in the presence of a P600 effect does not necessarily imply a temporary neural semantic illusion. The N400 and P600 components have similar scalp distributions and an overlapping posteriorly-distributed P600 effect might cancel out any appearance of the N400 effect (of opposite polarity) at the scalp surface (although note that such cancellation does not always occur: evidence from ERPs to semantic and syntactic 'double' violations suggests that these two component can, at least under some circumstances, be additive (Hagoort, 2003; Osterhout and Nicol, 1999)).

of a sentence that can be predicted purely on the basis of semantic combinatorial relationships and the structure that is actually assigned by the syntax (Culicover and Jackendoff, 2005; Levin and Rappaport Hovav, 2005).

In sum, I have suggested that a continued combinatorial analysis reflected by the P600 ERP component is most likely to occur as a consequence of conflicts in the output of two, or more than two, separable but interactive processing streams: (a) a conflict between a coherent semantic representation that is output by a semantic memory-based stream and a syntactic violation that is recognized by a syntactically-driven combinatorial processing stream; (b) a conflict between a coherent semantic representation that is output by the semantic memory-based stream and an anomalous semantic–thematic representation that is also output by a syntactically-driven combinatorial analysis but that is evaluated as semantically impossible with respect to our real-world knowledge; and/or (c) a conflict between a potentially coherent semantic–thematic representation that is output by an asyntactic *semantically-driven* combinatorial analysis and the anomalous semantic–thematic representation that is output by a *syntactically-driven* combinatorial analysis.

The output of a continued combinatorial analysis, reflected by the P600, is what will ultimately determine the final interpretation of the sentence: in the case of unambiguous syntactic or thematic–semantic violations, a continued combinatorial analysis will lead to the conclusion that there is a violation of morphosyntactic or semantic–thematic constraints and the comprehender will usually (although not always) correctly conclude that these sentences are unacceptable. However, in most garden path sentences, despite the perception of a temporary 'anomaly', the continued syntactically-driven combinatorial parse will usually succeed in assigning thematic roles and the parser will come to the correct conclusion that the sentence makes sense.

4.3. *Relationships with other models of language comprehension*

This view of a non-syntactocentric language comprehension system that is made up of processing streams that are independent but yet closely interactive is not new. In its assumptions that semantic processing occurs at least partly in parallel with morphosyntactic processing, it has much in common with constraint-based models of language processing (MacDonald et al., 1994). Most such models, however, have focused on the influence of semantic–thematic information (and other sources of contextual information) on the build-up of syntactic structure and have placed less weight on the influences of lexical semantic associative information. Moreover, most models of language processing – both constraint-based and serial – have focused primarily on the influences of non-syntactic information (including semantic–thematic relationships) on the resolution of syntactic ambiguity within sentences (Boland and Tanenhaus, 1991; MacDonald et al., 1994; Tanenhaus and Carlson, 1989; Trueswell and Tanenhaus, 1994) and, more recently, on the costs of processing syntactically complex, non-canonical sentences (Caplan and Chen, 2006; Chen et al., 2006; Traxler et al., 2002). The model described in this review, on the other hand, holds that semantic relationships (both semantic memory-based associations and semantic–thematic relationships) can challenge the build-up of syntactically determined structure, even when the syntax is very simple and non-ambiguous. It thus affords semantics a more powerful role in challenging the syntax than has often been assumed.

The idea that the build-up of syntactic structure can be challenged and, in some cases, even overcome by additional streams of processing also has features in common with language processing models that have emphasized the operation of heuristic mechanisms in influencing comprehension (Ferreira, 2003; Ferreira et al., 2002; Garrett, 2000; Townsend and Bever, 2001). In these models, heuristic strategies are thought to compete with deeper algorithmic (combinatorial) syntactically-driven analyses to influence sentence interpretation. Indeed, there is evidence that, in syntactically ambiguous sentences and in non-canonical, syntactically complex sentences, these heuristic mechanisms can sometimes lead participants to come to final interpretations ('good enough' representations) that are not syntactically licensed (Caplan et al., 1994; Christianson et al., 2001; Ferreira, 2003; Ferreira et al., 2002; Saffran et al., 1998; Sanford, 2002). Several heuristic mechanisms have been discussed in such models. One is a plausibility heuristic that is based on semantic relationships between individual words. This is similar to the semantic memory-based stream of processing discussed here: matching groups of words to what has been stored within semantic memory could be conceived of as a heuristic short-cut to deriving the gist of a proposition. A second heuristic mechanism that has been discussed as sometimes competing with a syntactically-driven combinatorial analysis, is one in which comprehenders assign roles based purely on the animacy of a NP, i.e. an inanimate entity is taken to be the Theme and an animate entity is taken to be the Agent of a sentence.[8] Future studies will determine whether such an asyntactic thematic assignment based on animacy alone is indeed heuristic in nature or whether it constitutes part of a more systematic semantically-driven combinatorial analysis that is subject to its own rules and representations (as discussed further below).

The existence of parallel competing but interacting neural streams mediating sentence comprehension is also similar to what has been proposed by both Kim and Osterhout (2005) as well as by Kolk, Chwilla and colleagues to explain the P600 effect evoked by certain types of semantic violations.

Kim and Osterhout (2005) have emphasized the role of 'semantic–thematic attraction' in overcoming morphosyntactic constraints (Section 3.1), whereas, in this review, I have subdivided semantic relationships into those that are associative and those that have implications for syntactic

[8] Note that, in canonical sentences such as *"the eggs would eat"*, one would have to assume that this heuristic was even stronger than another common heuristic that has been discussed: the comprehender's tendency to assume that the subject and object of a sentence are the Agent and Theme of the action denoted by the verb (the so-called NVN strategy). In other words, in these sentences, participants might assume that the inanimate entity *"eggs"* was the Theme of the sentence, rather than the Agent (as dictated by a NVN strategy), and this animacy heuristic would compete and conflict with the morphosyntactic assignment of the role of Agent to *"eggs"* by the verb.

structure, i.e. I have drawn a three-way distinction between (a) semantic associative or categorical memory-based relationships, (b) semantic–thematic relationships—those types of semantic relationships that are relevant for combinatorial processing and (c) morphosyntactic relationships. I have suggested that a P600 might arise when there are conflicts between any two or three of these types of representation. In addition, whereas Kim and Osterhout have argued that 'semantic–thematic attraction' can ultimately 'win' or override morphosyntax altogether, I have discussed lexical semantic associations and semantic–thematic relationships as posing a temporary 'challenge' to the syntax rather than completely overriding it. This is because most parsers, when asked, do come to the correct conclusion that the types of sentences illustrated in Table 1 are unacceptable. In other words, while a semantic memory-based analysis may detect a match between incoming associative lexical semantic relationships and what is stored in semantic memory, and although semantic–thematic relationships might bias towards a coherent interpretation, it is usually a syntactically-driven combinatory parse that ultimately wins out to determine final acceptability decisions. This may not always be the case, however: as discussed above, semantic–thematic relationships that are not syntactically licensed can, under some circumstances, determine participants' final interpretations of sentences (Caplan et al., 1994; Christianson et al., 2001; Ferreira, 2003; Ferreira et al., 2002; Saffran et al., 1998; Sanford, 2002).

Kolk and colleagues have conceived of the P600 as reflecting a monitoring process that, in cases of conflict between different possible sentence interpretations (such as those delivered by semantic memory-based and syntactically-driven combinatorial streams), functions to prevent comprehension errors. As proposed in the current review, monitoring is believed to reflect a continued algorithmic (or combinatorial) analysis that is what ultimately determines the sentence interpretation.[9] The monitoring account emphasizes that this continued analysis constitutes a reprocessing of the input and that this reprocessing (or reanalysis) plays a general role in determining whether what the comprehender heard or read was, in fact, correct. It therefore offers valuable insights by drawing analogies with monitoring reanalyses in other areas of cognition, including speech production (Levelt, 1983) and action monitoring (Yeung et al., 2004). The monitoring hypothesis also emphasizes that the continued analysis reflected by a P600 is not necessarily only syntactic in nature, and second, that it is primarily under executive control. Both these points are discussed in more detail below.

The idea of multiple independent but interactive streams of language processing also has much common with the spirit of the Parallel Architecture of language structure proposed by Jackendoff (2002). The Parallel Architecture suggests that components of language are distinct and yet that they must come together through 'interface rules': it affords phonology and semantic structure the same status as syntax in terms of language generativity. In discussing the implications of this architecture for processing, Jackendoff (2007-this issue) suggests that multiple streams are computed opportunistically and incrementally such that all relevant structures are processed at once in competition with one another. This sort of model predicts processing costs, perhaps reflected by a P600 effect, in cases of conflict between the outputs of these streams.

Jackendoff also considers the evolutionary role of protolanguages as discussed by Bickerton (1990), now manifest most clearly in pidgin languages and at early stages of language development in children, that make use of semantic combinations of individual words without syntax. It is possible that the semantic memory-based comprehension mechanism described above exists as a remnant of an earlier stage of language evolution, and that a system of continued combinatorial analysis, reprocessing and/or monitoring, reflected by the P600, evolved as an inevitable consequence of this double-tiered language system.

Finally, one of the main emphases of the Parallel Architecture is on a generative semantically-driven combination that that can build up sentence structure independently of the syntax. Note, once again, that this type of semantic combination is distinguishable from associative-based semantics: it may not necessarily make use of all semantic features of words, but only those semantic features that are directly relevant for combination. Although this hypothesis still remains to be explicitly tested in processing terms, I have raised the possibility that the combinatorial stream may be divisible into semantic and syntactic combinatorial streams, and that the P600 evoked by animacy violations reflects a continued syntactic combinatorial analysis resulting from a conflict between these semantically-driven and syntactically-driven combinatorial analyses. Also, as discussed further in section 5.3, the generation of a P600 effect (distinct from the N400 effect) by certain types of semantic violations during non-verbal visual event comprehension supports the existence of a neural stream supporting some sort of semantic combination in the absence of morphosyntax, but that is distinct from processing based purely on what is stored within semantic memory.

[9] This group has emphasized the idea that such monitoring does not include any attempt to reassign (or repair) thematic roles (van Herten et al., 2006; van Herten et al., 2005) as if such repair occurred, this might "lead the system away from a veridical sentence interpretation and would bring participants to erroneously evaluate the sentences as plausible". As discussed in Section 3.1, it is clear that the P600 is not only evoked by semantic–thematic violations that are easily thematically repairable. I therefore also view the P600 as primarily reflecting continued algorithmic analysis that does not necessarily involve repair (see Grodner et al., 2003 for a discussion of these types of processes in cases of syntactic ambiguity). However, at this stage, I do not think that we can exclude the possibility that participants make some *attempt* at repairing sentences such as in Table 1: the finding by Kuperberg et al. (2006a) that the P600 was slightly more positive to critical verbs in sentences that were more difficult to repair than in sentences that were easy to repair suggests that the continued analysis reflected by the P600 may have included some attempt at reassigning thematic roles, with a larger P600 evoked when such an attempted repair was more difficult (Kuperberg et al., 2006a). Note, however, that any such attempt at thematic reassignment would, in these sentences, be doomed to failure: it was ultimately the morphosyntax that determined the interpretation of the types of sentences given in Table 1 — participants concluded that they were anomalous.

4.4. *Open questions*

In sum, I have suggested that there exist at least two neural processing streams that are engaged during the online comprehension of verb argument relationships within sentences—a semantic memory-based stream and a combinatorial stream (or streams) that is sensitive to both morphosyntactic and thematic–semantic constraints. The existence of a semantic memory-based processing mechanism ensures that we make maximum use of our prior experience and the existence of combinatorial mechanisms of comprehension ensures that we can compute novel relationships between people, objects and actions. There remain, however, many questions about the nature and relationships between these streams of comprehension.

First, what is the precise temporal relationship between these streams? As highlighted by this review, the N400 and the P600 are often sensitive to the same variables and, at times, they appear to be reciprocally modulated with a P600 being evoked when the N400 is attenuated. This suggests that these streams are highly interactive. However, we also know that, in many situations, the N400 and the P600 can be additive and there is certainly evidence that they are dissociable (Hagoort, 2003; Osterhout and Nicol, 1999). This suggests that they can also act independently. What remains unclear is whether these streams begin at the same time or whether semantic memory-based processing begins prior to combinatorial processing, and/or whether semantic memory-based processing ends before a first pass of combinatorial processing. These questions are, unfortunately, inherently difficult to address using ERPs alone because the N400 and P600 components share similar scalp distributions and they overlap on the scalp surface. Future studies combining ERPs with MEG and/or fMRI may be able to examine the time courses of each of these neural mechanisms more precisely.

A second set of questions relates to the nature of the continued combinatorial analysis observed in response to thematic–semantic violations: is it syntactic in nature and, if so, how does it relate to morphosyntactic processing? Or is this stream divisible into distinct morphosyntactic and semantic sub-streams that each attempt to assign thematic roles? These questions have important implications for understanding how the brain deals with the syntax–semantics interface in processing terms and, more specifically, for understanding whether it recognizes a distinction between semantic associations and semantic features that are 'visible' to the syntax. Indeed, such questions may be relevant for understanding how the brain processes relationships other than those between a verb and its argument(s). For example, in a recent study, Kemmerer et al. (2007) showed that semantically anomalous adjectives that violated grammatical-semantic constraints on linear order (e.g. *"Jennifer rode a gray huge elephant"*), failed to evoke an N400 effect, but rather evoked a robust P600 effect (relative to non-violated adjectives), suggesting that the brain does indeed recognize 'grammatical' lexical semantic relationships as being distinct from associative lexical semantic relationships.

A third set of questions relates to how the P600 effect evoked by syntactic and semantic verb–argument violations relates to late positivities seen in other types of language paradigms. This review has focused on the semantic and syntactic aspects of verb argument structure. It has also been known for some time that late positivities can also be evoked by orthographic violations (Munte et al., 1998), and, more recently, Vissers, Chwilla and Kolk (2006) have reported that this effect is seen when such orthographic violations are derived from words that are semantically expected with respect to the preceding context (e.g. *"In that library the pupils borrow bouks…"*) but not when they are unpredictable (e.g. *"the pillows were stuffed with bouks…"*). They suggest that, in these cases, the P600 effect once again reflects a reanalysis or monitoring process that is triggered by a conflict between streams of processing, but this time the conflict is between the output of a coherent semantic memory-based system and orthographic processing.

This finding does not, of course, negate the implications of the N400 and P600 findings discussed in this review for understanding how semantic memory-based lexical information, thematic–semantic lexical information and morphosyntactic information interact during online neural processing. It does, however, raise some key questions about the underlying neurocognitive process that the P600 actually reflects. There are several possibilities.

The first is that there exist multiple neurocognitive processing streams (mediating different levels of language processing, e.g.. syntactic, semantic–thematic, orthographic), each subserved by a distinct neural network, and the P600 reflects a continued analysis within all of them simultaneously, regardless of the type of anomaly or ambiguity that originally triggered such continued analysis. This, as I understand it, is a claim of the monitoring hypothesis (Vissers et al., 2006).

A second possibility is that, rather than all such streams being reactivated simultaneously, the P600 reflects a continued analysis within the specific stream that detected the violation. On this account, there is little in common with the P600 evoked by different types of violations apart from it reflecting neural activity (and some kind of continued analysis) occurring within the same time window. A third possibility is that activity at these different levels of processing are, at least to some degree, subserved by the same neuroanatomical network and that the P600 reflects activity within this network.

Given the widespread distribution of the P600 effect on the scalp, these possibilities are very difficult to disentangle using ERPs alone and, once again, require the complementary use of techniques with better spatial resolution. The key challenges that therefore face us are to determine the precise triggers for a P600, the levels of language processing to which the P600 is sensitive, and the degree to which it reflects activity within neuroanatomically divisible circuits.

A related set of questions revolve around whether the functional processes reflected by the P600 are exclusively engaged during language processing. I suggest not. As discussed in Section 5.3, a P600 effect is seen during higher-order visual comprehension and we have suggested that it may reflect a continued attempt to assign semantic roles to characters, objects and entities (semantically-based combinatory processing) that is analogous to a continued semantic-thematic analysis during language comprehension. And it is

also possible that combinatorial linguistic processing engages neurocognitive algorithms or nueroanatomical systems that are common to those engaged in computing patterned rule-based sequences outside the language system (Coulson et al., 1998; Osterhout and Hagoort, 1999; Osterhout et al., 2007; Patel et al., 1998; Van Petten et al., 1999).

Finally, returning to the processing of semantic memory-based, thematic–semantic and morphosyntactic relationships that influence verb–argument structure, we have seen that there is a fluid balance in activity between the semantic memory-based processing and combinatorial processing streams: whether an N400 or a P600 is evoked is, to some degree, influenced by both task and by sentence and discourse context. This raises the question of the degree to which this balance can be influenced by top-down control. Indeed, as indicated above, one of the key claims of the monitoring hypothesis is that continued algorithmic analysis is primarily under executive control (see Kolk and Chwilla, 2007 for additional discussion). Determining the mechanisms by which such top-down processes impact on language comprehension is clearly a challenge for future research.

It is clear that there are many unknowns. However, regardless of the answers to all these questions, I suggest that this view of language comprehension as being composed of at least two distinct but interactive streams is important in our conceptualization of it not being at the mercy of syntax, and in particular for understanding the relationship between semantics and syntax in the brain (see also Osterhout et al., 2007 for discussion). I also believe that this view of the language processing system has widespread implications for understanding the nature of language disorders and individual variability, for understanding the neuroanatomical basis of language comprehension and, indeed, for understanding general mechanisms of comprehension outside language domain. In the next section, I discuss some of these implications.

5. Implications

5.1. *Implications for understanding language disorders and individual variability*

The way language disorders have often been understood is in terms of selective deficits at one level of language representation, e.g. semantic *or* syntactic. For example, patients with agrammatic aphasias are usually considered to have syntactic deficits (Caplan, 1992) while language abnormalities in patients with schizophrenia are often viewed as being primarily semantic in nature (Goldberg et al., 1998; Kuperberg and Caplan, 2003). But another way to conceptualize these disorders is in terms of an altered *balance* between the semantic memory-based and combinatorial mechanisms of language comprehension outlined above. This perspective may explain how abnormalities at more than one level of language processing might arise and may, in fact, reflect the opposite sides of the same coin. So, for example, a deficit in combinatorial analysis in brain-damaged, aphasic patients may lead to a relative dependence on the types of semantic memory-based mechanisms discussed here (see Pinango, 2006 for discussion, and, conversely, hyperactivity within the semantic system in schizophrenia (e.g. Kreher et al., submitted for publication) may lead to reduced dependence on combinatorial analyses (see Kuperberg et al., 2006c for discussion).

There is certainly evidence to support this perspective. It has long been recognized that agrammatic aphasic patients show particular problems with interpreting sentences in which the syntax assigns implausible thematic roles but in which an evaluation of items against information stored in semantic memory would lead to a plausible interpretation (Caramazza and Zurif, 1976; Grodzinsky, 2000; Kolk and Weijts, 1996; Saffran et al., 1998). And, using ERPs, Hagoort et al. (2003) reported a relative attenuation of the P600 but an abnormally increased N400 to grammatical violations in such patients.

In patients with schizophrenia, particularly those with clinical language disorganization or 'positive thought disorder', there is evidence both for increased activity to semantic associations between individual words (Kuperberg et al., 2007b; Minzenberg et al., 2002; Sitnikova et al., 2002; Spitzer et al., 1993) as well as for impairments in combining syntactic structure with the meaning of individual words to build up sentence context (Kuperberg et al., 2006b; Kuperberg et al., 1998; Kuperberg et al., 2000b). And, using ERPs, we have shown that, in schizophrenia patients, the P600 effect is absent to violations such as *"eat"* in sentences such as *"Every morning at breakfast the eggs would eat…"* (Kuperberg et al., 2006c).

Moreover, if, as discussed above, the dynamic interplay between these two processing mechanisms is normally modulated by working memory and executive top-down control, this might also explain how abnormalities of executive function and working memory function, including those seen in certain types of aphasias and in schizophrenia, could directly impact upon the language system, altering the balance between the semantic memory-based and syntactically-driven and semantically-driven combinatory mechanisms (see Kolk and Chwilla, 2007; Kolk, 2006 for further discussion in aphasia. It would also explain why individual variability in working memory function amongst healthy individuals predicts whether an N400 or a P600 is evoked by the types of semantic verb–argument violations described in Table 1 (Nakano and Swaab, 2004).

5.2. *The neuroanatomical basis of two mechanisms of language comprehension*

Understanding language comprehension in terms of two interacting processing mechanisms also has implications for understanding its underlying neuroanatomical circuitry. Our understanding of the neuroanatomy underlying the N400 and P600 effects is currently limited. This is because most evidence comes from the use of anomaly paradigms that parallel those used in ERP studies, but that use neuroimaging techniques, such as fMRI, whose temporal resolution is far inferior to that of ERPs, and that cannot index neural activity that is specifically time-locked to the critical anomalous words of interest. Rather, the hemodynamic response measured by such techniques reflects neural activity that is integrated across multiple words as well as across any task that participants are required to perform (see Kuperberg et al., 2003a for discussion). Despite many caveats in interpretation,

the available fMRI evidence suggests that the brain regions engaged to the types of anomalies that evoke N400s in ERP studies are distinct from the regions engaged to the types of anomalies that evoke P600s in ERP studies (both outright syntactic anomalies and semantic–thematic violations). More specifically, we (Kuperberg et al., 2003a; Kuperberg et al., 2000a) and others (Hagoort et al., 2004; Kiehl et al., 2002; Newman et al., 2001; Ni et al., 2000) have shown that semantic incongruities evoking N400s within sentences in ERP studies are associated with the recruitment of posterior superior and inferior temporal regions and/or the left anterior inferior prefrontal cortex.[10] Many of these same regions are activated in studies using pairs or groups of individual words to probe semantic memory function—both semantic encoding (Demb et al., 1995; Kirchhoff et al., 2000; Wagner et al., 1998) and semantic retrieval (Badre et al., 2005; Bokde et al., 2001; Fletcher et al., 2000; Moss et al., 2005; Thompson-Schill et al., 1997; Thompson-Schill et al., 1999; Wagner et al., 2001). Moreover, in semantic priming paradigms, some of the same temporal and inferior prefrontal regions are also modulated by semantic associative and/or categorical relationships between primes and targets (Copland et al., 2003; Giesbrecht et al., 2004; Kotz et al., 2002; Kuperberg et al., 2007a; Kuperberg et al., submitted for publication; Matsumoto et al., 2005; Mummery et al., 1999; Rissman et al., 2003; Rossell et al., 2003; Wheatley et al., 2005). These similarities lend further support to the idea that sentence comprehension involves a constant comparison between semantic associative relationships between incoming words and information stored within semantic memory.

On the other hand, syntactic anomalies of the type that evoke P600s in ERP studies are associated with activity within different sets of brain regions in fMRI studies (Friederici et al., 2003; Kuperberg et al., 2003a; Newman et al., 2001; Ni et al., 2000). Moreover, we have recently gathered data suggesting that some of the same regions that are activated to outright morphosyntactic violations (Kuperberg et al., 2003a) are also activated by the types of animacy semantic–thematic violation that we have shown evoke P600s rather than N400s (e.g. "*…the eggs would eat…*") (Kuperberg et al., 2006d). These regions are widespread and vary between studies, but include middle and superior prefrontal cortices, posterior inferior frontal and motor cortices, and parietal cortices (Friederici et al., 2003; Kuperberg et al., 2003a; Kuperberg et al., 2006d; Newman et al., 2001; Ni et al., 2000). Subcortical regions including the basal ganglia, can also be engaged (Friederici et al., 2003; Kuperberg et al., 2006d)—a finding that is consistent with lesion studies suggesting that these regions may be a source of the P600 (Friederici et al., 1999; Kotz et al., 2003).

The functional roles of each component of this widespread network, and how they relate to the P600, remain unclear, and their engagement may reflect the operation of more than one neurocognitive process. One possibility is that the prefrontal-basal ganglia circuitry – known to play a role in building sequences of actions (Graybiel, 1995; Graybiel, 1998) – evolved to play a specific role in syntactically-based language systems (see Osterhout et al., 2007 for discussion) and that the activation of posterior inferior frontal, motor and parietal cortices reflects the involvement of a mirror neuron system that provides an evolutionary link from motor action to aspects of syntax (Arbib, 2005; Kemmerer, 2006).

These ideas linking syntactic processing with action in the real-world are exciting (see also Section 5.3) but they are currently speculative. What we can say, at this stage, is that the existing functional imaging evidence is consistent with the existing ERP evidence in suggesting that at least two different neural processing streams operate during language comprehension—one that appears to evaluate incoming semantic associative and categorical information against information that is prestored within semantic memory (mediated by inferior prefrontal and temporal cortices), and another widespread network that appears to be more sensitive to both morphosyntactic and thematic–semantic relationships, and that is engaged when the rules governing these realtionships are violated.

5.3. *Two mechanisms of comprehension: insights based on non-verbal comprehension*

Finally, understanding language processing in terms of these two neural mechanisms has implications for considering the generalizabilty of such neural mechanisms beyond the language system. It has been known for some time that waveforms similar to the verbal N400 are also evoked by other meaningful stimuli such as faces and pictures. Just as for words, the N400 evoked by pictures is modulated by contextual congruity: more negative N400s are observed to pictures that are incongruous (*versus* congruous) with a single picture prime (Barrett and Rugg, 1990; Holcomb and McPherson, 1994; McPherson and Holcomb, 1999), with the context of a surrounding scene (Ganis and Kutas, 2003), and with a verbal sentence context (Federmeier and Kutas, 2001; Ganis et al., 1996). In addition, larger N400s are also reported to visual scenes that are incongruous (*versus* congruous) with a series of static pictures conveying stories (West and Holcomb, 2002) and with video depictions of common every-day events (Sitnikova et al., 2003). The distribution across the scalp of the N400 evoked by visual images tends to be more anterior than the distribution of the verbal N400, suggesting that the underlying neural generators of these effects may not be identical. But functionally they may be similar.

More recently, in addition to an anteriorly-distributed N400, we reported a Late Positivity with a similar temporal pattern to the P600, as participants viewed short, silent movie-clips depicting violations of actions in real-world events, e.g. a man attempting to shave with a rolling pin (Sitnikova et al., 2003; Sitnikova, et al., submitted for pubication, Fig. 11, left). In these events, the critical objects did not have the semantic properties to execute the target action: a rolling pin does not have the semantic features to carry out the action of shaving. In other words, these scenes depicted impossible actions. As in language, the Late Positivity evoked by such impossible event violations in the visual world could be dissociated from the N400: an N400 effect but no Late Positivity effect was evoked by movie scenes that did not violate a given action but that were

[10] Encouragingly, some of these regions have been reported as being time-locked to the onset of critical semantically anomalous words in studies that use MEG (Halgren et al., 2002) — a technique that does have the excellent temporal resolution of ERPs.

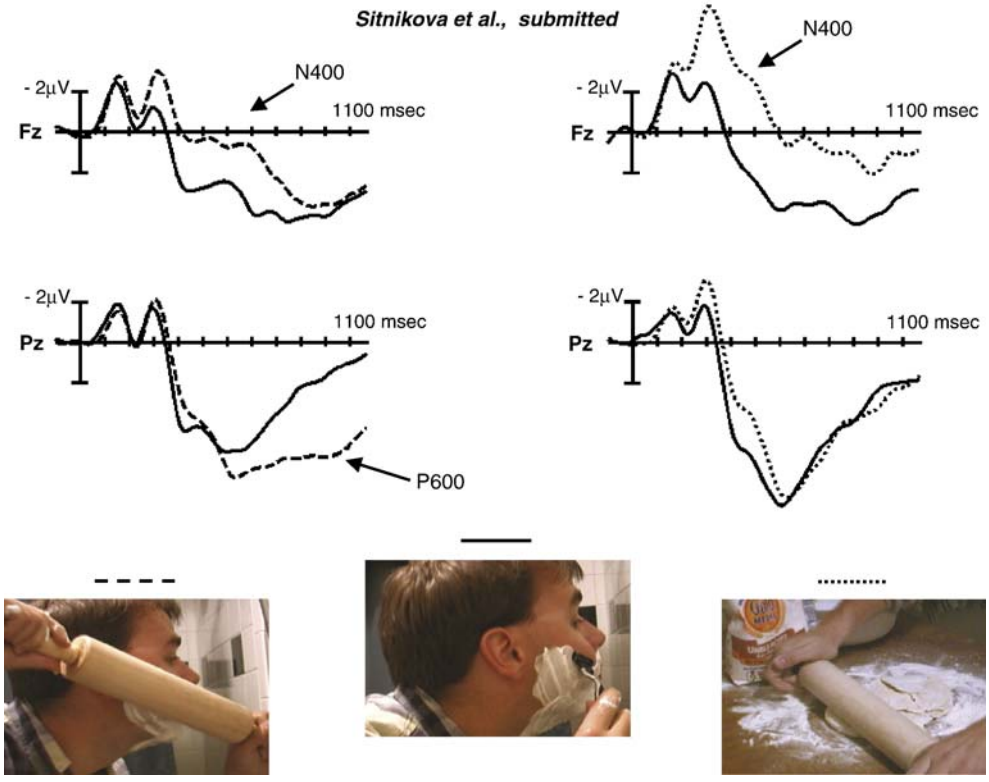

Fig. 11 – Disassociation between the anterior N400 effect and the Late Positivity effect in the comprehension of real-world visual events.

still incongruous with their preceding contexts (e.g. a scene depicting dough being rolled with a rolling pin after a man prepares to shave in a bathroom) (Sitnikova et al., submitted for publication) (Fig. 11, right).

We have suggested that the Late Positivity evoked by such action violations in these movie-clips reflects participants' registration of the impossibility of these actions and prolonged processing by computing the relationship between object, actors and actions. Such computation may be based on the semantic properties that are functionally necessary to perform the central action (Sitnikova et al., submitted for publication; Sitnikova et al., in press). More generally, we have suggested that this process may be analogous to the combinatorial analyses reflected by the P600 evoked by syntactic violations and the types of semantic verb–argument violations discussed in this review. In language, thematic roles are primarily assigned on the basis of functionally-necessary semantic constraints but they are closely linked to certain semantic constraints such as animacy that determine whether an event is possible or impossible. In the visual real-world, the roles of characters, actors and objects around an action may be assigned on the basis of functionally-necessary semantic constraints that once again determine what is possible or impossible for an action to be executed. Consistent with this idea, we have preliminary fMRI evidence suggesting that such visual event violations engage a similar neural circuitry to that engaged by semantic verb–argument and syntactic violations in language (Sitnikova et al., 2004). If this is the case, this would truly open up the idea of generalizabilty in comprehension mechanisms across linguistic and non-linguistic systems, and would allow us to make true biological links between the uniquely human capacity of language and comprehension in the visual real world.

6. Conclusion

I have presented evidence from a recent set of ERP studies suggesting that the language processing system engages at least two interactive but dissociable routes or streams to comprehension. The first, reflected in part by modulation of the N400, is a semantic memory-based system that constantly compares lexical associative and categorical relationships between incoming groups of words with pre-existing information stored within semantic memory. The second combinatorial stream (or streams) is sensitive to morphosyntactic as well as to thematic–semantic constraints and proceeds, to some degree, in parallel with semantic memory-based analysis. Rather than a syntactically-driven combinatorial thematic stream dominating language comprehension, as has been previously been assumed, I have suggested that the outcome of a semantic memory-based analysis and possibly a semantically-driven combinatorial thematic analysis can, under some circumstances, temporarily dominate online comprehension, even in simple, canonical unambiguous sentences. I have also suggested that, when this occurs, the conflict between the output of these streams leads to continued combinatorial analysis and that this continued analysis is reflected by the

P600. The balance between these neural streams of comprehension appears to be dynamic and can be modulated by task, by working memory function as well as by context. An abnormal balance between these systems may begin to explain the patterns of language dysfunction associated with some disorders of language and comprehension. Finally, I have suggested that these two routes to comprehension are not unique to language, and that they may share common neurocognitive mechanisms and neuroanatomical circuitry to those engaged in real-world visual comprehension.

The idea that there are multiple distinct but interactive processing streams underlying comprehension helps explain how, on the one hand, we make maximal use of what we have encountered again and again in the real world, and yet how, on the other hand, we are able to compute unusual relationships between people, objects and actions to understand novel events. The balanced operation of these distinct brain systems – one that links incoming semantic information with existing information stored in semantic memory, and another that combines relationships between people, objects and actions to construct new meaning – allows for comprehension that is both efficient and yet adaptive. The challenge ahead is to more carefully define the cognitive, temporal and neuroanatomical underpinnings of these two neural systems and the relationships between them.

Acknowledgments

The work conducted by Gina Kuperberg cited in this review was supported by NIMH (R01 MH071635), NARSAD (with the Sidney Baer Trust) and a Claflin Distinguished Scholars Award from Mass. General Hospital. The content is based on a talk given at a Satellite Symposium, "Unraveling the Mysteries of Meaning in the Brain: Contextual Cues to Language Comprehension", at the 2006 Annual Meeting of the Cognitive Neuroscience Society. I am very thankful to Phillip Holcomb, David Caplan and Tatiana Sitnikova for so many challenging discussions about N400s, P600s and language comprehension, and for their thoughts on this manuscript. I am also very grateful to Herman Kolk, Ray Jackendoff, David Kemmerer, Martin Paczynski, Tali Ditman, and two anonymous reviewers for all their insightful and clarifying comments.

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