# 61 Postlexical Integration Processes in Language Comprehension: Evidence from Brain-Imaging Research

#### COLIN M. BROWN, PETER HAGOORT, AND MARTA KUTAS

ABSTRACT Language comprehension requires the activation, coordination, and integration of different kinds of linguistic knowledge. This chapter focuses on the processing of syntactic and semantic information during sentence comprehension, and reviews research using event-related brain potentials (ERPs), positron emission tomography (PET), and functional magnetic resonance imaging (fMRI). The ERP data provide evidence for a number of qualitatively distinct components that can be linked to distinct aspects of language understanding. In particular, the separation of meaning and structure in language is associated with different ERP profiles, providing a basic neurobiological constraint for models of comprehension. PET and fMRI research on sentence-level processing is at present quite limited. The data clearly implicate the left perisylvian area as critical for syntactic processing, as well as for aspects of higher-order semantic processing. The emerging picture indicates that sets of areas need to be distinguished, each with its own relative specialization.

In this chapter we discuss evidence from cognitive neuroscience research on sentence comprehension, focusing on syntactic and semantic integration processes. The integration of information is a central feature of such higher cognitive functions as language, where we are obliged to deal with a steady stream of a multitude of information types. Understanding a written or spoken sentence requires bringing together different kinds of linguistic and nonlinguistic knowledge, each of which provides an essential ingredient for comprehension. One of the core tasks that faces us, then, is to construct an integrated representation. For example, if a listener is to understand an utterance, then at least the following processes need to be successfully completed: (a) recognition of the signal as speech (as opposed to some other kind of noise), (b) segmentation of the signal into constituent parts, (c) access to the mental lexicon based on

the products of the segmentation process, (d) selection of the appropriate word from within a lexicon containing some 30,000 or more entries, (e) construction of the appropriate grammatical structure for the utterance up to and including the word last processed, and (f) ascertaining the semantic relations among the words in the sentence. Each of these processes requires the activation of different kinds of knowledge. For example, segmentation involves phonological knowledge, which is largely separate from, for instance, the knowledge involved in grammatical analysis. But knowledge bases like phonology, word meaning, and grammar do not, on their own, yield a meaningful message. While there is no question that integration of these (and other) sources of information is a prerequisite for understanding, considerable controversy surrounds the details.

Which sources of knowledge actually need to be distinguished? Is the system organized into modules, each operating within a representational subdomain and dealing with a specific subprocess of comprehension? Or are the representational distinctions less marked or even absent? What is the temporal processing nature of comprehension? Does understanding proceed via a fixed temporal sequence, with limited crosstalk between processing stages and representations? Or is comprehension the result of more or less continuous interaction among many sources of linguistic and nonlinguistic knowledge? These questions, which are among the most persistent in language research, are now gaining the attention of cognitive neuroscientists. This is an emerging field, with a short history. Nevertheless, progress has been made, and we present a few specific examples in this chapter.

A cognitive neuroscience approach to language might contribute to language research in several ways. Neurobiological data can, in principle, provide evidence on the representational levels that are postulated by different language models-semantic, syntactic, and so on (see the section on PET/fMRI). Neurobiological data can

COLIN M. BROWN and PETER HAGOORT Neurocognition of Language Processing Research Group, Max Planck Institute for Psycholinguistics, Nijmegen, The Netherlands MARTA KUTAS Department of Cognitive Science, University

of California, San Diego, Calif.

reveal the temporal dynamics of comprehension, crucial for investigating the different claims of sequential and interactive processing models (see the sections on the N400 and the P600/SPS). And, by comparing brain activity within and between cognitive domains, neurobiological data can also speak to the domain-specificity of language. It is, for example, a matter of debate whether language utilizes a dedicated working-memory system or a more general system that subserves other cognitive functions as well (see the section on slow brain-potential shifts).

### Postlexical syntactic and semantic integration processes

In this chapter we focus specifically on what we refer to as postlexical syntactic and semantic processes. We do not discuss the processes that precede lexical selection (see Norris and Wise, chapter 60, for this subject), but rather concern ourselves with processes that follow word recognition. Once a word has been selected within the mental lexicon, the information associated with this word needs to be integrated into the message-level representation that is the end product of comprehension. If this integration is to be successful, both syntactic and semantic analyses need to be performed.

At the level of syntax, the sentence needs to be parsed into its constituents, and the syntactic dependencies among constituents need to be specified (e.g., What is the subject of the sentence? Which verbs are linked with which nouns?). At the level of semantics, the meaning of an individual word needs to be merged with the representation that is being built up of the overall meaning of the sentence, such that thematic roles like agent, theme, and patient can be ascertained (e.g., Who is doing what to whom?). These syntactic and semantic processes lie at the core of language comprehension. Although words are indispensable bridges to understanding, it is only in the realm of sentences (and beyond in discourses) that they achieve their full potential to convey rich and varied messages.

The field of language research lacks an articulated model of how we achieve (mutual) understanding. This lack is not too surprising when we consider the problems that confront us in devising a theory of meaning for natural languages, let alone the difficulties attendant on combining such a representational theory with a processing model that delineates the comprehension process at the millisecond level. However understandable, the lack of an overall model has meant that the processes involved in meaning integration at the sentential level have received scant experimental attention. The one area in which quite specific models of the relationship between semantic representations and on-line language processing have been proposed is the area of parsing research. Here, a major concern has been to assess the influence of semantic representations on the syntactic analysis of sentences, with a particular focus on the moments at which integration between meaning and structure occurs (cf. Frazier, 1987; Tanenhaus and Trueswell, 1995). Research in this area has concentrated on the on-line resolution of sentential-syntactic ambiguity (e.g., "The woman sees the man with the binoculars." Who is holding the binoculars?). The resolution of this kind of ambiguity speaks to the separability of syntax and semantics, as well as to the issue of sequential or interactive processing. The prevailing models in the literature can be broadly separated into autonomist and interactive accounts.

In autonomous approaches, a separate syntactic knowledge base is used to build up a representation of the syntactic structure of a sentence. The prototypical example of this approach is embodied in the Garden-Path model (Frazier, 1987), which postulates that an intermediate level of syntactic representation is a necessary and obligatory step during sentence processing. This model stipulates that nonsyntactic sources of information (e.g., message-level semantics) cannot affect the parser's initial syntactic analysis (see also Frazier and Clifton, 1996; Friederici and Mecklinger, 1996). Such sources come into play only after a first parse has been delivered. When confronted with a sentential-syntactic ambiguity, the Garden-Path model posits principles of economy, on the basis of which the syntactically least complex analysis of the alternative structures is chosen at the moment the ambiguity arises. If the chosen analysis subsequently leads to interpretive problems, this triggers a syntactic reanalysis.

In the most radical *interactionist approach*, there are no intermediate syntactic representations. Instead, undifferentiated representational networks are posited, in which syntactic and semantic information emerge as combined constraints on a single, unified representation (e.g., Bates et al., 1982; Elman, 1990; McClelland, St. John, and Taraban, 1989). In terms of the processing nature of the system, comprehension is described as a fully interactive process, in which all sources of information influence the ongoing analysis as they become available.

A third class of models sits somewhere in between the autonomous and radical interactionist approaches. In these so-called *constraint-satisfaction models*, lexically represented information (such as the animacy of a noun or the transitivity of a verb) but also statistical information about the frequency of occurrence of a word or of syntactic constructions play a central role (cf. MacDonald, Pearlmutter, and Seidenberg, 1994; Spivey-Knowlton and Sedivy, 1995). The approach emphasizes the interactive nature of comprehension, but does not exclude the existence of separate representational levels as a matter of principle. Comprehension is seen as a competition among alternatives (e.g., multiple parses), based on both syntactic and nonsyntactic information. In this approach, as in the more radical interactive approach, sentential-syntactic ambiguities are resolved by the immediate interaction of lexical-syntactic and lexicalsemantic information, in combination with statistical information about the relative frequency of occurrence of particular syntactic structures, and any available discourse information, without appealing to an initial syntax-based parsing stage or a separate revision stage (cf. Tanenhaus and Trueswell, 1995).

Although we have discussed these different models in the light of sentential-syntactic ambiguity resolution, their architectural and processing assumptions hold for the full domain of sentence and discourse processing. Clearly, the representational and processing assumptions underlying autonomous and (fully) interactive models have very different implications for an account of language comprehension. We will return to these issues after giving an overview of results from the brainimaging literature on syntactic and semantic processes during sentence processing.

Before discussing the imaging data, a few brief comments on the sensitivity and relevance for language research of different brain-imaging methods are called for. The common goal in cognitive neuroscience is to develop a model in which the cognitive and neural approaches are combined, providing a detailed answer to the very general question of where and when in the brain what happens. Methods like event-related brain potentials (ERPs), positron emission tomography (PET), and functional magnetic resonance imaging (fMRI) are not equally revealing or relevant in this respect. In terms of the temporal dynamics of comprehension, only ERPs (and their magnetic counterparts from magnetoencephalography, MEG) can provide the required millisecond resolution (although recent developments in noninvasive optical imaging indicate that near-infrared measurements might approach millisecond resolution; cf. Gratton, Fabiani, and Corballis, 1997). In contrast, the main power of PET and fMRI lies in the localization of brain areas involved in language processing (although recent advances in neuronal source-localization procedures with ERP measurements are making this technique more relevant for localizational issues; cf. Kutas, Federmeier, and Sereno, 1999). Recent analytic developments in PET and fMRI research further indicate that information on effective connectivity in the brain (i.e., the influence that one neuronal system exerts over an-

other) might begin to constrain our models of the language system (cf. Büchel, Frith, and Friston, 1999; Friston, Frith, and Frackowiak, 1993). However, localization as such does not reveal the nature of the activated representations: The hemodynamic response is a quantitative measure that does not of itself deliver information on the nature of the representations involved. The measure is maximally informative when separate brain loci can be linked, via appropriately constraining experimental conditions, with separate representations and processes. A similar situation holds for the ERP method: The polarity and scalp topography of ERP waveforms can, in principle, yield qualitatively different effects for qualitatively different representations and/or processes, but only appropriately operationalized manipulations will make such effects interpretable (cf. Brown and Hagoort, 1999; Osterhout and Holcomb, 1995). In short, whatever the brain-imaging technique being used, the value of the data critically depends on its relation to an articulated cognitive-functional model.

## Cognitive neuroscience investigations of postlexical integration

EVENT-RELATED BRAIN POTENTIAL MANIFESTATIONS OF SENTENCE PROCESSING Space limitations rule out an introduction on the neurophysiology and signalanalysis techniques of event-related brain potentials (see Picton, Lins, and Scherg, 1995, for a recent review). It is, however, important to bear in mind that, owing to the signal-to-noise ratio of the EEG signal, one cannot obtain a reliable ERP waveform in a standard language experiment without averaging over at least 20-30 different tokens within an experimental condition. Thus, when we speak of the ERP elicited by a particular word in a particular condition, we mean the electrophysiological activity averaged over different tokens of the same type.

Within the realm of sentence processing, four different ERP profiles have been related to aspects of syntactic and semantic processing: (1) A transient negativity over left-anterior electrode sites (labeled the left-anterior negativity, LAN) that develops in the period roughly 200-500 ms after word onset. The LAN has been related not only to the activation and processing of syntactic word-category information, but also to more general processes of working memory. (2) A transient bilateral negativity, labeled the N400, that develops between 200 and 600 ms after word onset: the N400 has been related to semantic processing. (3) A transient bilateral positivity that develops in the period between 500 and 700 ms. Variously labeled the syntactic positive shift (SPS) or the P600, this positivity has been related to syntactic processing. (4) A slow positive shift over the front of the

head, accumulating across the span of a sentence, that has been related to the construction of a representation of the overall meaning of a sentence. Let us discuss each of these ERP effects in turn.

Left-anterior negativities The LAN is a relative newcomer to the set of language-related ERP effects. Both its exact electrophysiological signature and its functional nature are still under scrutiny. Some researchers have suggested that the LAN is related to early parsing processes, reflecting the assignment of an initial phrase structure based on syntactic word-category information (Friederici, 1995; Friederici, Hahne, and Mecklinger, 1996). Other researchers propose that a LAN is a reflection of working-memory processes during language comprehension, related to the activity of holding a word in memory until it can be assigned its grammatical role in a sentence (Kluender and Kutas, 1993a,b; Kutas and King, 1995). Clearly more research is called for to decide between these quite separate views. One of the pending issues is the uniformity of the LAN. There is variability in both its topography and latency. It is possible, therefore, that more than one LAN exists (some researchers distinguish between an early left-anterior negativity and a later left-anterior negativity; cf. Friederici, 1995), with different functional interpretations.

An example of a left-anterior negativity is given in figure 61.1 (from work by Kluender and Münte, 1999), in which a preferred and a nonpreferred version (at least in standard Northern German dialects) of a so-called whmovement is contrasted. The particular wh-movement under investigation is the displacement of the direct object of a verb that occurs when a declarative sentence is transformed into a question-sentence-e.g., the transformation of the declarative "The cautious physicist has stored the data on a diskette" into the question-sentence "What has the cautious physicist stored on a diskette?" In the declarative sentence, the data is the direct object of its immediately preceding verb. In the question-sentence, the data has been replaced by the interrogative pronoun what, which, moreover, has been moved to the beginning of the sentence. (This is, therefore, an instance of wh-movement, where wh is a shorthand notation for the category of interrogative words, such as what, who, which, etc.) Although the data no longer appears in the question-sentence, syntactically speaking, the wh-element what is extracted from the direct-object position to sentence-initial position, leaving a trace after stored (i.e., "What, has the cautious physicist stored on a diskette?"). This trace is presumed to co-index the empty syntactic position after stored in the question-sentence with the pronoun *what* in sentence-initial position.

The comparison in the figure concerns a preferred and a nonpreferred wh-movement in standard Northern German dialect. The nonpreferred movement elicited a focal left-anterior negativity. This result is particularly interesting because it adds to the set of syntactic phenomena that have been associated with left-anterior negativities. The effect that Kluender and Münte obtained is incompatible with an interpretation in terms of a violation of expected syntactic word-category information: The word that elicits the LAN effect does not violate category constraints. One hypothesis is that the effect is reflecting a disruption in the primary parsing process of working out the co-index relationship that is indicated by the first part of the wh-question, with a concomitant sudden increase in working-memory load.

*The N400 component* Of all the ERP effects that have been related to language, the N400 is the most firmly established component (Kutas and Hillyard, 1980). This negative-polarity potential with a maximal amplitude at approximately 400 ms after stimulation onset is, as a rule, elicited by any meaningful word (especially nouns, verbs, and adjectives, sometimes referred to as openclass words) presented either in isolation, in word-word contexts (e.g., priming paradigms) or in sentences. The effect starts some 200-250 ms after word onset and can last for some 200-300 ms; it is widely distributed over the scalp, with a tendency toward greater amplitudes over more central and posterior electrode sites. Although originally demonstrated for sentence-final words that violate the semantic constraints of sentences (e.g., "The woman spread her toast with hypotheses"), more than 15 years of research has demonstrated that this component is not a simple incongruity detector; rather, it is a sensitive manifestation of semantic processing during on-line comprehension (for reviews see Kutas and Van Petten, 1994; Osterhout and Holcomb, 1995). An example of this sensitivity is given in figure 61.2, which shows the ERP waveform elicited by two visually presented words that differ in the extent of their semantic fit with preceding discourse. In this experiment subjects read sentences for comprehension, without having to perform any extraneous task. (This is an advantage of the ERP method compared to the reaction-time method, where one must always consider additional processes, such as lexical decision, due to the external task.) Subjects were presented with a short discourse followed by one of two sentences containing a critical word. The critical word was entirely acceptable within the restricted context of the final sentence itself, but in one case the critical word did not match the messagelevel meaning set up by the preceding discourse. For example:



FIGURE 61.1 Grammatical movement effect. The solid line represents the average ERP waveform for a grammatically preferred continuation. The dotted line represents the average waveform for the grammatically nonpreferred continuation. Preferred sentence (critical word in italics, to which the ERP waveform is time-locked): "Was denkst du, *hat* der umsichtige Physiker auf die Diskette gespeichert?" (literally translated: "What think you, has the cautious physicist on the disk stored?"). Nonpreferred sentence: "Was denkst du, *daß* der umsichtige Physiker auf die Diskette gespeichert hat?" (literally for the disk stored?").

*Discourse: "As* agreed upon, Jane was to wake her sister and her brother at 5 o'clock. But the sister had already washed herself, and the brother had even got dressed."

*Normal continuation:* "Jane told the brother that he was exceptionally *quick* today."

Anomalous continuation: 'Jane told the brother that he was exceptionally slow today."

As figure 61.2 shows, both words (*quick, slow*) elicit the N400 component, with an onset at about 200-250 ms. This underscores the general observation that each

translation: "What think you, that the cautious physicist on the disk stored has?"). In wh-question sentences in Northern German dialects, the complementizer  $da\beta$  at the beginning of an embedded clause is less preferred in combination with the movement of direct objects to sentence-initial position. Four electrode positions are shown, two over left- and right-anterior sites, and two over left and right temporal sites. Negative polarity is plotted upward, in microvolts. (Data from Kluender and Münte, 1999.)

meaningful word in a sentence elicits an N400. The difference in the match between the meaning of the critical word and the meaning of the discourse emerges as a difference in the overall amplitude of the N400, with the mismatching word eliciting the largest amplitude. The amplitude difference is referred to as the N400 effect. Clearly, this N400 effect can emanate only from an attempt to integrate the meaning of the critical word within the discourse. This testifies both to the semantic sensitivity of the N400 and to the integrational processes



FIGURE 61.2 Discourse-semantic N400 effect. The solid line represents the average ERP waveform for the normal continuation of the discourse, and the dotted line for the anomalous continuation. In the figure, the potential elicited by the critical word starts at 600 ms, and is preceded and followed by the po-

tentials elicited by the word before and after the critical word. Three electrode positions are shown: one over the posterior midline of the scalp (Pz), and one each on left and right lateral temporal-posterior sites (LTP and RTP). (Data from Van Berkum, Hagoort, and Brown, 1999.)

that are manifest in modulations of N400 amplitude (see also St. George, Mannes, and Hoffman, 1994, 1997). Note, moreover, that the onset latency of the effect reveals that these high-level processes are already operative within some 200 ms of the word's occurrence. The very early moment at which high-level discourse information is modulating the comprehension process is less readily compatible with strictly sequential models, in which lower-level analyses have to be completed before higher levels of information can affect comprehension.

For present purposes a synopsis of five main findings on the N400 suffices to exemplify its relevance for the study of postlexical processes: (1) The amplitude of the N400 is inversely related to the cloze probability of a word in sentence context. The better the semantic fit between a word and its context, the smaller the amplitude of the N400. (2) This inverse relationship holds for singleword, sentence, and discourse contexts. (3) The amplitude of the N400 varies with word position. Open-class words at the beginning of a sentence elicit larger negativities than open-class words in later positions. This most likely reflects the incremental impact of semantic constraints throughout the sentence. (4) The elicitation of the N400 is independent of input modality-naturally produced connected speech, sign language, or slow and fast visual stimulation. (5) Grammatical processes typically do not directly elicit larger N400s, although difficulty in grammatical processing subsequently gives rise to N400 activity in some cases.

On the basis of these findings it is by now widely accepted that, within the domain of language comprehension, the elicitation of the N400 and the modulations in N400 amplitude are indicative of the involvement of semantic representations and of differential semantic processing during on-line language comprehension. Note

that the claim is not that the N400 is a language-specific component (i.e., modulated solely by language-related factors); rather, in the context of language processing, N400 amplitude variation is linked to lexical and message-level semantic information. In terms of the functional interpretation of the N400 effect, it has been suggested that the effect is a reflection of lexical integration processes. After a word has been activated in the mental lexicon, its meaning has to be integrated into a message-level conceptual representation of the context within it occurs. The hypothesis is that it is this meaningintegration process that is manifest in the N400 effect. The more difficult the integration process is, the larger the amplitude of the N400 (Brown and Hagoort, 1993, 1999; Kutas and King, 1995; Osterhout and Holcomb, 1992).

The P600, or syntactic positive shift (SPS) The P600/SPS, which is of more recent origin, was first reported as a response to syntactic violations in sentences (Hagoort, Brown, and Groothusen, 1993; Osterhout and Holcomb, 1992). For example, in the sentence "The spoilt child throw the toy on the ground," the grammatical number marking on the verb throw does not agree with the fact that the grammatical subject of the sentence (i.e., the spoilt child) is singular. This kind of agreement error elicits a positive shift that starts at approximately 500 ms after the violating word (in this case throw) has been presented. The shift can last for more than 300 ms, and is widely distributed over the scalp, with posterior maxima. Since its discovery in the early nineties, the P600/SPS has been observed in a wide variety of syntactic phenomena (see Osterhout, McLaughlin, and Bersick, 1997, for a recent overview). In the realm of violations, it has been shown that the P600/SPS is elicited by violations of

(a) constraints on the movement of sentence constituents (e.g., "What was a proof of criticized by the scientist?"), (b) phrase structure rules (e.g., "The man was upset by the emotional rather *response* of his employer"), (c) verb subcategorization (e.g., "The broker persuaded *to* sell the stock"), (d) subject-verb number agreement (as in the above example), (e) reflexive-antecedent gender agreement (e.g., "The man congratulated *herself on* the promotion"), and (f) reflexive-antecedent number agreement (e.g., "The guests helped *himself* to the food").

It should be noted that these violations involve very different aspects of grammar. The fact that in each instance a P600/SPS is elicited points toward the syntactic sensitivity of the component. At the same time the heterogeneity of syntactic phenomena associated with the P600/SPS raises questions about exactly what the component is reflecting about the language process. We will return to this issue after presenting further evidence on the sensitivity of the P600/SPS.

The P600/SPS is not restricted to the visual modality, but is also observed for naturally produced connected speech (Friederici, Pfeifer, and Hahne, 1993; Hagoort and Brown, in press; Osterhout and Holcomb, 1993). Furthermore, it has been demonstrated that the P600/ SPS is not a mere violation detector. In fact, it can be used to investigate quite subtle aspects of parsing, such as are involved in the resolution of sentential-syntactic ambiguity. For example, in the written sentence "The sheriff saw the cowboy and the Indian spotted the horse in the canyon," the sentence is syntactically ambiguous until the verb *spotted* The ambiguity is between a conjoined noun-phrase reading of the cowboy and the Indian, and a reading in which the Indian is the subject of a second clause, thereby signaling a sentence conjunction. At the verb spotted this ambiguity is resolved in favor of the second-clause reading. It has been suggested in the parsing literature that the conjoined noun-phrase analysis results in a less complex syntactic structure than the sentence-conjunction analysis. Furthermore, as we noted above, it has been claimed that the parser operates economically, such that less complex syntactic analyses are preferred over more complex ones. This would imply that during the reading of the ambiguous example sentence, subjects would experience difficulty in parsing the sentence at the verb *spotted*, despite the fact that in terms of its meaning and in terms of the grammatical constraints of the language, the sentence is perfectly in order. This difficulty should become apparent in a comparison with the same sequence of words in which the ambiguity does not arise, and in which the sentence-conjunction reading is the only option, due to the inclusion of an appropriately placed comma: "The sheriff saw the cowboy, and the Indian spotted the

horse in the canyon." Note that this particular disambiguation obviously only holds for the visual modality.

When we compare the waveform elicited by the critical written verb spotted in the ambiguous sentence to that elicited by the same verb in the control sentence, a P600/SPS is seen in the ambiguous sentence. This is shown in figure 61.3, which depicts the ERP waveform, over four representative electrode sites, for the verb spotted in the ambiguous and nonambiguous sentence, preceded and followed by one word. This finding demonstrates that the P600/SPS does not depend on grammatical violations for its elicitation. The component can reflect on-line sentence-processing operations related to the resolution of sentential-syntactic ambiguity. Interestingly, the more frontal scalp distribution of the P600/ SPS to sentential-syntactic ambiguity resolution differs from the predominantly posterior distribution elicited by syntactic violations. It might be the case, therefore, that there is more than one positive shift under the general heading of P600/SPS (cf. Brown and Hagoort, 1998; Hagoort and Brown, in press).

Given the sensitivity of the P600/SPS to processes related to the resolution of syntactic ambiguity, it is a good tool with which to investigate the impact of lexicalsemantic and higher-order (e.g., discourse) meaning representations on parsing. The impact of semantic information during sentence processing is one of the issues that we raised earlier on the processing nature of the parser. Namely, can nonsyntactic knowledge immediately contribute to sentential-syntactic analysis, or is a first-pass structural analysis performed on the basis of only syntactic knowledge? So, in the written sentence "The helmsman repairs the mainsail and the skipper varnishes the mast after the storm," the same syntactic ambiguity is present as in the cowboy-and-Indian example. But since the meaning of the verb repair is compatible only with inanimate objects, a noun-phrase conjunction of the mainsail and the skipper can be excluded on semantic grounds (i.e., the helmsman cannot repair the skipper). Nevertheless, parsing models claiming that the first-pass structural assignment is based solely on syntactic information maintain that the conjoined noun-phrase analysis will be initially considered, and preferred over a sentence-conjunction analysis. This claim has been assessed by investigating the ERP waveform to the verb repair in the ambiguous sentence and a nonambiguous control (again realized by appropriately inserting a comma, in this case after *the mainsail*). The results were clear: No difference was seen between the unpunctuated ambiguous and the punctuated nonambiguous sentences (cf. Hagoort, Brown, Vonk, and Hoeks, 1999). This indicates that the semantic information carried by the verb was immediately used to





syntactically unambiguous: The sheriff saw the cowboy, and the indian spotted the horse in the canyon. syntactically ambiguous: The sheriff saw the cowboy and the indian spotted the horse in the canyon.



FIGURE 61.3 Sentential-syntactic ambiguity effect. The dotted line represents the average ERP waveform for initially syntactically ambiguous sentences. At the point of disambiguation (at 686 ms) the sentence continued with a grammatically correct but nonpreferred reading. The solid line represents the control condition, in which unambiguous versions of the same nonpreferred structures were presented. In the figure, the critical

constrain the ongoing analysis, and thus argues against models that propose an autonomous first-pass structural analysis.

The functional interpretation of the P600/SPS has not yet been fully clarified. Some researchers claim that the late positivity is a member of the P300 familynamely, the so-called P3b component (Coulson, King, and Kutas, 1998; Gunter, Stowe, and Mulder, 1997; but see Osterhout et al., 1996). Other researchers have suggested that the P600/SPS is a reflection of specifically grammatical processing, related to (re)analysis processes that occur whenever the parser is confronted with a failed or nonpreferred syntactic analysis (Friederici and Mecklinger, 1996; Hagoort, Brown, and Groothusen, 1993; Osterhout, 1994; Münte, Matzke, and Johannes, 1997). Note that this position does not necessarily entail any commitment to the language specificity of the component. Rather, the claim advanced by Hagoort, Brown, and Groothusen (1993) and Osterhout (1994) is



word is preceded and followed by one word. The region within which the P600/SPS developed is shaded. Four electrode positions are shown, two over left- and right-anterior temporal sites, and two over left and right temporal sites. (From Brown and Hagoort, 1999. © 1999 Cambridge University Press.)

that, within the domain of sentence processing, the P600/SPS is a manifestation of processes that can be directly linked to the grammatical properties of language (cf. Osterhout et al., 1996; Osterhaut and Hagoort, 1999).

The issue of the functional characterization of the P600/SPS clearly stands to benefit from other areas of brain-imaging research. In particular, localizational techniques such as PET and fMRI could provide crucial information on the commonalities and divergences in the neural circuitry underlying the P600/SPS and the P300.

Despite our still incomplete understanding of the functional nature of the P600/SPS, one important fact already stands out-namely, this component is electrophysiologically distinct from the N400, implying at least a partial separation in the neural tissue that underlies the two components. These electrophysiological findings are therefore directly relevant for the question

#### Good comprehenders



FIGURE 61.4 Differential comprehension skill effect. Average ERP waveforms recorded at one left-frontal electrode site for object-relative (dotted line) and subject-relative (solid line) sentences, for a group of 12 good and 12 poor comprehenders.

of the possible separation in the brain of syntactic and semantic knowledge. Sentence-processing models that conflate the processing and/or representational distinctions between syntax and semantics (e.g., McClelland, St. John, and Taraban, 1989) cannot account for these findings.

*Slow shifts* Language processing beyond the level of the individual word is revealed in ERPs averaged across clauses and sentences (see Kutas and King, 1995). These slow potentials show systematic variation in a variety of sentence types, none of which has to contain any violation. Kutas and King have identified several such slow potentials with different distributions over the left and right side of the head. Of particular relevance is their finding of an ultraslow frontal positivity which has been hypothesized to reflect the linking of

Waveforms are aligned on the first word of each sentence type. The shaded regions indicate areas of statistically significant difference between the two sentence types. (From King and Kutas, 1995. ©1995 MIT Press.)

information in working and long-term memory during the creation of a message-level representation of a sentence.

An example of such a slow frontal-positivity from the work of King and Kutas (1995) is shown in figure 61.4. This effect was elicited by the relative processing difficulty of so-called object-relative sentences, compared to subject-relative sentences. In an object-relative sentence, e.g., "The reporter who the senator harshly attacked admitted the error," the subject of the main clause (*The reporter*) is the object of the relative-clause verb (*attacked*). Such sentences have consistently been shown to be much harder to process than subject-relative sentences, where the subject of the main clause is also the subject of the relative clause (e.g., "The reporter who harshly attacked the senator admitted the error"). This processing difficulty is attributed to the greater working-memory

demands of object-relative sentences, where information has to be maintained in memory over longer stretches of time than for subject-relative sentences.

The figure shows separate pairs of waveforms for two groups of subjects-those with high language comprehension scores and those with low scores. This separation in two groups of subjects is informative because differences in comprehension performance have been linked to differences in working-memory capacity (e.g., King and Just, 1991). Two aspects are particularly noteworthy in these data. First, the waveforms for the object-relative sentences diverge from the slow-frontal positive shift for the subjectrelative sentences at the first possible moment of workingmemory load difference, i.e., when the second nounphrase (the senator) had to be added to working memory. Second, there are substantial processing differences as a function of comprehension skill and hence, by hypothesis, of working-memory capacity. The slow positivity is present only in the good comprehenders, for whom the increased memory demands of the object-relative sentences emerge as a negative-going deflection from the slow positivity that is characteristic of the subject-relative sentences. In contrast, the poor comprehenders show basically the same ERP profile for the two types of sentences, both being as negative as the waveform elicited by the object-relative sentences in the good comprehenders. It would seem that the poor comprehenders are already maximally taxed by having to cope with any kind of embedded clause.

This finding of differential effects for readers with differing degrees of comprehension skills bears on the question of whether language uses a dedicated workingmemory system or draws upon a general system shared by other cognitive functions (Caplan and Waters, in press). A systematic investigation of the (non)linguistic variables that modulate the slow-potential shift will be of direct relevance for this issue. More generally, the finding of long-lasting potentials linked to sentence processing opens the way for investigating the more sustained and incremental effects that wax and wane over the course of an entire sentence.

*Summary* We have discussed several qualitatively distinct ERP components that can be reliably linked to distinct aspects of language comprehension. On the basis of their different electrophysiological profiles, we can conclude that nonidentical brain systems underlie the various aspects of linguistic processing that are manifest in these different components. This provides a neurobiological constraint for models of language comprehension-models that will need to account for these different patterns of ERP effects.

An important working hypothesis concerns how the basic distinction of meaning and structure in language is

linked to the N400 and the P600/SPS. Research that has used these components to address the basic processing nature of parsing has yielded evidence that is incompatible with strict autonomous characterizations of sentence processing. Furthermore, slow potential shifts that develop over entire clauses and sentences have been linked to integrational processes at the message level, and have demonstrated considerable effects of betweensubject working memory differences.

At the temporal level, the millisecond resolution of the electrophysiological signal provides a dynamic picture of the ongoing comprehension process. Different language-related ERP effects are observed to arise at different moments and to persist for differing stretches of time. Within some 200 ms after stimulation, processes related to lexical meaning and integration emerge in the ERP waveform. Some researchers argue that syntactic processes can be seen preceding and partly overlapping with this early onset (cf. LAN effects). Processes related to modifying the ongoing syntactic analysis can be seen at some 500 ms in the ERP waveform. Various co-occurrences of LAN, N400, and P600/SPS effects have been reported, in ways that can be sensibly linked to the online comprehension process (e.g., N400 semantic processing effects as a consequence of preceding P600/SPS syntactic processing effects).

LESION AND HEMODYNAMIC DATA ON BRAIN AREAS INVOLVED IN SENTENCE PROCESSING In the previous section we discussed the relevance of ERP data for models of sentence comprehension. The processing of syntactic ambiguities has been a major testing ground for such models. The classical lesion studies and the more recent PET/fMRI studies on sentence comprehension have a slightly different focus. These studies attempt to determine areas that are involved in sentence processing, or to isolate and localize a specific subcomponent of sentence comprehension. This aim is independent of the issue of whether and when different processing components influence each other during sentence comprehension.

Until fairly recently most of the evidence on the neural circuitry of sentence processing came from lesion studies. One of the central issues in this work has been the identification of areas involved in the computation of syntactic structure during language comprehension. The general picture that has emerged from this research is complicated (for a more extensive overview, see Hagoort, Brown, and Osterhout, 1999). Despite the classical association between Broca's area and syntactic functions (e.g., Caramazza and Zurif, 1976; Heilman and Scholes, 1976; Von Stockert and Bader, 1976; Zurif, Caramazza, and Myerson, 1972), detailed lesion analyses have made it doubtful that lesions restricted to this area result in lasting syntactic deficits (e.g., Mohr et al., 1978). More recent analyses confirm that the left perisylvian cortex is critically involved in both parsing and syntactic encoding. Within this large cortical area it has been difficult to pinpoint a more restricted area that is crucial for syntactic processing. One reason is that lesions in any one part of this cortex can result in syntactic deficits (Caplan, Hildebrandt, and Makris, 1996; Vanier and Caplan, 1990). Moreover, the left anterior-temporal cortex, which has classically not been associated with any particular linguistic function, nonetheless appears to be consistently associated with syntactic deficits (Dronkers et al., 1994). This area is claimed to be involved in morphosyntactic processing, in addition to other areas in the left perisylvian cortex.

The lesion data thus suggest that it is impossible to single out one brain area that is dedicated to syntactic processing. There are at least two reasons for this complicated picture. One is that within the perisylvian cortex, individual variation in the neural circuitry for higher-order language functions might be substantially larger than for functions subserved by the primary sensorimotor cortices (cf. Bavelier et al., 1997; Ojemann, 1991). In addition, the wide variety of "syntactic" manipulations across studies makes it difficult to pinpoint the causal factors underlying the reported variation in brain areas. It is important to keep in mind that the areas involved in parsing (i.e., comprehension) are not necessarily the same as those involved in grammatical encoding (i.e., production), and that processing of wordcategory information or morphosyntactic features is different from establishing the syntactic dependencies among constituents. While all of these involve syntactic processing at some level, they clearly refer to very different aspects of syntactic processing. Comparing results across studies therefore requires an appreciation of the different syntactic manipulations employed.

*Hemodynamic studies* So far, PET and fMRI studies on language comprehension have largely focused on single word processing. Very few studies investigated integration processes at the sentence level or beyond (Bavelier et al., 1997; Caplan, Alpert, and Waters, 1998; Indefrey et al., 1996; Mazoyer et al., 1993; Nichelli et al., 1995; Stowe et al., 1994; Stromswold et al., 1996). In all but one of these (Mazoyer et al., 1993), the sentences were presented visually.

Two studies tried to isolate activations related to sentence-level processes from lower-level verbal processing, such as the reading of consonant strings (Bavelier et al., 1997) and single word comprehension (Mazoyer et al., 1993). The very nature of the comparisons in these studies makes it difficult to distinguish between sentencelevel activations related to prosody, syntax, and sentencelevel semantics.

The remaining brain-imaging studies on sentence processing were aimed at isolating the syntactic processing component (Caplan, Alpert, and Waters 1998; Indefrey et al., 1996; Just et al., 1996; Stowe et al., 1994; Stromswold et al., 1996). Although these different studies show nonidentical patterns of activation, all five report activation in the left inferior-frontal gyrus, including Broca's area.

Four studies manipulated the syntactic complexity of the sentence materials (Caplan, Alpert, and Waters, 1998; Just et al., 1996; Stowe et al., 1994; Stromswold et al., 1996). For instance, Stromswold et al. (1996). compared sentences that were similar in terms of their propositional content, but differed in syntactic complexity. In one condition sentences with center-embedded structures were presented (e.g., "The juice that the child spilled stained the rug"). The other condition consisted of sentences with right-branching structures (e.g., "The child spilled the juice that stained the rug"). The former structures are notoriously harder to process than the latter. A direct comparison between the structurally complex (center-embedded) and the less complex sentences (right-branching) resulted in activation of Broca's area, particularly in the pars opercularis.

Caplan, Alpert, and Waters (1998) performed a partial replication of this study. They also observed increased activation in Broca's area for the center-embedded sentences. However, although the activation was in the pars opercularis, the blood flow increase was more dorsal and more anterior than in the previous study. Factors related to subject variation between studies may account for this regional activation difference within Broca's area.

In contrast to the other studies on syntactic processing (Caplan, Alpert, and Waters, 1998; just et al., 1996; Stowe et al., 1996; Stromswold et al., 1996), the critical comparisons in the Indefrey study were not between conditions that differed in syntactic complexity, but rather those that did and did not require syntactic computations. Subjects were asked to read sentences consisting of pseudowords and function words in German [e.g., "(Der Fauper) (der) (die Lüspeln) (febbt) (tecken) (das Baktor)"]. Some of the sentences contained a syntactic error (e.g., *tecken*, a number agreement error with respect to the singular subject Fauper). In one condition, subjects were asked to detect this error (parsing) and to produce the sentence in its correct syntactic form ("Der Fauper, der die Lüspeln febbt, teckt das Baktor"). The latter task requires grammatical encoding in addition to parsing. In another condition, subjects were only asked to judge the grammaticality of the input string as they read it out. In a third condition, they were asked to make phonological acceptability judgments for the same pseudowords and

function strings, presented without syntactic structure and with an occasional element that violated the phonotactic constraints of German. The experimental conditions were contrasted with a control condition in which subjects were asked to read out unstructured strings of the same pseudowords and function words used in the other conditions. All three syntactic conditions (including the syntactic error detection) were associated with activation of the inferior frontal sulcus between dorsal Broca's area and adjacent parts of the middle frontal gyrus. Both acceptability judgment tasks (syntactic and phonological) showed activation in bilateral anterior inferior frontal areas, as well as in the right hemisphere homologue of Broca's area. These results suggest that the right hemisphere activation that has also been found by others (Just et al., 1996; Nichelli et al., 1995) might reflect error detection. The syntactic processing component that is common across studies seems to be subserved by the left frontal areas.

The first fMRI study at 4 tesla on sentence processing was performed by Bavelier and colleagues (1997). They compared activations due to sentence reading with the activations induced by consonant strings presented like the sentences. Although the design does not allow the isolation of different sentence-level components (e.g., phonological, syntactic, and semantic processing), it nevertheless contains a number of relevant results. Overall, activations were distributed throughout the left perisylvian cortex, including the classical language areas (Broca's area, Wernicke's area, angular gyrus, and supramarginal gyrus). Other parts of the perisylvian cortex were also activated, such as left prefrontal areas and the left anterior-temporal lobe. At the individual subject level, these activations were in several small and distributed patches of cortex. In other visual but nonlanguage tasks, local activations were much less patchy, i.e., containing more contiguous activated voxels than the activations during visual sentence reading. Moreover, the precise pattern of activations varied substantially across individuals. For instance, the activations in Broca's area varied significantly in the precise localization with respect to an individual's main sulci.

If this patchy pattern of activations and the substantial differences across subjects during sentence reading reflect a basic difference between the neural organization of linguistic integration processes and the neural organization of sensory processing, this might in part explain the inconsistency of the lesion and brain-imaging data on sentence-level processing.

*Conclusion* The data indicate that syntactic processing is based on the concerted action of a number of different areas, each with its own relative specialization. These rela-

tive specializations may include memory requirements for establishing long-distance structural relations, the retrieval of lexical-syntactic information (word classes, such as nouns and verbs; grammatical gender; argument structure; etc.), the use of implicit knowledge of the structural constraints in a particular language to group words into well-formed utterances, and so on. All these operations are important ingredients of syntactic processing. At the same time, they are quite distinct and hence unlikely to be the province of one and the same brain area. The same conclusions apply, *mutatis mutandis*, to semantic integration processes.

In light of the available evidence, it can be argued that sets of areas in the left perisylvian cortex, each having its own relative specialization, contribute to syntactic processing and to important aspects of higher-order semantic processing. Exactly what these specializations are needs to be determined in studies that successfully isolate the relevant syntactic and semantic variables, as specified in articulated cognitive models of listening and reading. In addition, there appears to be restricted but nonetheless salient individual variation in the organization of the language processing networks in the brain, which adds to the complexity of determining the neural architecture of sentence processing (cf. Bavelier et al., 1997).

Broca's area has been found to be especially sensitive to the processing load involved in syntactic processing. It thus might be a crucial area for keeping the output of structure-building operations in a temporary buffer (working memory). The left temporal cortex, including anterior portions of the superior-temporal gyrus is presumably involved in morphosyntactic processing (Dronkers et al., 1994; Mazoyer et al., 1993). The retrieval of lexical-syntactic information, such as word class, supposedly involves the left frontal and left temporal regions (Damasio and Tranel, 1993; Hillis and Caramazza, 1995).

Although lesion and PET/fMRI studies on sentence comprehension have not yet reached the sophistication of bearing results with clear implications for our functional models of parsing and other sentence-level integration processes, they have begun to demarcate the outlines of the neural circuitry involved. Moreover, these studies have raised a number of important issues that have to be dealt with in future studies on the cognitive neuroscience of language. Prime among them is the issue of individual variation.

## Cognitive neuroscience research on language comprehension: The next millennium

The ERP work offers us a rich collection of potentials that can be fruitfully related to language comprehension,

providing important constraints on the architecture and mechanisms of the language system. The PET and fMRI research on sentence processing has complemented the lesion work, further delimiting language-related areas in the brain. At the very least, we have a solid basis on which to continue building a cognitive neuroscience research program on language understanding. However, various challenges still lie ahead, two of which we briefly mention here.

First, an appreciation of the differences between the various brain-imaging methods has led to the view that cognitive neuroscience research must bring together the more temporally and spatially sensitive research tools. In fact, it is becoming something of a dogma that ERP/ MEG. PET, and fMRI measurements should be combined, preferably in the same experiment. However, a note of caution is called for here: We have, as yet, very little understanding of how the electrophysiological and the hemodynamic signals are related. Without such knowledge, it is difficult to ascertain in what way a particular component of the ERP/MEG signal relates to a hemodynamic response in a specific area of the brain and vice versa. Therefore, any response to the call for a spatiotemporal integrative approach is, at present, more a promise for the future than an actual, substantive research program. For the moment, cognitive neuroscience research on language mirrors the standard methodological division in the brain-imaging field, with separate experiments with ERP and/or MEG methodology, and others with PET or fMRI. Much basic research is needed before it will be clear whether a meaningful (as opposed to a mere technical) marriage of electromagnetic and hemodynamic approaches is possible (see for further discussion Rugg, 1999).

A second issue concerns the PET and fMRI work on sentence processing. Most PET and fMRI language researchers have, perhaps understandably, steered clear of the complexities of integrational processes during comprehension; however, the field needs a concerted effort in this area. Language understanding entails much more than word recognition, and we must expand our knowledge of the neural architecture to include the circuitry involved in postlexical integration. A particular challenge for PET and fMRI work will be to implement research that does justice to the elegance and richness of human language.

ACKNOWLEDGMENTS We thank Robert Kluender, Pim Levelt, Jacques Mehler, Tom Münte, and Richard Wise for helpful comments, and Inge Doehring for graphical assistance. Colin Brown and Peter Hagoort are supported in part by grant 400-56-384 from the Netherlands Organization for Scientific Research. Marta Kutas is supported in part by grants HD22614, AG08313, M1152893.

#### REFERENCES

- BATES, E., S. MCNEW, B. MACWHINNEY, A. DEVESCOVI, and S. Smith, 1982. Functional constraints on sentence processing: A cross-linguistic study. *Cognition* 11:245-299.
- BAVELIER, D., D. CORINA, P. JEZZARD, S. PADMANABHAN, V P. CLARK, A. KARNI, A. PRINSTER, A. BRAUN, A. LALWANI, J. P. RAUSCHECKER, R. TURNER, and H. NEVILLE, 1997 Sentence reading: A functional MRI study at 4 tesla. J. Cogn. Neurosci. 9:664-686.
- BROWN, C. M., and P. HAGOORT, 1993. The processing nature of the N400: Evidence from masked priming. *J Cogn. Neuro*sci. 5:34-44.
- BROWN, C. M., and P. HAGOORT, 1999. On the electrophysiology of language comprehension: Implications for the human language system. In *Architectures and Mechanisms for Language Processing*, M. Crocker, M. Pickering, and C. Clifton, eds. Cambridge: Cambridge University Press, pp. 213-237.
- BÜCHEL,C., C. FRITH, and K. FRISTON, 1999. Functional integration: Methods for assessing interactions among neuronal systems using brain imaging. In *Neurocognition of Language*,
- C. M. Brown and P. Hagoort, eds. Oxford: Oxford University Press, pp. 337-358.
- CAPLAN, D., N. ALPERT, and G. WATERS, 1998. Effects of syntactic structure and propositional number on patterns of regional cerebral blood flow.). *Cogn. Neurosci.* 10:541-552.
- CAPLAN, D., N. HILDEBRANDT, and N. MAKRIS, 1996. Location of lesions in stroke patients with deficits in syntactic processing in sentence comprehension. *Brain* 199:933-949.
- CAPLAN, D., and G. WATERS, in press. Verbal working memory and sentence comprehension. *Brain Behav. Sci.*
- CARAMAZZA, A., and E. B. ZURIF, 1976. Dissociation of algorithmic and heuristic processes in language comprehension: Evidence from aphasia. *Brain Lang.* 3:572-582.
- COULSON, S., J. W KING, and M. KUTAS, 1998. Expect the unexpected: Event-related brain response to morphosyntactic violations. *Lang. Cogn. Proc.* 13:21-58.
- DAMASIO, A. R., and D. TRANEL, 1993. Verbs and nouns are retrieved from separate neural systems. *Proc. Natl. A cad. Sci. U.S.A.* 90:4957-4960.
- DRONKERS, N. F., D. P. WILKINS, R. D. VAN VALIN, JR., B. B. REDFERN, and J. J. JAEGER, 1994. A reconsideration of the brain areas involved in the disruption of morphosyntactic comprehension. *Brain Lang.* 47:461-463.
- ELMAN, J. L., 1990. Representation and structure in connectionist models. In *Cognitive Models of Speech Processing: Psycholinguistic and Computational Perspectives*, G. T M. Altmann, ed. Cambridge, Mass.: MIT Press, pp. 345-382.
- FRAZIER, L., 1987 Sentence processing: A tutorial review. In *The Psychology of Reading, Attention and Performance X11, M. Colt*heart, ed. Hillsdale, N.J.: Lawrence Erlbaum, pp. 559-586.
- FRAZIER, L., and C. CLIFTON, 1996. Construct. Cambridge, Mass.: MIT Press.
- FRIEDERICI, A. D., 1995. The time course of syntactic activation during language processing: A model based on neuropsychological and neurophysiological data. *Brain Lang.* 50:259-281.
- FRIEDERICI, A. D., A. HAHNE, and A. MECKLINGER, 1996. Temporal structure of syntactic parsing: Early and late event-related brain potential effects elicited by syntactic anomalies.) Exp. *Psychol.: Learn. Mem. Cognit.* 22:1219-1248.
- FRIEDERICI, A. D., and A. MECKLINGER, 1996. Syntactic parsing as revealed by brain responses: First-pass and

second-pass parsing processes. J. Psycholinguistic Res. 25:157-176.

- FRIEDERICI, A. D., E. PFEIFER, and A. HAHNE, 1993. Eventrelated brain potentials during natural speech processing: Effects of semantic, morphological and syntactic violations. Cogn. Brain Res. 1:183-192.
- FRISTON, K., C. FRITH, and R. S. J. FRACKOWIAK, 1993. Timedependent changes in effective connectivity measured with PET. Hum. Brain Mapp. 1:69-80.
- GRATTON, G., M. FABIANI, and P. M. CORBALLIS, 1997. Can we measure correlates of neuronal activity with non-invasive optical methods? In Optical Imaging of Brain Function and Metabolism II, A. Villringer and U. Dirnagl, eds. New York: Plenum Press, pp. 53-62.
- GUNTER, T. C., L. A. STOWE, and G. M. MULDER, 1997 When syntax meets semantics. Psychophysiol. 34:660-676.
- HAGOORT, P., and C. M. BROWN, in press. Semantic and syntactic ERP effects of listening to speech compared to reading. Neuropsychologia.
- HAGOORT, P., C. M. BROWN, and J. GROOTHUSEN, 1993. The syntactic positive shift (SPS) as an ERP-measure of syntactic processing. Lang. Cogn. Proc. 8:439-483.
- HÁGOORT, P., C. M. BROWN, and L. OSTERHOUT, 1999. The neurocognition of syntactic processing. In Neurocognition of Language, C. M. Brown and P. Hagoort, eds. Oxford: Oxford University Press, pp. 273-316.
- HAGOORT, P., C. M. BROWN, W VONK, and J. HOEKS, 1999. Manuscript in preparation.
- HEILMAN, K. M., and R. J. SCHOLES, 1976. The nature of comprehension errors in Broca's conduction and Wernicke's aphasics. Cortex 12:258-265.
- HILLIS, A. E., and A. CARAMAZZA, 1995. Representation of grammatical knowledge in the brain. J. Cogn. Neurosci. 7:397-407.
- INDEFREY, P., P. HAGOORT, C. M. BROWN, H. HERZOG, and R. J. SEITZ, 1996. Cortical activation induced by syntactic processing: A [150]-butanol PET study. NeuroImage 3:5442.
- JUST, M. A., P. A. CARPENTER, T A. KELLER, W F. EDDY, and K. R. THULBORN, 1996. Brain activation modulated by sentence comprehension. Science 274:114-116.
- KING, J. W, and M. A. JUST, 1991. Individual differences in syntactic processing: The role of working memory load. J. Mem. Lang. 30:580-602.
- KING, J. W, and M. KUTAS, 1995. Who did what and when? Using word- and clause-related ERPs to monitor working memory usage in reading. J. Cogn. Neurosci. 7:378-397.
- KLUENDER, R., and M. KUTAS, 1993a. The interaction of lexical and syntactic effects in the processing of unbounded dependencies. Lang. Cogn. Proc. 8:573-633.
- KLUENDER, R., and M. KUTAS, 1993b. Bridging the gap: Evidence from ERPs on the processing of unbounded dependencies. J. Cogn. Neurosci. 2:196-214.
- KLUENDER, R., and T F. MONTE, 1999. Wh-strategies in German: The influence of universal and language-specific variation on the neural processing of wh-questions. In preparation.
- KUTAS, M., K. D. FEDERMEIER, and M. I. SERENO, 1999. Current approaches to mapping language in electromagnetic space. In Neurocognition of Language, C. M. Brown and P. Hagoort, eds. Oxford: Oxford University Press, pp. 359-392.
- KUTAS, M., and S. A. HILLYARD, 1980. Reading senseless sentences: Brain potentials reflect semantic incongruity. Science 207:203-205.

- KUTAS, M., and J. W KING, 1995. The potentials for basic sentence processing: Differentiating integrative processes. In Attention and Performance XVI: Information Integration in Perception and Communication, T Inui and J. McClelland, eds. Cambridge, Mass.: MIT Press, pp. 501-546.
- KUTAS, M., and C. VAN PETTEN, 1994. Psycholinguistics electrified: Event-related brain potential investigations. In Handbook of Psycholinguistics, M. Gernsbacher, ed. New York: Academic Press, pp. 83-144.
- MACDONALD, M. A., N. J. PEARLMUTTER, and M. S. SEIDEN-BERG, 1994. The lexical nature of syntactic ambiguity resolution. Psych. Rev. 101:676-703.
- MAZOYÉR, B., N. TZOURIO, V FRAK, A. SYROTA, N. MU-RAYAMA, O. LEVRIER, G. SALAMON, S. DEHAENE, L. CO-HEN, and J. MEHLER, 1993. The cortical representation of speech. J. Cogn. Neurosci. 5:467-479.
- MCCLELLAND, J. L., M. ST. JOHN, and R. TARABAN, 1989. Sentence comprehension: A parallel distributed processing approach. Lang. Cogn. Proc. 4:287-335.
- MOHR, J. P., M. S. PESSIN, S. FINKELSTEIN, H. H. FUNKEN-STEIN, G. W DUNCAN, and K. R. DAVIS, 1978. Broca aphasia: Pathologic and clinical. Neurology 28:311-324.
- MÜNTE, T. F., M. MATZKE, and S. JOHANNES, 1997. Brain activity associated with syntactic incongruities in words and pseudo-words. J. Cogn. Neurosci. 9:300-311.
- NICHELLI, P., J. GRAFMAN, P. PIETRINI, K. CLARK, K. Y LEE, and R. MILETICH, 1995. Where the brain appreciates the moral of a story. NeuroReport 6:2309-2313.
- OJEMANN, G., 1991. Cortical organization of language and verbal memory based on intraoperative investigation. Prog. Sens. Physiol. 12:193-210.
- OSTERHOUT, L., 1994. Event-related brain potentials as tools for comprehending sentence comprehension. In Perspectives on Sentence Processing, C. Clifton, L. Frazier, and K. Rayner, eds. Hillsdale, N.J.: Erlbaum, pp. 15-44.
- OSTERHOUT, L., and P. HAGOORT, 1999. A superficial resemblance does not necessarily mean you are part of the family: Counterarguments to Coulson, King, and Kutas (1998) in the P600/SPS-P300 debate. Lang. Cogn. Proc. 14: 1-14.
- OSTERHOUT, L., and P. J. HOLCOMB, 1992. Event-related brain potentials elicited by syntactic anomaly. J. Mem. Lang. 31:785-806.
- OSTERHOUT, L., and P. J. HOLCOMB, 1993. Event-related potentials and syntactic anomaly: Evidence of anomaly detection during the perception of continuous speech. Lang. Cogn. Proc. 8:413-437.
- OSTERHOUT, L., and P. J. HOLCOMB, 1995. Event-related potentials and language comprehension. In Electrophysiology of Mind: Event-Related Brain Potentials and Cognition, M. D. Rugg and M. G. H. Coles, eds. New York: Oxford University Press, pp. 171-215.
- OSTERHOUT, L., R. MCKINNON, M. BERSICK, and V COREY, 1996. On the language-specificity of the brain response to syntactic anomalies: Is the syntactic positive shift a member of the P300 family?J. Cogn. Neurosci. 8:507-526.
- OSTERHOUT, L., J. MCLAUGHLIN, and M. BERSICK, 1997. Event-related brain potentials and human language. Trends Cogn. Sci. 1:203-209.
- PICTON, T. W, O. G. LINS, and M. SCHERG, 1995. The recording and analysis of event-related potentials. In Handbook of Neuropsychology, Vol. 10, F. Boller and J. Grafman, eds. Amsterdam: Elsevier, pp. 3-73.

- RUGG, M., 1999. Functional neuroimaging in cognitive neuroscience. In *Neurocognition of Language*, C. M. Brown and P. Hagoort, eds. Oxford: Oxford University Press, pp. 15-36.
- SPIVEY-KNOWLTON, M. J., andj. C. SEDÍVY, 1995. Resolving attachment ambiguities with multiple constraints. *Cognition* 55:227-267.
- ST. GEORGE, M., S. MANNES, andj. E. HOFFMAN, 1994. Global semantic expectancy and language comprehension. J. *Cogn. Neurosci.* 6:70-83.
- ST. GEORGE, M., S. MANNES, andj. E. HOFFMAN, 1997. Individual differences in inference generation: An ERP analysis. J. Cogn. Neurosci. 9:776-787.
- STOWE, L. A., A. A. WIJERS, A. T M. WILLEMSEN, E. REU-LAND, A. M. J. PAANS, and W VAALBURG, 1994. PET studies of language: An assessment of the reliability of the technique. *J. Psycholinguistic Res.* 23:499-527.
- STROMSWOLD, K., D. CAPLAN, N. ALPERT, and S. RAUCH, 1996. Localization of syntactic comprehension by positron emission tomography. *Brain Lang.* 52:452-473.

- TANENHAUS, M. K., and J. C. TRUESWELL, 1995. Sentence comprehension. In *Handbook of Perception and Cognition, Vol.* 11: Speech, Language, and Communication, J. Miller and P. Eimas, eds. New York: Academic Press, pp. 217-262.
- VAN BERKUM, J. J. A., P. HAGOORT, and C. M. BROWN, in press. Semantic integration in sentences and discourse: Evidence from the N400. J. *Cogn. Neurosci.*
- VANIER, M., and D. CAPLAN, 1990. CT scan correlates of agrammatism. In *Agrammatic Aphasia: A Cross-Language Narrative Source Book*, L. Menn and L. K. Obler, eds. Amsterdam: John Benjamins, pp. 37-114.
- VON STOCKERT, T R., and L. BADER, 1976. Some relations of grammar and lexicon in aphasia. *Cortex* 12:49-60.
- ZURIF, E. B., A. CARAMAZZA, and R. MYERSON, 1972. Grammatical judgments of agrammatic aphasics. *Neuropsychologia* 10:405-417.