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The neurocognitive processing of plausibility and real-world knowledge: A cross-linguistic investigation

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To my wonderful parents,

Peter and Anne Tune

"Music is to the soul what words are to the mind"

Thank you for being the tunes of my life!

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PART I

1   INTRODUCTION

Our knowledge about concepts and meanings is at the very heart of human cognition. In everyday life, we have to interact with our environment in a variety of different ways. Our actions are guided by what we know and believe about the world and this knowledge derives primarily from previous sensory and perceptual experiences. The fact that we are capable of engaging with our environment in an appropriate and efficient way means that we have learnt (how) to make sense of the events and entities we are faced with in day-to-day life. We are thus able to recognise and name both physical objects and abstract concepts, to categorise and associate them based on their specific properties, to interpret other people's intentions, and to judge cause and effect of their actions as well as our own. Moreover, the ability to represent this wealth of knowledge about the real world in the conceptualised and symbolic form of language is believed to be exclusive to humans. Our language capacity allows us to communicate with others about past and future events or to describe fictitious scenarios by combining previously acquired concepts in a novel way without the need for external stimulation. Thus language forms a primary means of interacting with those around us by allowing us to express our own thoughts and comprehend those of others. As long as language processing proceeds in an undisturbed manner, we are largely unaware of the underlying mechanisms that support the seemingly effortless interpretation of linguistic input. The importance of these processes for successful communication, however, becomes all the more apparent when language processing is disrupted, for example, by brain lesions that render semantic analysis difficult or impossible.

Scientific research that aims to uncover and define cognitive or neural mechanisms underlying semantic processing is inevitably faced with the complexity and wealth of semantic relationships that need to be taken into account. In absence of non-invasive neurocognitive methods and insights gleaned from modern neurobiology, early research had a limited impact on our understanding of how semantic processing is implemented in the human brain. Traditional neurological models of language have been based primarily on lesion-deficit data, and thus supported the view that certain areas of the brain were exclusively dedicated to the processing of language-specific functions (Geschwind, 1970; Lichtheim, 1885; Wernicke, 1874). Furthermore, classical theories of sensory processing viewed the brain as a purely stimulus-driven system

that retrieves and combines individual low-level aspects or features in an automated, passive and context-independent manner (Biederman, 1987; Burton & Sinclair, 1996; Hubel & Wiesel, 1965; Massaro, 1998).

After a recent paradigm shift in the cognitive neurosciences, current theories of sensory processing are now based on the concept of the brain as a highly active, adaptive and dynamic device. In this sense, language comprehension, like many other higher-cognitive functions, is shaped by a flexible interaction of a number of different processes and information sources that include so-called *bottom-up* signals, i.e., the actual sensory input and processes related to their forward propagation, and *top-down* processes that generate predictions and expectations based on prior experience and perceived probabilities. Therefore, accounts that view semantic processing as a dynamic and active construction of meaning that is highly sensitive to contextual influences seem most probable from a neurobiological perspective. Results from electrophysiological and neuroimaging research on semantic analysis in sentence and discourse context have provided evidence for top-down influences from the very beginning. In addition, recent ERP results have suggested that the interaction between top-down and bottom-up information is more flexible and dynamic than previously assumed. Yet, the importance of predictions and expectations has long been neglected in models of semantic processing and language comprehension in general.

Neuroimaging data have provided us with a long list of brain regions that have been implicated in different aspects of semantic analysis. We are only beginning to understand the role(s) that these regions play and how they interact to support the flexible and efficient construction of meaning.

The aim of the present thesis is to gain a more comprehensive view on the computational mechanisms underlying language processing by investigating how bottom-up and top-down information and processes interactively contribute to the semantic analysis in sentences and discourse. To this end, we conducted a total of five studies that used either event-related potentials or functional neuroimaging to shed light on this matter from different perspectives.

The thesis is divided into two main parts: Part I (chapters 1-5) provides an overview on previous results from electrophysiology and neuroimaging on semantic processing as well as a description and discussion of the studies conducted in the

present thesis. Part II (chapters 6-9) consists of three research articles that describe and discuss the results of five experimental studies.

In Part I, Chapter 2 gives a brief introduction to the event-related potential and functional neuroimaging techniques and reviews the most relevant results and theories that have emerged from studies on sentence and discourse processing. Chapter 3 highlights the research questions targeted in each of the experimental studies and describes and discusses the most relevant findings against the background established by Chapter 2. Chapters 4 and 5 conclude Part I by placing the presented results in a broader context and by briefly outlining future directions.

Part II begins with a survey of the three studies reported in the subsequent chapters. Chapter 7 highlights the results of the first study, a German ERP experiment that investigated the impact of capitalisation, i.e., a purely form-based and contextually independent bottom-up manipulation, on the processing of semantic anomalies in single sentences. Chapter 8 comprises three ERP experiments that used both easy and hard to detect semantic anomalies in German and English to corroborate the assumption that the weighting of top-down and bottom-up information cues might be determined in a language-specific way. Chapter 9, the final chapter of the thesis, describes and discusses the results of the third study, in which the impact of embedding context on the required depth of semantic processing was examined using functional neuroimaging.

2   EMPIRICAL EVIDENCE ON SEMANTIC PROCESSING

Scientific studies aiming to examine semantic processing in the human brain can be categorised along several dimensions. One way is to broadly differentiate studies based on the research questions they tried to answer. In this respect, research has focused on three aspects of language processing that are thought to represent distinct aspects of semantic analysis: representation, access and integration. At the same time, research questions and the experimental manipulations used to test existing hypotheses critically hinge on the characteristics of the applied research technique. Studies aiming to uncover the time course of semantic processing are thus different from investigations that set out to identify and describe the role of brain areas involved in certain processes.

The experiments that are presented in detail in Part II used either EEG or fMRI to shed light on different aspects of semantic processing. To establish a background against which the results of the studies can be discussed, this chapter reviews the most relevant findings separately for the domains of electrophysiological and neuroimaging research.

2.1   Electrophysiological research on semantic processing

The so-called N400 component is the most important dependent measure in neurocognitive studies that use event-related potentials to investigate the neural bases of semantic processing. This chapter begins with a brief introduction to the basic principles of the event-related potential technique. The focus of this chapter lies on a review of important findings that led to the postulate of the most prominent theories on its functional significance. These theories are described and contrasted in the last section of this chapter.

2.1.1   Basic principles

The human electroencephalogram (EEG) – measured non-invasively via scalp electrodes – is thought to emerge primarily as the result of summed postsynaptic potentials of large assemblies of neocortical pyramidal cells. To produce externally detect-

able voltage fluctuations, hundreds of thousands of these neurons that are symmetrically aligned and oriented perpendicularly to the surface of the scalp need to be activated in a synchronised fashion (Kutas & Dale, 1997). Changes in neurophysiological activity of the brain triggered by and time-locked to cognitive, sensory or motor events are known as event-related potentials (ERPs). The extraction of these stimulus-related brain signals by repeated averaging procedures is a technique that allows the tracking of information processing with excellent temporal precision on the order of milliseconds. The method is thus extensively employed in experimental psychology, cognitive neuroscience, psycho- and neurolinguistics, as well as many related fields to study the time course of cognitive and neural processes underlying higher-cognitive functions such as language, memory or attention. In this endeavour, ERP effects, i.e., the relative difference in brain activity elicited by two experimental conditions, are of primary interest. Individual ERP components or effects can be distinguished and compared along four dimensions: amplitude, latency, polarity and topography. Even though the spatial distribution of ERPs is one of the features used to describe and compare ERP patterns, there is no straightforward mapping of effects measured on the surface of the scalp to their underlying neural generators. This is due to the so-called "inverse problem", i.e., the fact that there is no unique mathematical solution to the attempted reconstruction of an intracranial current source for a pattern of scalp-recorded EEG activity. Despite recent methodological advances made in the quest to create sophisticated algorithms to derive neural sources of event-related potentials, one still needs to proceed cautiously in interpreting the results, as the localisations will always remain approximate in nature.

2.1.2   Characterisation of the N400

First reported in 1980 in the seminal article by Kutas and Hillyard (Kutas & Hillyard, 1980), the N400 component is defined as a negative-going signal deflection in the ERP that typically occurs in a time window of 250 to 600ms after stimulus onset and reaches its peak at approximately 400ms. The N400 shows a relatively broad distribution across both hemispheres but tends to be most pronounced at central and parietal electrode sites. For visually presented words, it has a small but robust bias towards the right hemisphere, whereas the processing of auditory words is characterised by a more anterior and left-sided negativity (Holcomb & Neville, 1990). Since its discovery, a

great deal of electrophysiological research has focused on delineating the functional significance of the N400. To this end, scientific studies aimed to examine which stimulus types would generally elicit N400 activity, and to arrive at a fine-grained description of factors that exert a modulating influence on amplitude, distribution or latency of this electrophysiological response.

Having been discovered in a linguistic context – or more precisely – in response to anomalous sentence-final words, an interpretation of the N400 as a language-specific correlate of semantic processing appeared highly attractive because it was in line with the ideas of modularity and domain specificity that were at the heart of many models of language comprehension at that time (Fodor, 1983; Forster, 1979; 1989). In fact, this view of the N400 has been surprisingly persistent despite an extensive body of literature that refuted this perspective. Electrophysiological evidence accrued over the past thirty years shows N400 activity elicited not only by spoken, written or signed words, but by a wide range of meaningful (or potentially meaningful) stimuli, including pronounceable pseudowords, familiar and unfamiliar acronyms (Holcomb & Neville, 1990; Kutas, Neville, & Holcomb, 1987; Laszlo & Federmeier, 2007; 2008), faces (Barrett & Rugg, 1989; Bobes, Valdessosa, & Olivares, 1994; Germain-Mondon, Silvert, & Izaute, 2011), videos (Sitnikova, Holcomb, Kiyonaga, & Kuperberg, 2008), gestures (Kelly, Kravitz, & Hopkins, 2004; Wu & Coulson, 2005), line drawings, pictures and scenes (Barrett & Rugg, 1990; Ganis & Kutas, 2003; McPherson & Holcomb, 1999; Willems, Özyürek, & Hagoort, 2008), as well as environmental sounds (Chao, Nielsen-Bohlman, & Knight, 1995; Orgs, Lange, Dombrowski, & Heil, 2006; Van Petten & Rheinfelder, 1995).

In addition, some of these N400 effects have been observed in studies that examined whether semantic priming effects reported for verbal prime-target pairs presented in the same modality (visual or auditory) would not only generalise across modalities but also extend to nonverbal stimuli. Indeed, effects of semantic priming, i.e., a reduction in N400 amplitude for the target of a semantically related stimulus pair, have been found for words across modalities, in pairs combining verbal and nonverbal stimuli, as well as among nonverbal stimulus types such as pictures, gestures, faces or even odours (Castle, Van Toller, & Milligan, 2000; Gottfried & Dolan, 2003; Sarfarazi, 1999). Taken together, these findings provide strong evidence against a view of the N400 as a language-specific index of semantic processes that operate in a do-

main-specific fashion and independent of additionally available sensory or perceptual information. On the contrary: the data suggest that the N400 marks the brain's default response to a wide variety of potentially meaningful stimuli, thus reflecting cognitive processes that contribute to a dynamic, interactive and multimodal[1] construction of meaning. In conclusion, the overall sensitivity of the N400 to a wide range of stimuli speaks for a differentiation between meaningful and meaningless events, and not for a discrimination of linguistic and non-linguistic stimuli (cf. Kutas & Federmeier, 2011).

2.1.3   N400 as a dependent measure in language comprehension

The fact that the N400 cannot be taken as marker of semantic processes in language alone does not preclude it as a dependent variable in investigations on cognitive mechanisms that support semantic analysis in language. Over the past thirty years, much insight has been gained from studies that used the N400 to examine the time course of word and sentence processing, and to identify the factors that dynamically shape how the brain constructs meaning. From scientific studies that employed different experimental manipulations including the classic anomalous sentence paradigm, but also priming and repetition designs, we know that it is the amplitude of the N400 that shows the most variation, while latency and topography remain relatively stable.

The combined results of a large number of scientific studies provide a comprehensive and complex description of the variety of factors that bear on the amplitude of the N400. Today, we are still adding new pieces to the puzzle. The following summary of the most influential findings on the N400 in studies investigating language comprehension will show that we are still far away from completely understanding the functional significance of this measure and even further away from mapping it to precise and neurobiologically plausible mechanisms.

The first report of the N400 in 1980 by Kutas and Hillyard already provided us with some important details about its sensitivity. Across three experiments, the

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[1] It is a matter of debate whether the N400 reflects semantic processes that rely on purely amodal representations of conceptual knowledge (see Binder & Desai, 2011 for a recent review of different accounts on the representation of semantic knowledge). Differences in topography observed for N400 effects across different modalities and stimulus types (and sometimes within a given modality as a function of concreteness, e.g., West & Holcomb, 2000) seem to speak against a purely amodal representation, as the N400 appears to be at least sensitive to different modalities. While differences in topography of ERPs do not allow for a precise identification of underlying cognitive or neural processes, a possible characterisation of the N400 is that it reflects a number of partially modality-specific but functionally similar processes that are supported by a more or less overlapping configuration of brain regions.

authors compared the electrophysiological response to non-anomalous sentence-final words (1a) with the response to sentence completions that were either semantically (1b+c) or physically (1d) unexpected:

> (1)   a. It was his first day at work.
>
>   b. He took a sip from the waterfall.
>
>   c. He took a sip from the transmitter.
>
>   d. She put on her high-heeled SHOES.

The comparison revealed three main findings: (i) relative to non-anomalous words, sentence-final words that expressed mildly or strongly unexpected events led to an increase in N400 amplitude; (ii) the magnitude of this change in amplitude reflected the relative expectedness of the critical word within the provided sentence context; and (iii) stimuli that were unexpected with respect to their physical appearance elicited a qualitatively different response. These results allowed an initial assessment of the cognitive processes that the N400 might be reflecting. From the observed data pattern, it was obvious that the N400 was not merely an index of the brain's reaction to surprising or unexpected stimuli of all kinds as deviations from the orthographical norm were treated differently. Furthermore, the comparison of unexpected, yet in principle plausible, and grossly violating words showed that the N400 was sensitive to language processing at a complex level as it mirrored the degree of a word's contextual fit by a graded increase in amplitude.

Subsequent research extended these initial findings in numerous ways. While several studies replicated the finding that semantic anomalies engendered large N400 effects, further evidence showed that semantic violations were, however, not a necessary prerequisite for the elicitation of such effects as they have also been observed in response to plausible yet unexpected sentence completions relative to more predictable continuations (Kutas & Hillyard, 1984). More precisely, it was shown that the amplitude of the N400 was inversely correlated with the so-called "cloze probability" of a word (Taylor, 1953). The term cloze probability describes the proportion of people that choose a particular word as the most plausible continuation of a sentence fragment in an offline paper and pencil test. This means that words with a high cloze probability elicit smaller N400 amplitudes than words with a low cloze probability that are less expected in a given sentence or discourse context. These results con-

firmed that expectations and predictions play an important part in language comprehension and that amplitude modulations are closely related to a word's predictability. As discussed in more detail below, the sources driving these expectancies and the mechanisms by which they are implemented at a cognitive or neural level remain a matter of open debate.

At the same time, studies investigating language comprehension at the single word level revealed that N400 effects were not a phenomenon emerging in the context of higher-order structures only, as even isolated words were associated with variable N400 amplitudes determined by different stimulus characteristics. Investigations aiming to describe the functional sensitivity of the N400 in a systematic manner have focused on different aspects: at the one end of the spectrum are studies examining the influence of low-level, local and stimulus-dependent (bottom-up) influences on single word processing, while other studies concentrated on the impact of higher-level, global and context-driven (top-down) information. Lastly, there are a number of studies that explored the interaction between the two types of information sources.

2.1.3.1 Word level effects

In spite of initial evidence for a modulating influence of contextually derived expectations, many of the early experiments on the N400 focused on the impact of stimulus-related factors such as frequency, orthographic neighbourhood, repetition, concreteness, and word-level lexical associations. This emphasis was most likely due to the influence of early psycholinguistic models of language comprehension that argued for a priority of bottom-up information in serial and integrative models of word recognition and reading (e.g., Forster, 1989; Marslen-Wilson, 1989; Norris, 1994). These models advocated a view in which word recognition was initiated by an automatic and passive spread of activation across nodes of a semantic network or "mental lexicon" that was completely independent of more global, contextual information (Collins & Loftus, 1975; see Neely, 1991 for a review).

In fact, a large number of electrophysiological experiments revealed that the size of the N400 amplitude was shaped by a variety of bottom-up information sources. Given that all other factors are kept constant, high frequency open-class words tend to elicit an N400 of smaller, i.e., more positive, amplitude than low-frequency words. This effect was observed for words in unstructured lists (Rugg, 1990) or embedded in

sentences. In sentences, however, frequency effects interact with the position of the critical word within the sentence, as the advantage for frequent over infrequent words was found to be largest in sentence-initial and attenuated in sentence-final positions (Van Petten & Kutas, 1990; 1991b). Repetition causes a similar change in amplitude size, with repeated words engendering a reduced N400 compared to non-repeated words. This effect is most robust for words presented as part of unstructured word lists (Rugg, 1985), but can also be observed in higher-order structure such as sentences or discourse (Van Petten & Kutas, 1991a) as long as repetition is licensed within that context (Swaab, Camblin, & Gordon, 2004).

As with frequency effects, repetition effects also interact with temporal aspects, such that they are strongest for immediate repetition and decline with increasing distance between the initial presentation of a word and its repetition. Furthermore, N400 amplitude varies as a function of a word's orthographic neighbourhood size, i.e., the number of existing words that can be formed by altering one letter only. Words that have a high number of lexical neighbours trigger stronger N400 activity than words with a small lexical neighbourhood – a findings that also extends to pseudowords (Holcomb, Grainger, & O'Rourke, 2002).

2.1.3.2 Contextual influences

Many studies focused on effects of semantic priming that lead to a reduced N400 amplitude for target stimuli compared to words that are not preceded by semantically related primes. In this context, the N400 has served as a dependent measure to test the assumption that priming effects observed at the word level are due to automatic mechanisms during a presumed autonomous stage of word recognition, whereas context-level facilitation are driven by controlled post-lexical computations. To probe this hypothesis, Kutas (Kutas, 1993) compared of the effects of lexical and sentential context during on-line word processing in a within-subject design. The results showed that both types of contexts elicited N400 effects that were highly similar with respect to their spatial distribution, latency and overall morphology. The only apparent difference concerned the size of the amplitude: it was smaller for related words in sentences than for words in semantically related word pairs. The author argued that this effect reflected differences in contextual constraint between word pairs and sentences, since sentential context led to an accumulation of semantic constraint over time. In sum-

mary, the study provided strong evidence against the proposition that facilitation aris-ing from word-level lexical-semantic associations and sentential context are inde-pendent of one another. However, this does not entail that sentence context effects are simply the results of additive lexical-semantic associations, as similar but independent effects were found when both information sources were available (van Petten, 1993).

As alluded to above, several studies found interactions of sentence-level ef-fects with factors like word frequency and repetition, as well as lexical associations – all of which argue against a strict temporal dissociation of bottom-up and top-down influences. Yet, when both information sources are present, there is a general ten-dency for higher-level effects to cancel out the impact of bottom-up information sour-ces (Coulson, Federmeier, Van Petten, & Kutas, 2005; Van Petten & Kutas, 1991b; Van Petten, Kutas, Kluender, Mitchiner, & McIsaac, 1991).

The influence of global information sources on the interpretation of contex-tually embedded words was further corroborated by studies finding N400 differences between words that confirmed or disproved discourse level expectations. One such experiment conducted by van Berkum and colleagues (Berkum, Hagoort, & Brown, 1999; Hagoort & van Berkum, 2007; Van Berkum, Zwitserlood, Hagoort, & Brown, 2003) presented participants with short stories in which they manipulated the contex-tual fit of a word in the last sentence. Importantly, anomalous words were only in con-flict with the discourse theme and not with the meaning of the sentence in which they appeared. For example, story-final sentences such as *"Jane told her brother that he was exceptionally slow/quick"* are equally plausible as long as only the sentential con-text is considered. In a wider discourse context that describes Jane's brother as having been quite fast, however, the word *"slow"* is highly unexpected. Indeed, the authors reported a larger N400 for discourse-anomalous relative to discourse-coherent words. The comparison of N400 anomaly effects at the discourse- and sentence-level showed that they were highly similar, especially in regard to the observed topography, as well as onset and peak latency. In reference to this perceived similarity, Hagoort and van Berkum (2007, p. 803) assume that the two effects are based on *"the activity of a largely overlapping or identical set of underlying neural generators, indicating simi-lar functional processes"*.

2.1.4   Theories of the N400

In light of the reviewed data, what can be concluded about the nature of the N400 obtained in linguistic contexts? One general conclusion is that the N400 response to a word is dynamically influenced by both local and global information sources. In this sense, it appears to reflect a single or multiple processes that support the flexible construction of a word's meaning as shaped by the interaction between bottom-up and top-down information. Naturally then, the question arises as to the details of these processes and how they relate to the sequence of distinct processing steps that were postulated for some psycholinguistic models of sentence processing. Moreover, if the goal to understand how meaning is derived in the human brain is to be taken seriously, one needs to ask how the identified functions could be implemented by neurally plausible mechanisms.

The proposed functional interpretations of the N400, of which three are discussed in more detail below, differ with respect to the level at which they attempt to sketch out underlying mechanisms. Most of the electrophysiological research on language processing grew out of theoretically grounded and behaviourally tested conceptions of how language comprehension (and production) is carried out in our "minds". Therefore, the debate on the functional interpretation of the N400 has mainly focused on the question which of the processes assumed to contribute to language comprehension was reflected by the N400. Indeed, recent years have seen a slow but steady shift toward accounts that aim to relate the N400 to neural networks and neural computations involved in the convergence of single features onto a unified concept (e.g., Federmeier & Laszlo, 2009; Laszlo & Plaut, 2012; Lau, Phillips, & Poeppel, 2008; Van Petten & Luka, 2006).

2.1.4.1 The integration view

As one of the most prominent theories of the N400, the "integration view" postulates that changes of N400 amplitude arise due to relatively late, post-lexical processes that mediate the controlled and strategic integration of a current word with the contextual information accrued up to that point (e.g., Brown & Hagoort, 1993; Hagoort, 2008; Hagoort & van Berkum, 2007; Hagoort, Baggio, & Willems, 2009). This account is in line with one-step models of language comprehension that build on the so-called "immediacy assumption" (Altmann, 1997; Just & Carpenter, 1980; MacDonald,

Pearlmutter, & Seidenberg, 1994; Tanenhaus & Trueswell, 1995), the idea that interpretation is driven by the instantaneous and parallel impact of all available information sources including those that co-occur in a different modality (e.g., syntax, lexical-semantic associations at the word level, sentence and discourse context, speaker identity, co-speech gestures, etc.).

In contrast, a two-step model of language interpretation would predict that the meaning of a word is first computed within the local sentence context before it is integrated with global discourse information. The integration account interprets modulation of N400 amplitude as an index of the processing costs caused by combining a word with the higher-order representation held in working memory. For words that have a close fit to context and are therefore highly expected, *"semantic unification"*, i.e., the *"constructive process in which a semantic representation is constructed that is not already available in memory"* (Hagoort et al., 2009, p. 833), is easier than for less expected and anomalous words.

Importantly, while the proponents of this account acknowledge that language processing is highly predictive, they assume that the mechanisms underlying the N400 are essentially non-predictive in nature as they do not reflect the process by which expectations are generated, but index the match or mismatch between existing expectations and the current input. From this line of argumentation follows that the size of the N400 should strongly correlate with the plausibility of an utterance (commonly measured via offline plausibility judgements) as words that are highly expected and therefore easier to integrate tend to be perceived as more plausible. While this correlation appears to be confirmed in a number of studies, as will be discussed below, there are also notable exceptions that challenge this functional interpretation of the N400.

The integration account is strongest in explaining the influence and – in some cases – the dominance of higher-level information sources over lower-level ones. It is supported by studies that provide evidence for the impact of a number of such higher-level cues on language comprehension. As mentioned above, multiple studies showed that N400 effects for semantic anomalies at the word, sentence or discourse level were highly similar in their time-course, topography and overall morphology (Berkum et al., 1999; Kutas, 1993; Van Berkum et al., 2003). In similar spirit, Hagoort and colleagues (2004) compared violations of world knowledge, i.e., sentences that allow for the construction of coherent propositions that were nevertheless factually incorrect, to

semantic anomalies that induced a conflict at a more basic level. In accordance with previous findings, the authors observed virtually identical N400 effects for both anomaly types compared to plausible control conditions.

Additional studies corroborated the view that information sources at a global level such as the identity of the speaker (Van Berkum, 2008) or the overall discourse topic (George, Mannes, & Hoffinan, 1994; Nieuwland & Van Berkum, 2005; 2006) could override the impact of local cues such as word-level semantic associations or animacy constraints. The study by Nieuwland and van Berkum (2006) found an N400 effect for sentences like *"The peanut was salted"* compared to *"The peanut was in love"* when they were embedded in a cartoonlike story that described the inanimate object with human features. Taken together, these findings can be readily derived from a theory that assumes an interaction of all accessible information sources at the same stage of language processing. Finally, the integration account provides a straightforward explanation for the sensitivity of the N400 to cross-modal information in priming but also sentence paradigms (Özyürek, Willems, Kita, & Hagoort, 2007; for the integration of verbal content with iconic co-speech gestures or pictures, see Willems et al., 2008).

The account fails to explain the genesis of all those effects that are related to purely bottom-up factors such as frequency or orthographic neighbourhood size that bear on N400 amplitude in absence of any context. In principle, under the assumption that the N400 is a marker for post-lexical integration processes only, all changes in amplitude that are temporally localised to pre-lexical or lexical processes are not predicted by this theory. Moreover, as semantic integration appears to be mediated by top-down control processes, this should preclude N400 modulation in the absence of conscious attention. However, there are multiple studies that obtained N400 effects from non-conscious paradigms such as masked priming (Deacon, Hewitt, Yang, & Nagata, 2000; Eddy, Schmid, & Holcomb, 2006; Kiefer, 2002), the attentional blink (Luck, Vogel, & Shapiro, 1996; Maki, Frigen, & Paulson, 1997) and even during different stages of sleep (e.g., Brualla, Romero, Serrano, & Valdizán, 1998; López, Carmenate, & Alvarez, 2001; for a review see Ibáñez, Martín, Hurtado, & López, 2009). Lastly, the integration account does not provide an explanation for recent findings that showed N400 activity not only for real, existing words but also for pronounceable pseudowords and familiar acronyms presented in unstructured lists and for unfamiliar,

illegal acronyms when embedded in sentences (Laszlo & Federmeier, 2007; 2008; 2009; 2011).

2.1.4.2 The lexical "preactivation" view

While the integration view had been the prevailing functional interpretation of the N400 for many years, the number of results that could not be derived from this theory increased steadily. It became obvious that any functional interpretation that aimed to account for the entire range of available results needed to map out a mechanisms that incorporated the influence of both top-down and bottom-up processes as well as possible interactions between the two processing routes. This led to the postulate of the "lexical (preactivation) view" (e.g., Brouwer, Fitz, & Hoeks, 2012; Federmeier & Kutas, 1999; Kutas & Federmeier, 2000; Lau et al., 2008; Stroud & Phillips, 2011).

In this theory, a reduction in N400 amplitude, as for example observed for semantically related target stimuli in priming paradigms or for highly expected words in sentences, is thought to reflect a facilitated access to semantic information in long-term memory. More precisely, this ease of processing is achieved by a strong predictive component that uses contextual information to *"pre-activate the perceptual and semantic features of forthcoming items, such that information congruent with the context or the prediction it has engendered is subsequently easier to assimilate and process"* (Kutas & Federmeier, 2000, p. 468). Importantly, while the cause for lexical "preactivation" might be based on output from combinatorial operations, the N400 itself is assumed to arise from a non-combinatorial mechanism.

There are different opinions on the precise nature and organisation of the representations of meaning that are "stored" in semantic memory and the lines between ideas that represent constructs of purely cognitive psychological nature and those concepts that are proposed to be neurobiologically grounded are more than blurry at times (for comprehensive reviews see Binder, Desai, Graves, & Conant, 2009; Martin, 2007; McRae & Jones, 2012). One prominent view that lies at the heart of the lexical view is that semantic knowledge is represented in a distributed fashion across several areas of the brain and that the building blocks or units of this distributed network encode semantic or conceptual features that converge onto unified semantic concepts.

The lexical view is supported by studies reporting the absence of N400 effects for violations that were clearly semantic in nature. The earliest evidence stems from a study that used event-related potentials to compare the processing of true or false affirmative and negative statements about categorical membership (Fischler, Bloom, Childers, Roucos, & Perry, 1983). For affirmative sentences (e.g., *"A robin is a bird/tree"*), the authors found the N400 amplitude to be larger for false compared to true statements. The electrophysiological pattern observed for negative statements, however, was less expected: here, true negative statements (*"A robin is not a tree"*) elicited a more negative N400 than negative statements that were factually false (*"A robin is not a bird"*). These findings indicate that the observed N400 effect does not reflect differences in truth between statements, but instead might be driven by the degree of semantic association between individual words. Importantly, these results could not be derived from an integration account that capitalises on the plausibility of an utterance.

The assumption that changes in N400 amplitude are at least in part influenced by lexical-semantic associations between individual elements of a sentence was further supported by the research literature on so-called "semantic reversal anomalies", i.e., constructions that induce a conflict between form and meaning. These violations are characterised by a reversed and therefore implausible assignment of thematic roles to nominal arguments that exhibit a close semantic relation to the described event. In English and Dutch, sentences such as *"The hearting meal was <u>devouring</u>…"* (Kim & Osterhout, 2005) or *"De speer heeft de athleten <u>geworpen</u>"* ('The javelin has thrown the athletes') (Hoeks, Stowe, & Doedens, 2004) did not engender N400 but late positivity effects at the position of the verb (underlined) when compared to plausible sentences. Notably, analogous sentences that lacked a strong semantic association between the subject and the expressed action (*"The dusty tabletops were devouring…"*) did elicit the expected N400 effects. While findings from English and Dutch alone point towards a strong influence of lexical-semantic associations (see e.g., Brouwer et al., 2012; Stroud & Phillips, 2011), Chapter 3 will describe and discuss cross-linguistic differences in the processing of semantic reversal anomalies that complicate this interpretation.

In 1999, Federmeier and Kutas reported the results of an ERP study that were highly influential for the evolution of the lexical theory of the N400 (Federmeier &

Kutas, 1999). The authors extended the traditional sentence violation paradigm by introducing a context sentence that determined the contextual constraint, i.e., the degree to which the context led to high cloze probabilities for the sentence-final word. In addition, they presented participants with three kinds of sentence completions: those that were highly expected and contextually congruent, and two types of incongruent words with an equally low cloze probability either belonging to the same semantic category or to a different one. Moreover, as assessed by a pre-test, the two incongruent words led to equally low plausibility judgements. Thus, if the size of the N400 critically hinged on the ease of contextual integration, there should be no difference in N400 activity for the anomalous words. However, if context-independent aspects – like the idea that concepts within a semantic category share more features than concepts that belong to different categories – had an impact on semantic processing, differences would be expected. Importantly, the latter hypothesis implies that language comprehension was indeed guided by (specific) predictions for upcoming items.

Below are examples for all types of completions in sentences following high (2a) and low (2b) contextual constraints.

(2)   a. They wanted to make the hotel look more like a tropical resort.

               So along the driveway they planted row of palms/pines/tulips.

          b. Eleanor offered to fix her visitor some coffee.

               Then she realized she didn't have a clean cup/bowl/spoon.

The comparison of the brain's activity in response to the critical stimuli (underlined) yielded the following main findings: (i) both high and low constraining context engendered graded levels of N400 activity; (ii) N400 amplitude was smallest for congruent completions, intermediate for within-category violations and largest for between-category violations; (iii) contextual constraint interacted with the ERP response such that within-category violations elicited a larger N400 under low than high semantic constraint; and (iv) plausibility ratings were affected in the opposite direction by sentential constraint.

These findings allow for several important conclusions. First of all, results (i) and (ii) not only support the idea that the brain generates predictions about upcoming words, but also that these predictions are relatively precise. Thus, two items that are

fairly similar in their characteristics due to a considerable overlap in semantic features, still elicit distinct level of N400 activity as one of the two fulfils the existing predictions to higher degree. Furthermore, semantic processing seems to be sensitive to context-independent relationships between concepts that could be represented in long-term memory structure or dynamically generated. Lastly, Federmeier and Kutas (1999) argue that in terms of on-line processing, within-category violations benefit from contextual constraint as it leads to more precise predictions for plausible sentence completions. In this sense, the N400 is assumed to reflect the match or feature overlap between the expected (but not presented) and the actually encountered item. The higher the feature overlap and the stronger the "preactivation" of features for the predicted item, the easier is the switch from one processing state to the next.

This functional interpretation can easily derive priming effects as well as data that underscore the predictive nature of language processing (DeLong, Urbach, & Kutas, 2005; Van Petten, Coulson, Rubin, Plante, & Parks, 1999). However, there are several results that cannot be reconciled with this account of the N400. On the one hand, there are several studies that found N400 effects for the mismatch between information structure and prosodic cues (Hruska & Alter, 2004; Li, Hagoort, & Yang, 2008; Toepel & Alter, 2004). In one of these studies, Schumacher and Baumann (2010) used sentence pairs such as *"Sabine repairs an old shoe. In doing so, she cuts the sole"* in which the referent introduced in the second sentence (underline) is accessible via an inference (in this case, a whole-part relation) from another active discourse referent. Accessible referents marked with a pitch accent that signalled the introduction of a new referent engendered an N400 effect relative to an appropriate pitch accent. This finding cannot be explained by contextual influences on the critical word since the propositional content of the second sentence remained unchanged. The observed N400 effect appears to reflect a conflict induced by the bottom-up information of the critical word itself in conjunction with the information structure of the sentence pairs.

On the other hand, there are robust cross-linguistic differences in the processing of semantic reversal anomalies. In contrast to English and Dutch that only show a late positivity, German, Turkish and Chinese do show N400 effects that are in some languages followed by a late positivity (Bornkessel-Schlesewsky et al., 2011). Again, on the basis of the lexical account these cross-linguistic differences cannot be ex-

plained in a straightforward way as the degree of semantic association between the nominal arguments and the verb was comparable across the tested languages. Chapter 3 describes these findings in more detail and proposes how these findings could be explained in an extended account of the N400.

Finally, as the integration view, this functional interpretation fails to account for N400 activity and effects observed for pseudowords and orthographically illegal strings such as familiar and unfamiliar acronyms.

2.1.4.3 The interaction and "obligatory semantics" view

The most recent account put forward by Kutas and Federmeier (Kutas & Federmeier, 2011) describes the N400 as an index of (attempted) semantic access and the size of the N400 amplitude as correlated with the amount of activation induced in a spatially distributed semantic network supporting the mapping between form and meaning. This functional specification of the N400 is built on a number of important hypotheses that are motivated by recent ERP findings.

First of all, this theory challenges the prevailing assumption that access and retrieval of semantic information linked to a perceptual input must follow (visual) word recognition, i.e., the identification of an appropriate lexical entry. This postulate that forms the basis of many psycholinguistic models of reading (Forster, 1999; Forster & Davis, 1984) and that is crucial to the lexical preactivation view described above entails that semantic access should only be attempted for stimuli that have lexical status and furthermore, that the retrieved semantic information is restricted to the selected lexical entry. However, these predictions are not borne out by the available ERP literature. Recent results show N400 activity elicited by orthographically legal but meaningless pseudowords as well as by orthographically illegal but familiar acronyms when these are presented as part of unstructured word lists (Laszlo & Federmeier, 2007). Moreover, unfamiliar acronyms that are both meaningless and unpronounceable elicit N400 activity when are they are embedded in sentences (Laszlo & Federmeier, 2008). This suggests that semantic access is attempted for all incoming and potentially meaningful stimuli irrespective of their lexical status. The outcome of this process, i.e., the amount of distributed activity in the assumed semantic network appears to be reflected in N400 amplitude. In addition, a study by Laszlo and Federmeier (2009) found a reduction in N400 amplitude for unexpected sentence comple-

tions that were orthographic neighbours of the predicted sentence-final word as compared to non-neighbour stimuli. Importantly, this modulation was independent of the lexical status of the critical stimuli (words, pseudowords or illegal strings) and indicates that even illegal words benefits from co-activation due to orthographical similarity to predicted items.

The second assumption inherent to this recent theory of the N400 is that the level of induced activity in the semantic network is not only determined by stimulus-related activation. By contrast, the N400 is viewed as a measure of both bottom-up integrative and top-down predictive comprehension "strategies" that form two processing routes operating in parallel and interactively. Motivated by the wealth of ERP results that attest to the important role of top-down processes the authors argue that *"any complete theory of language processing will have to acknowledge the separate contributions of these two processing streams and explain how they come together to serve comprehension goals"* (Kutas & Federmeier, 2011, p. 634).

In this sense, the "interaction view" aims to derive a functional interpretation that is not tied to a specific sub-process of semantic analysis. Instead it is based on an interpretation that softens the lines between presumably distinct stages of processing by postulating that the N400 samples a temporally delimited interval in the continuous construction of meaning. Rather than linking the N400 to a specific operation such as lexical access or integration, or localising it to a restricted and invariant set of brain areas, this view focuses on the dynamic synergy between stimulus-induced feed-forward activity and a current state of activation in the *"multimodal long-term memory system"* (p. 640). In other words, the N400 is seen as an index of the spread of activation through a spatially distributed network that is jointly mediated by top-down and bottom-up information. The balance between the ongoing state of activation in the neural network as determined by top-down processes and the stimulus-induced activity can be dynamically modulated by a number of internal and external factors that affect either or both of these processing routes. These factors include recent inputs of all available modalities, allocation of attention in response to given tasks or targeted goals, previous experiences and perceived probabilities, as well as more stimulus-related properties such as frequency, concreteness or number of orthographical neighbours. Moreover, based on findings from visual half-field experiments (reviewed in Federmeier, 2007), Kutas and Federmeier (2011) argue that there is a sub-

stantial difference in the contribution of the two hemispheres: whereas the left hemisphere is predominantly implicated in top-down prediction processes, the right hemisphere is thought to largely engage in stimulus-related bottom-up processing.

Within this assumed framework, a reduction in N400 amplitude observed for a given stimulus reflects the degree to which the ongoing activation state matches the state induced by bottom-up activity. If many of the current stimulus' features are already active due to top-down processes, the transition from one activation state to the next should be less costly. The absence of N400 effects for anomalies that are clearly semantic in nature (e.g., for false negative statements or semantic reversal anomalies; see the previous section) are derived from the assumption that the N400 does not mark the end state of semantic analysis. Consequently, some types of information might not be available in time to impact the construction of meaning as reflected by the N400. For violations of thematic role assignment, Federmeier and Laszlo (2009, p. 30) argue *"that the time required to map the semantics of particular words onto the syntactic phrase structure information in order to determine each word's thematic role exceeds the point at which the N400 is triggered"*. While this might in principle be plausible, it does not offer a straightforward explanation for the cross-linguistic differences found for the processing of semantic reversal anomalies.

2.1.5   Summary

The short review on how the N400 component and its modulation have been used in investigations of language comprehension shows that we have gained significant insight on the sensitivity of this dependent measure. Yet, there are still many unanswered questions. The comparison of the most prominent theories of the N400 has illustrated that neither can account for the enormous bandwidth of results that have been accumulated over more than three decades. In fact, these theories only aim to account for N400 modulations that are driven by lexical-semantic factors. However, there are also a number of N400 effects that are elicited by morphological or syntactic information (for a comprehensive overview, see Bornkessel-Schlesewsky & Schlesewsky, 2009). N400 effects have been found for case violations in languages like German, Japanese or Hindi (Frisch & Schlesewsky, 2001; Mueller, Hahne, Fujii, & Friederici, 2005; Choudhary, Schlesewsky, Roehm, & Bornkessel-Schlesewsky, 2009), as well as in response to legal but dispreferred word order variations (Bornkes-

sel, Fiebach, & Friederici, 2004a; Bornkessel, McElree, Schlesewsky, & Friederici, 2004b; Haupt, Schlesewsky, Roehm, Friederici, & Bornkessel-Schlesewsky, 2008) and to violations of word formation restrictions (Janssen, Wiese, & Schlesewsky, 2006).

The questions that have been posed, and the suggested functional interpretations reflect how the scientific field concerned with the examination of language-related processes has been shaped by the different prevailing trends or discussions. During the last two decades, the increasing focus on the importance of predictions and expectations in all aspects of cognitive processing (Friston, 2005; Friston & Kiebel, 2009; Hohwy, 2007; Rao & Ballard, 1999; 2004; Vuust, Ostergaard, Pallesen, Bailey, & Roepstorff, 2009) led to discussions and new ideas on how this principle could be incorporated in theories of language processing. While all of the discussed theories of the N400 attempt to acknowledge the predictive nature of language comprehension (though to different degrees), there are, at this point, no straightforward mappings between the proposed functions of the N400 and neural mechanisms. The interaction and obligatory semantics view is most comprehensive and some of the hypotheses derived from this perspective have been tested in a neurally plausible neurocomputational model of the N400 (Laszlo & Plaut, 2012). At the moment, this model is restricted to the feed-forward processing of bottom-up information and as such does not include a mechanism for the interaction of top-down and bottom-up processing routes. Moreover, all of these models are based on electrophysiological evidence alone which precludes precise hypotheses on the involvement and interaction of specific brain areas. The next section describes how studies using functional neuroimaging have tried to answer this question.

2.2   Evidence from neuroimaging studies

The advent of modern non-invasive neuroimaging techniques such as positron emission tomography (PET) or functional magnetic resonance imaging (fMRI) marked the beginning of a new chapter in the field of cognitive neuroscience. Up to that point, research on the neural foundation of language and other cognitive processes had been dominated by lesion-deficit analyses that led to *large-module conceptualization of functional organization, an approach in which rather widespread territories of cortex are deemed responsible for broad categories of functions"*(Bookheimer, 2002, p.

151). The limitations inherent to this approach were also reflected in early neurological models of language that argued for the existence of two core language centres – located in the left inferior frontal gyrus and left posterior superior temporal gyrus – supporting speech production and speech comprehension, respectively (Geschwind, 1970; Lichtheim, 1885; Wernicke, 1874).[2] The results of neuroimaging studies on language processing have changed and extended this view in many ways (Stowe, Haverkort, & Zwarts, 2005).

This chapter provides a very brief introduction to the basic principles of functional neuroimaging and then goes on to summarise the findings on semantic processing that are most relevant to the experiments discussed in Chapter 3 and presented in detail in Part II of the present thesis.

2.2.1 Basic principles of functional neuroimaging

Given the steadily increasing number of research articles published per year on experiments using fMRI (or PET) to examine higher-cognitive functions, it is easy to forget that these techniques have been around for less than thirty years. Both fMRI and PET are essentially activation-based techniques, i.e., they identify brain areas that are actively involved in a specific task. Yet, it is important to emphasise that the observed engagement of a brain region in an investigated task does not mean that its execution critically hinges on the involvement of this region. The identification of brain regions showing a change in neural activity in correlation with task performance is dependent on the functional link between the triggered increase in energy demands and cerebral blood flow. fMRI takes advantage of the blood oxygenation level dependent (BOLD) mechanism (Ogawa, Lee, Kay, & Tank, 1990), i.e., the fact that variation in the ratio of oxygenated to deoxygenated blood leads to measurable signal changes (for a review, see Logothetis, 2002).

Neuroimaging techniques provide a way to study the neural bases of language functions at an excellent spatial resolution. Apart from this advantage, there are several limitations that one needs to keep in mind both in the experimental design of

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[2] However, it only seems fair to mention that this overly simplistic description of early neurological models of language (that is still present in many textbooks) actually fails to do justice to the work of neurologists like Carl Wernicke and Ludwig Lichtheim, who advocated ideas on the neural representation of language that are more sophisticated and modern than they are commonly depicted (see e.g., Gage & Hickok (2005) for a review of some aspects of the original work by Carl Wernicke).

studies and in the interpretation of obtained results. First of all, compared to the ERP technique, fMRI offers a relatively poor temporal resolution. This is due to the fairly slow vascular response to increased energy demands in the brain. Thus, there is no synchrony between the onset of neural activity and a measurable change in BOLD signal, which causes a delay in the onset of about 2 seconds and in the peak of about 5-7 seconds. Furthermore, the assessment of performance-related brain activity commonly relies on the computation of the difference in signal observed for a condition of interest and a baseline condition, and in many cases, a subsequent comparison of two conditions of interest. This means that the choice of both baseline and critical conditions can vastly influence the outcome of an experiment. Therefore, great care is needed in the development of experimental designs to avoid or control potential confounds and to maximise the chances of isolating the cognitive processes in which one is interested.

2.2.2   Neuroimaging results on sentence and discourse processing

The neuroimaging literature on the processing of meaning in language shows a myriad of studies concerned with various aspects of the neural organisation of semantic processing. It is beyond the scope of the present thesis to portray the actual bandwidth of research questions and experimental paradigms, therefore the reader is referred to comprehensive reviews and meta-analyses reported elsewhere (Binder et al., 2009; Binder & Desai, 2011; Bookheimer, 2002; Martin, 2007; Patterson, Nestor, & Rogers, 2007). The following section is devoted to neuroimaging studies that investigated semantic processing in sentence or discourse context and more precisely to those studies that compared the brain response to different types of semantic anomalies to that observed for congruent control conditions.

Many of the early neuroimaging studies on semantic (and syntactic) processing can be jointly characterised by their aim to identify brain areas that are functionally specialised for discrete language domains such as syntax or semantics. Moreover, the design of these experiments was greatly influenced by the prevailing view in the electrophysiological literature that suggested a one-to-one mapping between ERP components and language processes as conceived in psycholinguistic models. In this sense, the N400 was correlated with the processing of meaning, while the P600 was thought of as a marker of syntactic operations. With the increased availability of

neuroimaging methods came the aspiration to test whether this assumed functional and temporal segregation of linguistic functions would be further corroborated by dissociations in the spatial domain. Therefore, many of the employed experimental designs were adaptations of the semantic priming and anomaly paradigms commonly used in ERP studies. The application of semantic or syntactic violations in neuroimaging experiments relied on the assumption that anomalous sentences of a certain type would engender relatively higher levels of neural activation in areas that were also engaged in the processing of the same kind of operation in non-anomalous sentences.

2.2.2.1 Evidence from single sentence studies

In spite of the fact that many neuroimaging studies used the anomalous sentence paradigm to examine changes in brain activity related to language comprehension, these studies varied with respect to the specific aspects of sentence processing in which they were interested. Some studies aimed to test whether semantic and syntactic analysis were supported by distinct or overlapping areas of the brain (Friederici, Meyer, & Cramon, 2000; Friederici, Rüschemeyer, Hahne, & Fiebach, 2003; Newman, Pancheva, Ozawa, Neville, & Ullman, 2001; Ni et al., 2000; Rüschemeyer, Zysset, & Friederici, 2006; Rüschemeyer, Fiebach, Kempe, & Friederici, 2005). Others studies asked if the processing of different types of semantic anomalies would yield distinct patterns of increased brain activity across the brain. To this end, the authors manipulated the characteristics of sentence final words so that they showed different levels of congruence, predictability, or plausibility against the background of real-world knowledge (Baumgaertner, Weiller, & Büchel, 2002; Cardillo, Aydelott, Matthews, & Devlin, 2004; Dien et al., 2008; Hagoort et al., 2004; Kiehl, Laurens, & Liddle, 2002; Kuperberg et al., 2003; Kuperberg, Sitnikova, & Lakshmanan, 2008; Raposo & Marques, 2013; Stringaris, Medford, Giampietro, Brammer, & David, 2007). All studies used anomalies that were embedded in a single sentence and in most of them participants were asked to perform a binary acceptability/plausibility judgement task after each trial.

The findings that are most relevant to the questions asked in the present studies stem from experiments comparing brain regions involved in the comprehension of very obvious semantic violations (e.g. *"The pilot flies the book"*, (Baumgaertner et al., 2002)) and anomalies describing events that are in principle possible but either

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unlikely or factually false. Kuperberg et al. (2000) conducted a series of block-design fMRI experiments that included the following conditions (amongst others):

> (3)   a. The boy counted the <u>ducks.</u>
>
>   b. The woman painted the <u>insect.</u>
>
>   c. The mother ironed the <u>kiss.</u>
>
>   d. The young man slept the <u>guitar.</u>

Sentences like (3c) induce a semantic anomaly because the final word (underlined) is not included in the set of possible direct objects that match the verb's semantic selection constraints (here, because they do not belong to the category of objects that could be ironed). These violations are different from sentences that describe scenarios that do not fit our knowledge about probable events in the real world (3b). The authors found the left superior temporal gyrus to be more involved in the processing of "world knowledge anomalies" than in simple semantic violations and sentences that violate subcategorisation constraints (3d). Additionally, simple semantic anomalies produced stronger responses in the right middle and superior temporal gyrus than subcategorisation violations. The authors suggest that these findings may point to distinct contributions of the left and right superior temporal cortex in the processing of lexical-semantic information and the application of real-world knowledge.

Hagoort and colleagues (2004) conducted matched ERP and fMRI experiments that targeted a very similar research question. However, in contrast to Kuperberg et al. (2000) they included real-world anomalies expressing propositions that could be readily classified as being factually false. For example, a sentences such as *"The Dutch trains are white…"* describes a scenario in conflict with the well-known fact (among Dutch people) that the trains in the Netherlands are yellow. In comparison to non-anomalous sentences (*"The Dutch trains are yellow…"*) both real-world and simple semantic violations (*"The Dutch trains are sour…"*) led to increased activation in the pars triangularis and orbitalis of the left IFG. The authors argue for a role of these regions in the retrieval and integration of lexical-semantic information and world knowledge.

The overall pattern of results in the literature on single sentence studies is relatively heterogeneous and shows that there is not a single brain region (or not even a single set of regions) that could be interpreted as being specialised for semantic pro-

cessing. Regions frequently reported for showing higher levels of neural activity for anomalous compared to non-anomalous sentences include the pars opercularis, triangularis and orbitalis of the inferior frontal gyrus, the anterior insula, various portions of the superior, middle and inferior temporal gyrus, the temporal pole, and the angular gyrus. There is an overall tendency for a more extensive involvement of left hemisphere regions, but this does not necessarily mean that the analysis of meaning is indeed left lateralised. Rather, the apparent bias towards the left hemisphere found across these studies may have to do with the unnatural format of presenting large numbers of single sentences out of context. As several studies have shown, the overall pattern of brain activity in response to longer sequences of text such as sentence pairs, mini discourses or short stories tends to be much more balanced between the two hemispheres (see e.g., Mazoyer et al., 1993; St George, Kutas, Martinez, & Sereno, 1999; Xu, Kemeny, Park, Frattali, & Braun, 2005).

When comparing the results of individual studies it becomes apparent that the findings can be rather diverse – even in studies that used highly similar stimuli and procedures. The most consistent finding across many of the single sentence studies is the increased involvement of the left (and in some cases right) IFG for anomalous sentences compared to non-anomalous controls. Across the three sub-regions of the IFG, the pars orbitalis (roughly corresponding to BA 47) is reported most frequently, followed by the pars triangularis (BA 45) and pars opercularis (BA 44). The role of these regions in semantic processing continues to be a topic of open debate. Bookheimer proposes that the anterior ventral portion of the IFG (BA47) is involved in *"executive aspects of semantic processing that involve semantic working memory, directing semantic search, or drawing comparisons between semantic concepts in working memory"* (Bookheimer, 2002, p. 168). The view that anterior parts of the IFG are critically engaged in semantic processing in terms of controlled retrieval of semantic information, is shared by several others (Badre, Poldrack, Paré-Blagoev, Insler, & Wagner, 2005; Dapretto & Bookheimer, 1999; Fiez, 1997; Friederici, 2002; Newman et al., 2001; Stringaris et al., 2007; Wagner, Paré-Blagoev, Clark, & Poldrack, 2001). Hagoort and colleagues are amongst those researchers that implicate the pars orbitalis and triangularis in processes of semantic integration (Hagoort et al., 2004; Kuperberg et al., 2008; Menenti, Petersson, Scheeringa, & Hagoort, 2009). In contrast to these interpretations stands the view that increased activation in the left

IFG does not reflect semantic processing *per se,* but domain-general processes of cognitive control (Moss et al., 2005; Thompson-Schill, D'Esposito, & Kan, 1999; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997). Some have argued for a functional segregation within the left IFG since the foci of increased activation due to higher selection demands reported by Thompson-Schill et al. (1997) appeared to be located in a more posterior part of the IFG (BA 44/45).

In addition to inferior frontal regions many studies have reported increased activation for anomalous sentences relative to non-anomalous sentences in several areas of the left and/or right middle and superior temporal lobe (Baumgaertner et al., 2002; Friederici et al., 2003; Hagoort et al., 2004; Kuperberg et al., 2000; 2003; Ni et al., 2000; Rüschemeyer et al., 2005; Stringaris et al., 2007). However, as Dien and O'Hare (2008, p.180) note, even when the comparison is restricted to the left temporal lobe, there is little consistency in the localised activation foci. The interpretation of the functional role(s) of these regions is just as variable. Some authors of the original fMRI studies on semantic anomalies implicate the posterior middle temporal gyrus (and the adjacent superior temporal sulcus (STS) and inferior temporal cortex (IT)) in the storage of semantic information and emphasise that increased MTG activation is in line with results from localisation studies of the N400 using MEG source localisation or intracranial recordings (reviewed in Van Petten & Luka, 2006). Activation in the posterior STG is generally assumed to reflect early stages in the of the sound-to-meaning mapping (cf. Lau et al., 2008), while Friederici (2003) proposed that this region might be involved in the integration of syntactic, semantic and pragmatic information at the sentence level. Furthermore, Obleser and Kotz (2010) found evidence for top-down processes that modulate activation in the left STS and STG due to an interaction between intelligibility and cloze probability.

Despite the fact that activation in parts of the anterior temporal lobe is one of the most stable findings in meta-analyses of text comprehension (Ferstl, Neumann, Bogler, & Cramon, 2008), contrasts of anomalous and non-anomalous sentences rarely yield activation in this region.[3] This might be due to two reasons: the inferior portion of the anterior temporal lobe is prone to susceptibility artefacts which lead to decreased BOLD signal (Devlin et al., 2000), and thus activation in these areas might

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[3] However, there are a number of studies that report increased activation in parts of the anterior temporal lobe for sentences compared to word lists (Bottini et al., 1994; Brennan et al., 2012; Friederici et al., 2000; Mazoyer et al., 1993; Stowe et al., 1998; Xu et al., 2005).

have gone undetected. On the other hand, it is possible that activation in parts of the anterior temporal lobe depends on the presentation of longer and more naturalistic text sequences.

Lastly, the studies by Stringaris et al. (2007) and Newman et al. (2001) found increased activation in the left and/or right angular gyrus (AG) for semantic violations relative to congruent control sentences, however the authors did not elaborate on the functional role that this region might play in language comprehension.

In summary, the results from single sentence studies suggest that the analysis of meaning in sentential context is supported by variable configurations of brain areas located in the prefrontal cortex, the temporal lobes and posterior parts of the inferior parietal lobule. However, as these findings emerged from highly controlled contrasts between conditions it is likely that they may not reflect the entire extent of brain regions engaged in semantic processing at the sentence level.

2.2.2.2 Evidence from discourse processing

There is a constantly growing body of literature on neuroimaging studies aiming to examine aspects of language comprehension that arise in more ecologically valid paradimgs (Caplan & Dapretto, 2001; Ferstl & Cramon, 2001; 2002; Ferstl, Rinck, & Cramon, 2005; Mazoyer et al., 1993; Menenti et al., 2009; Siebörger, Ferstl, & Cramon, 2007; St George, Kutas, Martinez, & Sereno, 1999; Xu, Kemeny, Park, Frattali, & Braun, 2005). Results obtained from experiments that used stimuli ranging from sentence pairs to short stories indicate that semantic analysis in a broader context engages a number of brain regions beyond those reported for closely matched contrasts between single sentence. These include medial portions of the superior frontal gyrus bilaterally, the left posterior cingulate cortex and inferior precuneus, as well as the temporal poles and angular gyri. Interestingly, many of these regions report higher levels of neural activity for congruent relative to incongruent sentences or paragraphs.[4] The involved brain regions have been implicated in processes required for the comprehension of longer text sequences, such as deductive reasoning, inferencing, and the establishment of coherence. Furthermore, the overall results point to more balanced involvement of the left and right hemisphere. This led to the hypothesis that

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[4] Note that a common finding in single sentence studies are stronger neural responses for anomalous compared to non-anomalous sentences but little or no activation for the reverse contrast.

right hemisphere regions in the medial and lateral parietal lobe as well as the medial prefrontal cortex are important for higher-order language processes such as metaphor comprehension or theory of mind (ToM) (see Ferstl et al., 2008 for a recent meta-analysis of discourse studies).

St. George et al. (1999) asked participants to read titled or untitled paragraphs, each consisting of 10-15. Importantly, the presence or absence of a title critically changed the degree of coherence that could be established between individual senten-ces. Untitled paragraph led to increased levels of neural activity across both hemi-spheres that were, however, more pronounced in the right hemisphere. The authors observed more extensive activation in the right superior, middle and inferior temporal sulci for untitled relative to titled paragraphs. Interestingly, the reverse pattern was found for the left middle and superior temporal sulci. St George et al. suggest that the right middle and inferior temporal cortex might play a crucial role in the establish-ment of global coherence.

Ferstl and von Cramon (2001; 2002) extended these findings by investigating the establishment of coherence in a paradigm that manipulated coherence and cohe-sion in sentence pairs. Cohesion is commonly defined as the semantic link between individual sentences of larger text sequences as achieved by means of lexical or grammatical features such as conjunctive adverbs (e.g., therefore, then, thus, hence) or co-reference between nouns and pronouns. Thus, cohesion strategies can support inferencing processes aiming to establish a coherent meaning.

The authors found higher levels of neural activity for coherent relative to in-coherent sentence pairs in the left posterior cingulated cortex, inferior precuneus and in medial portions of the superior frontal gyrus. The suggestion that parts of the me-dial prefrontal cortex (roughly corresponding to medial portions of BA 8, 9, 10, as well as BA 32) contribute to the establishment of coherence was further corroborated by a second study that replicated the observed results.

Another brain region that has been the topic of many discussions is the inferior parietal lobule, which can be subdivided into the supramarginal gyrus (BA40) and angular gyrus (BA39). There are a number of studies on discourse comprehension (and a few on single sentences or word pairs) that found contributions of the left and right angular gyrus. However, the precise role of the angular gyrus in semantic pro-cessing remains to be elucidated, as the findings are relatively diverse.

Ni et al. (2000) and Raposo and Marques (2013) who used single sentences reported higher levels of brain activity in the right angular gyrus for semantic violations compared to control sentences, while other studies observed a reversed pattern (Humphries, Binder, Medler, & Liebenthal, 2006; 2007; Siebörger et al., 2007). Menenti et al. (2009) compared the influence of neutral and mitigating context on the processing of world knowledge violations and found the left angular gyrus (and possibly also right angular gyrus[5]) to be sensitive to the relative strength of semantic coherence between the context and the critical sentence. More precisely, the degree to which world knowledge violations elicited stronger neural responses than control sentences depended on the preceding context. Mitigating context allowing for a coherent interpretation attenuated the difference in neural activation for anomalous and non-anomalous sentences. These findings suggest that the angular gyri might play a role in semantic integration at a more complex level that is not only sensitive to sentence-level associations but also to the degree of global coherence. This hypothesis appears to be plausible as the inferior parietal lobule is part of the heteromodal association cortex that receives auditory, visual and somatosensory inputs from many other cortical and subcortical brain areas (Seghier, 2013).

2.2.3   Summary

Piecing together the results from individual studies at the single sentence and discourse level leads to a complex mosaic that does not yet yield a clear picture of how semantic processing is implemented in the human brain. The overall pattern shows an involvement of areas located in the inferior and medial frontal cortices, the temporal and inferior parietal lobes. There is significant evidence against the existence of "core language areas" that are selectively devoted to the processing of very specific language functions, as many studies observed an overlap in brain regions supporting different linguistic and non-linguistic functions. One of the most robust findings is the involvement of the left inferior frontal gyrus in response to semantic anomalies; however, no consensus has been reached on the question if this activation does indeed reflect semantic processing or if it indicates strategic control processes.

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[5] The authors report that a comparable interaction between context type and congruency was also present in the right angular gyrus though only at a less stringent statistical threshold.

Comparing the set of brain regions engaged in semantic analysis at an elementary and more complex level shows that the contextual (and task) environment has a crucial influence on the range of recruited brain areas. Owing to the recent trend to study language comprehension under more naturalistic conditions we are beginning to move toward to a better characterisation of the involvement and interaction of cortical and subcortical regions in the construction of meaning at a more complex level.

2.3   Combining results from electrophysiology and neuroimaging

From the very beginning scientists who made use of event-related potentials to study the neural underpinnings of language comprehension (or other higher-cognitive functions) have wondered about the neural generators of scalp-recorded brain activity. Due to the poor spatial resolution of the EEG technique, differences in the topography of N400 effects observed across different modalities (see section 2.1) are difficult to interpret. The availability of neuroimaging data on semantic processing in context opened up the possibility to compare data with a high spatial resolution to those with an excellent temporal precision. However, a mapping of different data types is not trivial, as this would imply that the BOLD signal measured in fMRI and low-frequency field potentials recorded by means of electrodes placed on the scalp reflected the same underlying neural activity. Nevertheless, several researchers have proposed comprehensive models aiming to derive the neural generators of the N400 from evidence obtained from lesion studies, magnetoencephalography experiments as well as from intracranial recordings (see e.g., Baggio & Hagoort, 2011; Brouwer, 2013; Lau et al., 2008; Van Petten & Luka, 2006 and the localisation studies reviewed therein). The focus of this chapter lies on the account put forward by Lau et al. (2008), as it is one of the most prominent models of the N400.

2.3.1   Lau et al. (2008): A cortical network for semantics: (de)constructing the N400

In their review of the N400, Lau and colleagues propose a framework for the study of semantic processes that is motivated by two main assumptions: (i) delineating the functional significance of the N400 is of critical importance for neural models of language comprehension, and (ii) that this can be achieved by testing predictions derived

from a neuroanatomical model of semantic processing grounded in psycholinguistic notions with available data from functional neuroimaging, MEG source localisation, lesion data and intracranial recordings.

The neuroanatomical model that serves as framework for the analysis of spatial data is based on the belief that it is possible to define a set of brain regions specialised for different aspects of semantic processing. These processing steps that are derived from psycholinguistic models of language comprehension include the representation and retrieval of lexical-semantic information, and the combination or integration of smaller units into more complex conceptual structures.

Motivated by evidence gleaned from lesion-deficit data and neuroimaging, Lau et al. describe and define five cortical regions of the left hemisphere that form the structural and functional architecture of their model: the posterior temporal cortex, the anterior temporal cortex, the angular gyrus of the inferior parietal lobule, and the inferior frontal gyrus sub-divided into an anterior and posterior part. The authors argue that the posterior temporal cortex, or more precisely, the mid-posterior portion of the MTG and adjacent STS and IT are involved in the storage of and access to lexical representations. The anterior part of the inferior frontal gyrus is thought to be involved in the controlled retrieval of lexical information while the posterior part mediates selection among competing lexical candidates. In addition, they propose that the inferior frontal gyrus might also be engaged in the application of world knowledge. For the anterior temporal cortex, defined as encompassing the anterior portion of the STS and MTG as well as the temporal pole, they envisage a role in basic combinatorial processes at the sentence level. Finally, the angular gyrus in concert with the anterior temporal cortex is thought to engage in the final integration of words with the preceding context to form conceptual representations of increasing complexity. The output of this integration process serves as input to the anterior inferior frontal gyrus that implements prediction processes based on this information. The basic architecture of the model builds on a feed-forward mechanism with multiple processing steps. In order to account for contextual influences on lexical access, the model includes a top-down connection from the anterior inferior frontal gyrus to the posterior temporal cortex that implements predictions in the form of facilitated access due to lexical "preactivation".

Against this background, the authors derive the following hypotheses to disentangle different views on the functional significance of N400 effects. Under the assumption that the N400 largely reflects combinatorial integration processes or the controlled retrieval and selection of lexical information, spatial data from different neurocognitive methods should localise these processes to the inferior frontal gyrus, anterior temporal cortex and/or the angular gyrus. On the other hand, if N400 modulations predominantly index the relative ease with which a lexical representation can be accessed from long-term memory, then, according to the proposed model, these processes should be localised to the posterior temporal cortex.

In order to test these hypotheses, the authors systematically review fMRI data from studies using N400 priming or anomaly paradigms, MEG source localisation data, lesion data and findings derived from intracranial recordings collected from epilepsy patients. The overview of data collected with these "localisation techniques" shows that all of the model's regions, with the exception of the angular gyrus, have been repeatedly implicated in the processes targeted in priming or anomaly paradigms. Evidence for the lexical account of the N400 stems from fMRI priming studies showing that the MTG (BA 21) is the only region that is consistently reported in both long and short stimulus-onset asynchrony (SOA) studies. Other regions include the temporal pole (BA38), inferior temporal cortex (BA37) and superior temporal gyrus (BA22). The inferior frontal gyrus is reliably engaged in studies using SOAs of at least 600ms. Lau and colleagues argue that this pattern is line with the model's prediction, as facilitated access to lexical representations should be observable in the MTG and possibly in adjacent areas, irrespective of the used SOA. In short SOAs, priming effects are assumed emerge due to an automatic and passive spread of activation, while they are caused by top-down predictions at long SOAs. The resultant facilitation in lexical access supported by the MTG should thus be the same in both cases. Based on the observed pattern in priming studies Lau et al. suggest that the left mid-posterior MTG might indeed be one of the neural generators of the scalp-recorded N400 priming effect.

The comparison of fMRI studies on the processing of semantic anomalies shows a less homogeneous pattern. As already discussed in section 2.2, increased activation for anomalous relative to non-anomalous sentences was most consistently reported for the inferior frontal gyrus, though the involvement of the different sub-

regions did not seem to follow a systematic pattern. While increased recruitment of the anterior and posterior inferior frontal gyrus can be derived from their postulated role in controlled retrieval or selection processes, the absence of reliable effects in the middle temporal gyrus challenge the lexical access account of the N400 as built on the proposed neuroanatomical model.

Finally, the data available from MEG source localisations and intracranial recordings exhibit a considerable degree of variation. However, among implicated regions, the left MTG is indeed one of the most consistently identified sources across different N400 paradigms and applied source estimation models. There are several reasons for why results of intracranial recordings from epilepsy patients can only make a limited contribution to the identification of brain areas involved in semantic processing and in the genesis of the N400 effect. First of all, the placement of subdural or depth electrodes and the extent of covered brain area is determined by clinical considerations and may vary considerably across patients. Secondly, this entails that some areas of the brain are tested more often than others, which introduces a bias in the overall pattern of results.

One of the areas consistently sampled in epilepsy patients is the anterior medial temporal lobe. Nobre and colleagues measured a potential in this part of the brain that shared many of its characteristics (time course, sensitivity to experimental manipulations) with the scalp-recorded N400 and might therefore be among its neural generators (Nobre & McCarthy, 1994; 1995).

Capitalising on the findings from fMRI studies on semantic priming and MEG source localisation results, Lau and colleagues conclude that the interpretation of the reviewed data within the proposed neuroanatomical framework lends more support for the lexical view than for accounts that interpret the N400 as reflecting integration processes, only. They acknowledge that integration processes play an important role in the generation of predictions based on contextual influences but argue that brain activity related to the implementation of these processes should have a limited influence on the scalp-recorded N400 signal.

2.3.2 Critical evaluation of the postulated account

It seems important to note that there are several caveats and limitations that concern both the proposed neuroanatomical model and the derived interpretation of the func-

tional significance of the N400 in language comprehension. First of all, the neuroanatomical framework models semantic processing in a relatively isolated way. It only includes a small set of left hemisphere regions, thus leaving aside brain areas recruited in more ecological valid processing of language, including contributions of the right hemisphere and potential hemispheric interactions and differences. Secondly, the definition of the functional role of brain areas included in the model are based in part on psycholinguistic considerations and in part on neuroimaging results and lesion data. While some interpretations appear well supported by the available literature, others are more controversial than the authors make them out to be. What is most problematic about the chosen approach, however, is the fact that the same kind of data used to define the functional roles of the model's units is then applied to test the predictions derived from the model. Moreover, the data used to motivate and test the model represent only a small subset of the overall N400 literature. In absence of independent evidence on the neural implementation of semantic processing it does not seem surprising that the available data match many of the model's predictions. Consequently, the conclusions to be drawn about the neural generators and the functional interpretation of the N400 critically hinge on the roles assigned to brain region in in the neuroanatomical model.

Apart from these methodological limitations, one could generally challenge the assumptions that resolving the debate on the functional interpretation of the N400 would have important consequences for neural models of language comprehension. As long as this discussion is centred on processes that are primarily grounded in psycholinguistic models, a convergence of data onto one of the two accounts would only have an impact on psycholinguistic models of language comprehension. To arrive at a better understanding of the neurobiological grounding of semantic processing, the focus needs to be shifted toward hypotheses and predictions that relate to basic functional principles of the brain.

2.4   Summary

This chapter provided an overview on neurocognitive research on semantic processing by highlighting the most relevant results reported in the ERP and fMRI literature. The review of the N400 literature illustrated the sensitivity of the N400 to a variety of manipulations. Some of these factors are examples of early bottom-up influences like a

word's log frequency or orthographical neighbourhood while others are instances of top-down cues based on contextual information. It was shown that these factors are not independent of one another but that they jointly impact on the construction of meaning, though with the general tendency of global contexts overwriting the effects of local influences like word-level semantic associations. The overview also covered three of the most prominent accounts of the N400 that were proposed on the basis of electrophysiological data. The comparison of these perspectives on the N400 illustrated that no consensus has been reached with respect to the functional interpretation of this dependent measure and that neither of the theories can account for the entire range of available data.

The review of functional neuroimaging studies on semantic processing in the context of single sentences or larger text sequences found several brain areas located in the frontal, temporal and inferior parietal lobes of the left and right hemisphere engaged in the construction of meaning. The comparison of local and global context revealed that the latter involves a larger set of brain areas supporting additional cognitive processes like reasoning, inferencing and the establishment of coherence. Thus, the available or absence of embedding context crucially influences the recruitment of processes underlying sentence comprehension.

The last part of the overview chapter focused on the question of how ERP and neuroimaging results could be integrated into a single account using the example of the framework postulated by Lau et al. (2008).

In summary, despite the vast number of studies aiming to uncover the neural implementation of semantic processing, we are only beginning to understand how the individual pieces might fit together in a larger context. The current challenge for theories on the N400 and more general models of semantic processing is to account for the dynamic and adaptive interaction of top-down and bottom-up factors. At the moment, many of the assumed processes that contribute to the construction of meaning are motivated by theoretical considerations. Thus, there is still a wide gap between these postulated processing steps and their implementation at the neurobiological level. Future studies need to focus on hypotheses that respect what has been learnt about the functionality of the human brain.

3   EVIDENCE FROM THE PRESENT STUDIES

The aim of the experiments presented in detail in Part II was to shed more light on the impact of top-down and bottom-up information sources on semantic processing both within a single language and across languages. As highlighted in Chapter 2, recent ERP results suggest that the interaction between top-down and bottom-up information is more extensive than previously assumed. Moreover, systematic cross-linguistic variation found in response to certain semantic manipulations poses an additional challenge to existing accounts of the N400. To further investigate the mechanisms that allow for such dynamic interactions, we conducted a total of five experiments: the first four experiments measured ERPs, while the last experiment used fMRI.

The first ERP study investigated the impact of a novel form-based manipulation on the processing of semantic anomalies in German, whereas the remaining ERP experiments focused on the questions of whether cross-linguistic differences previously observed for semantic reversal anomalies would extend to other anomaly types as well. To this end, the processing of easy to detect and more subtle "borderline anomalies" embedded in context was compared across German and English. To gain a more comprehensive view of how these different types of anomalies are processed, we conducted an fMRI study on German that used the same paradigm and stimuli.

In the first ERP experiment, which is reported in Chapter 7, we wanted to test the hypothesis that a purely form-based and contextually independent manipulation could modulate the brain's reaction to semantic anomalies. This hypothesis was in part based on N400 effects reported for a mismatch between information structure and prosodic cues that were not predicted by existing accounts of the N400 (Hruska & Alter, 2004; Li et al., 2008; Schumacher & Baumann, 2010; Toepel & Alter, 2004). While bottom-up effects like frequency and orthographic neighbourhood size have been studied previously, most results showed that in sentence-final positions the "baseline effect" of such factors tends to be neutralised by contextual top-down influences (see section 2.1). To test our hypothesis we developed an experimental paradigm, which manipulated the contextual fit of sentence-final words both in terms of their physical appearance and their plausibility. We presented single sentences in written form and used capitalisation to introduce a change in physical properties. We chose capitalisation because it is a highly salient and potentially meaningful deviation

from standard orthographic rules. In some cases it may be used to express emphasis, but more generally, it serves to signal high information content. To allow conclusions about the role of capitalisation as a marker for changes in information content, we contrasted it with a physical change in the opposite direction that was included as a between-subject factor.

We speculated that sentence-final anomalous words printed in all capital letters (*"What we need now are real and democratic BLATHERERS"*; English translation given) would be processed differently from anomalous words whose physical properties did not differ from that of the preceding context (*"What we need now are real and democratic blatherers"*). More precisely, we expected a reduction in N400 amplitude for anomalous words whose physical appearance signalled high information status. Since a change from uppercase to normal letters is not associated with a particular paralinguistic function, we did not expect a comparable modulating influence for this type of physical deviation.

Our results showed that this was indeed the case. In the UP group (i.e., with a change to uppercase letters), the comparison of congruent words with or without physical change (*"What we need now are real and democratic ELECTIONS / elections"*) to anomalous words printed in normal or uppercase letters yielded a pattern of graded N400 amplitude. Whereas a change to uppercase letters did not influence the processing of plausible sentence-final words, it caused a substantial reduction in N400 amplitude for anomalous sentence completions. Importantly, no such attenuation was observed for the change from uppercase to lowercase letters (i.e., in the DOWN group). Apart from the N400 modulation, we found another difference in the electrophysiological response across the two groups: in the UP group, final words that deviated from the preceding context in terms of their case type elicited an early positivity effect in comparison to sentence-final words without a change. Again, no such effect was elicited in the DOWN group.

Since the applied physical change was completely independent of the propositional message expressed by the sentences, its modulating effect cannot be explained by the integration account of the N400 (Hagoort & van Berkum, 2007). There is no apparent reason to assume that the degree to which the anomalous word matches the preceding context should have been increased by capitalisation. This is further supported by the behavioural data that indicate that capitalising the last word did not ren-

der the implausible sentence more acceptable. The lexical preactivation account (Lau et al., 2008) does not provide a straightforward explanation for the observed attenuation, either. In order to derive the observed results from the core postulations of this theory, one would have to assume that the case change introduced additional context information that would have led to facilitation in the access to the critical word. This is clearly not the case. While the interaction account includes a flexible interaction between bottom-up and top-down information, it does not provide explicit hypotheses for the processing of the tested form-based and potentially meaningful bottom-up manipulation of the present study.

We therefore propose a new account of the lexical-semantic N400 termed the "bidirectional coding account", which takes some of the core assumptions from the lexical preactivation account and extends them to derive an explanation for the present results and for the data that motivated this experiment. In the following, the basic ideas of the postulated account are briefly summarised; for a more detailed motivation of the assumed architecture see Chapter 7.

In contrast to the lexical account by Lau et al. (2008) we explicitly include a separation of access to lexical and conceptual representations and assume that N400 modulation reflects the relative ease or difficulty of access at the level of concepts or referents rather than at the level of lexical representations. However, we propose a link between these stages in the sense that the degree of "preactivation" of lexical representations built up via semantic associations between words or contextual information contributes to the level of concept or referent accessibility. However, the N400 does not simply reflect the relative ease or difficulty with which a concept or referent can be accessed. Rather, it is an indicator for the match between the actual level of accessibility for the current concept or referent and its predicted accessibility. This prediction is in turn determined by the interaction between purely form-based bottom-up cues like prosody or capitalisation and top-down predictions on referent/concept accessibility derived from contextual information.

The attenuated N400 response to capitalised anomalies can then be explained as follows: the actual accessibility of the critical word is fairly low due to the lack of strong lexical "preactivation" that could be relayed to the level of accessibility for the referent in the example sentence. The very salient and meaningful change in case signals high informativity, thus a change from the default that assumes accessible refer-

ents or concepts. In interaction with top-down predictions this bottom-up cue leads to an expectation of decreased accessibility. Thus, there is greater compatibility of the predicted and actual referent accessibility, which is reflected in the attenuated N400 response.

Another way of looking at this is to say that capitalisation is a bottom-up cue processed fast enough that it can alter concomitant top-down predictions (that are based on the preceding context) before they interact with the output of a more thorough bottom-up analysis of the critical word. Taking a hierarchical processing architecture incorporating both feed-forward and feed-back mechanisms as a basic framework, this interpretation would in principle amount to the claim that there are fast connections between the lowest and highest level of the hierarchy allowing for low-level bottom-up information to precede directly to the highest (or a higher) level where it would exert a modulating influence on top-down predictions.

Evidence that this is in principle possible stem from the domain of visual object recognition. Most current models of visual object recognition are based on the assumption that recognition is achieved by both bottom-up analysis and controlled top-down processes (see Bar, 2003; and Cheung & Bar, 2013 and the literature reviewed therein). However, facilitation in object recognition caused by top-down predictions can also be observed in the absence of context. This gives rise to the question of how top-down prediction can be instantiated in these cases. Bar (2003) argues for top-down facilitation based on rapid projections of low frequency images from V2 to the prefrontal cortex via "anatomical shortcuts" or more precisely via the magnocellular pathway. These relatively coarse low frequency images give rise to "initial guesses" on perceptual input that are back-projected to the inferior temporal cortex where this information is integrated with the results of the bottom-up analysis. In those cases where additional predictions derived from context are available as well, the low frequency images projected from V2 are combined with existing prediction to form "educated guesses", which constrain the set of possible objects even further.

While there is, of course, no straightforward mapping of the model proposed by Bar (2003) to the assumed mechanisms of the N400, it nevertheless seems worthwhile to consider that such rapid connections might be involved in the processing of form-based bottom-up cues in language comprehension as well. To sketch out a precise model of how such a mechanism could be implemented in semantic processing is

beyond the scope of the present discussion. It would involve defining anatomical connections that could support rapid projections to prefrontal cortex for both visual and auditory input. Furthermore, it is unclear at this point what the nature of the rapidly projected information (a low frequency image in the case of visual object recognition) would be in language processing, as these could be coarse visual or auditory representations of the perceived input or projections of fuzzy lexical information. Finally, it would require a more precise definition of the types of bottom-up information that would trigger such a processing mechanism.

There is some limited evidence that such a mechanisms might in fact be implemented at a smaller scale in visual word recognition. A study by Kim and Vai (2012) found evidence for rapid interactions between representations at a lexical and sublexical level. They presented participants with contextually embedded illegal letter strings and two types of pseudowords that differed in terms of their similarity to the congruent real word (*"She measured the flour so that she could bake the cake/ceke/tont/srtd"*). Interestingly, although the study was predominantly focused on differences in early ERP components, the authors also report an attenuated N400 response to the pseudoword "ceke" relative to the N400 effect elicited for the pseudoword "tont" that showed little resemblance with the congruent word. It thus appears plausible to argue that the observed modulation was derived via a mechanism that incorporates rapid feed-forward and feed-back projections between lower and higher levels of the processing architecture.

Another findings stems from a study by Delaney-Busch and Kuperberg (2013), who found an attenuated N400 effect for emotional critical words as opposed to neutral critical words. The critical emotion stimuli that carried positive or negative valence appeared in sentences that were preceded by emotional (pleasant or unpleasant) discourse context while critical neutral words followed neutral discourse context. It is thus possible that the emotionally charged discourse context led to a processing "strategy" focused on the rapid evaluation of a word's emotional salience, which in turn altered the top-down expectations for the same word.

In sum, based on the data from the first ERP experiment, we proposed a new account of the N400 that incorporates a more dynamic interaction of top-down and contextually independent, form-based bottom-up information sources. This account could potentially be extended to account for "non-semantic" N400 effects and might

serve as a basic framework for the aim to derive testable hypothesis on the neural mechanisms of semantic processing.

Study 2, which is described in Chapter 8, comprises three ERP experiments that compared the processing of hard and easy to detect semantic anomalies in German and English. The more subtle semantic violation, also termed "borderline anomalies", were related to the so-called Moses Illusion which describes the relatively robust failure to detect a semantic distortion because the anomalous term has a close fit to the context. The most famous example is the question *"How many animals did Moses take onto the ark?"* that most people answer with "two" without noticing that it was Noah, not Moses, who built the ark (Erickson & Mattson, 1981).

We wanted to test whether the robust cross-linguistic differences observed for semantic reversal anomalies (Bornkessel-Schlesewsky et al., 2011) would generalise to this type of semantic anomaly. Bornkessel-Schlesewsky and colleagues suggested that the cross-linguistic differences in the processing of semantic reversal anomalies could be explained by taking into consideration the degree to which interpretation in a given language is driven by word order cues. English and Dutch both have a relatively rigid word order, which makes the linear order of sentence elements one of the most important cues in semantic analysis (MacWhinney, Bates, & Kliegl, 1984). On the other hand, in languages like German or Chinese, which allow for much more flexibility in the linear order of sentential elements, a larger set of cues including animacy or case marking needs to be evaluated. Bornkessel-Schlesewsky and colleagues thus conclude that the cross-linguistic modulation indicates that the N400 is sensitive to the language-specific weighting of top-down influences, i.e., predictions based in part on the linear order of elements, and bottom-up cues like case marking or animacy.

The decision to focus on borderline anomalies was in part motivated by the results of a recent ERP study by Sanford and colleagues (Sanford, Leuthold, Bohan, & Sanford, 2011) who found the absence of N400 effect for both detected and non-detected borderline anomalies, compared to non-anomalous control sentences. The only distinguishing feature was a late positivity effect for detected anomalies relative to the non-detected and correct control condition. Easy to detect anomalies, on the other hand, did elicit an N400 effect followed by a late positivity in comparison to non-anomalous sentences.

For the first experiment of Study 2 (section 8.2), we used German translations of the materials used by Sanford et al. (2011) to investigate if the language-specific weighting of top-down and bottom-up information sources proposed for semantic reversal anomalies would also lead to different ERP results for the processing of borderline anomalies in German. In contrast to English, we did observe an N400 effect for detected borderline anomalies relative to non-detected anomalies as well as correct control sentences. Non-detected anomalies and control sentences did not differ in N400 amplitude, which suggests that missed borderline anomalies might in fact be treated like non-anomalous sentences. Similar to the English data, detected anomalies engendered an additional late positivity effect that followed the N400. In addition, easy to detect anomalies elicited a strong N400 effect that was again followed by a late positivity.

The suggestion that observed cross-linguistic modulation of the N400 might indicate substantial differences in the neural implementation of semantic processing in German and English was further corroborated by Experiments 2a and 2b (section 8.3.1 and 8.3.2). These experiments on German and English used a slightly adapted paradigm that reduced the impact of the behavioural task effects. Both experiment replicated the results of the original studies.

Taken together, the cross-linguistic variation found for the processing of correctly detected borderline anomalies poses a challenge for the lexical preactivation account of the N400. Based on the English results alone, this account would have provided a straightforward explanation for the absence of the N400: the close fit of the anomalous word to both the global context and the correct concept or referent leads to a fair amount of top-down induced "preactivation" causing a substantial reduction or neutralisation of the N400 effect. However, this account cannot explain the divergent results observed for the analysis of borderline anomalies in German.

We argue that the bi-directional coding account proposed in Study 1 seems well suited to derive the observed cross-linguistic variation in the N400 as it incorporates more than purely top-down lexical preactivation. As outlined above, we suggest that modulations of the N400 reflect the mismatch between top-down and bottom-up information sources. Top-down sources include semantic cues such as the global context information, and grammatical cues such as position and word order. The absence of the N400 could then explained by the high degree of position-based predictability

of upcoming elements that dominates interpretation in languages with strict word order such as English. Since the anomalous word has a very good fit to the context it also fulfils semantic expectations to a considerable degree.

German on the other hand shows a stronger weighting of bottom-up information sources, which in turns leads to weaker or less precise top-down predictions and higher chances for a mismatch between bottom-up cues and the local sentence context. However, it is important to note that we do not mean to suggest that the absence or presence of the N400 is a direct index of the detectability of an anomaly but rather that is reflects one part of the semantic analysis that may ultimately lead to the correct detection of an anomaly.

As the final study of the present thesis, we conducted a German fMRI experiment to examine the brain regions involved in the interpretation of the same easy to detect and borderline anomalies. We were particularly interested in how the processing of words and concepts interacts with the expectations from local and global context to lead to deep or superficial interpretations. We hypothesised that the influence of the embedding context would have a different effect in easy to detect and borderline anomalies. This was motivated by the assumption that the provided context might play a less important role for the detection of obvious semantic anomalies since the anomalous word mismatches with predictions both at the global and local context level. In borderline anomalies, the context might actually strengthen the illusion effect, which is why a more thorough and extensive evaluation of the encountered proposition is needed for successful detection of an anomaly.

In line with the literature on discourse comprehension that was reviewed in Chapter 2, we found that the processing of both anomaly types engaged a complex set of brain region located across the frontal, temporal and parietal lobes and that the contributions of the two hemispheres were relatively balanced. Relative to non-anomalous control sentences detected borderline anomalies showed higher levels of neural activity in prefrontal, inferior parietal and inferior temporal regions of the left and right hemisphere. Frontal regions included parts of the anterior insula bilaterally and the right pars triangularis; inferior parietal regions encompassed the angular gyrus bilaterally and the left supramarginal gyrus, while increased activation relative to control was only found in the left and right inferior temporal gyrus.

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Contrasting detected easy anomalies to non-anomalous control sentences revealed stronger neural responses in the left and right temporal lobe for the former. These regions included the left inferior temporal gyrus, parahippocampal gyrus and well at the transverse temporal gyrus and the right superior temporal gyrus and inferior temporal cortex. Interestingly, congruent control sentences revealed large clusters of increased bilateral frontal activation in comparison to detected easy anomalies. We suggest that this pattern reflects the relative difficulty in decision making since obvious anomalies are easily categorised as anomalous once the critical word has been processed whereas non-anomalous sentences require a more extensive and complete processing. This interpretation is supported by accounts that implicate the prefrontal cortex in domain-general aspects of cognitive control (Bornkessel-Schlesewsky & Schlesewsky, 2013; Miller & Cohen, 2001; Moss et al., 2005; Stowe et al., 2005; 1998; Thompson-Schill et al., 1997). It cannot be reconciled with the postulations that the left (and possibly also the right) inferior frontal gyrus, in particular the pars orbitalis and triangularis serve as a "unification space" where the integration of different information takes place (Baggio & Hagoort, 2011; Hagoort, 2008; Hagoort et al., 2004). It also does not follow from the neuroanatomical model proposed by Lau and colleagues who do not comment on the role of the right prefrontal cortex but implicate the left pars triangularis in controlled retrieval of semantic information and thus in semantic processing *per se*. Importantly, both accounts would postulate that non-anomalous sentences should lead to higher levels of neural activity than plausible control sentences. These predictions are not borne out by the present data.

The difference observed with respect to the increased involvement of temporal and inferior parietal regions relative to control sentences is in line with previous findings suggesting that the left and right inferior parietal lobule and in particular the angular gyri may engage in a more thorough analysis that builds on the integration of all relevant information (e.g., Binder et al., 2009; Menenti et al., 2009). Increased recruitment of temporal regions for detected easy anomalies may reflect mismatches at a more local context level. We therefore conclude that the distinction in the involvement of inferior parietal and temporal regions across anomaly types reflects differences in the required depth of semantic processing.

4   SUMMARY AND FUTURE DIRECTIONS

Part I of the present work described how the scientific field concerned with the neural underpinnings of semantic analysis in sentence and discourse context has gradually evolved and matured other the last thirty years. Yet, as the research questions and results of the present experiments have highlighted, there are still many unknown variables in the mechanisms that underlie semantic processing. The present studies found additional evidence for an extensive interaction of factors relating to the sensory and perceptual quality of a stimulus with those that generate predictions against the background of previous experiences and learned associations between words or concepts. The results of the three ERP experiments on the processing of easy and hard to detect semantic anomalies in German and English illustrate how cross-linguistic investigations provide a window onto the adaptive nature of the brain. We observed N400 modulations both within a language as well across languages and developed the bi-directional coding account that can derive these findings by assuming that the interaction between top-down and bottom-up effects occurs in both directions. In current models of the N400, the emphasis had largely been on contextual facilitation due to top-down predictions.

The fMRI experiment on different types of semantic anomalies revealed an extensive assembly of brain areas that are engaged in the comprehension of auditory sentences. The complexity and diversity of results reported in previous studies (reviewed in section 2.2) illustrates that it seems almost impossible to assign individual and clearly delineated functions to these areas. In fact, for higher-cognitive functions such as language this attempt might be doomed to failure as individual brain region engage in a variety of tasks and individual task may be supported by a flexible set of brain regions.

It appears that after early years of neuroimaging were characterised by constant methodological testing and refinements, we have now reached a level of understanding that can be used to ask questions that are not restricted to assignment of functional label to individual labels of the brain. Indeed, recent years have seen an increasing interest in the characterisation of neural processes rather than functional localisation (Hasson & Honey, 2012). At the current moment, most models of language comprehension, including the bi-directional coding account presented here, in-

corporate processes such as lexical access, preactivation, retrieval and integration. Unfortunately, not all of the accounts acknowledge that these are in most instances cognitive notions that are grounded in theoretical rather than neurobiological assumptions about the functionality of the human brain. Admittedly, the gap between neural activity in the form of firing rates of individual neurons and higher-cognitive functions is far too wide to be bridged in the near future. It seems that research questions and analyses that are situated at the level of neural networks and that incorporate knowledge about the structural and functional principles of the brain are a feasible approach to study the neurobiological underpinnings of semantic processing.

As already discussed in section 2.3, what we need are models of semantic processing (or language processing in general) that are at least in part built on independent assumptions about the basic structural and computational principles of the brain. Furthermore, the study of auditory language processing could benefit from knowledge accrued for other modalities and domains like the visual or the sensorimotor system. In fact, semantic processing seems to be one of the best examples to illustrate that language cannot be studied in isolation. The construction of meaning is at the very heart of our interactions and communications with the environment, yet the close link between action, perception and cognition has been largely overlooked in early psycholinguistic and neurocognitive research.

Drawing on accumulated knowledge from research on auditory processing in non-human primates and the organisation of the visual system in both animals and humans, recent publications on the neural circuitry supporting human language show an increasing focus on models with dual stream architecture (Bornkessel-Schlesewsky & Schlesewsky, 2013; Friederici, 2009; 2011; Hickok & Poeppel, 2004; Rauschecker, 1998; Rauschecker & Scott, 2009; Saur et al., 2008; Ueno, Saito, Rogers, & Lambon Ralph, 2011). Models of this kind, which attempt to describe human language processing within a neurobiologically plausible framework, may be a promising framework for the derivation of concrete, testable hypotheses that respect what we have learnt about language and about the human brain.

Proceeding from the perspective that the N400 – or semantic processing in general – is crucially modulated by the our expectations regarding the properties of upcoming items; with expectations determined by the interaction of top-down and bottom-up information, one of the future challenges will be to arrive at a precise de-

scription of the sources, implementation and consequences of predictive processing. There are many unanswered questions with respect to the generation, application, and the nature of predictions in language comprehension. Focusing on the investigation of processes underlying prediction seems to be a particularly promising path to a better understanding of the neurobiology of language, as the neural computation of predictions and the correction of prediction errors play a key role in all our actions. As such, predictive processing may well be one of the most essential, effective and potentially unifying functions of the human cortex.

There are different flavours of "predictive coding" accounts that explain the implementation of prediction by internal forward and/or reverse models that derive expectations from previous input and continuously match them against incoming input (Clark, 2013; Friston, 2005; Friston & Price, 2001; Hohwy, 2007; Rao & Ballard, 1999). While most of these accounts were postulated an as explanation for visual perception and motor control they have also been adapted for higher-cognitive functions such as language processing (e.g., Bornkessel-Schlesewsky & Schlesewsky, 2013; Friston, 2012; Pickering & Garrod, 2013; Rauschecker & Scott, 2009).

However, the specific impact of prediction processes on ERP components of language comprehension remains a matter of debate. While Bornkessel-Schlesewsky and Schlesewsky (n.d.) argue that language-related negativities such as the N400 or the left anterior negativity (LAN) could be interpreted as reflecting prediction errors during language processing, others have challenged the idea that the N400 marks increased costs due to failed predictions (Van Petten & Luka, 2012). To arrive at a better understanding of the role of prediction for semantic processing, several questions will need to be answered. The first question concerns the precise nature of prediction in language processing. In sentence or discourse comprehension we can generate predictions about both the quality of an upcoming referent or concept as well as about the time frame in which we expect to encounter this concept. Are expectations about the "what" and "when" implemented in the same way?

Another interesting aspect concerns the relative strength of predictions – does it make sense to talk about weaker and stronger predictions or is predictive processing an "all or nothing" principle? If predictions can in fact be more or less precise, how does this impact on the match between top-down and bottom-up information?

The results of the present ERP experiments on borderline anomalies suggest that the relative strength and reliability of predictions can cause to a more permanent shift in the balance of top-down and bottom-up influences. Furthermore, the results of the fMRI study showed that predictions can be met or failed at different level of the processing hierarchy as the increased involvement of temporal regions for easy anomalies may have indicated a mismatch at a more elementary level. The detection of borderline anomalies, on the other hand, relied on the application of real-world knowledge that was potentially supported by regions of the left and right inferior parietal lobule.

If the interpretation of the N400 amplitude as a marker for failed predictions is indeed correct than this would entail that qualitatively similar N400 effects could emerge from very different underlying configurations of brain areas. However, more comprehensive insight into the processes that enable the computation and implementation of predictions in language processing may ultimately help to derive testable hypotheses about the dynamic network of brain regions that could be involved in such a mechanism.

5   REFERENCES

Altmann, G. (1997). *The ascent of Babel: An exploration of language, mind, and understanding*. New York, NY, US: Oxford University Press.

Badre, D., Poldrack, R. A., Paré-Blagoev, E. J., Insler, R. Z., & Wagner, A. D. (2005). Dissociable Controlled Retrieval and Generalized Selection Mechanisms in Ventrolateral Prefrontal Cortex. *Neuron*, *47*(6), 907–918. doi:10.1016/j.neuron.2005.07.023

Baggio, G., & Hagoort, P. (2011). The balance between memory and unification in semantics: A dynamic account of the N400. *Language and Cognitive Processes*, *26*(9), 1338–1367.

Bar, M. (2003). A cortical mechanism for triggering top-down facilitation in visual object recognition. *Journal of Cognitive Neuroscience*, *15*(4), 600–609.

Barrett, S. E., & Rugg, M. D. (1989). Event-related potentials and the semantic matching of faces. *Neuropsychologia*, *27*(7), 913–922. doi:10.1016/0028-3932(89)90067-5

Barrett, S. E., & Rugg, M. D. (1990). Event-related potentials and the semantic matching of pictures. *Brain and Cognition*, *14*(2), 201–212. doi:10.1016/0278-2626(90)90029-N

Baumgaertner, A., Weiller, C., & Büchel, C. (2002). Event-Related fMRI Reveals Cortical Sites Involved in Contextual Sentence Integration. *NeuroImage*, *16*(3), 736–745. doi:10.1006/nimg.2002.1134

Berkum, J. J. V., Hagoort, P., & Brown, C. M. (1999). Semantic integration in sentences and discourse: Evidence from the N400. *Journal of Cognitive Neuroscience*, *11*(6), 657–671.

Biederman, I. (1987). Recognition-by-components: A theory of human image understanding. *Psychological review*, *94*(2), 115–117. doi:10.1037/0033-295X.94.2.115

Binder, J. R., & Desai, R. H. (2011). The neurobiology of semantic memory. *Trends in Cognitive Sciences*, *15*(11), 527–536. doi:10.1016/j.tics.2011.10.001

Binder, J. R., Desai, R. H., Graves, W. W., & Conant, L. L. (2009). Where Is the Semantic System? A Critical Review and Meta-Analysis of 120 Functional Neuroimaging Studies. *Cerebral Cortex*, *19*(12), 2767–2796. doi:10.1093/cercor/bhp055

Bobes, M. A., Valdessosa, M., & Olivares, E. (1994). An ERP Study of Expectancy Violation in Face Perception. *Brain and Cognition*, *26*(1), 1–22. doi:10.1006/brcg.1994.1039

Bookheimer, S. (2002). Functional MRI of Language: New Approaches to Understanding the Cortical Organization of Semantic Processing. *Annual Review of Neuroscience*, *25*(1), 151–188. doi:10.1146/annurev.neuro.25.112701.142946

Bornkessel, I. D., Fiebach, C. J., & Friederici, A. D. (2004a). On the cost of syntactic ambiguity in human language comprehension: an individual differences approach. *Cognitive Brain Research*, *21*(1), 11–21. doi:10.1016/j.cogbrainres.2004.05.007

Bornkessel, I., McElree, B., Schlesewsky, M., & Friederici, A. D. (2004b). Multi-dimensional contributions to garden path strength: Dissociating phrase structure from case marking. *Journal of Memory and Language*, *51*(4), 495–522. doi:10.1016/j.jml.2004.06.011

Bornkessel-Schlesewsky, I., & Schlesewsky, M. (2009). Processing syntax and morphology: A neurocognitive perspective. Oxford: Oxford University Press.

Bornkessel-Schlesewsky, I., & Schlesewsky, M. (2013). Reconciling time, space and function: A new dorsal–ventral stream model of sentence comprehension. *Brain and Language*, *125*(1), 60–76.

Bornkessel-Schlesewsky, I., & Schlesewsky, M. (submitted). The Argument Dependency Model. To G. Hickok & S. L. Small (Eds.), *Neurobiology of Language*. Elsevier.

Bornkessel-Schlesewsky, I., Kretzschmar, F., Tune, S., Wang, L., Genç, S., Philipp, M., et al. (2011). Think globally: Cross-linguistic variation in electrophysiological activity during sentence comprehension. *Brain and Language*, *117*(3), 133–152. doi:10.1016/j.bandl.2010.09.010

Bottini, G., Corcoran, R., Sterzi, R., Paulesu, E., Schenone, P., Scarpa, P., et al. (1994). The role of the right hemisphere in the interpretation of figurative aspects of language. A positron emission tomography activation study. *Brain*, *117*(6), 1241-1253.

Brennan, J., Nir, Y., Hasson, U., Malach, R., Heeger, D. J., & Pylkkänen, L. (2012). Syntactic structure building in the anterior temporal lobe during natural story listening. *Brain and Language*, *120*(2), 163–173. doi:10.1016/j.bandl.2010.04.002

Brouwer, H. & Hoeks, J. C. J. (2013). A time and place for language comprehension: mapping the N400 and the P600 to a minimal cortical network. *Frontiers in Human Neuroscience 7*(758), 1–12. doi:10.3389/fnhum.2013.00758

Brouwer, H., Fitz, H., & Hoeks, J. (2012). Getting real about Semantic Illusions: Rethinking the functional role of the P600 in language comprehension. *Brain Research*, *1446*(C), 127–143. doi:10.1016/j.brainres.2012.01.055

Brown, C., & Hagoort, P. (1993). The Processing Nature of the N400: Evidence from Masked Priming. *Journal of Cognitive Neuroscience*, *5*(1), 34–44. doi:10.1016/0010-0277(89)90013-9

Brualla, J., Romero, M. F., Serrano, M., & Valdizán, J. R. (1998). Auditory event-related potentials to semantic priming during sleep. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section*, *108*(3), 283–290.

Burton, H., & Sinclair, R. (1996). Somatosensory cortex and tactile perceptions. *Pain and touch*, 105–77.

Caplan, R., & Dapretto, M. (2001). Making sense during conversation: an fMRI study. *NeuroReport*, *12*(16), 3625–3632.

Cardillo, E. R., Aydelott, J., Matthews, P. M., & Devlin, J. T. (2004). Left Inferior Prefrontal Cortex Activity Reflects Inhibitory Rather Than Facilitatory Priming. *Journal of Cognitive Neuroscience*, *16*(9), 1552–1561. doi:10.1016/S0167-7152(99)00149-2

Castle, P. C., Van Toller, S., & Milligan, G. J. (2000). The effect of odour priming on cortical EEG and visual ERP responses. *International Journal of Psychophysiology*, *36*(2), 123–131.

Chao, L. L., Nielsen-Bohlman, L., & Knight, R. T. (1995). Auditory event-related potentials dissociate early and late memory processes. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section*, *96*(2), 157–168.

Cheung, O. S., & Bar, M. (2013). The resilience of object predictions: Early recognition across viewpoints and exemplars. *Psychonomic Bulletin & Review*. doi:10.3758/s13423-013-0546-5.

Choudhary, K. K., Schlesewsky, M., Roehm, D., & Bornkessel-Schlesewsky, I.

(2009). The N400 as a correlate of interpretively relevant linguistic rules: Evidence from Hindi. *Neuropsychologia*, *47*(13), 3012–3022.

Clark, A. (2013). Whatever next? Predictive brains, situated agents, and the future of cognitive science. *Behavioral and brain sciences*, *36*(03), 181–204. doi:10.1017/S0140525X12000477

Collins, A. M., & Loftus, E. F. (1975). A spreading-activation theory of semantic processing. *Psychological review*, *82*(6), 407–428. doi:10.1037/0033-295X.82.6.407

Coulson, S., Federmeier, K. D., Van Petten, C., & Kutas, M. (2005). Right Hemisphere Sensitivity to Word- and Sentence-Level Context: Evidence From Event-Related Brain Potentials. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *31*(1), 129–147. doi:10.1037/0278-7393.31.1.129

Dapretto, M., & Bookheimer, S. Y. (1999). Form and content: dissociating syntax and semantics in sentence comprehension. *Neuron*, *24*(2), 427–432.

Deacon, D., Hewitt, S., Yang, C.-M., & Nagata, M. (2000). Event-related potential indices of semantic priming using masked and unmasked words: evidence that the N400 does not reflect a post-lexical process. *Cognitive Brain Research*, *9*(2), 137–146. doi:10.1016/S0926-6410(99)00050-6

Delaney-Busch, N., & Kuperberg, G. (2013). Friendly drug-dealers and terrifying puppies: Affective primacy can attenuate the N400 effect in emotional discourse contexts. *Cognitive, Affective, & Behavioral Neuroscience*, *13*(3), 473–490. doi:10.3758/s13415-013-0159-5

DeLong, K. A., Urbach, T. P., & Kutas, M. (2005). Probabilistic word pre-activation during language comprehension inferred from electrical brain activity. *Nature Neuroscience*, *8*(8), 1117–1121. doi:10.1038/nn1504

Devlin, J. T., Russell, R. P., Davis, M. H., Price, C. J., Wilson, J., Moss, H. E., et al. (2000). Susceptibility-Induced Loss of Signal: Comparing PET and fMRI on a Semantic Task. *NeuroImage*, *11*(6), 589–600. doi:10.1006/nimg.2000.0595

Dien, J., & O'Hare, A. J. (2008). Evidence for automatic sentence priming in the fusiform semantic area: Convergent ERP and fMRI findings. *Brain Research*, *1243*, 134–145. doi:10.1016/j.brainres.2008.09.045

Dien, J., Franklin, M. S., Michelson, C. A., Lemen, L. C., Adams, C. L., & Kiehl, K. A. (2008). fMRI characterization of the language formulation area. *Brain Research*, *1229*, 179–192. doi:10.1016/j.brainres.2008.06.107

Eddy, M., Schmid, A., & Holcomb, P. J. (2006). Masked repetition priming and event-related brain potentials: A new approach for tracking the time-course of object perception. *Psychophysiology*, *43*(6), 564–568. doi:10.1111/j.1469-8986.2006.00455.x

Erickson, T. D., & Mattson, M. E. (1981). From words to meaning: A semantic illusion. *Journal of Verbal Learning and Verbal Behavior*, *20*(5), 540–551.

Federmeier, K. D. (2007). Thinking ahead: The role and roots of prediction in language comprehension. *Psychophysiology*, *44*(4), 491–505. doi:10.1111/j.1469-8986.2007.00531.x

Federmeier, K. D., & Kutas, M. (1999). A Rose by Any Other Name: Long-Term Memory Structure and Sentence Processing. *Journal of Memory and Language*, *41*(4), 469–495. doi:10.1006/jmla.1999.2660

Federmeier, K. D., & Laszlo, S. (2009). Time for meaning: Electrophysiology Provides Insights into the Dynamics of Representation and Processing in Semantic Memory. In B. Ross (Ed.), *Psychology of Learning and Motivation* (Vol.

51, pp. 1–44). Psychology of Learning and Motivation. doi:10.1016/S0079-7421(09)51001-8

Ferstl, E. C., & Cramon, von, D. Y. (2001). The role of coherence and cohesion in text comprehension: an event-related fMRI study. *Cognitive Brain Research*, *11*(3), 325–340. doi:10.1016/S0926-6410(01)00007-6

Ferstl, E. C., & Cramon, von, D. Y. (2002). What does the frontomedian cortex contribute to language processing: coherence or theory of mind? *NeuroImage*, *17*(3), 1599–1612.

Ferstl, E. C., Neumann, J., Bogler, C., & Cramon, von, D. Y. (2008). The extended language network: A meta-analysis of neuroimaging studies on text comprehension. *Human brain mapping*, *29*(5), 581–593. doi:10.1002/hbm.20422

Ferstl, E. C., Rinck, M., & Cramon, D. Y. V. (2005). Emotional and Temporal Aspects of Situation Model Processing during Text Comprehension: An Event-Related fMRI Study. *Journal of Cognitive Neuroscience*, *335*(5), 724–739. doi:10.1016/S0304-3940(02)01196-5

Fiez, J. A. (1997). Phonology, semantics, and the role of the left inferior prefrontal cortex. *Human brain mapping*, *5*(2), 79–83.

Fischler, I., Bloom, P. A., Childers, D. G., Roucos, S. E., & Perry, N. W. (1983). Brain Potentials Related to Stages of Sentence Verification. *Psychophysiology*, *20*(4), 400–409. doi:10.1111/j.1469-8986.1983.tb00920.x

Fodor, J. A. (1983). *The Modularity of Mind*. MIT Press.

Forster, K. I. (1979). Levels of processing and the structure of the language processor. In W. E. Cooper & E. Walker (Eds.) *Sentence processing: Psycholinguistic studies presented to Merrill Garrett*, 27–85, Hillsdale, NJ.

Forster, K. I. (1989). *Basic issues in lexical processing*. The MIT Press.

Forster, K. I. (1999). The microgenesis of priming effects in lexical access. *Brain and Language*, *68*(1), 5–15.

Forster, K. I., & Davis, C. (1984). Repetition priming and frequency attenuation in lexical access. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *10*(4), 680–698. doi:10.1037/0278-7393.10.4.680

Friederici, A. D. (2002). Towards a neural basis of auditory sentence processing. *Trends in Cognitive Sciences*, *6*(2), 78–84.

Friederici, A. D. (2009). Pathways to language: fiber tracts in the human brain. *Trends in Cognitive Sciences*, *13*(4), 175–181. doi:10.1016/j.tics.2009.01.001

Friederici, A. D. (2011). The brain basis of language processing: from structure to function. *Physiological reviews*, *91*(4), 1357-1392.

Friederici, A. D., Meyer, M., & Cramon, von, D. Y. (2000). Auditory Language Comprehension: An Event-Related fMRI Study on the Processing of Syntactic and Lexical Information. *Brain and Language*, *75*(3), 465–477. doi:10.1006/brln.2000.2313

Friederici, A. D., Rüschemeyer, S.-A., Hahne, A., & Fiebach, C. J. (2003). The role of left inferior frontal and superior temporal cortex in sentence comprehension: localizing syntactic and semantic processes. *Cerebral Cortex*, *13*(2), 170–177.

Frisch, S., & Schlesewsky, M. (2001). The N400 reflects problems of thematic hierarchizing. *NeuroReport*, *12*(15), 3391–3394.

Friston, K. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *360*(1456), 815-836.

Friston, K. (2012). Prediction, perception and agency. *International Journal of Psychophysiology*, *83*(2), 248–252. doi:10.1016/j.ijpsycho.2011.11.014

Friston, K. J., & Price, C. J. (2001). Dynamic representations and generative models

of brain function. *Brain research bulletin*, *54*(3), 275–285.

Friston, K., & Kiebel, S. (2009). Predictive coding under the free-energy principle. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1521), 1211–1221. doi:10.1038/335311a0

Gage, N. Y. Y., & Hickok, G. (2005). Multiregional Cell Assemblies, Temporal Binding and the Representation of Conceptual Knowledge in Cortex: a Modern Theory by a "Classical" Neurologist, Carl Wernicke. *Cortex, 41*(6), 823–832. doi:10.1016/S0010-9452(08)70301-0

Ganis, G., & Kutas, M. (2003). An electrophysiological study of scene effects on object identification. *Brain research. Cognitive brain research*, *16*(2), 123–144.

George, M. S., Mannes, S., & Hoffinan, J. E. (1994). Global Semantic Expectancy and Language Comprehension. *Journal of Cognitive Neuroscience*, *6*(1), 70–83. doi:10.1016/0010-0285(77)90005-6

Germain-Mondon, V., Silvert, L., & Izaute, M. (2011). N400 modulation by categorical or associative interference in a famous face naming task. *Neuroscience Letters*, *501*(3), 188–192. doi:10.1016/j.neulet.2011.07.014

Geschwind, N. (1970). The organization of language and the brain. *Science*, *170*(961), 940-944.

Gottfried, J. A., & Dolan, R. J. (2003). The nose smells what the eye sees: crossmodal visual facilitation of human olfactory perception. *Neuron*, *39*(2), 375–386.

Hagoort, P. (2008). The fractionation of spoken language understanding by measuring electrical and magnetic brain signals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1493), 1055–1069.

Hagoort, P., & van Berkum, J. (2007). Beyond the sentence given. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1481), 801–811. doi:10.1037/0033-2909.123.2.162

Hagoort, P., Baggio, G., & Willems, R. M. (2009). Semantic unification. *The cognitive neurosciences*, *4*, 819–836.

Hagoort, P., Hald, L. A., Bastiaansen, M., & Petersson, K. M. (2004). Integration of Word Meaning and World Knowledge in Language Comprehension. *Science*, *304*(5669), 438–441. doi:10.1126/science.1095455

Hasson, U., & Honey, C. J. (2012). Future trends in Neuroimaging: Neural processes as expressed within real-life contexts. *NeuroImage*, *62*(2), 1272–1278. doi:10.1016/j.neuroimage.2012.02.004

Haupt, F. S., Schlesewsky, M., Roehm, D., Friederici, A. D., & Bornkessel-Schlesewsky, I. (2008). The status of subject–object reanalyses in the language comprehension architecture. *Journal of Memory and Language*, *59*(1), 54–96. doi:10.1016/j.jml.2008.02.003

Hickok, G., & Poeppel, D. (2004). Dorsal and ventral streams: a framework for understanding aspects of the functional anatomy of language. *Cognition*, *92*(1-2), 67–99. doi:10.1016/j.cognition.2003.10.011

Hoeks, J. C. J., Stowe, L. A., & Doedens, G. (2004). Seeing words in context: the interaction of lexical and sentence level information during reading. *Cognitive Brain Research*, *19*(1), 59–73. doi:10.1016/j.cogbrainres.2003.10.022

Hohwy, J. (2007). Functional Integration and the Mind. *Synthese*, *159*(3), 315–328.

Holcomb, P. J., & Neville, H. J. (1990). Auditory and Visual Semantic Priming in Lexical Decision: A Comparison Using Event-related Brain Potentials. *Language and Cognitive Processes*, *5*(4), 281–312.

Holcomb, P. J., Grainger, J., & O'Rourke, T. (2002). An Electrophysiological Study of the Effects of Orthographic Neighborhood Size on Printed Word Percep-

tion. *Journal of Cognitive Neuroscience*, *14*(6), 938–950. doi:10.1016/S0926-6410(01)00129-X

Hruska, C., & Alter, K. (2004). Prosody in dialogues and single sentences. In A. Steube (Ed.), *Information Structure: Theoretical and Empirical Aspects* (pp. 211–226). Berlin: Walter de Gruyter: Information structure: Theoretical and Empirical Aspects.

Hubel, D. H., & Wiesel, T. N. (1965). Receptive fields and functional architecture in two nonstriate visual areas (18 and 19) of the cat. *Journal of Neurophysiology*.

Humphries, C., Binder, J. R., Medler, D. A., & Liebenthal, E. (2006). Syntactic and Semantic Modulation of Neural Activity during Auditory Sentence Comprehension. *Journal of Cognitive Neuroscience*, *18*(4), 665–679. doi:10.1006/nimg.2001.0933

Humphries, C., Binder, J. R., Medler, D. A., & Liebenthal, E. (2007). Time course of semantic processes during sentence comprehension: An fMRI study. *NeuroImage*, *36*(3), 924–932. doi:10.1016/j.neuroimage.2007.03.059

Ibáñez, A. M., Martín, R. S., Hurtado, E., & López, V. (2009). ERPs studies of cognitive processing during sleep. *International Journal of Psychology*, *44*(4), 290–304. doi:10.1080/00207590802194234

Janssen, U., Wiese, R., & Schlesewsky, M. (2006). Electrophysiological responses to violations of morphosyntactic and prosodic features in derived German nouns. *Journal of Neurolinguistics*, *19*(6), 466–482. doi:10.1016/j.jneuroling.2006.04.002

Just, M. A., & Carpenter, P. A. (1980). A theory of reading: From eye fixations to comprehension. *Psychological review*, *87*, 329–354.

Kelly, S. D., Kravitz, C., & Hopkins, M. (2004). Neural correlates of bimodal speech and gesture comprehension. *Brain and Language*, *89*(1), 253–260.

Kiefer, M. (2002). The N400 is modulated by unconsciously perceived masked words: Further evidence for an automatic spreading activation account of N400 priming effects. *Brain research. Cognitive brain research*, *13*(1), 27–39.

Kiehl, K. A., Laurens, K. R., & Liddle, P. F. (2002). Reading Anomalous Sentences: An Event-Related fMRI Study of Semantic Processing. *NeuroImage*, *17*(2), 842–850. doi:10.1006/nimg.2002.1244

Kim, A., & Lai, V. (2012). Rapid interactions between lexical semantic and word form analysis during word recognition in context: evidence from ERPs. *Journal of Cognitive Neuroscience*, *24*(5), 1104–1112.

Kim, A., & Osterhout, L. (2005). The independence of combinatory semantic processing: Evidence from event-related potentials. *Journal of Memory and Language*, *52*(2), 205–225. doi:10.1016/j.jml.2004.10.002

Kuperberg, G. R., Holcomb, P. J., Sitnikova, T., Greve, D., Dale, A. M., & Caplan, D. (2003). Distinct Patterns of Neural Modulation during the Processing of Conceptual and Syntactic Anomalies. *Journal of Cognitive Neuroscience*, *15*(2), 272–293. doi:10.1017/S0048577299971202

Kuperberg, G. R., McGuire, P. K., Bullmore, E. T., Brammer, M. J., Rabe-Hesketh, S., Wright, I. C., et al. (2000). Common and distinct neural substrates for pragmatic, semantic, and syntactic processing of spoken sentences: an fMRI study. *Journal of Cognitive Neuroscience*, *12*(2), 321–341.

Kuperberg, G. R., Sitnikova, T., & Lakshmanan, B. M. (2008). Neuroanatomical distinctions within the semantic system during sentence comprehension: Evidence from functional magnetic resonance imaging. *NeuroImage*, *40*(1), 367–388. doi:10.1016/j.neuroimage.2007.10.009

Kutas, M. (1993). In the company of other words: Electrophysiological evidence for single-word and sentence context effects. *Language and Cognitive Processes*, *8*(4), 533–572. doi:10.1080/01690969308407587

Kutas, M., & Dale, A. (1997). Electrical and magnetic readings of mental functions. *Cognitive Neuroscience*, *1974242*.

Kutas, M., & Federmeier, K. D. (2000). Electrophysiology reveals semantic memory use in language comprehension. *Trends in Cognitive Sciences*, *4*(12), 463–470. doi:10.1016/S1364-6613(00)01560-6

Kutas, M., & Federmeier, K. D. (2011). Thirty years and counting: finding meaning in the N400 component of the event-related brain potential (ERP). *Annual Review of Psychology*, *62*, 621–647.

Kutas, M., & Hillyard, S. A. (1980). Reading senseless sentences: Brain potentials reflect semantic incongruity. *Science*, *207*(4427), 203–205.

Kutas, M., & Hillyard, S. A. (1984). Brain potentials during reading reflect word expectancy and semantic association. *Nature*, *307*(5947), 161–163. doi:10.1038/307161a0

Kutas, M., Neville, H. J., & Holcomb, P. J. (1987). A preliminary comparison of the N400 response to semantic anomalies during reading, listening and signing. *Electroencephalography Clinical Neurophysiology*, *39*, 325–330.

Laszlo, S., & Federmeier, K. D. (2007). Better the DVL You Know: Acronyms Reveal the Contribution of Familiarity to Single-Word Reading. *Psychological Science*, *18*(2), 122–126. doi:10.1111/j.1467-9280.2007.01859.x

Laszlo, S., & Federmeier, K. D. (2008). Minding the PS, queues, and PXQs: Uniformity of semantic processing across multiple stimulus types. *Psychophysiology*, *45*(3), 458–466. doi:10.1111/j.1469-8986.2007.00636.x

Laszlo, S., & Federmeier, K. D. (2009). A beautiful day in the neighborhood: An event-related potential study of lexical relationships and prediction in context. *Journal of Memory and Language*.

Laszlo, S., & Federmeier, K. D. (2011). The N400 as a snapshot of interactive processing: Evidence from regression analyses of orthographic neighbor and lexical associate effects. *Psychophysiology*, *48*(2), 176–186. doi:10.1111/j.1469-8986.2010.01058.x

Laszlo, S., & Plaut, D. C. (2012). A neurally plausible Parallel Distributed Processing model of Event-Related Potential word reading data. *Brain and Language*, *120*(3), 271–281. doi:10.1016/j.bandl.2011.09.001

Lau, E. F., Phillips, C., & Poeppel, D. (2008). A cortical network for semantics: (de)constructing the N400. *Nature Reviews Neuroscience*, *9*(12), 920–933. doi:10.1038/nrn2532

Li, X., Hagoort, P., & Yang, Y. (2008). Event-related Potential Evidence on the Influence of Accentuation in Spoken Discourse Comprehension in Chinese. *Journal of Cognitive Neuroscience*, *20*(5), 906–915. doi:10.1016/j.cognition.2005.07.001

Lichtheim, L. (1885). On aphasia. *Brain*, *7*(4), 433–484.

Logothetis, N. K. (2002). The neural basis of the blood-oxygen-level-dependent functional magnetic resonance imaging signal. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *357*(1424), 1003–1037. doi:10.1098/rstb.2002.1114

López, V., Carmenate, L., & Alvarez, A. (2001). N400 effect during different sleep stages. *Clinical Neurophysiology*, *112*, 12–51.

Luck, S. J., Vogel, E. K., & Shapiro, K. L. (1996). Word meanings can be accessed

but not reported during the attentional blink. *Nature*, *383*(6601), 616–618.

MacDonald, M. C., Pearlmutter, N. J., & Seidenberg, M. S. (1994). Lexical nature of syntactic ambiguity resolution. *Psychological review*, *101*(4), 676–703.

MacWhinney, B., Bates, E., & Kliegl, R. (1984). Cue validity and sentence interpretation in English, German, and Italian. *Journal of Verbal Learning and Verbal Behavior*, *23*(2), 127–150.

Maki, W. S., Frigen, K., & Paulson, K. (1997). Associative priming by targets and distractors during rapid serial visual presentation: Does word meaning survive the attentional blink? *Journal of Experimental Psychology: Human Perception and Performance*, *23*(4), 1014.

Marslen-Wilson, W. (1989). Access and integration: Projecting sound onto meaning. In Marslen-Wilson, William (Ed). *Lexical representation and process*., 3-24. Cambridge, MA, US: The MIT Press.

Martin, A. (2007). The representation of object concepts in the brain. *Annual Review of Psychology*, *58*, 25–45.

Massaro, D. W. (1998). *Perceiving talking faces: From speech perception to a behavioral principle*. MIT Press.

Mazoyer, B. M., Tzourio, N., Frak, V., Syrota, A., Murayama, N., Levrier, O., et al. (1993). The cortical representation of speech. *Journal of Cognitive Neuroscience*, *5*(4), 467–479.

McPherson, W. B., & Holcomb, P. J. (1999). An electrophysiological investigation of semantic priming with pictures of real objects. *Psychophysiology*, *36*(01), 53–65.

McRae, K., & Jones, M. N. (2012). Semantic memory. *The Oxford handbook of cognitive psychology*.

Menenti, L., Petersson, K. M., Scheeringa, R., & Hagoort, P. (2009). When elephants fly: differential sensitivity of right and left inferior frontal gyri to discourse and world knowledge. *Journal of Cognitive Neuroscience*, *21*(12), 2358–2368.

Miller, E. K., & Cohen, J. D. (2001). An Integrative Theory of Prefrontal Function. *Annual Review of Neuroscience*, *24*(1), 167–202. doi:10.1146/annurev.neuro.24.1.167

Moss, H. E., Abdallah, S., Fletcher, P., Bright, P., Pilgrim, L., Acres, K., & Tyler, L. K. (2005). Selecting among competing alternatives: selection and retrieval in the left inferior frontal gyrus. *Cerebral Cortex*, *15*(11), 1723–1735.

Mueller, J. L., Hahne, A., Fujii, Y., & Friederici, A. D. (2005). Native and Nonnative Speakers' Processing of a Miniature Version of Japanese as Revealed by ERPs. *Journal of Cognitive Neuroscience*, *17*(8), 1229–1244. doi:10.1162/jocn.1996.8.3.231

Neely, J. H. (1991). Semantic priming effects in visual word recognition: A selective review of current findings and theories. *Basic processes in reading: Visual word recognition*, *11*.

Newman, A. J., Pancheva, R., Ozawa, K., Neville, H. J., & Ullman, M. T. (2001). An Event-Related fMRI Study of Syntactic and Semantic Violations. *Journal of Psycholinguistic Research*, *30*(3), 339–364. doi:10.1023/A:1010499119393

Ni, W., Constable, R. T., Mencl, W. E., Pugh, K. R., Fulbright, R. K., Shaywitz, S. E., et al. (2000). An Event-related Neuroimaging Study Distinguishing Form and Content in Sentence Processing. *Journal of Cognitive Neuroscience*, *12*(1), 120–133. doi:10.1006/brln.1996.0024

Nieuwland, M. S., & Van Berkum, J. J. A. (2005). Testing the limits of the semantic illusion phenomenon: ERPs reveal temporary semantic change deafness in

discourse comprehension. *Cognitive Brain Research*, *24*(3), 691–701. doi:10.1016/j.cogbrainres.2005.04.003

Nieuwland, M. S., & Van Berkum, J. J. A. (2006). When Peanuts Fall in Love: N400 Evidence for the Power of Discourse. *Journal of Cognitive Neuroscience*, *18*(7), 1098–1111. doi:10.1037/0033-2909.123.2.162

Nobre, A. C., & McCarthy, G. (1994). Language-Related ERPs: Scalp Distributions and Modulation by Word Type and Semantic Priming. *Journal of Cognitive Neuroscience*, *6*(3), 233–255. doi:10.3109/00207458808985695

Nobre, A. C., & McCarthy, G. (1995). Language-related field potentials in the anterior-medial temporal lobe: II. Effects of word type and semantic priming. *The Journal of Neuroscience*, *15*(2), 1090–1098.

Norris, D. (1994). Shortlist: a connectionist model of continuous speech recognition. *Cognition*, *52*(3), 189–234. doi:10.1016/0010-0277(94)90043-4

Obleser, J., & Kotz, S. A. (2010). Expectancy constraints in degraded speech modulate the language comprehension network. *Cerebral Cortex*, *20*(3), 633–640.

Ogawa, S., Lee, T. M., Kay, A. R., & Tank, D. W. (1990). Brain magnetic resonance imaging with contrast dependent on blood oxygenation. *Proceedings of the National Academy of Sciences*, *87*(24), 9868–9872.

Orgs, G., Lange, K., Dombrowski, J.-H., & Heil, M. (2006). Conceptual priming for environmental sounds and words: An ERP study. *Brain and Cognition*, *62*(3), 267–272. doi:10.1016/j.bandc.2006.05.003

Özyürek, A., Willems, R. M., Kita, S., & Hagoort, P. (2007). On-line Integration of Semantic Information from Speech and Gesture: Insights from Event-related Brain Potentials. *Journal of Cognitive Neuroscience*, *19*(4), 605–616. doi:10.1111/j.1469-8986.2005.00356.x

Patterson, K., Nestor, P. J., & Rogers, T. T. (2007). Where do you know what you know? The representation of semantic knowledge in the human brain. *Nature Reviews Neuroscience*, *8*(12), 976–987. doi:10.1038/nrn2277

Petten, C. V. (1993). A comparison of lexical and sentence-level context effects in event-related potentials. *Language and Cognitive Processes*, *8*(4), 485–531. doi:10.1080/01690969308407586

Pickering, M. J., & Garrod, S. (2013). An integrated theory of language production and comprehension. *Behavioral and brain sciences*, *36*(04), 329–347. doi:10.1017/S0140525X12001495

Rao, R. P. N., & Ballard, D. H. (1999). Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects. *Nature Neuroscience*, *2*(1), 79–87. doi:10.1038/4580

Rao, R. P., & Ballard, D. H. (2004). Probabilistic models of attention based on iconic representations and predictive coding. *Neurobiology of Attention*, 553–561.

Raposo, A., & Marques, J. F. (2013). The contribution of fronto-parietal regions to sentence comprehension: Insights from the Moses illusion. *NeuroImage*, *83*, 431–437.

Rauschecker, J. P. (1998). Parallel processing in the auditory cortex of primates. *Audiology and Neurotology*, *3*(2-3), 86–103.

Rauschecker, J. P., & Scott, S. K. (2009). Maps and streams in the auditory cortex: nonhuman primates illuminate human speech processing. *Nature Neuroscience*, *12*(6), 718–724. doi:10.1038/nn.2331

Rugg, M. D. (1985). The Effects of Semantic Priming and Word Repetition on Event-Related Potentials. *Psychophysiology*, *22*(6), 642-647.

Rugg, M. D. (1990). Event-related brain potentials dissociate repetition effects of

high-and low-frequency words. *Memory & Cognition*, *18*(4), 367–379. doi:10.3758/BF03197126

Rüschemeyer, S. A., Zysset, S., & Friederici, A. D. (2006). Native and non-native reading of sentences: An fMRI experiment. *NeuroImage*, *31*(1), 354-365.

Rüschemeyer, S.-A., Fiebach, C. J., Kempe, V., & Friederici, A. D. (2005). Processing lexical semantic and syntactic information in first and second language: fMRI evidence from German and Russian. *Human brain mapping*, *25*(2), 266–286. doi:10.1002/hbm.20098

Sanford, Anthony J, Leuthold, H., Bohan, J., & Sanford, A. J. (2011). Anomalies at the borderline of awareness: An ERP study. *Journal of Cognitive Neuroscience*, *23*(3), 514–523.

Sarfarazi, M. (1999). Visual Event Related Potentials Modulated by Contextually Relevant and Irrelevant Olfactory Primes. *Chemical Senses*, *24*(2), 145–154. doi:10.1093/chemse/24.2.145

Saur, D., Kreher, B. W., Schnell, S., Kümmerer, D., Kellmeyer, P., Vry, M.-S., et al. (2008). Ventral and dorsal pathways for language. *PNAS*, *19*(4), 777–785. doi:10.1093/cercor/bhn124

Schumacher, P. B., & Baumann, S. (2010). Pitch accent type affects the N400 during referential processing. *NeuroReport*, *21*(9), 618–622. doi:10.1097/WNR.0b013e328339874a

Seghier, M. L. (2013). The Angular Gyrus Multiple Functions and Multiple Subdivisions. *The Neuroscientist*, *19*(1), 43–61.

Siebörger, F. T., Ferstl, E. C., & Cramon, von, D. Y. (2007). Making sense of non-sense: An fMRI study of task induced inference processes during discourse comprehension. *Brain Research*, *1166*, 77–91. doi:10.1016/j.brainres.2007.05.079

Sitnikova, T., Holcomb, P. J., Kiyonaga, K. A., & Kuperberg, G. R. (2008). Two Neurocognitive Mechanisms of Semantic Integration during the Comprehension of Visual Real-world Events. *Journal of Cognitive Neuroscience*, *20*(11), 2037–2057. doi:10.1037/0033-2909.127.1.3

St George, M., Kutas, M., Martinez, A., & Sereno, M. I. (1999). Semantic integration in reading: engagement of the right hemisphere during discourse processing. *Brain*, *122*(7), 1317–1325. doi:10.1093/brain/122.7.1317

Stowe, L. A., Broere, C. A., Paans, A. M., Wijers, A. A., Mulder, G., Vaalburg, W., & Zwarts, F. (1998). Localizing components of a complex task: sentence processing and working memory. *NeuroReport*, *9*(13), 2995–2999.

Stowe, L. A., Haverkort, M., & Zwarts, F. (2005). Rethinking the neurological basis of language. *Lingua*, *115*(7), 997–1042. doi:10.1016/j.lingua.2004.01.013

Stringaris, A. K., Medford, N. C., Giampietro, V., Brammer, M. J., & David, A. S. (2007). Deriving meaning: Distinct neural mechanisms for metaphoric, literal, and non-meaningful sentences. *Brain and Language*, *100*(2), 150–162. doi:10.1016/j.bandl.2005.08.001

Stroud, C., & Phillips, C. (2011). Examining the evidence for an independent semantic analyzer: An ERP study in Spanish. *Brain and Language*, *120*(2), 108-126. doi:10.1016/j.bandl.2011.02.001

Swaab, T. Y., Camblin, C. C., & Gordon, P. C. (2004). Electrophysiological Evidence for Reversed Lexical Repetition Effects in Language Processing. *Journal of Cognitive Neuroscience*, *16*(5), 715–726. doi:10.1016/0028-3932(95)00017-W

Tanenhaus, M. K., & Trueswell, J. C. (1995). Sentence comprehension. Miller, J. L.

& Eimas, P. D. (Eds). *Speech, language, and communication. Handbook of perception and cognition (2nd ed.), 11*, 217-262. San Diego, CA, US: Academic Press

Taylor, W. L. (1953). "Cloze procedure": a new tool for measuring readability. *Journalism quarterly.*

Thompson-Schill, S. L., D'Esposito, M., & Kan, I. P. (1999). Effects of repetition and competition on activity in left prefrontal cortex during word generation. *Neuron*, *23*(3), 513–522.

Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K., & Farah, M. J. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. *Proceedings of the National Academy of Sciences*, *94*(26), 14792–14797.

Toepel, U., & Alter, K. (2004). On the independence of information structural processing from prosody. In A. Steube (Ed.), *Information structure: Theoretical and empirical aspects.*, 227–240. Berlin: Walter de Gruyter.

Ueno, T., Saito, S., Rogers, T. T., & Lambon Ralph, M. A. (2011). Lichtheim 2: synthesizing aphasia and the neural basis of language in a neurocomputational model of the dual dorsal-ventral language pathways. *Neuron*, *72*(2), 385–396.

Van Berkum, J. J. A. (2008). Understanding Sentences in Context: What Brain Waves Can Tell Us. *Current Directions in Psychological Science*, *17*(6), 376–380. doi:10.1111/j.1467-8721.2008.00609.x

Van Berkum, J. J. A., Zwitserlood, P., Hagoort, P., & Brown, C. M. (2003). When and how do listeners relate a sentence to the wider discourse? Evidence from the N400 effect. *Cognitive Brain Research*, *17*(3), 701–718. doi:10.1016/S0926-6410(03)00196-4

Van Petten, C., & Kutas, M. (1990). Interactions between sentence context and word frequency in event-related brain potentials. *Memory & Cognition*, *18*(4), 380–393.

Van Petten, C., & Kutas, M. (1991a). Electrophysiological evidence for the flexibility of lexical processing. *Understanding word and sentence*, 129–174.

Van Petten, C., & Kutas, M. (1991b). Influences of semantic and syntactic context on open- and closed-class words. *Memory & Cognition*, *19*(1), 95–112. doi:10.3758/BF03198500

Van Petten, C., & Luka, B. J. (2006). Neural localization of semantic context effects in electromagnetic and hemodynamic studies. *Brain and Language*, *97*(3), 279–293. doi:10.1016/j.bandl.2005.11.003

Van Petten, C., & Luka, B. J. (2012). Prediction during language comprehension: Benefits, costs, and ERP components. *International Journal of Psychophysiology*, *83*(2), 176–190. doi:10.1016/j.ijpsycho.2011.09.015

Van Petten, C., & Rheinfelder, H. (1995). Conceptual relationships between spoken words and environmental sounds: Event-related brain potential measures. *Neuropsychologia*, *33*(4), 485–508. doi:10.1016/0028-3932(94)00133-A

Van Petten, C., Coulson, S., Rubin, S., Plante, E., & Parks, M. (1999). Time course of word identification and semantic integration in spoken language. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *25*(2), 394–417. doi:10.1037/0278-7393.25.2.394

Van Petten, C., Kutas, M., Kluender, R., Mitchiner, M., & McIsaac, H. (1991). Fractionating the Word Repetition Effect with Event-Related Potentials. *Journal of Cognitive Neuroscience*, *3*(2), 131–150. doi:10.1016/0028-3932(74)90071-2

Vuust, P., Ostergaard, L., Pallesen, K. J., Bailey, C., & Roepstorff, A. (2009). Predic-

tive coding of music – Brain responses to rhythmic incongruity. *Cortex*, *45*(1), 80–92. doi:10.1016/j.cortex.2008.05.014

Wagner, A. D., Paré-Blagoev, E. J., Clark, J., & Poldrack, R. A. (2001). Recovering meaning: left prefrontal cortex guides controlled semantic retrieval. *Neuron*, *31*(2), 329–338.

Wernicke, C. (1874). *Der Aphasische Symptomencomplex* (Cohn & Weigert.). Breslau.

West, W. C., & Holcomb, P. J. (2000). Imaginal, Semantic, and Surface-Level Processing of Concrete and Abstract Words: An Electrophysiological Investigation. *Journal of Cognitive Neuroscience,* *12*(6), 1024–1037. doi:10.1162/jocn.1997.9.6.714

Willems, R. M., Özyürek, A., & Hagoort, P. (2008). Seeing and Hearing Meaning: ERP and fMRI Evidence of Word versus Picture Integration into a Sentence Context. *Journal of Cognitive Neuroscience*, *20*(7), 1235–1249. doi:10.1093/cercor/bhl141

Wu, Y. C., & Coulson, S. (2005). Meaningful gestures: Electrophysiological indices of iconic gesture comprehension. *Psychophysiology*, *42*(6), 654–667.

Xu, J., Kemeny, S., Park, G., Frattali, C., & Braun, A. (2005). Language in context: emergent features of word, sentence, and narrative comprehension. NeuroImage, 25(3), 1002–1015. doi:10.1016/j.neuroimage.2004.12.013

6 EXPERIMENTAL STUDIES

Study 1:

Lotze, N., Tune, S., Schlesewsky, M. & Bornkessel-Schlesewsky, I. (2011). Meaningful physical changes mediate lexical-semantic integration: Evidence for the interplay between top-down and bottom-up information sources in the N400. *Neuropsycholgia*, 49(13), 3573–3582.

Study 2:

Tune, S., Schlesewsky, M., Small, S. L., Sanford, A.J., Bohan, J., Sassenhagen, J., Bornkessel- Schlesewsky, I. (accepted). Cross-linguistic variation in the neurophysiological response to semantic processing: Evidence from anomalies at the borderline of awareness. *Neuropsychologica*.

Study 3:

Tune, S., Schlesewsky, M., Nagels, A., Small, S.L., Bornkessel-Schlesewsky, I. (submitted). Depth of semantic processing in discourse context modulates contributions of temporal and parietal regions: fMRI evidence. *Cortex*.

PART II

7   STUDY 1

Meaningful physical changes mediate lexical-semantic integration:

Top-down and form-based bottom-up information sources interact in the N400

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ABSTRACT

Models of how the human brain reconstructs an intended meaning from a linguistic input often draw upon the N400 event-related potential (ERP) component as evidence. Current accounts of the N400 emphasise either the role of contextually-induced lexical preactivation of a critical word (Lau, Phillips, & Poeppel, 2008) or the ease of integration into the overall discourse context including a wide variety of influencing factors (Hagoort & van Berkum, 2007). The present ERP study challenges both types of accounts by demonstrating a contextually-independent and purely form-based bottom-up influence on the N400: the N400 effect for implausible sentence-endings was attenuated when the critical sentence-final word was capitalised (following a lowercase sentence context). By contrast, no N400 modulation occurred when the critical word involved a change from uppercase (sentence context) to lowercase. Thus, the N400 was only affected by a change to uppercase letters, as is often employed in computer-mediated communication as a sign of emphasis. This result indicates that N400 amplitude is reduced for unexpected words when a bottom-up (orthographic) cue signals that the word is likely to be highly informative. The lexical-semantic N400 thereby reflects the degree to which the semantic informativity of a critical word matches expectations, as determined by an interplay between top-down and bottom-up information sources, including purely form-based bottom-up information.

Keywords: language comprehension, semantics, lexicon, physical deviance, computer-mediated communication, N400, late positivity, bidirectional coding account.

7.1   Introduction

Language provides us, as humans, with an immensely powerful and expressive means of communication. We can use it not only to convey facts about the world, and thereby states of affairs which may already be familiar to the addressee, but also to talk about events that have never taken place and never will. For example, if one were to tell a friend that *Martians have landed on the banks of the Rhine*, he/she will likely never have experienced such an event, but would nevertheless understand what the utterance means (though he/she might not believe it). In view of this vast expressive potential of language, it is not surprising that the question of how the brain reconstructs the intended meaning from a linguistic input has received a lot of attention in the literature on the neuroscience of language.

One position that has come to be highly influential in this regard has been described as a "one-step model of language interpretation" (Hagoort & van Berkum, 2007, p. 802). This model essentially claims that all available information sources (e.g. syntax, semantics, prosody, discourse context, world knowledge etc.) are all taken into account immediately and simultaneously in the brain's computation of meaning (Crain & Steedman, 1985; MacDonald, Pearlmutter, & Seidenberg, 1994; Trueswell & Tanenhaus, 1994; e.g. Hagoort & van Berkum, 2007). This means, for example, that a new word that is encountered in a particular sentence and discourse context is *not* first integrated into the meaning of the sentence and, only in a second stage, related to the broader discourse. Evidence for the one-stage view has primarily been based on the N400 event-related brain potential (ERP), an electrophysiological response that has been known to be sensitive to meaning ever since it was first reported by Kutas and Hillyard (1980) for semantically anomalous (*He spread the warm bread with socks*) or unexpected (*He took a sip from the waterfall*) continuations. Specifically, a range of recent studies has demonstrated that the N400 is influenced by a number of diverse factors such as discourse context (Van Berkum, Brown, Hagoort, & Zwitserlood, 2003), world knowledge (Hagoort, Hald, Bastiaansen, & Petersson, 2004) and even the identity of the speaker (Van Berkum, van den Brink, Tesink, Kos, & Hagoort, 2008).[1] Since none of these studies provided any evidence

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[1] Van Berkum et al. (2008) demonstrated speaker effects on the N400 by showing that this component can be modulated by an incompatibility between speaker and message (e.g. a child's voice saying "*Every evening I drink some wine before I go to sleep*" or a male voice saying "*If only I looked like Britney Spears in her latest video*").

for measurable differences between N400 effects which are engendered by a violation of sentence-external factors (e.g. contextual or world knowledge) and N400 effects which reflect sentence-internal incongruities, they appear to provide strong evidence for the one-step view of interpretation. In the words of Van Berkum and colleagues (2008, p. 589): "to the brain of the language user, there is no context-free meaning".

It has, however, been argued that findings such as these can also be derived via a lexical view of the N400 in concert with the assumption of a strong predictive component in language processing (Lau et al., 2008). A schematic representation of Lau and colleagues' model is given in Figure 1. As is apparent from the figure, it explains N400 modulations in terms of variations in the degree of lexical preactivation of a lexical item and these are influenced by top-down processes (e.g. contextual influences). In this view, therefore, one does not necessarily need to appeal to a one-step interpretation mechanism "in which knowledge about the context and the world, concomitant information from other modalities, and the speaker are brought to bear immediately, by the same fast-acting brain system that combines the meanings of individual words into a message-level representation" (Hagoort & van Berkum, 2007, p. 801). In principle, then, a feed-forward model including multiple interpretation steps is compatible with the data, provided that it incorporates a feed-back loop that can modulate the degree of lexical preactivation of an upcoming word via a predictive mechanism.
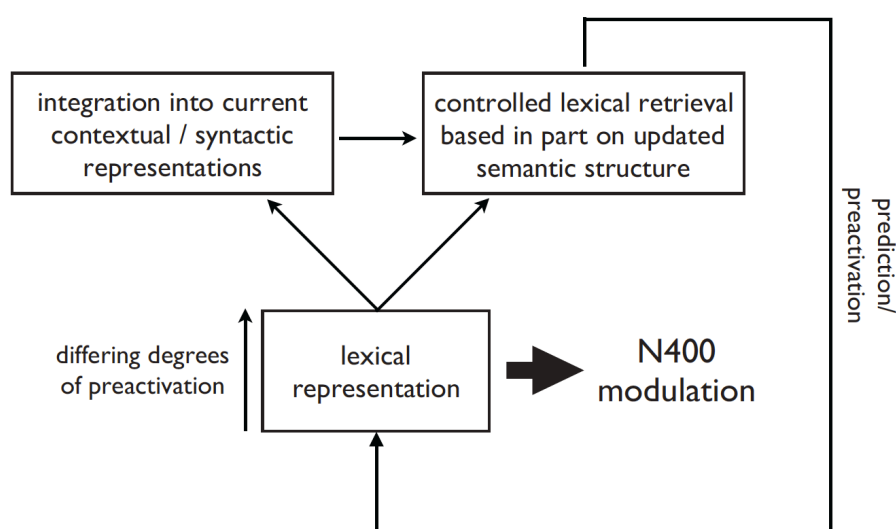
Figure 1: Schematic depiction of the lexical account of the N400 (Lau et al., 2008). Note that the neuroanatomical designations in Lau and colleagues' model are omitted here since they are not directly relevant to the present article.

As is apparent from Figure 1, the lexical model relies on the assumption that, prior to a critical word being encountered, there is a sufficient build-up of context for the word in the control condition to become more highly preactivated than its counterpart in the critical condition. In Van Berkum and colleagues' (2008) study, for example, one would need to assume that an adult voice in conjunction with the lead-in "*Every evening I drink some...*" is sufficient to lead to a stronger preactivation of *wine* than the same words spoken by a child's voice. In principle, this appears plausible. However, other recent results appear to present more of a challenge to the lexical account of the N400. For example, Schumacher and Baumann (2010) examined the processing of accessible referents[2] with different types of pitch accents (given, new, accessible) and found that inappropriate pitch accents engendered an increased N400 (followed by a late positivity in the case of the givenness accent). (For other reports of N400 effects for mismatches between prosody and information structure, see Hruska & Alter, 2004; Toepel & Alter, 2004; Li, Hagoort, & Yang, 2008.) Results such as these are not easily explained via a contextual modulation of lexical preactivation, since the N400 effects occurred for identical critical words and sentence contexts, with only the pitch information *on the critical word itself* changing across conditions. Rather, they appear to suggest that N400 amplitude is sensitive to the interplay of top-down and bottom-up factors: the former include contextually-induced lexical preactivation, while the latter encompass form-based aspects of the critical word (e.g. its prosodic realisation).[3] A possible consequence of this tentative "bottom-up/top-down" account of the N400 is that a low degree of lexical (pre-)activation per se need not lead to an increase in N400 amplitude provided that the form-based bottom-up information associated with the critical word signals this low activation status. In other words, one role of focus (new information) marking in the languages of the world, either prosodically or otherwise, would be to provide a bottom-up "alert" to the low degree of preactivation / high degree of informativity of the word in question.

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[2] Accessible referents were not directly mentioned in the prior discourse context, but were accessible via an inference from another active discourse referent. Schumacher and Baumann (2010) present the following example (English translation of the German original; *sole* is the accessible referent): *Sabine repairs an old shoe. In doing so, she cuts the sole*.

[3] Note that bottom-up influences on the N400 have, of course, long been described with regard to factors such as lexical frequency (see Kutas & Federmeier, 2000, for an overview). These types of influences are clearly compatible with an activation-based account, since frequency is often thought to affect the base activation (or recognition threshold) of a lexical entry (e.g. Morton, 1969). Here, however, we focus specifically on *form-based* bottom-up information, for which it appears considerably less clear how it might exert a direct influence on the activation of a concept or lexical entry.

In summary, previous results suggest that N400 modulations may result from a combination of form-based bottom-up and top-down factors. Most crucially, they indicate that N400 increases need not always reflect the low preactivation/contextual fit of a critical word, but can also be elicited when there is a mismatch between the bottom-up information provided with that word (e.g. its prosodic realisation) and its information status (i.e. whether it provides old or new information). In the present study, we sought to examine whether form-based bottom-up influences on the N400 can also be observed when they do not lead to a mismatch with top-down information such as context or information structure. To this end, we employed a novel orthographic manipulation, namely capitalisation.

7.2   The present study

Capitalisation is an orthographic strategy that is used in computer-mediated communication (CMC), which, in the day and age of blogs, chats and iPads, is becoming an increasingly important part of our everyday lives (e.g. Herring, 2008). In the language domain, one of the defining characteristics of these new communication modes is that, in contrast to traditional writing styles, they employ "a complex set of orthographic strategies designed to compensate for the lack of intonation and paralinguistic cues that interactive written discourse imposes on its users" (Werry, 1996, pp. 56-57). Capitalisation of words, as one of the simplest and most clearly definable strategies of this type, essentially serves to signal a (virtual) increase in speech volume and is thus often referred to as "shouting". In addition to serving as a possible means for emphasis, it therefore bears a negative connotation such that guides on web etiquette advise against its use, especially in multiword sequences.[4]

The interest of capitalisation for the present study is that it is an orthographic deviation that serves to signal high information content. Thus, if the hypothesis advanced above about the interplay of form-based bottom-up and top-down factors in the N400 is correct, a less expected (implausible) sentence continuation may be processed differently when it is realised via a capitalised critical word as opposed to a critical word that does not signal a change in information content. To test this, we

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[4] For example, the Department of Education and Training of the Australian state of Queensland's state government advises on its website: "Don't type in ALL CAPITALS - it is called shouting and is considered to be rude" (http://education.qld.gov.au/learningplace/communication/chat/chatiquette.html, accessed on July 16th 2010).

manipulated both the plausibility of the sentence-final word (factor PLAUSibility) and whether it induced a physical change or not (factor CHANGE) in a fully crossed design (see Table 1). In addition, we manipulated the type of the physical change as a between-participants factor (GROUP): for one participant group, physically deviating final words changed from normal text to uppercase (potentially meaningful, signalling high information content); for a second group, sentences were generally presented in uppercase letters and physically deviating final words were changed to normal (i.e. lowercase) text (non-meaningful).[5] Note that, while case changes have been examined in several previous ERP studies on language (Kutas & Hillyard, 1980; Osterhout, McKinnon, Bersick, & Corey, 1996), none of these crossed the physical change with a plausibility manipulation. Furthermore, in contrast to the prosodic manipulations used in previous studies, case changes cannot, in and of themselves, induce a conflict with the content of the message being conveyed.

Our hypotheses were as follows. If lexical-semantic integration of a critical word is indeed modulated by purely form-based bottom-up factors, the N400 effect for implausible vs. plausible continuations should be reduced when bottom-up information signals a high information status (i.e. when the critical word is capitalised). We predict that this N400 reduction should be specific to capitalisation as a meaningful physical change and that it should therefore not be observable in the case of a physical change from upper- to lowercase.

7.3 Methods

7.3.1 Participants

40 monolingually raised native speakers of German participated in the present study after giving informed consent (18 women; mean age: 24.4; range 20-32 years). All participants were right-handed (Edinburgh handedness inventory, Oldfield, 1971), had normal or corrected-to-normal vision and no known neurological disorders.

7.3.2 Materials

The critical stimulus materials consisted of 80 sets of the 8 conditions shown in

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[5] Note that the deviating (lowercase) words nevertheless adhered to the regularities of German orthography, i.e. nouns always began with a capital letter.

Table1. All sentences had a length of seven words. In order to guarantee for maximal naturalness of the sentences, we selected 80 sentences with a capitalised final word from the "Dortmunder Chat-Korpus" (http://www.chatkorpus.tu-dortmund.de/), a corpus of over 140 000 chat entries. The sentences stem primarily from media-related chats (e.g. about politics), since these provide relatively natural contexts in which capitalisation occurs in full and grammatical sentences as opposed to single phrases or one word turns in capitals (e.g. "NO!"), which are of high frequency in private chats and typical for the register. In political chats, by contrast, the register is more formal, but users nevertheless interact as emotionally as in private chats. Thus, "shouting" (i.e. capitalisation) is quite frequent, but occurs in grammatical sentences. The 80 sentences (40 ending with a noun and 40 ending with a verb) were adapted to fit the seven word length constraint (e.g. via the deletion of subordinate clauses). Implausible sentences were generated by exchanging the final words of the sentences selected from the corpus so that, across all items, the critical words for plausible and implausible sentences were lexically identical. (For the example in Table 1, the corresponding plausible sentence was *Ich wähle doch keinen grinsenden, albernen Schwätzer,* 'I won't vote for a grinning, inane blatherer.') From these 80 pairs of plausible and implausible sentences, the full set of conditions in Table 1 was generated, thus resulting in 640 sentences in total (320 sentences of the "UP" variant of the physical change and 320 sentences of the "DOWN" variant). The UP and DOWN materials were both subdivided into two lists of 160 sentences each (40 per condition and 2 from each lexical set). The two sentences in a list from a single set always included one plausible and one implausible continuation, with combinations of change and no-change variants rotated across sets. Repetitions from a single set were presented at least 40 sentences apart, i.e. never occurred within the same experimental block. Two constrained randomisations were prepared for each list. Each participant saw a single list of materials and list presentation was counterbalanced across participants.

Table 1. Examples of the critical conditions in the present study.

Type of change (between participants)	Condition (within participants)	Example
UP (meaningful)	Plausible- No change	Wir brauchen jetzt echte und demokratische Neuwahlen. we need now real and democratic elections 'What we need now are real and democratic elections.'
	Plausible- Change	Wir brauchen jetzt echte und demokratische NEUWAHLEN. we need now real and democratic ELECTIONS
	Implausible- No change	Wir brauchen jetzt echte und demokratische Schwätzer. we need now real and democratic blatherers 'What we need now are real and democratic blatherers.'
	Implausible- Change	Wir brauchen jetzt echte und demokratische SCHWÄTZER. we need now real and democratic BLATHERERS
DOWN (not meaningful)	Plausible- No change	WIR BRAUCHEN JETZT ECHTE UND DEMOKRATISCHE NEUWAHLEN. WE NEED NOW REAL AND DEMOCRATIC ELECTIONS
	Plausible- Change	WIR BRAUCHEN JETZT ECHTE UND DEMOKRATISCHE Neuwahlen. WE NEED NOW REAL AND DEMOCRATIC elections
	Implausible- No change	WIR BRAUCHEN JETZT ECHTE UND DEMOKRATISCHE SCHWÄTZER. WE NEED NOW REAL AND DEMOCRATIC BLATHERERS
	Implausible- Change	WIR BRAUCHEN JETZT ECHTE UND DEMOKRATISCHE Schwätzer. WE NEED NOW REAL AND DEMOCRATIC blatherers

7.3.3   Procedure

Experimental sessions were conducted in a dimly lit, sound attenuated room. Sentences were presented in a word-by-word manner in the centre of a computer screen (presentation rate: 400 ms / word followed by an inter-stimulus interval (ISI) of 100 ms). Each trial began with the presentation of a fixation asterisk (300 ms, 200 ms ISI) and ended with 500 ms of blank screen, after which participants performed a plausibility judgement task by pressing one of two hand-held pushbuttons (cued by a question mark). The maximal response time was set to 2000 ms and the assignment of left and right buttons to the "plausible" and "implausible" responses was counterbalanced across participants. After a further 1500 ms of blank screen, the next trial started. Participants were asked to avoid movements and to only blink their eyes between the onset of the judgement task and the beginning of the next sentence.

Following a short practise session, the experiment consisted of four blocks of 40 sentences each, between which participants took short breaks.

7.3.4   EEG recording and analysis

The EEG was recorded from 25 Ag/AgCl electrodes (ground: AFZ) fixed at the scalp by means of an elastic cap (Easycap GmbH, Herrsching, Germany). The electrooculogram (EOG) was monitored by means of electrodes at the outer canthus of each eye (horizontal EOG) and above and below the participant's right eye (vertical EOG). EEG and EOG channels were amplified by means of a Refa (Twente Medical Systems, Enschede, The Netherlands) / BrainAmp (Brain Products, Gilching, Germany) amplifier and digitised with a sampling rate of 250 Hz.[6] Recordings were referenced to the left mastoid but rereferenced to linked mastoids offline.

In order to eliminate slow signal drifts, a 0.3-20 Hz band-pass filter was applied to the raw EEG data. Subsequently, average ERPs were calculated per condition per participant from the onset of the critical verb to 1000 ms post onset, before grand-averages were computed over all participants. Trials containing EEG or EOG artifacts were excluded from the averaging procedure (the EOG rejection criterion was 40μV).

For the statistical analysis of the ERP data, repeated-measures ANOVAs involving the factors PLAUSibility, CHANGE, GROUP and region of interest (ROI) were calculated for mean amplitude values per time window per condition. Lateral ROIs were defined as follows: *left-anterior* (F3, F7, FC1, FC5); *left-posterior* (CP1, CP5, P3, P7); *right-anterior* (F4, F8, FC2, FC6); *right-posterior* (CP2, CP6, P4, P8). For midline sites, each electrode (FZ, FCZ, CZ, CPZ, PZ) was treated as a ROI of its own. For analyses involving more than one degree of freedom in the numerator, significance values were corrected when sphericity was violated (Huynh & Feldt, 1970).

For the analysis of the behavioural data (error rates and reaction times), repeated-measures analyses of variance (ANOVAs) were calculated including the factors PLAUS, CHANGE and GROUP. We only computed analyses by participants (and not by items), since the GROUP factor was a by-participant and not a by-item factor.

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[6] The change of amplifier was necessitated by the closure of a laboratory after the first half of the experiment had been conducted. Data were acquired from an equal number of participants with both amplifiers and amplifier type was also distributed equally across both participant groups (UP and DOWN).

7.4   Results

7.4.1   Behavioural data

Mean accuracies for the plausibility judgement task were as follows (standard deviations are given in parentheses): PLAUSIBLE- NO CHANGE (UP) = 96.3% (4.6%); PLAUSIBLE- NO CHANGE (DOWN) = 97.3% (3.5%); PLAUSIBLE- CHANGE (UP) = 96.3% (3.4%); PLAUSIBLE- CHANGE (DOWN) = 96.1% (4.5%); IMPLAUSIBLE- NO CHANGE (UP) = 80.4% (11.3%); IMPLAUSIBLE- NO CHANGE (DOWN) = 82.8% (10.1%); IMPLAUSIBLE- CHANGE (UP) = 83.4% (9.9%); IMPLAUSIBLE- CHANGE (DOWN) = 84.1% (8.7%). A repeated measures ANOVA revealed a main effect of PLAUS ($F(1,38) = 66.24$, $p < 0.0001$) but no effects of or interactions with the other critical factors.

Mean reaction times for correct responses were as follows: PLAUSIBLE- NO CHANGE (UP) = 493 ms (174 ms); PLAUSIBLE- NO CHANGE (DOWN) = 455 ms (183 ms); PLAUSIBLE- CHANGE (UP) = 480 ms (165 ms); PLAUSIBLE- CHANGE (DOWN) = 443 ms (167 ms); IMPLAUSIBLE- NO CHANGE (UP) = 538 ms (170 ms); IMPLAUSIBLE- NO CHANGE (DOWN) = 501 ms (196 ms); IMPLAUSIBLE- CHANGE (UP) = 509 ms (185 ms); IMPLAUSIBLE- CHANGE (DOWN) = 488 ms (183 ms). For the reaction times, a repeated-measures ANOVA showed main effects of PLAUS ($F(1,38) = 13.28$, $p < 0.001$) and CHANGE ($F(1,38) = 6.65$, $p < 0.02$) but no interactions and no effects involving the factor GROUP.

In summary, the behavioural data indicate that participants processed the sentences attentively and accurately, though they were less accurate in classifying the implausible sentences as implausible than in classifying the plausible sentences as plausible. In other words, participants accepted some of the implausible sentences as plausible, which is not completely unexpected seeing our implausible sentences mainly involved violations of word knowledge – and might therefore be considered plausible under certain circumstances. Crucially, however, the behavioural data showed no interactions between PLAUS and CHANGE or PLAUS, CHANGE and GROUP.

7.4.2   ERP data

In view of the accuracy differences between the plausible and implausible sentence

conditions, we computed ERP averages over all artefact-free trials (i.e. trials for which participants did not give the expected response were not excluded from the final data analysis in order to avoid systematic differences between the numbers of trials across conditions). However, as shown in the Supplementary Materials, similar results obtain when trials for which participants did not give the expected response are excluded.

Figure 2: Grand average ERPs (N=20) at the position of the critical clause-final word (onset at the vertical bar) for the UP group (direction of physical change: from normal text to uppercase). Negativity is plotted upwards.

Grand average ERPs for the critical clause-final word are shown for the UP group (physical deviation involved a change to uppercase) and for the DOWN group (physical deviation involved a change to normal text) in Figures 2 and 3, respectively. As is apparent from Figures 2 and 3, an implausible sentence ending engendered an N400 in both groups. However, in the UP group, this effect appears to be substantially reduced when the implausibility was accompanied by a physical change. In this group, physically deviating stimuli also seem to engender an early positivity preceding the N400. For the DOWN group, by contrast, visual inspection of the ERPs indi-

cates that the physical change had very little effect. Finally, implausible vs. plausible sentences engender a late positivity in both groups.

These effects were analysed statistically by means of ANOVAs in successive 50 ms time windows between 200 and 800 ms. Effects were only interpreted when they reached significance in at least two consecutive time windows (e.g. Gunter, Friederici, & Schriefers, 2000). The results of the statistical analyses are summarised in Table 2.
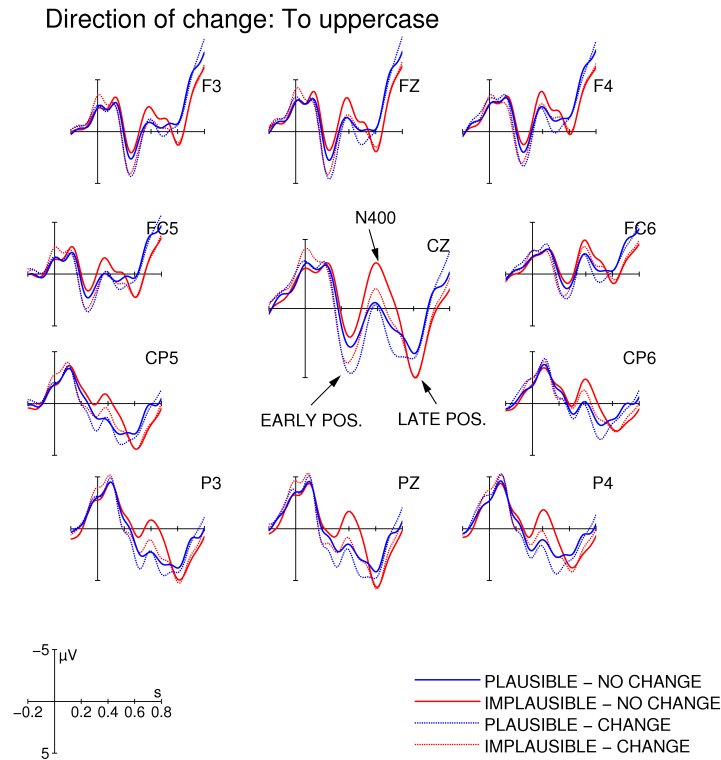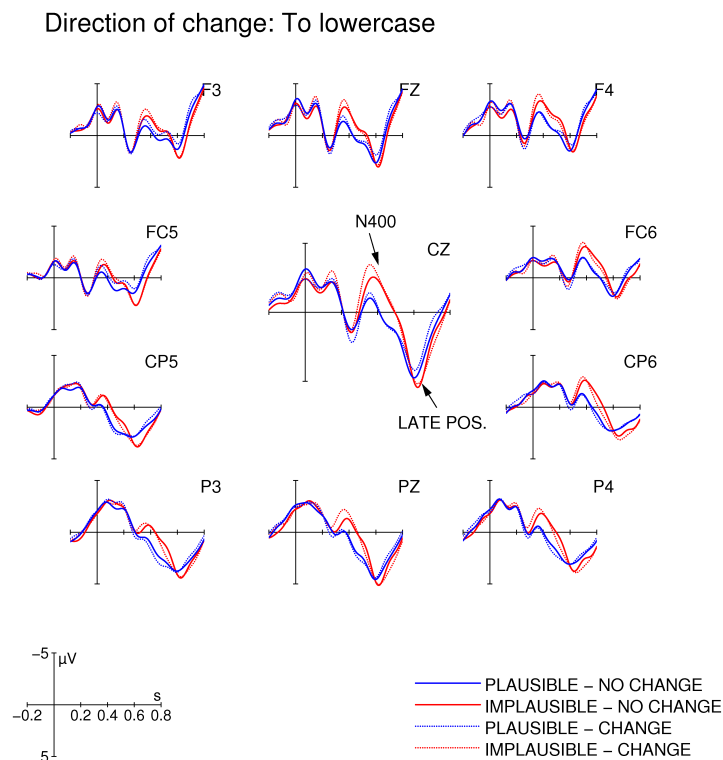

Figure 3: Grand average ERPs (N=20) at the position of the critical clause-final word (onset at the vertical bar) for the DOWN group (direction of physical change: from uppercase to normal text). Negativity is plotted upwards.

Table 2 (Part 1). Summary of the statistical analysis in successive 50 ms time windows from 200 to 500 ms post onset of the critical sentence-final word. Only effects that reached significance in at least two consecutive time windows were considered significant (Gunter et al., 2000). In order to increase readability, only significant effects are reported (i.e. if an effect is not listed, it did not reach significance). Partial η^2 values are reported in parentheses. Abbreviations for statistical significance: *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; marginal = $p < 0.07$. Abbreviations for lateral ROIs: 1 = left-anterior, 2 = left-posterior, 3 = right-anterior, 4 = right-posterior. Abbreviations for midline ROIs: 1 = FZ, 2 = FCZ, 3 = CZ, 4 = CPZ, 5 = PZ.

200-250	250-300	300-350

GROUP x CHANGE x ROI
LAT: * (0.09)
    GROUP x CHANGE
    L-ANT: *** (0.33)
           UP: CHANGE *** (0.68)
    L-POST: * (0.10)
           UP: CHANGE * (0.30)
    R-ANT: * (0.13)
           UP: CHANGE *** (0.46)
    R-POST: --
 	
MID: ** (0.10)
    GROUP x CHANGE
    FZ: *** (0.28)
        UP: CHANGE *** (0.60)
    FCZ: *** (0.27)
        UP: CHANGE *** (0.60)
    CZ: *** (0.25)
        UP: CHANGE ** (0.56)
    CPZ: ** (0.18)
        UP: CHANGE ** (0.47)
    PZ: * (0.13)
        UP: CHANGE ** (0.33)
	GROUP x CHANGE x ROI
	LAT: *** (0.17)
	    GROUP x CHANGE
	    L-ANT: ** (0.21)
	           UP: CHANGE *** (0.47)
	    L-POST: m (0.08)
	           UP: CHANGE *** (0.54)
	    R-ANT: --
	
	    R-POST: --
	
	GROUP x CHANGE
	MID: *** (0.16)
	        UP: CHANGE ** (0.47)	

350-400	400-450	450-500

GROUP x CHANGE x PLAUS
LAT: * (0.14)
    UP: CHANGE x PLAUS * (0.21)
        NO-CHANGE: PLAUS *** (0.57)
 	
MID: * (0.15)
    UP: CHANGE x PLAUS *** (0.23)
        NO-CHANGE: PLAUS *** (0.57)
	GROUP x CHANGE x PLAUS x ROI
	LAT: * (0.09)
	    GROUP x CHANGE x PLAUS
	    L-ANT: --
	    L-POST: * (0.14)
	    UP: CHANGE x PLAUS * (0.29)
	      CHANGE: PLAUS * (0.21)
	      NO-CHANGE: PLAUS *** (0.71)
	    R-ANT: --
	    R-POST: --
	
	MID: ** (0.11)
	    GROUP x CHANGE x PLAUS
	    FZ: --
	    FCZ: --
	    CZ: --
	    CPZ: --
	    PZ: * (0.14)
	    UP: CHANGE x PLAUS * (0.25)
	      CHANGE: PLAUS * (0.19)
	      NO-CHANGE: PLAUS *** (0.68)
		GROUP x CHANGE x PLAUS x ROI
		LAT: ** (0.12)
		    GROUP x CHANGE x PLAUS
		    - no effect in any ROI -
		
		MID: *** (0.26)
		    GROUP x CHANGE x PLAUS
		    FZ: --
		    FCZ: --
		    CZ: --
		    CPZ: --
		    PZ: m (0.16)
		    UP: CHANGE x PLAUS * (0.25)
		      CHANGE: PLAUS ** (0.34)
		      NO-CHANGE: PLAUS *** (0.65)

Table 2 (Part 2). Summary of the statistical analysis in successive 50 ms time windows from 500 to 800 ms post onset of the critical sentence-final word. Only effects that reached significance in at least two consecutive time windows were considered significant (Gunter et al., 2000). In order to increase readability, only significant effects are reported (i.e. if an effect is not listed, it did not reach significance). Partial η^2 values are reported in parentheses. Abbreviations for statistical significance: *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; marginal = $p < 0.07$. Abbreviations for lateral ROIs: 1 = left-anterior, 2 = left-posterior, 3 = right-anterior, 4 = right-posterior. Abbreviations for midline ROIs: 1 = FZ, 2 = FCZ, 3 = CZ, 4 = CPZ, 5 = PZ.

500-550	550-600	600-650

		PLAUS x ROI
		LAT: ** (0.15)
		    PLAUS
		      L-ANT: --
		      L-POST: *** (0.30)
		      R-ANT: *** (0.26)
		      R-POST: *** (0.27)
		
		PLAUS
		MID: *** (0.30)

650-700	700-750	750-800

PLAUS x ROI
LAT: * (0.09)
    PLAUS
      L-ANT: * (0.40)
      L-POST: *** (0.35)
      R-ANT: *** (0.31)
      R-POST: *** (0.39)
 	
PLAUS
MID: *** (0.33)
	PLAUS
	LAT: *** (0.39)
	
	MID: *** (0.30)
		PLAUS
		LAT: *** (0.31)
		
		MID: *** (0.22)

The analysis in Table 2 confirms the impressions based on visual inspection. A physical change from normal text to uppercase (UP group) engendered a positivity between 200 and 300 ms post word onset and led to a significantly reduced N400 effect for implausible sentences in the (interaction between GROUP, TYPE and PLAUS between 300 and 500 ms). Finally, implausible sentences elicited a late positivity (600-800 ms) which did not differ between groups.

Topographical maps for the statistically significant effects are shown in Figure 4. These illustrate the differing distributions for the early positivity and the N400 effect, thus showing that the case change effects in the N400 time window are unlikely to simply have "carried over" from the early positivity.

CHANGE EFFECT   PLAUSIBILITY EFFECT

NO CHANGE   CHANGE

CHANGE:
TO UPPERCASE

0.200 .. 0.300 s   0.350 .. 0.500 s   0.350 .. 0.500 s

−3.5   µV   +3.5

CHANGE:
TO LOWERCASE

0.350 .. 0.500 s   0.350 .. 0.500 s
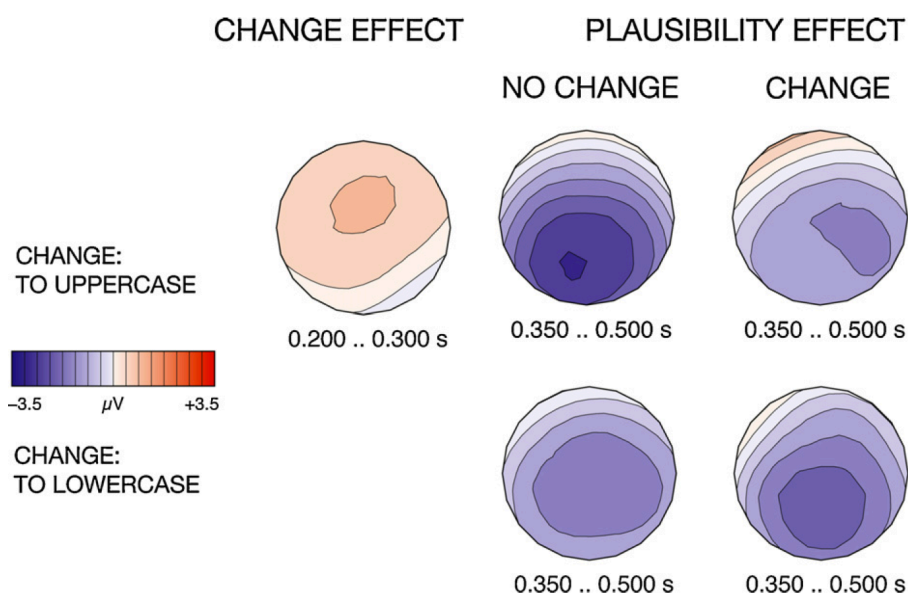
Figure 4: Topographical maps for the differences between change vs. no change stimuli (change effect) and implausible vs. plausible stimuli (plausibility effect). For the plausibility effect, effects for the two groups (UP vs. DOWN) and change vs. no-change conditions are shown separately in view of the three-way interaction between PLAUS, CHANGE and GROUP (see Table 2). For the change effect, only the main effect for the UP group is shown, since this is the only effect that reached significance in this early time window.

7.5   Discussion

The results of the present study indicate that orthographic changes in a linguistic stimulus can mediate lexical-semantic integration: sentences involving a physical change from normal text to uppercase showed a significant reduction of the N400 effect for implausible sentence endings. Changes from uppercase to normal text had no such effect, thus indicating that the communicative meaningfulness of the physical change was crucial for the N400 modulation. Recall that, while a change to uppercase adds emphasis and is interpreted as "shouting" in computer-mediated communication (CMC) (for German, see Runkehl, Schlobinski, & Siever, 1998), a change from uppercase to normal text is a purely physical deviation that is not communicatively meaningful. In addition to the N400 modulation, the present results also yielded two positivity effects, which we will discuss briefly in the following before turning to a more extensive discussion of the N400.

7.5.1   The early and late positivity effects

Firstly, for uppercase physical deviants, we observed an early positivity (as also re-

ported by Kutas & Hillyard, 1980). The fact that this effect did not occur for changes to lowercase suggests that it is not a target-related P3b (see, for example, Polich, 2004), since a P3b interpretation would predict a symmetrical effect for physical changes in both directions (i.e. from lowercase to uppercase and vice versa). However, since the case change was not task-relevant, the absence of a P3b is not overly surprising. Rather, the early positivity may be an instance of a frontal P200 effect, which has been shown to be modulated by the processing of visual "pop-outs" (based, for example, on colour and size) (Luck & Hillyard, 1994), is reduced for repeated stimuli (e.g. Freunberger, Klimesch, Doppelmayr, & Höller, 2007) and has therefore been linked to repetition suppression (Wiggs & Martin, 1998). From this perspective, the early positivity in the UP group could be taken to reflect a physically salient, but task-irrelevant physical change, while the change in the DOWN group was not salient enough to elicit a pop-out response (see Melloni, Schwiedrzik, Müller, Rodriguez, & Singer, for evidence that the amplitude of the P200 is sensitive to the visual saliency of a stimulus). Perhaps most importantly for present purposes, the differences in the early positivity time window – though sensitive to the distinction between changes to upper- vs. lowercase – cannot explain the pattern observed in the N400 time window: (a) in contrast to the early positivity, the N400 effect interacted with plausibility; and (b) the topographies of the two effects differed (see Table 2 and Figure 4).

Secondly, all implausible continuations engendered a late positivity and this effect was not modulated by the physical change. This result is in line with previous findings of biphasic N400 - late positivity patterns in response to semantic incongruities (e.g. Gunter, Jackson, & Mulder, 1992; Faustmann, Murdoch, Finnigan, & Copland, 2007; Roehm, Bornkessel-Schlesewsky, Rösler, & Schlesewsky, 2007a). While it has not yet been shown conclusively under which conditions semantic incongruities engender a late positivity in addition to an N400, van de Meerendonk et al. (2010) suggest that this may be related to the strength of the incongruity. However, the manipulation employed in the present study is not suited to shedding further light on this question.

7.5.2   The N400 modulation

Returning now to the N400 modulation, the fact that a concurrent change to uppercase letters almost completely neutralised the N400 effect for implausible sentence endings

is particularly striking in view of the fact that this change did not alter the propositional meaning of the sentence. It clearly also did not provide any lexical or semantic context that could have increased the predictability of the implausibility-inducing word and the overall ERP pattern is not predictable on the basis of participants' behavioural performance (which did not show an interaction between PLAUS, CHANGE and GROUP). This physically-based modulation of the lexical-semantic N400 is thus problematic for purely lexical accounts of the N400 (Lau et al., 2008, see Figure 1). It is also not straightforwardly explained by the one-step account of sentence interpretation (Hagoort & van Berkum, 2007), since capitalisation of the critical word does not change the degree of compatibility between this word and the context. In this way, capitalisation differs fundamentally from all previous factors that have been shown to influence the N400, including the prosodic manipulations described in the introduction: here, the physical change is independent of the content of the message being conveyed. This study is thus, to the best of our knowledge, the first to demonstrate a genuine influence of form-based bottom-up information on the N400 that does not in some way involve an incongruity with top-down factors.

A possible alternative explanation that appears worth considering is that the use of a capitalised critical word may have induced a "semantic illusion", i.e. a situation in which a semantic incongruity is overlooked by the processing system (see Sanford & Sturt, 2002).[7] In a study that examined the interplay between lexical-semantic integration and information structure, Wang, Hagoort, & Yang (2009) found that the N400 effect for a contextually inappropriate vs. appropriate continuation was reduced when the critical word was not in focus. To explain this result, they argue that focused words (i.e. words that provide new information) are allocated more processing resources than words that are not in focus, thus increasing the propensity for semantic illusions in the latter case.[8] However, an explanation along these lines does not appear to be applicable to the present findings. Firstly, the fact that the plausibility judgement task was performed with an accuracy of over 80% in all conditions demonstrates that

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[7] The most famous example of a semantic illusion is the so-called *Moses illusion*, in which someone asked "*How many animals of each sort did Moses put on the ark?*" will typically answer "two" rather than "none" (Erickson & Matteson, 1981).

[8] An alternative explanation for this finding, which essentially resulted from an increased N400 effect for the appropriate non-focused continuation rather than from a reduced N400 effect for the inappropriate non-focused continuation, is that the appropriate non-focused continuation involved an accessible referent in the sense of Schumacher and Baumann (2010) (see the introduction) rather than a referent that had already been introduced. Accessible referents ("indirect anaphors") have been shown to induce increased N400 effects in previous studies (Burkhardt, 2006; Burkhardt & Roehm, 2007).

participants detected the semantic incongruity even when the critical word involved a change to uppercase. In addition, the pattern of results did not change when only those trials for which participants gave the expected judgement response were included in the analysis (see the Supplementary Materials). Secondly, the ERP findings for the critical word also do not provide any evidence for a reduced allocation of processing resources to this word when it was capitalised. On the one hand, the change to uppercase engendered an increased P200, an effect which has been shown to be related to the allocation of attention (see, for example, Mangels, Picton, & Craik, 2001, for the finding of larger P200 amplitudes for stimuli processed under full as opposed to divided attention). On the other hand, the late positivity effect for implausible continuations occurred independently of the physical change. By contrast, it has been demonstrated that semantic anomalies that are prone to engendering semantic illusions (i.e. anomalies analogous to the Moses illusion, see Footnote 7) only elicit late positivities when they are detected (Sanford, Leuthold, Bohan, & Sanford, 2011). Overall, then, there is no evidence that a change to a capitalised critical word produced a semantic illusion in the present study.

In summary, the present findings demonstrate a purely form-based bottom-up modulation of the lexical-semantic N400 via a paralinguistic orthographic strategy (capitalisation) that is not predicted by any existing accounts of the N400.[9]

7.5.3   The bidirectional coding account: A new model of the lexical-semantic N400 and the neural processing of linguistic meaning

In the following, we propose a new account of the lexical-semantic N400, which extends and modifies the lexical account of the N400 (Lau et al., 2008) in order to incorporate the present results as well as previous findings on discourse and information structure-related N400 effects and prosodic manipulations. The architecture of the model, the "bidirectional coding account", is shown in Figure 5.

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[9] An anonymous reviewer raised the concern that the N400 modulation observed here, and specifically the interaction between PLAUS and CHANGE for the UP group, could have resulted from a case change-induced floor effect in the N400. This possibility is addressed in the Supplemetary Materials via a split-half analysis of the data from the UP group.
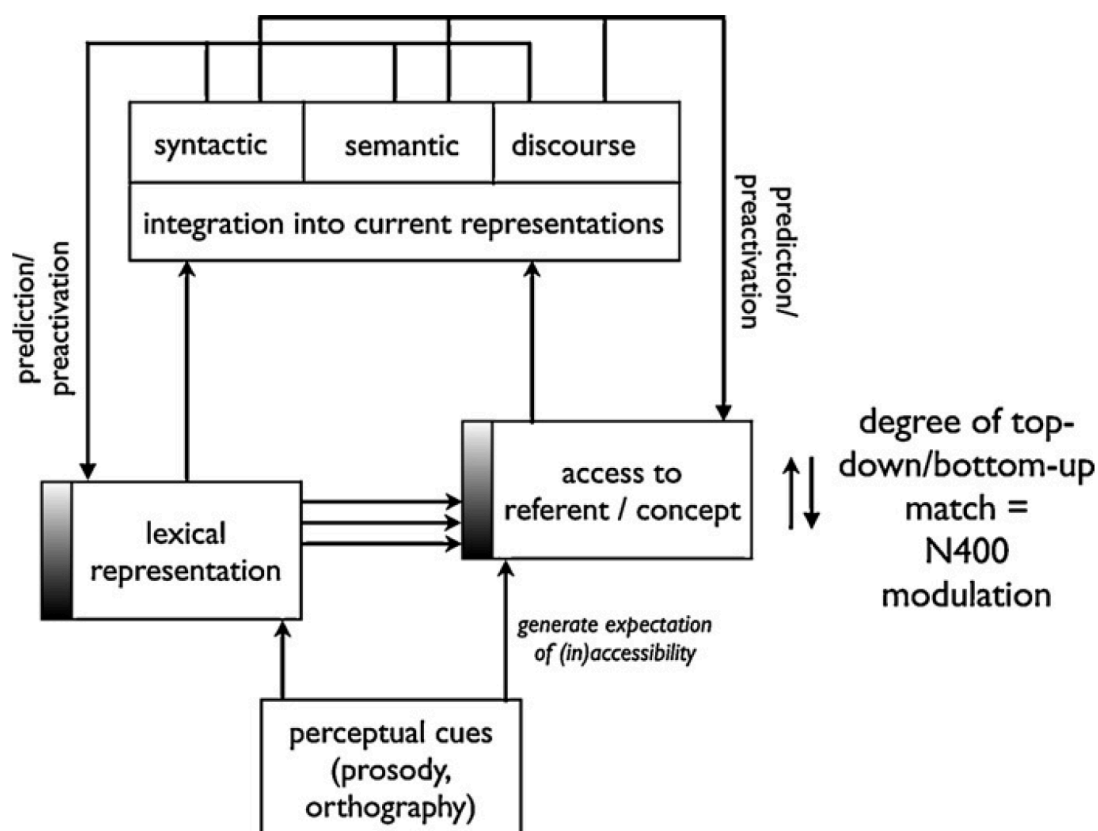
Figure 5: Schematic depiction of the architecture of the bidirectional coding account of the N400. The shaded bars represent varying degrees of activation. For further details, see the main text. Note that, at present, the model is only designed to account for lexical-semantic N400 effects (see Footnote 10). Note also that the clear-cut separation between syntactic, semantic and discourse information in the figure is for illustrative purposes only and serves to highlight the information types involved in generating relevant top-down influences. However, empirical research suggests that syntactic and semantic information may, in fact, be tightly intertwined in the brain (see Bornkessel-Schlesewsky & Schlesewsky, 2009a, 2009b, for an overview).

As is apparent from Figure 5, the bidirectional coding account includes several key additions in comparison to the lexical account (see Figure 1). Firstly, while the lexical account leaves open the possibility of a differentiation between lexical and conceptual access (Lau et al., 2008; for the importance of conceptual features, see, for example, Federmeier, 2007), we assume that N400 modulations reflect access to referents or concepts rather than lexical representations. This assumption is necessary, in our view, in order to account for discourse-based N400 effects such as those reported by Burkhardt (2006) and Schumacher (2009). These studies consistently showed the following N400 gradation: new referent > accessible referent > old (previously mentioned) referent, thus suggesting that N400 amplitude increases with decreasing accessibility of the referent. Burkhardt and Roehm (2007) additionally demonstrated that, for accessible referents, the salience of the inferential anchor (i.e. the referent in the context that is related to the critical word) also modulates N400 ampli-

tude. These findings provide evidence for the top-down influence of discourse representations to referent / concept accessibility in the model. We further assume that pre-activation of a lexical entry, as produced via lexical-semantic associations between individual words (see Lau et al., 2008) feeds into the level of referent accessibility.

The second, and most crucial, assumption of the bidirectional coding account – and the main claim that goes beyond the assumptions of previous accounts – is that N400 modulations are not simply an indication of referent accessibility. Rather, N400 amplitude reflects the degree of match between top-down expectations about referent accessibility / lexical preactivation and bottom-up information on how accessible the referent or concept is likely to be. The bottom-up route included here is needed in order to account for the fact that new referents do not elicit increased N400 responses when they are focused, i.e. when it is clear from the combination of context and target sentence that a critical word provides new information (Bornkessel, Schlesewsky, & Friederici, 2003; Wang et al., 2009). In the study by Bornkessel and colleagues, which examined question-answer pairs in German, the case marking of the critical noun phrase signalled that it matched the wh-word in the question. In the experiment by Wang and colleagues, which was conducted in Chinese, it is likely that the position of the critical word in the sentence was crucial: in the subject-verb-object orders employed in this study, the focused noun must occur in the post-verbal position (Li & Thompson, 1981). Thus, in both cases, form-based information indicated that the referent in question would provide new information and thus should not be highly accessible. N400 amplitude therefore reflects a combination of bottom-up (including purely form-based) and top-down information sources. We propose that the long-standing assumption that the N400 reflects accessibility itself rather than the degree of match between the accessibility of a referent and its predicted accessibility can be attributed to the fact that, by default, the system expects referents to be accessible and deviations form this default expectation require additional information (e.g. prosodic marking).

Further converging support for this account stems from the observation of increased negativity effects, typically interpreted as N400 modulations, when the prosodic realisation of a critical word does not match the information status of that word (new, accessible, or old; Hruska & Alter, 2004; Toepel & Alter, 2004; Li et al., 2008; Schumacher & Baumann, 2010). Syntactic indications of new information (informa-

tion structural focus) give rise to the same result: Cowles, Kluender, Kutas, & Polinsky (2007) reported an N400-like effect for clefted nouns that were already mentioned in the context and thus inappropriate in that position (e.g. *It was the queen* ... following a context question such as "Who did the queen silence?").

Finally, the form-based bottom-up influence assumed here is required in order to account for the present finding of a reduction in the implausibility N400 for a capitalised critical word. As described in detail in the introduction, capitalisation is a common orthographic strategy in computer-mediated communication that serves to signal extreme emphasis. As such, it is a clear bottom-up indicator of high informativity and, thereby, of low referent/concept accessibility. Under these circumstances, the N400 effect for an implausible continuation – i.e. a continuation that employs a referent/concept with a particularly low level of accessibility in the given sentence context – is significantly attenuated. These findings, which are the first to employ a form-based bottom-up information type that does not result in a (potential) mismatch with the message being conveyed, provide strong support for the assumption that the lexical-semantic N400 reflects the degree to which the semantic informativity of a critical word matches expectations, with expectations crucially determined by an interplay between top-down and bottom-up information sources.[10]

7.6   Conclusions

The present ERP results show that lexical-semantic N400 effects in language comprehension are crucially influenced by (form-based) bottom-up information that is inde-

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[10] Note that, at present, the bidirectional coding account only aims to account for lexical-semantic N400 effects. While these types of N400 effects are arguably best-known, the literature on the electrophysiology of language processing also includes reports of a number of N400 modulations which are not lexical-semantic in nature, e.g. for case violations in German (Frisch & Schlesewsky, 2001), Japanese (Mueller, Hahne, Fujii, & Friederici, 2005) and Hindi (Choudhary, Schlesewsky, Roehm, & Bornkessel-Schlesewsky, 2009); violations of (productive) morphological rules (Janssen, Wiese, & Schlesewsky, 2005); and word order variations (Bornkessel, McElree, Schlesewsky, & Friederici, 2004; Haupt, Schlesewsky, Roehm, Friederici, & Bornkessel-Schlesewsky, 2008). For these types of manipulations, in which N400 modulations result from syntactic or morphological information (see Bornkessel-Schlesewsky & Schlesewsky, 2009a, for an overview) an account in terms of referent/concept accessibility is not straightforwardly applicable. In addition, it has been shown that "grammatical" N400 effects show different characteristics to lexical-semantic N400s in the frequency domain (Roehm, Bornkessel-Schlesewsky, & Schlesewsky, 2007b), thus demonstrating that they are not directly comparable to one another. However, it appears the claim that the N400 is crucially influenced by the interplay between top-down and bottom-up information sources in generating expectations about a current input item could potentially also be extended to cover these other types of N400 effects. Yet this is beyond the scope of the present paper and will need to be investigated in more detail in future work.

pendent of the message being conveyed. On the basis of these findings, we have proposed a new model of the lexical-semantic N400, the bidirectional coding account. In contrast to other current models of the N400, which emphasise the role of lexical preactivation (Lau et al., 2008) or the ease of integrating a critical word into the current discourse (Hagoort & van Berkum, 2007), the bidirectional coding account postulates that the interaction between top-down and form-based bottom-up information is crucial to explaining N400 modulations. Specifically, it proposes that the lexical-semantic N400 reflects the degree to which a critical word meets expectations about referent/concept accessibility based on the degree of match between bottom-up and top-down information sources.

7.7   References

Bornkessel-Schlesewsky, I., & Schlesewsky, M. (2009a). *Processing syntax and morphology: A neurocognitive perspective*. Oxford: Oxford University Press.

Bornkessel-Schlesewsky, I., & Schlesewsky, M. (2009b). The role of prominence information in the real time comprehension of transitive constructions: A cross-linguistic approach. *Language and Linguistics Compass, 3*, 19-58.

Bornkessel, I., McElree, B., Schlesewsky, M., & Friederici, A. D. (2004). Multi-dimensional contributions to garden path strength: Dissociating phrase structure from case marking. *Journal of Memory and Language, 51*, 495-522.

Bornkessel, I., Schlesewsky, M., & Friederici, A. D. (2003). Contextual information modulates initial processes of syntactic integration: The role of inter- vs. intra-sentential predictions. *Journal of Experimental Psychology: Learning, Memory and Cognition, 29*, 269-298.

Burkhardt, P. (2006). Inferential bridging relations reveal distinct neural mechanisms: Evidence from event-related brain potentials. *Brain and Language, 98*, 159-168.

Burkhardt, P., & Roehm, D. (2007). Differential effects of saliency: An event-related brain potential study. *Neuroscience Letters, 413*, 115-120.

Choudhary, K. K., Schlesewsky, M., Roehm, D., & Bornkessel-Schlesewsky, I. (2009). The N400 as a correlate of interpretively-relevant linguistic rules: Evidence from Hindi. *Neuropsychologia, 47*, 3012-3022.

Cowles, H. W., Kluender, R., Kutas, M., & Polinsky, M. (2007). Violations of information structure: An electrophysiological study of anserws to wh-questions. *Brain and Language, 102*, 228-242.

Crain, S., & Steedman, M. (1985). On not being led up the garden path: The use of context by the psychological parser. In D. Dowty, L. Karttunen, & A. Zwicky (Eds.), *Natural language parsing: Psychological, computational, and theoretical perspectives* (pp. 320-357). Cambridge: Cambridge University Press.

Erickson, T. A., & Matteson, M. E. (1981). From words to meaning: A semantic illusion. *Journal of Verbal Learning and Verbal Behavior, 20*, 540-552.

Faustmann, A., Murdoch, B. E., Finnigan, S. P., & Copland, D. A. (2007). Effects of advancing age on the processing of semantic anomalies in adults: Evidence from event-related brain potentials. *Experimental Aging Research, 33*, 439-460.

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

Freunberger, R., Klimesch, W., Doppelmayr, M., & Höller, Y. (2007). Visual P2 component is related to theta phase-locking. *Neuroscience Letters, 426*, 181-186.

Frisch, S., & Schlesewsky, M. (2001). The N400 indicates problems of thematic hierarchizing. *Neuroreport, 12*, 3391-3394.

Gunter, T. C., Friederici, A. D., & Schriefers, H. (2000). Syntactic gender and semantic expectancy: ERPs reveal early autonomy and late interaction. *Journal of Cognitive Neuroscience, 12*, 556-568.

Gunter, T. C., Jackson, J. L., & Mulder, G. (1992). An electrophysiological study of semantic processes in young and middle-aged academics. *Psychophysiology, 29*, 38-54.

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

438-441.

Hagoort, P., & van Berkum, J. J. A. (2007). Beyond the sentence given. *Philosophical Transactions of the Royal Society B*, *362*, 801-811.

Haupt, F. S., Schlesewsky, M., Roehm, D., Friederici, A. D., & Bornkessel-Schlesewsky, I. (2008). The status of subject-object reanalyses in the language comprehension architecture. *Journal of Memory and Language*, *59*, 54-96.

Herring, S. C. (2008). Language and the internet. In W. Donsbach (Ed.), *International encycopedia of communication* (pp. 2640-2645). Oxford: Blackwell.

Hruska, C., & Alter, K. (2004). Prosody in dialogues and single sentences: How prosody can influence speech perception. In A. Steube (Ed.), *Information structure: Theoretical and empirical aspects* (pp. 211-226). Berlin: Walter de Gruyter.

Huynh, H., & Feldt, L. S. (1970). Conditions under which the mean-square ratios in repeated measurement designs have exact F-distributions. *Journal of the American Statistical Association*, *65*, 1582-1589.

Janssen, U., Wiese, R., & Schlesewsky, M. (2005). Electrophysiological responses to violations of morphosyntactic and prosodic features in derived German nouns. *Journal of Neurolinguistics*, *19*, 466-482.

Kutas, M., & Federmeier, K. (2000). Electrophysiology reveals semantic memory use in language comprehension. *Trends in Cognitive Sciences, 4,* 463-469.

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

Lau, E., Phillips, C., & Poeppel, D. (2008). A cortical network for semantics: (de)constructing the N400. *Nature Reviews Neuroscience*, *9*(12), 920-933.

Li, C. N., & Thompson, S. A. (1981). *Mandarin Chinese: A functional reference grammar*. Berkeley/Los Angeles, CA: The University of California Press.

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

Luck, S. J., & Hillyard, S. A. (1994). Electrophysiological correlates of feature analysis during visual search. *Psychophysiology*, *31*, 291-308.

MacDonald, M. C., Pearlmutter, N. J., & Seidenberg, M. S. (1994). The Lexical Nature of Syntactic Ambiguity Resolution. *Psychological Review*, *101*, 676-703.

Mangels, J. A., Picton, T. W., & Craik, F. I. M. (2001). Attention and successful episodic encoding: an event-related potential study. *Cognitive Brain Research*, *11*, 77-95.

Melloni, L., Schwiedrzik, C.M., Müller, N., Rodriguez, E., & Singer, W. (2011). Expectations change the signatures and timing of electrophysiological correlates of perceptual awareness. *The Journal of Neuroscience, 31,* 1386-1396.

Morton, J. (1969). Interaction of information in word recognition. *Psychological Review, 76,* 165-178.

Mueller, J. L., Hahne, A., Fujii, Y., & Friederici, A. D. (2005). Native and nonnative speakers' processing of a miniature version of Japanese as revealed by ERPs. *Journal of Cognitive Neuroscience*, *17*, 1229-1244.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*, 97-113.

Osterhout, L., McKinnon, R., Bersick, M., & Corey, V. (1996). On the language specificity of the brain response to syntactic anomalies: Is the syntactic positive shift a member of the P300 family? *Journal of Cognitive Neuroscience*, *8*, 507-526.

Polich, J. (2004). Neuropsychology of the P3a and P3b: A theoretical overview. In C. Moore & K. Arikan (Eds.), *Brainwaves and mind: Recent developments* (pp. 15-29). Wheaton, IL: Kjelberg Inc.

Roehm, D., Bornkessel-Schlesewsky, I., Rösler, F., & Schlesewsky, M. (2007a). To predict or not to predict: Influences of task and strategy on the processing of semantic relations. *Journal of Cognitive Neuroscience*, *19*, 1259-1274.

Roehm, D., Bornkessel-Schlesewsky, I., & Schlesewsky, M. (2007b). The internal structure of the N400: frequency characteristics of a language-related ERP component. *Chaos and Complexity Letters*, *2*, 365-395.

Runkehl, J., Schlobinski, P., & Siever, T. (1998). *Sprache und Kommunikation im Internet. Überblick und Analysen [= "Language and communication on the internet. Overview and analyses"]*. Opladen: Westdeutscher Verlag.

Sanford, A. J., Leuthold, H., Bohan, J., & Sanford, A. J. S. (2011). Anomalies at the Borderline of Awareness: An ERP Study. *Journal of Cognitive Neuroscience*, *93*, 514-523.

Sanford, A. J., & Sturt, P. (2002). Depth of processing in language comprehension: not noticing the evidence. *Trends in Cognitive Sciences*, *6*, 382-386.

Schumacher, P. B. (2009). Definteness marking shows late effects during discourse processing: Evidence from ERPs. In S. L. Devi, A. Branco, & R. Mitkov (Eds.), *Anaphora processing and applications* (pp. 91-106). Heidelberg: Springer.

Schumacher, P. B., & Baumann, S. (2010). Pitch accent type affects the N400 during referential processing. *Neuroreport*, *21*, 618-622.

Toepel, U., & Alter, K. (2004). On the independence of information structural processing from prosody. In A. Steube (Ed.), *Information structure: Theoretical and empirical aspects* (pp. 227-240). Berlin: Walter de Gruyter.

Trueswell, J. C., & Tanenhaus, M. K. (1994). Toward a lexicalist framework for constraint-based syntactic ambiguity resolution. In C. Clifton, Jr., L. Frazier, & K. Rayner (Eds.), *Perspectives in sentence processing*. Hillsdale, NJ: Erlbaum.

Van Berkum, J. J. A., Brown, C., Hagoort, P., & Zwitserlood, P. (2003). Event-related brain potentials reflect discourse-referential ambiguity in spoken language comprehension. *Psychophysiology*, *40*, 235-248.

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

van de Meerendonk, N., Kolk, H. H. J., Vissers, C. T. W. M., & Chwilla, D. J. (2010). Monitoring in Language Perception: Mild and Strong Conflicts Elicit Different ERP Patterns. *Journal of Cognitive Neuroscience*, *22*, 67-82.

Wang, L., Hagoort, P., & Yang, Y. (2009). Semantic illusion depends on information structure: ERP evidence. *Brain Research*, *1282*, 50-56.

Werry, C. C. (1996). Linguistic and interactional features of internet relay chat. In S. C. Herring (Ed.), *Computer-mediated communication. Linguistic, social and cross-cultural perspectives* (pp. 47-63). Amsterdam: John Benjamins.

Wiggs, C. L., & Martin, A. (1998). Properties and mechanisms of perceptual priming. *Current Opinion in Neurobiology*, *8*, 227-233.

8   STUDY 2

Cross-linguistic variation in the neurophysiological response to semantic processing: Evidence from anomalies at the borderline of awareness

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ABSTRACT

The N400 event-related brain potential (ERP) has played a major role in the examination of how the human brain processes meaning. For current theories of the N400, classes of semantic inconsistencies which do not elicit N400 effects have proven particularly influential. Semantic anomalies that are difficult to detect are a case in point ("borderline anomalies", e.g. "After an air crash, where should the survivors be buried?"), engendering a late positive ERP response but no N400 effect in English (Sanford, Leuthold, Bohan, & Sanford, 2011). In three auditory ERP experiments, we demonstrate that this result is subject to cross-linguistic variation. In a German version of Sanford and colleagues' experiment (Experiment 1), detected borderline anomalies elicited both N400 and late positivity effects compared to control stimuli or to missed borderline anomalies. Classic easy-to-detect semantic (non-borderline) anomalies showed the same pattern as in English (N400 plus late positivity). The cross-linguistic difference in the response to borderline anomalies was replicated in two additional studies with a slightly modified task (Experiment 2a: German; Experiment 2b: English), with a reliable LANGUAGE x ANOMALY interaction for the borderline anomalies confirming that the N400 effect is subject to systematic cross-linguistic variation. We argue that this variation results from differences in the language-specific default weighting of top-down and bottom-up information sources, concluding that N400 amplitude reflects the interaction between the two information sources in the form-to-meaning mapping.

Keywords: Language processing, cross-linguistic differences, borderline anomalies, shallow processing, N400, P600, late positivity, bidirectional coding account, top-down, bottom-up.

8.1   Introduction

In everyday life, we use language to express our thoughts and to comprehend those around us. We make use of language in such a natural and seemingly effortless way that we are mostly unaware of the complex cognitive system that makes this possible. When processing speech or written language, we are faced with a difficult task, requiring us not only to combine words to form complex meanings, but also to assess whether the state of affairs described is consistent with what we already know about the world.

While the matching of linguistic meaning to world knowledge may appear *prima facie* to be straightforward, it is not always performed completely. Rather, under certain circumstances, we miss violations of our real world knowledge. A case in point is the so-called Moses illusion (Erickson & Matteson, 1981), a relatively robust failure to detect a distorted meaning in cases where a locally implausible phrase nevertheless exhibits a close fit to the global context. Erickson and Matteson asked people the now famous question "How many animals of each kind did Moses take on the Ark?" and reported that most people answered the question with "two" in spite of the fact that it was Noah, not Moses, who built and sailed the ark.

This type of "semantic illusion" has given rise to a great deal of research in theoretical and psychological linguistics, aiming to shed light on the linguistic basis of such illusions and the mechanisms involved in processing them (e.g. Ferreira, Ferraro, & Bailey, 2002; Sanford & Sturt, 2002; Sanford & Graesser, 2006). While the studies concerned with this particular phenomenon have employed a variety of materials and paradigms, there are several common results: First is that the Moses illusion effect generalises to other sentence materials (e.g. the "survivors illusion" in (1), cited from Sanford et al., 2011).

(1)   When an airplane crashes on a border with debris on both sides,
        where should the survivors be buried?

Further, the illusion occurs at comparable rates independent of the number of times it is presented (detection rates at approximately 60%) or the task demands, i.e., incidental detection or an explicit judgement task (e.g. Reder & Kusbit, 1991; Barton & Sanford, 1993; Daneman, Reingold, & Davidson, 1995; Hannon & Daneman,

2001; Hannon & Daneman, 2004). However, detection rates are subject to more substantial variation when linguistic factors such as focus, sentence structure or semantic relatedness are manipulated (Shafto & McKay, 2000; Büttner, 2007). In accordance with the terminology in Sanford et al. (2011), we shall refer to sentences constructed in the spirit of the Moses Illusion (such as 1) as "borderline anomalies", as an abbreviation of "anomalies at the borderline of awareness".

From the perspective of sentence understanding, a main interest in examining borderline anomalies such as (1) relates to questions about depth of processing. Specifically, it has been argued that referents with a good fit to the global discourse context (such as *survivors* in the context of an airplane crash) give rise to *shallow processing*, i.e. are not as deeply probed for their meaning in comparison to referents with a lower degree of contextual fit (Sanford & Garrod, 1998). In support of this proposal, Barton and Sanford (1993) found that the "survivor-anomaly" in (1) is detected much more readily in the context of a bicycle crash than in the context of an airplane crash, since, statistically, the word *survivors* is much more likely to be used in the latter case.

More recent studies have examined how borderline anomalies are processed during on-line comprehension, focusing particularly on whether they disrupt processing even when they are not detected. Results from both eye tracking (Bohan & Sanford, 2008) and event related brain potentials (Sanford et al., 2011) suggest that this is not the case: neither eye movement nor event-related potential (ERP) records reveal differences between the non-detected borderline anomalies and their plausible counterparts. On the basis of their results, Sanford and colleagues conclude that borderline anomalies are indeed subject to shallow processing, arguing against an alternative account in which such anomalies disrupt processing, but not enough to reach conscious awareness. A sample item from Sanford et al. (2011) is given in (2). ERPs were measured at the underlined word, with the context words differentiating between the borderline anomaly and the plausible control given in italics and curly brackets.

(2)   Child abuse cases are being reported much more frequently these days.
       In a recent trial, a 10-year {sentence / care order} was given to the <u>victim</u>, but this was subsequently appealed.

Of particular interest is that the detected anomalies in Sanford and colleagues'

(2011) study engendered a late positivity but no N400 effect, when compared to control stimuli. These findings may contribute to a better understanding of N400 effects more generally, an important issue that is the subject of active debate, particularly related to the on-line processing of sentence meaning. Since first reported by Kutas and Hillyard (1980), the N400 has been viewed as a correlate of lexical-semantic processing. However, there are differing perspectives on the reasons for this correlation (for a recent review, see Lau, Phillips, & Poeppel, 2008). According to the "integration" view, N400 amplitude reflects the ease or difficulty with which a new word can be semantically integrated into an existing sentence context (e.g. Hagoort & van Berkum, 2007; Hagoort, 2008). By contrast, the "lexical pre-activation" view is that the N400 reflects the ease with which that word can be accessed in semantic memory (e.g. Kutas & Federmeier, 2000; Lau et al., 2008; Brouwer, Fitz, & Hoeks, 2012; Stroud & Phillips, 2012). Sanford et al.'s (2011) findings appear to support the lexical view: in the borderline anomalies, the critical word that would be considered "preactivated" in light of its good lexical semantic fit to the global context induced an anomaly but no increased N400 effect. Similar conclusions follow from research on so-called "semantic reversal anomalies". In these sentences, exemplified by *For breakfast, the eggs would only <u>eat</u> toast and jam* (Kuperberg, Sitnikova, Caplan, & Holcomb, 2003) and *The hearty meals were <u>devouring</u> the kids* (Kim & Osterhout, 2005), the thematic roles and their arguments are misaligned (i.e. *eggs* and *hearty meals* are highly plausible Theme arguments of *eat* and *devour*, respectively, but implausible Agents). Like the borderline anomalies, semantic reversal anomalies have been shown to engender late positivity but not N400 effects in English (e.g. Kuperberg et al., 2003; Kim & Osterhout, 2005) and Dutch (e.g. Kolk, Chwilla, van Herten, & Oor, 2003; Hoeks, Stowe, & Doedens, 2004). This result, which sparked a great deal of discussion (for recent reviews, see Bornkessel-Schlesewsky & Schlesewsky, 2008; van de Meerendonk, Kolk, Chwilla, & Vissers, 2009), appears to follow straightforwardly from the lexical preactivation account of the N400: as in the borderline anomalies, the critical word is lexically associated with the sentence context, but is anomalous within the sentence *per se*. The absence of an increased N400 effect for these sentences seems to suggest that lexical preactivation, rather than semantic integration or composition, is the critical factor determining N400 amplitude.

Interestingly, cross-linguistic variation in ERP responses to semantic reversal

anomalies represents an additional complicating factor in characterizing the N400. In contrast to English and Dutch, German, Turkish and Chinese do show N400 effects for reversal anomalies (Bornkessel-Schlesewsky et al., 2011; Schlesewsky and Bornkessel-Schlesewsky, 2009). In German, this N400 forms part of a biphasic response, incorporating an N400 followed by a late positivity.[1] Bornkessel-Schlesewsky and colleagues (2011) argue that the presence or absence of the N400 for reversal anomalies is determined by the extent to which sentence interpretation relies on word order (termed "sequence dependence" in Bornkessel-Schlesewsky et al., 2011). In English and Dutch, word order is by far the most important cue for sentence interpretation (MacWhinney, Bates, & Kliegl, 1984; Bates, Devescovi, & Wulfeck, 2001), while a variety of cues must be taken into account in German, Turkish and Chinese (including, for example, case marking and animacy).[2] These cross-linguistic results present a challenge for the lexical preactivation view of the N400, since all the sentences examined in each of these languages contained strongly associated nouns and verbs. From the cross-linguistic results, it appears that the N400 is sensitive to the differential weighting of information sources across languages. Moreover, this suggests that semantic inconsistencies are processed differently in languages that rely primarily on one information source during sentence comprehension (such as English) compared to languages which rely on more than one (such as German). Therefore, it may be the case that these "single source" languages (i.e. languages with one dominant cue) are more susceptible to a temporary "blindness" to semantic anomalies, as reflected by the absence of an N400 for detected anomalies.

In the present study, we aimed to examine whether this type of cross-linguistic variation does in fact generalise to borderline anomalies, which in English appear analogous to reversal anomalies. If borderline anomalies also engender a biphasic N400-late positivity response in German, this would provide us with strong evidence against a purely lexical account of the N400.

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[1] The presence or absence of the late positivity for reversal anomalies is also subject to cross-linguistic variation, though along a different dimension to the N400. However, since it is the presence or absence of the N400 that is central to the present paper, we refer the interested reader to Bornkessel-Schlesewsky et al. (2011) for details on the variation of the positivity.

[2] This proposal was further supported by an experiment on Icelandic, in which Bornkessel-Schlesewsky et al. (2011) examined reversal anomalies with different verb classes, one of which called for strongly sequence-dependent interpretation, while the other did not. Strikingly, results revealed an English-type response (a monophasic late positivity with no N400) for the sequence-dependent verbs, but a German-type response for the other verb class (a biphasic N400 - late positivity pattern).

8.2   Experiment 1

Experiment 1 was designed as a German version of Sanford et al.'s (2011) ERP study. Materials were kept as closely comparable to those used in the original experiment as possible (given that they had to be translated) and the experimental task and procedure was identical.

8.2.1   Materials and Methods

8.2.1.1 Participants

Twenty-nine monolingually raised native speakers of German participated in the experiment after giving informed consent (15 women, mean age 23.8, range 18-31). All were right-handed (as assessed by an adapted German version of the Edinburgh Handedness Inventory; (Oldfield, 1971), had normal or corrected-to-normal vision and no known neurological or auditory disorders. Six participants were excluded from the analyses: two due to excessive artifacts and/or incomplete recording of the EEG data and four because of exceptionally high detection rates of above 80%, leaving fewer than 15 artifact-free missed anomaly trials for the averaging procedures.

8.2.1.2 Materials

The materials used in the present study were a translated and adapted version of the English stimuli employed by Sanford et al. (2011). The pool of items contained both hard-to-detect ("borderline") anomalies and more classic easy-to-detect anomalies (i.e., words with a poor fit to the context) that served as filler trials. Some items needed to be excluded because the strength of the semantic illusion was weakened by translation to German or because they relied on knowledge that could not be presumed for German participants. Other items were modified in the sense that British characters, places and names were replaced by German equivalents to render the materials more relevant and applicable to the targeted test subjects.

All materials were pre-tested in two questionnaire studies. Questionnaire 1 (n=70) ensured that borderline anomalies were reliably missed some of the time (hence allowing for an analysis of both detected and undetected borderline anomalies in the ERP study) and that classic easy-to-detect ("poor fit") anomalies were detected

at least 95% of the time. For this purpose the stimuli were distributed across ten lists, each containing 13 borderline anomalies, 16 easy-to-detect anomalies and equal numbers of non-anomalous control items for both anomaly types (i.e. 58 stimuli in total per list). The lists were then pseudo-randomised and each final version was presented to seven participants, who were asked to indicate and explain any detected anomalies. Borderline anomalies detected at a rate of 75% or higher were modified or excluded. The results of the questionnaire study showed that 68% of the presented borderline anomalies were correctly judged as being implausible. To attain the same number of sentences used in the English ERP study by Sanford and colleagues, 20 new items were created to replace excluded trials.

The final set of materials was further subjected to an additional questionnaire study (Questionnaire 2), in which we tested the contextual fit of the critical word. As in Sanford et al.'s (2011) study, this was accomplished by asking participants to judge the relevance of the critical word to the situation on a 7-point Likert scale (1 = "does not fit", 7 = "perfect fit"). Twenty participants rated the materials that were equally distributed across two lists. Borderline anomalies and poor fit anomalies yielded mean ratings of 5.02 and 2.20, respectively. Thus, borderline anomalies showed a significantly better contextual fit than their poor fit counterparts (t(210.201) = 18.54, $p <$ 0.0001). To account for unequal variances as indicated by Levene's test for homogeneity of variance, Welch's correction for the degrees of freedom was used. Importantly, the mean values for both anomaly types were highly comparable to those of Sanford and colleagues' materials (borderline anomalies: 5.16; poor fit anomalies: 2.17), thus demonstrating that contextual fit did not vary as a function of language.

In total, 215 stimulus pairs consisting of an anomalous condition and a corresponding plausible control condition were constructed, 135 pairs for the borderline anomalies and 80 pairs for the easy-to-detect "poor fit" anomalies. All stimuli were composed of two semantically connected sentences, with the first sentence providing context, and a second, critical sentence, containing a target word to which ERPs were timelocked. All critical sentences consisted of 17 words; however, sentence structures and linguistic methods of inducing the anomalies differed across anomaly types. In the following, the different layouts will be described on the basis of German and English examples.

Borderline anomalies

A sample borderline anomaly stimulus together with word-by-word translation from the present study in given in (3a).[3] The corresponding item from Sanford et al. (2011) is shown in (3b).

(3a)   Ein amerikanischer Jumbojet wurde von bewaffneten Extremisten gezwungen,
       An american   jumbo jet was   by   armed   extremists   forced
       in Kanada   zu landen und Experten waren schnell vor Ort, um zu vermitteln.
       in Canada   to land   and experts   were quickly on site for to mediate.
       Die Lage   beruhigte sich   durch die *{Verhandlungen/Kontaktaufnahme}*
       The situation calmed   itself   by   the {negotiations/ communications}
       der   Behörden   mit den verängstigten <u>Geiseln</u>, die im   Flugzeug saßen.
       of-the authorities with the   scared   hostages who in-the plane   sat.

(3b)   A North American jumbo jet was forced at gunpoint to land in Canada, experts
       were quickly on hand to help.
       First of all the authorities' initial *{negotiations/communications}* with the scared
       and desperate <u>hostages</u> helped calm the situation.

For the stimuli containing borderline anomalies, the second sentence was a thematic continuation of the first sentence and contained two alternative local context words (highlighted in italics) and the critical target word (underlined). The target word was always the 13th word position and separated by five words from the contextual manipulation. For most items, the local context was altered by replacing one word only, while for a few items more words needed to be changed. It is the relation between local context word/phrase and target word that determines whether the latter is perceived to be anomalous. Therefore, upon encountering the target word, the listener/reader should be able to judge whether the sentence is plausible without needing any further input. However, borderline anomalies are often missed because the target word is highly associated semantically to the overall context, despite its implausibility for the meaning of the particular sentence in which it appears.

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[3] Additional German and English examples as well as a detailed description of the critical words in terms of lexical category, case marking and grammatical function can be found in Appendix A.

Easy-to-detect anomalies

Eighty easy-to-detect anomaly sentence sets were used. These sentence pairs were constructed in a similar manner to the borderline anomalies, but the internal structure of the critical sentences was less standardised because in these cases the anomaly is evoked by a single word with a very poor fit to both local and global context. The critical words (highlighted in italics) appeared in different positions across stimulus sentences. This ensured that participants had to pay close attention to the whole sentence and could not predict the critical region in the stimuli presented. An example is given below (4a), again with the corresponding item from Sanford et al. (2011):

(4a)   Christian und Julias   gemeinsamer Abend   in dem   neuen Restaurant
       Christian and Julia's shared   evening in the   new   restaurant
       war ein richtiger Reinfall.
       was a   proper letdown.
       Zuerst servierte ihnen der *{Maler/Kellner}* die falschen Gerichte und dann
       First   served   them the {painter/waiter} the wrong   meals   and then
       wurde ihnen auch noch zu viel   berechnet.
       was   them also still too much charged.

(4b)   Denise and Fred's date to the new restaurant was a complete disaster.
       They were given the wrong meals by the *{painter/waiter}* and then they were overcharged for their meals.

The target words in all sentences were controlled for frequency (using the on-line Wortschatz corpus of the University of Leipzig) and length. The mean frequency class[4] for the target words was 12.79 for borderline anomaly items, 13.47 for anomalous target words in easy-to-detect items and 12.37 for their plausible counterparts ($F < 2$). There were also no significant differences in the average length of target words across anomaly types (mean length of target words: 8.1 letters for the borderline condition, 8.1 for poor fit to context anomalies and 7.5 for poor fit to context controls; $F < 2$).

        All auditory stimuli were recorded by a native female speaker of German who

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[4] Frequency classes are computed in relation to the most frequent word found in the corpus for a particular language. For example, if a word is placed in frequency class 11 this means that the most frequent word has 2^{11} times the number of occurrences of the selected word.

read the sentences with clear and natural intonation. To ensure equal volume levels, the stimuli were normalised digitally. After recording, trigger points for averaging ERPs were inserted at the spoken onset of each target word.

The stimuli were distributed across six lists, each composed of 215 sentence pairs, consisting of 135 borderline and 80 poor fit stimuli. While poor fit stimuli were divided evenly, of the 135 borderline items, 90 contained an anomaly and the remaining 45 were plausible controls. We employed this asymmetrical design, adopted from Sanford et al. (2011), to obtain a similar number of trials for each of the three experimental conditions (detected anomalies, missed anomalies, plausible controls) for the ERP analysis (based on the results of pre-test Questionnaire 1, in which the detection rate for borderline anomalies was ~60%). Within a final list, an item appeared as either anomalous or control condition, while across all lists, each condition of a stimulus pair was presented at least once. Thus, for borderline stimuli, this was achieved by rotating the materials over three lists with 135 stimuli each. Poor fit materials were divided into two lists consisting of 80 stimuli. Merging each borderline list with each poor fit list yielded the six final lists that were pseudo-randomised for presentation.

8.2.1.3 Procedure

For the experimental sessions, participants were seated in a dimly lit, sound attenuated booth, and listened to stimuli on loudspeakers. Participants were cued visually on a computer monitor. Each trial started with the presentation of a fixation asterisk in the centre of the screen, which was followed after 500 ms by the auditory presentation of the first sentence. After sentence offset, the asterisk remained on the screen for another 500 ms, after which participants were asked to press one of two active buttons on a hand-held game controller to initiate the presentation of the second sentence. Again, visual display of the fixation asterisk preceded auditory presentation by 500ms. After the second sentence ended, the asterisk was presented for another 1000 ms before being replaced by a question mark. The question mark served as a cue for the participants to indicate via button press whether they had detected an anomaly. The maximal response time was set to 3500 ms and the assignment of right and left buttons to the responses "plausible" and "implausible" was counterbalanced across participants. When a sentence was rated as plausible, the next trial started after a 2000 ms blank screen (the inter-trial interval). If participants judged a sentence as implau-

sible, they were asked to verbally explain their decision to the experimenter, who wrote down the explanation and recorded via button press whether the anomaly was indeed detected. There was no time limit for the verbal explanations given for detected anomalies.

Participants were asked to fixate on the asterisk throughout the duration of its presentation (from 500 ms before sentence onset to 1000 ms after sentence offset) and to avoid movements and eye blinks during the presentation of the second sentence. Before the start of the actual experimental session, a training session was conducted to ensure that participants were familiar with the task. Each participant was presented with one of the six lists split into experimental sessions with seven blocks of 27 sentence pairs and a final block of 26 sentence pairs. Between blocks, participants took short breaks.

Since a successful detection of some of the borderline anomalies required a certain level of general knowledge, participants completed a post-experiment multiple-choice test to determine if they understood all borderline anomalies as being semantically implausible. Depending on the experimental list presented, participants answered 32-35 multiple choice questions that contained the critical word and asked for the correct local context word. Five answer options were given, including the presented, incorrect local context word (e.g. „Who built the ark?" A: Noah, B: Moses, C: Jona, D: Adam, E: I don't know). Questions to which incorrect or no answers were given resulted in exclusion of the respective trial from subsequent analyses. A total of 108 trials (5.2%) and a mean of 4.7 (sd:2.2; range: 1-9) trials per participant were excluded.

8.2.1.4 EEG recording and preprocessing

The EEG was recorded from 25 Ag/AgCl scalp electrodes positioned according to the international 10/10 system by means of an elastic cap (Easycap GmbH, Herrsching, Germany). The horizontal and vertical electrooculogram (EOG) was monitored by placing electrodes at the outer canthi of both eyes and above and below the right eye, respectively. All EEG and EOG channels were amplified with a BrainAmp amplifier (Brain Products, Gilching, Germany) and digitised at a rate of 500 Hz (ground: AFZ). In recording, the left mastoid served as the online reference electrode, but the EEG signals were rereferenced to linked mastoids offline. Scalp impedances were kept be-

low 5 kΩ.

As a first step of processing, the EEG data were filtered with a 0.3-20 Hz band-pass filter to eliminate slow signal drifts. Automatic and manual rejections (with an EOG rejection threshold of 40 µV) were carried out to discard trials containing EEG or EOG artifacts. Single-subject ERP averages were computed per experimental condition and electrode from -200 to 1200ms relative to the onset of the critical target word. Trials that contained false alarm responses to plausible control sentences, detected anomalies with incorrect explanations, missed easy-to-detect anomalies and items for which false answers were given in the multiple-choice post-test were excluded from the averaging procedure (resulting in an overall loss of approximately 8.7% of the trials). Finally, grand-averages were computed over all participants.[5] Despite the exclusion of six participants, the different experimental lists were still presented equally often (one list was only presented three times, all other lists four times).

8.2.1.5 Data analysis

For the statistical analysis of the ERP data, separate analyses were computed for borderline and easy-to-detect anomalies, since they contained different lexical material. In both cases, repeated-measures ANOVAs involving the factors ANOMALY (for borderline anomalies: detected anomalies vs. missed anomalies vs. plausible controls; for easy-to-detect anomalies: anomalous vs. non-anomalous) and region of interest (ROI) were calculated for mean amplitude values per time window per condition. There were four lateral ROIs consisting of 4 electrodes each: left-anterior (F3, F7, FC1, FC5), right-anterior (F4, F8, FC2, FC6), left-posterior (CP1, CP5, P3, P7) and right-posterior (CP2, CP6, P4, P8). For midline sites, each of the six electrodes (FZ, FCZ, CZ, CPZ, PZ, POZ) made up a ROI of their own. Analyses for lateral and midline ROIs were performed separately. Whenever statistical computation included a factor with more than one degree of freedom in the numerator and sphericity was violated, Huynh-Feldt-corrected significance values are reported (Huynh & Feldt, 1970).

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[5] Descriptive statistics for the number of trials averaged per condition and experiment are given in Appendix B.

8.2.2 Results

8.2.2.1 Detection rates

Analysis of the behavioural data showed that easy-to-detect anomalies were correctly judged as implausible at a rate of 95.5% (sd: 4.9%), whereas for borderline anomalies the detection rate was only 61.3% (sd: 8.8%). Clearly the participants had little difficulty in categorising easy-to-detect anomalies as implausible, but had more difficulty with the borderline anomalies.

8.2.2.2 ERP data

Figure 1 displays the grand-average ERPs time-locked to the target word for detected borderline anomalies compared to missed anomalies and plausible controls, while the comparison of anomalous and non-anomalous easy-to-detect items is shown in Figure 2.

As is apparent from both figures, both types of correctly detected semantic anomalies elicited a negativity between approximately 200-500 ms followed by a late positivity between approximately 600-1100 ms post-onset of the critical word.[6] However, no comparable effects were apparent for the comparison of missed borderline anomalies and plausible controls. Separate statistical analyses were carried out for both anomaly types as well as for lateral and midline regions of interest to confirm the impressions based on visual inspection.

Borderline anomalies

A repeated-measures ANOVA for lateral electrode sites in the time window of 200-500ms revealed a main effect of ANOMALY [$F(2,44) = 7.21, p < 0.002$] as well as an interaction of ANOMALY x ROI [$F(6,132) = 4.21, p < 0.003$]. Resolving the observed interaction by ROI showed significant effects of ANOMALY in all four lateral ROIs (min: $F(2,44) = 3.41, p < 0.5$ for the left-anterior ROI; max: $F(2,44) = 10.19, p < 0.001$ for the right-posterior ROI). We further analysed the main effect of ANOMALY in each of the ROIs by computing pairwise comparisons, correcting for multiple comparisons using a modified Bonferroni procedure (Keppel, 1991). The

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[6] For detected borderline anomalies we also found an additional negative effect before the onset beginning of the critical word. See for Appendix C for a detailed analysis of this pre-onset negativity.

results showed no significant difference between missed anomalies and plausible controls [all Fs < 2.2]. At the same time, detected anomalies differed from both missed anomalies and plausible controls in all lateral ROIs [all Fs > 5.2].
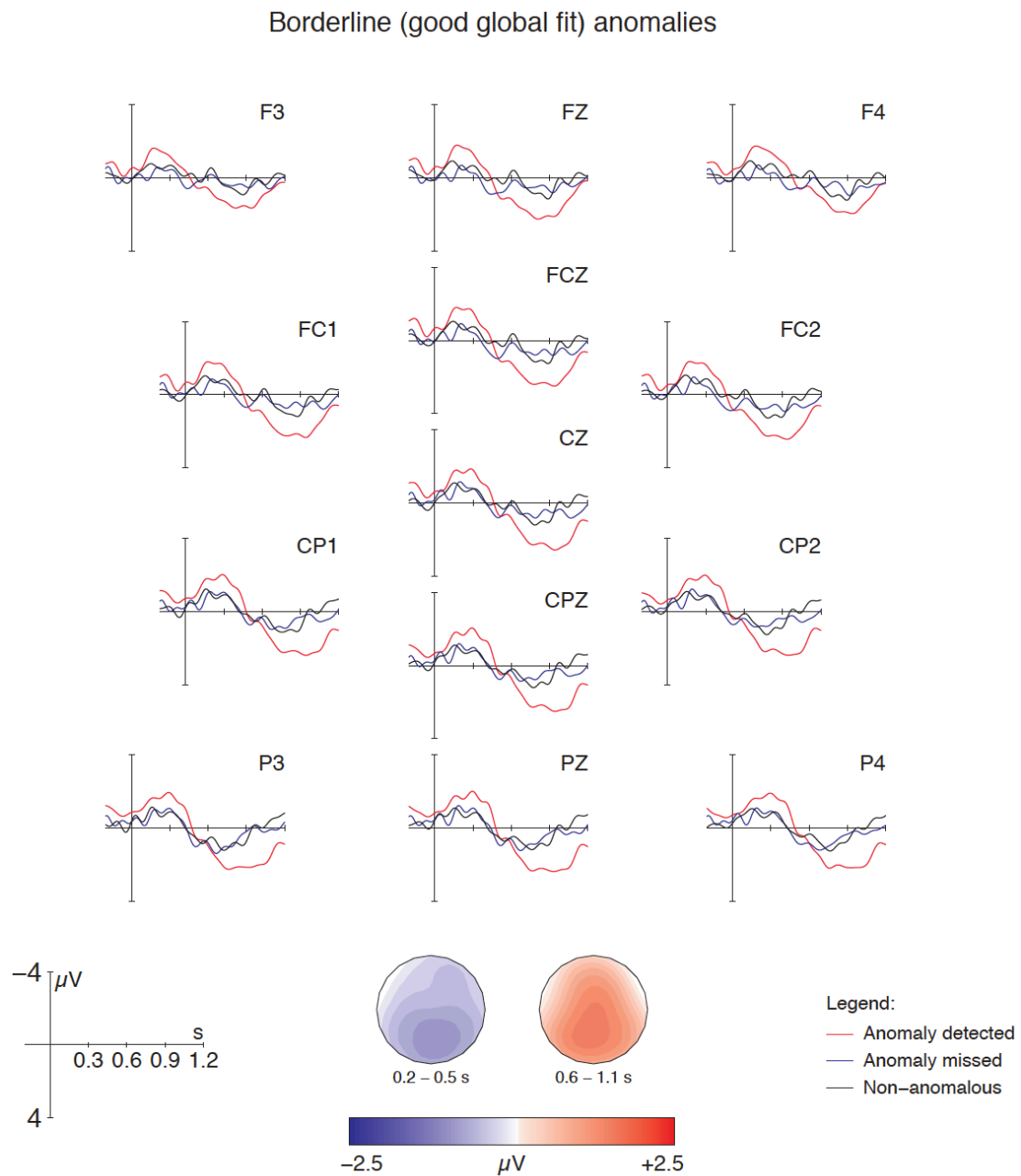
Figure 1: Grand average ERPs at the position of the critical word (onset at the vertical bar) in the borderline (good global fit) anomaly conditions at 13 selected electrodes in Experiment 1. The figure contrasts ERP responses to detected anomalies (red traces), missed anomalies (blue traces) and plausible controls (black traces). Negativity is plotted upwards. The topographical maps show the scalp distribution for the voltage difference between detected anomalies and plausible sentences in the N400 and late positivity time windows, respectively.

Figure 2: Grand average ERPs at the position of the critical word (onset at the vertical bar) in the easy-to-detect (poor global fit) anomaly conditions at 13 selected electrodes in Experiment 1. The figure contrasts ERP responses to anomalous (red traces) and non-anomalous sentences (blue traces). Negativity is plotted upwards. The topographical maps show the scalp distribution for the voltage difference between anomalous and plausible sentences in the N400 and late positivity time windows, respectively.

The global ANOVA for midline electrodes showed comparable results: a main effect of ANOMALY [$F(2,44) = 6.9$, $p < 0.01$] and an interaction of ANOMALY and ROI [$F(10,220) = 3.8$, $p < 0.01$]. When resolving the interaction by ROI, significant effects of ANOMALY were found at all midline sites, with the strongest effect at posterior electrodes [min: $F(2,44) = 4.6$, $p < 0.02$ at FCZ, max: $F(2,44) = 10.4$, $p < 0.001$

at POZ]. Resolving the ANOMALY effect in each of the midline ROIs showed a pattern similar to that found for lateral ROIs: detected anomalies differed significantly from missed anomalies in all ROIs [all Fs > 7.4], while the central and posterior electrodes CZ, PCZ, PZ and POZ also showed a significant distinction between detected anomalies and plausible sentences [all Fs > 7.2; FZ and FCZ: Fs < 3.9]. Importantly, no such difference was found for the contrast of missed anomalies and plausible sentences in any of the ROIs [all Fs < 2.9].

In the 600-1100 ms time window, the statistical analysis revealed a main effect of ANOMALY for both lateral and midline electrode sites [lateral: $F(2,44) = 29.3$, $p < 0.001$; midline: $F(2,44) = 42.1$, $p < 0.001$], while only lateral sites showed an interaction ANOMALY x ROI [$F(6, 132) = 4.6$, $p < 0.03$]. Again, all regions showed effects of ANOMALY, with the interaction due to more pronounced effects of ANOMALY at posterior electrode sites [max: $F(2,44) = 38.8$, $p < 0.001$ at the left-posterior ROI; min: $F(2,44) = 11.6$, $p < 0.001$ at the left-anterior ROI]. When the individual levels of ANOMALY were compared in a pairwise fashion for each of the lateral ROIs and across all midline electrodes, similar results were found: Detected anomalies differed significantly from both missed anomalies and plausible controls [lateral: all Fs > 24.3 (detected vs. missed) and all Fs > 13.3 (detected vs. plausible); midline: $F(1,22) = 73.3$, $p < 0.001$ (detected vs. missed) and $F(1,22) = 67.7$, $p < 0.001$ (detected vs. plausible)], while there was no difference between missed anomalies and plausible sentences [lateral: all Fs < 0.3; midline: $F(1,22) = 0.02$, $p = 0.89$].

Easy-to-detect anomalies

In line with previous results for this type of anomaly, statistical analyses confirmed that implausible words elicited a considerably larger negativity than plausible words in the 200-500 ms time window [lateral: $F(1,22) = 171.4$, $p < 0.001$; midline: $F(1,22) = 168.6$, $p < 0.001$]. Interactions of ANOMALY x ROI for both lateral and midline electrode sites [lateral: $F(3,66) = 51.7$, $p < 0.001$; midline: $F(5,110) = 75.8$, $p < 0.001$] reflected the centro-parietal distribution of the anomaly effect that is typical for an N400. For midline ROIs, the effect increased from anterior to posterior electrodes [min: $F(1,22) = 47.6$, $p < 0.001$ at FZ; max: $F(1,22) = 224.8$, $p < 0.001$ at POZ]. A similar pattern of results was observed in the analysis of lateral sites [min: $F(1,22) = 49.5$, $p < 0.001$ for the left-anterior ROI; max: $F(1,22) = 247.2$, $p < 0.001$ for the

right-posterior ROI].

As is apparent from Figure 2, anomalous words also elicited a larger late positivity in a time window between 600-1100 ms. Statistical analyses confirmed a main effect of ANOMALY [lateral: $F(1,22) = 39.8, p < 0.001$; midline: $F(1,22) = 59.2, p < 0.001$] and an interaction of ANOMALY x ROI [lateral: $F(3,66) = 54.5, p < 0.001$; midline: $F(5,110) = 32.7, p < 0.001$]. Resolving the interaction by ROI indicated that the positivity effect increased from anterior to posterior electrode sites for both lateral [min: $F(1,22) = 4.9, p < 0.05$ for the left-anterior ROI; max: $F(1,22) = 72.2, p < 0.001$ for the left-posterior ROI] and midline regions of interest [min: $F(1,22) = 16.9, p < 0.001$ at FZ; max: $F(1,22) = 77.9, p < 0.001$ at POZ].

In summary, detected borderline anomalies elicited an N400 effect followed by a late positivity in comparison to both missed anomalies and plausible controls. However, no differences were found between missed anomalies and plausible controls. Classic easy-to-detect anomalies triggered the emergence of an N400 followed by a late positivity.

Comparison of N400 amplitude for borderline versus easy-to-detect anomalies

Figures 1 and 2 suggest that the N400 effect is considerably more pronounced for easy-to-detect anomalies (approximately -6 μV) than for borderline anomalies (approximately -2 μV). To examine whether there was indeed a difference in magnitude, we compared ERP amplitude differences (anomaly-control) in the N400 time window (200-500 ms) with an ANOVA including the factors ANOMALY-TYPE and ROI. This analysis revealed main effects of ANOMALY-TYPE [lateral: $F(1,22) = 58.76; p < 0.001$; midline: $F(1,22) = 59.38; p < 0.001$] and interactions of ANOMALY-TYPE and ROI [lateral: $F(3,66) = 24.65; p < 0.001$; midline: $F(5,110) = 28.95; p < 0.001$]. Resolving the interactions by ROI showed significant effects of ANOMALY-TYPE in all regions, with effects more pronounced at posterior sites [lateral min.: $F(1,22) = 21.16, p < 0.001$ in the left-anterior region; max: $F(1,22) = 85.21, p < 0.001$ in the right-posterior region; midline min: $F(1,22) = 11.70, p < 0.01$ at FZ; max: $F(1,22) = 93.07, p < 0.001$ at PZ]. Thus, easy-to-detect anomalies indeed showed an N400 effect with a larger magnitude than borderline anomalies and this difference in amplitude was most pronounced in those regions in which the N400 effect was maximal.

8.2.3   Discussion

In terms of detection rates, Experiment 1 showed very similar results to those observed by Sanford et al. (2011). As before, the mean detection rate for borderline anomalies was considerably lower than that for easy-to-detect anomalies. For these anomalies, we observed a biphasic N400 – late positivity pattern, as also observed for English. By contrast, the comparison of electrophysiological responses to detected and non-detected borderline anomalies and their plausible controls revealed a deviation from previous findings for English: in the present study, detected borderline anomalies elicited an N400 effect followed by a late positivity in contrast to missed anomalies and plausible controls, which did not differ from each other. Recall that in the case of closely matched English borderline anomalies, the neural response to detected anomalies resembled that to non-detected and plausible stimuli in the N400 time range, with a differential effect arising only in the late positivity (Sanford et al., 2011). The results of Experiment 1 thus point to cross-linguistic differences in the processing of detected borderline anomalies (i.e., those that show a close fit to global context).

8.3   Experiment 2

The comparison between Experiment 1 and the previous findings by Sanford and colleagues (2011) indicates that the neural processing of borderline anomalies differs across languages: while German showed a biphasic N400 - late positivity response to detected anomalies, only a late positivity was observable in English. More recent results, however, suggest that it may be possible to induce N400-like effects for borderline anomalies in English, too, by manipulating task environment. Bohan, Leuthold, Hijikata, and Sanford (2012) report an ERP study using similar materials to those used in their original 2011 experiment, but employing visual presentation and an additional task. After judging whether a given passage was plausible or not (and, in the case of an "implausible" answer, reporting the nature of the anomalous content), participants rated how certain they were of their answer on a 6-point scale. Bohan and colleagues speculate that the difference between their results and the previous findings by Sanford et al. (2011) might be attributable to changes in task demands.

We shall return to the question of how task demands and the cross-linguistic

differences proposed here might be integrated within one account of the N400 in the General Discussion. Before addressing this question, however, we sought additional support for task-independent, cross-linguistic variation in the electrophysiological response to borderline anomalies. To this end, we conducted two additional ERP studies (one in German, Experiment 2a; one in English, Experiment 2b) with completely parallel design and analysis procedures. In these experiments, we aimed to reduce the impact of the judgement task as much as possible in order to allow us to examine the "basic" pattern that emerges in each language when task influences are minimised. To this end, we modified the design of Experiment 1 in three ways: (a) context and target sentences were presented with a fixed inter-stimulus interval, thus eliminating participants' control over target sentence presentation; (b) the judgement task only comprised a button press ("plausible" versus "implausible") but did not require participants to explain the nature of the anomaly following an "implausible" judgement; and (c) the number of trials in the experiment was decreased from 215 to 180 to reduce participants' exposure to the critical manipulation (i.e., the processing and classification of semantically anomalous and non-anomalous sentences).

8.3.1.1 Experiment 2a

8.3.1.2 Materials and Methods

Participants

Twenty-six monolingually raised native speakers of German participated in the experiment after having given informed consent (13 women, mean age 23.3, range 19-29). None of the participants had taken part in Experiment 1 and parameters for participant inclusion were the same as for Experiment 1. Four participants were excluded due to excessive EEG artefacts.

Materials

The materials were identical to those employed in Experiment 1 with the exceptions already noted above: the number of critical sentences was reduced from 215 to 180 by removing sentences from the easy-to-detect anomalies and the plausible borderline condition. In Experiment 2a, each participant thus heard 90 borderline anomaly sentences and 30 controls, as well as 30 sentences in each of the easy-to-detect anomaly

and control conditions, respectively. The borderline anomalies were selected on the basis of detection rates in Experiment 1, i.e. the items that were excluded were those that had shown the highest by-item detection rates in Experiment 1.

Procedure

The experimental procedure was identical to that in Experiment 1 with the two exceptions mentioned above: (a) context and target sentences were presented with a fixed ISI of 1000 ms; (b) the plausibility judgement consisted only of a button press, i.e. participants were not required to explain why they considered sentences implausible. The maximal reaction time was set at 2000 ms. In addition, in order to avoid anticipatory motor response preparation following the processing of the critical word, Experiment 2 did not employ a fixed assignment of push-buttons to the "plausible" and "implausible" categorisations per participant. Rather, the assignment of the left and right buttons to "plausible" and "implausible" responses varied on a trial-by-trial basis and was signalled by two smiley faces (one laughing and one frowning). Across each session, the assignment of the "plausible" and "implausible" categories to the left and right buttons was counterbalanced.

EEG data recording and preprocessing

EEG data recording and preprocessing was identical to Experiment 1 with the exception that eye movement artefacts were corrected using an independent component-analysis (ICA) based correction method. The ICA correction was employed in order to ensure that data analysis was comparable to Experiment 2b, in which it was necessary in order to avoid the loss of too many trials due to eye movement artefacts. To this end, we calculated an Extended Infomax ICA for each participant and subsequently selected template ICs for blinks and saccades, respectively. The two ICs best correlating with vertical and horizontal EOG templates were identified using an automatic procedure (Viola et al., 2009) and subsequently subtracted from the raw EEG data.

Data analysis

Data analysis was undertaken in an identical manner to Experiment 1.

8.3.1.3 Results

Detection rates

Analysis of the behavioural data showed that easy-to-detect anomalies were correctly judged as implausible at a rate of 95.6% (sd: 4.2%), whereas for borderline anomalies the detection rate was 71.2% (sd: 9.4%). To compare whether accuracy in Experiment 2a differed from that of Experiment 1, we computed a behavioural analysis for Experiment 1 that included only the materials that were used both German experiments. This yielded a detection rate for borderline anomalies of 63.5% (sd:9.3%) that differed significantly from that of Experiment 2a [$t(42.878) = -2.79$, $p = 0.008$] and an accuracy of 95.3% (sd:4.6) for easy-to-detect anomalies that did not differ from that of Experiment 2a [$t(42.871) = -0.21$, $p = 0.83$].

ERP data: Borderline anomalies

Figure 3 shows grand average ERPs timelocked to the critical word in the borderline anomaly conditions and the corresponding plausible controls. As is apparent from the Figure, the findings from Experiment 2a replicate those of Experiment 1: detected borderline anomalies engendered a biphasic N400 - late positivity response in comparison to missed anomalies as well as plausible controls.[7]

A repeated-measures ANOVA for lateral electrode sites in the time window of 200-500ms revealed a main effect of ANOMALY [$F(2,42) = 11.48$, $p < 0.001$]. We further analysed the main effect of ANOMALY by computing pairwise comparisons, correcting for multiple comparisons using a modified Bonferroni procedure (Keppel, 1991). The results showed no significant difference between missed anomalies and plausible controls [$F < 1$]. At the same time, detected anomalies differed from both missed anomalies [$F(1,21) = 14.86$, $p < 0.001$] and plausible controls [$F(1,21) = 24.06$, $p < 0.0001$].

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[7] As in Experiment 1, for detected borderline anomalies an early negativity prior to the onset of the critical word was observed relative to non-detected and plausible control sentences. See Appendix C for analysis and discussion of this effect.

Figure 3: Grand average ERPs at the position of the critical word (onset at the vertical bar) in the borderline (good global fit) anomaly conditions at 13 selected electrodes in Experiment 2a. The figure contrasts ERP responses to detected anomalies (red traces), missed anomalies (blue traces) and plausible controls (black traces). Negativity is plotted upwards. The topographical maps show the scalp distribution for the voltage difference between detected anomalies and plausible sentences in the N400 and late positivity time windows, respectively.

The global ANOVA for midline electrodes showed comparable results: a main effect of ANOMALY [$F(2,42) = 11.00, p < 0.001$] and an interaction of ANOMALY and ROI [$F(10,210) = 2.03, p < 0.05$]. When resolving the interaction by ROI, significant effects of ANOMALY were found at all midline sites except FZ, with the effect strongest at CPZ [$F(2,42) = 13.89, p < 0.0001$]. Resolving the ANOMALY effect in

each of the midline ROIs showing a significant main effect of ANOMALY revealed a pattern similar to that found for lateral ROIs: detected anomalies differed significantly from missed anomalies in all ROIs [all Fs > 5.7] as did detected anomalies and plausible sentences [all Fs > 4.8]. As in Experiment 1, no difference was found for the contrast of missed anomalies and plausible sentences in any of the ROIs [all Fs < 1].

In the 650-1100 ms time window,[8] the statistical analysis revealed a main effect of ANOMALY for both lateral and midline electrode sites [lateral: $F(2,42) = 8.14$, $p < 0.01$; midline: $F(2,42) = 9.27$, $p < 0.001$], while only lateral sites showed an interaction ANOMALY x ROI [$F(6, 126) = 2.95$, $p < 0.05$]. Again, all regions showed effects of ANOMALY, with the interaction due to more pronounced effects of ANOMALY at posterior electrode sites [max: $F(2,42) = 10.76$, $p < 0.001$ at the left-posterior ROI; min: $F(2,42) = 3.24$, $p < 0.05$ at the left-anterior ROI]. When the individual levels of ANOMALY were compared in a pairwise fashion for each of the lateral ROIs and across all midline electrodes, similar results were found: Detected anomalies differed significantly from plausible controls in all regions [lateral: all Fs > 5.3; midline: $F(1,21) = 19.6$, $p < 0.001$] and from missed anomalies in posterior lateral ROIs [all Fs > 5.3] as well as for midline sites [$F(1,21) = 7.92$, $p < 0.05$]. A difference between missed anomalies and plausible sentences was observed in the left-posterior ROI [$F(1,21) = 6.30$, $p < 0.05$].

ERP data: Easy-to-detect anomalies

ERP results for the easy-to-detect anomalies are shown in Figure 4. Here, the findings of Experiment 2a again replicate those of Experiment 1, with the semantically anomalous condition eliciting a biphasic N400 - late positivity pattern in comparison to the plausible control condition.

The statistical analyses in the 200-500 ms time window showed a main effect of ANOMALY [lateral: $F(1,21) = 42.19$, $p < 0.0001$; midline: $F(1,21) = 43.91$, $p < 0.0001$]. Interactions of ANOMALY x ROI for both lateral and midline electrode sites [lateral: $F(3,63) = 19.1$, $p < 0.0001$; midline: $F(5,105) = 21.8$, $p < 0.0001$] reflected the centro-parietal distribution of the effect. For midline ROIs, the effect increased from anterior to posterior electrodes [min: $F(1,21) = 6.55$, $p < 0.05$ at FZ;

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[8] The time window chosen for the late positivity in Experiment 2a (650-1100 ms) differed slightly from that in Experiment 1 (600-1100 ms) on account of visual inspection of effect onset in the grand average ERPs. This amounts to a reduction of the window size by 10% of the sample points.

max: $F(1,21) = 74.10$, $p < 0.0001$ at POZ]. A similar pattern of results was observed in the analysis of lateral sites [min: $F(1,21) = 4.40$, $p < 0.005$ for the right-anterior ROI; max: $F(1,21) = 85.2$, $p < 0.0001$ for the right-posterior ROI].
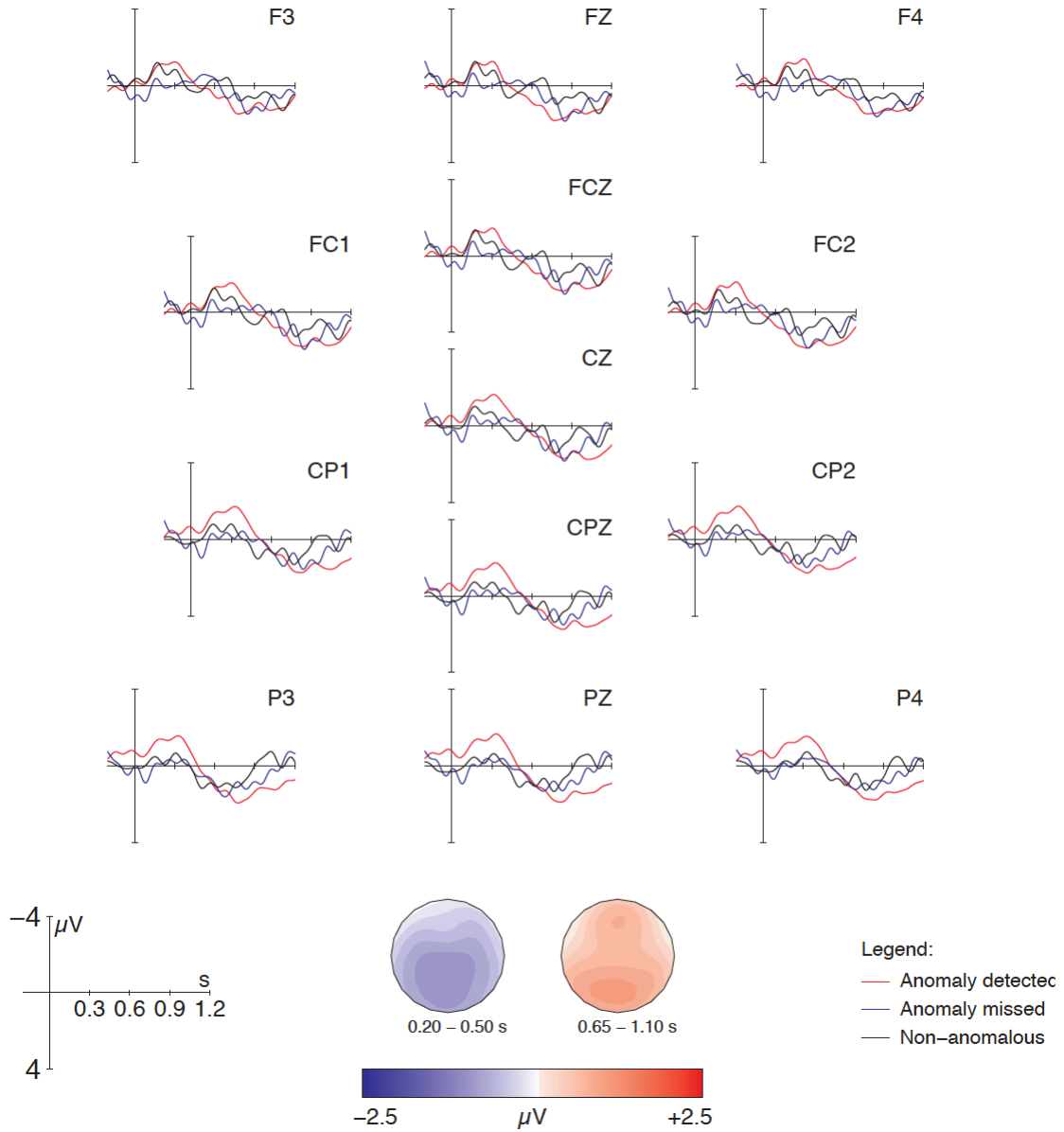

Figure 4: Grand average ERPs at the position of the critical word (onset at the vertical bar) in the easy-to-detect (poor global fit) anomaly conditions at 13 selected electrodes in Experiment 2a. The figure contrasts ERP responses to anomalous (red traces) and non-anomalous sentences (blue traces). Negativity is plotted upwards. The topographical maps show the scalp distribution for the voltage difference between anomalous and plausible sentences in the N400 and late positivity time windows, respectively.

For the late time window (650-1100 ms), statistical analyses showed a marginal main effect of ANOMALY for midline sites [$F(1,21) = 3.80$, $p < 0.07$] and a significant interaction of ANOMALY x ROI [lateral: $F(3,63) = 23.44$, $p < 0.0001$; midline: $F(5,105) = 9.11$, $p < 0.0001$]. Resolving the interaction by ROI indicated that the positivity effect only reached significance in posterior lateral ROIs [Fs > 9.3; ps < 0.01] and for midline sites PZ and POZ [Fs > 10.4; ps < 0.01].

8.3.2   Experiment 2b

8.3.2.1 Materials and Methods

Participants

Twenty-four monolingually raised native speakers of American English (students at the University of California, Irvine) participated in the experiment after giving informed consent (15 women, mean age 21.5, range 18-29). Parameters for participant inclusion were the same as for Experiments 1 and 2a. Six participants were excluded due to excessive EEG artefacts.

Materials

The materials were adapted from Sanford et al.'s (2011) stimuli for American participants (i.e. passages that required specifically British world knowledge were altered to fit into an American context and British expressions were replaced by appropriate counterparts in American English).[9] Materials were recorded by a trained speaker of American English using the same recording parameters as for Experiment 1.

As in Experiment 2a, each participant in Experiment 2 heard 180 passages in total: 90 borderline anomaly sentences and 30 controls, as well as 30 sentences in each of the easy-to-detect anomaly and control conditions, respectively.

Procedure

The experimental procedure was identical to that in Experiment 2a.

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[9] See Appendix A for a more detailed description of the differences between the materials used here and in Sanford et al. (2011).

EEG data recording and preprocessing

The EEG data were recorded using an EGI net amps 300 amplifier and a 256-channel HydroCel Geodesic Sensor Net (Electrical Geodesics, Inc., Eugene, OR) with a 500 Hz sampling rate. The data were recorded using a vertex reference, but re-referenced to linked mastoids offline. Impedances were kept below 50 kΩ.

In order to ensure maximal comparability of the data analysis to Experiments 1 and 2a, the entire data preprocessing and analysis procedure was restricted to the 32 channels that were recorded in our previous studies. Data preprocessing was accomplished in an identical manner to Experiment 2a. For this data set, some participants showed significant EMG contamination at occipital electrodes; accordingly, additional IC components representing muscle artefacts (Jung et al., 2000) were also removed for some participants. These components were identified by their location and significant high-frequency content in their power spectra. On average, 7.4 (sd: 2.4) ICs were removed per participant. The mean weight at electrode CPZ for all artefact ICs was low (0.02), indicating that these ICs did not substantially represent or influence activity measured at centroparietal sites.

Data analysis

Data analysis was undertaken in an identical manner to Experiments 1 and 2a.

8.3.2.2 Results

Detection rates

Analysis of the behavioural data showed that easy-to-detect anomalies were correctly judged as implausible at a rate of 91.3% (sd: 4.9%), whereas for borderline anomalies the detection rate was 55.6% (sd: 11.4%). Comparing these results to the detection rates of Experiment 2a revealed significant differences for both anomaly types [Borderline anomalies: $t(32.81) = 4.66, p < 0.001$, easy-to-detect-anomalies: $t(33.67) = 2.97, p = 0.005$].

ERP data: Borderline anomalies

Figure 5 shows ERPs for borderline anomaly sentences and their plausible controls. The data pattern replicates that observed by Sanford et al. (2011): detected borderline

anomalies elicited a late positivity in comparison to missed anomalies and plausible controls, but no N400 effect.
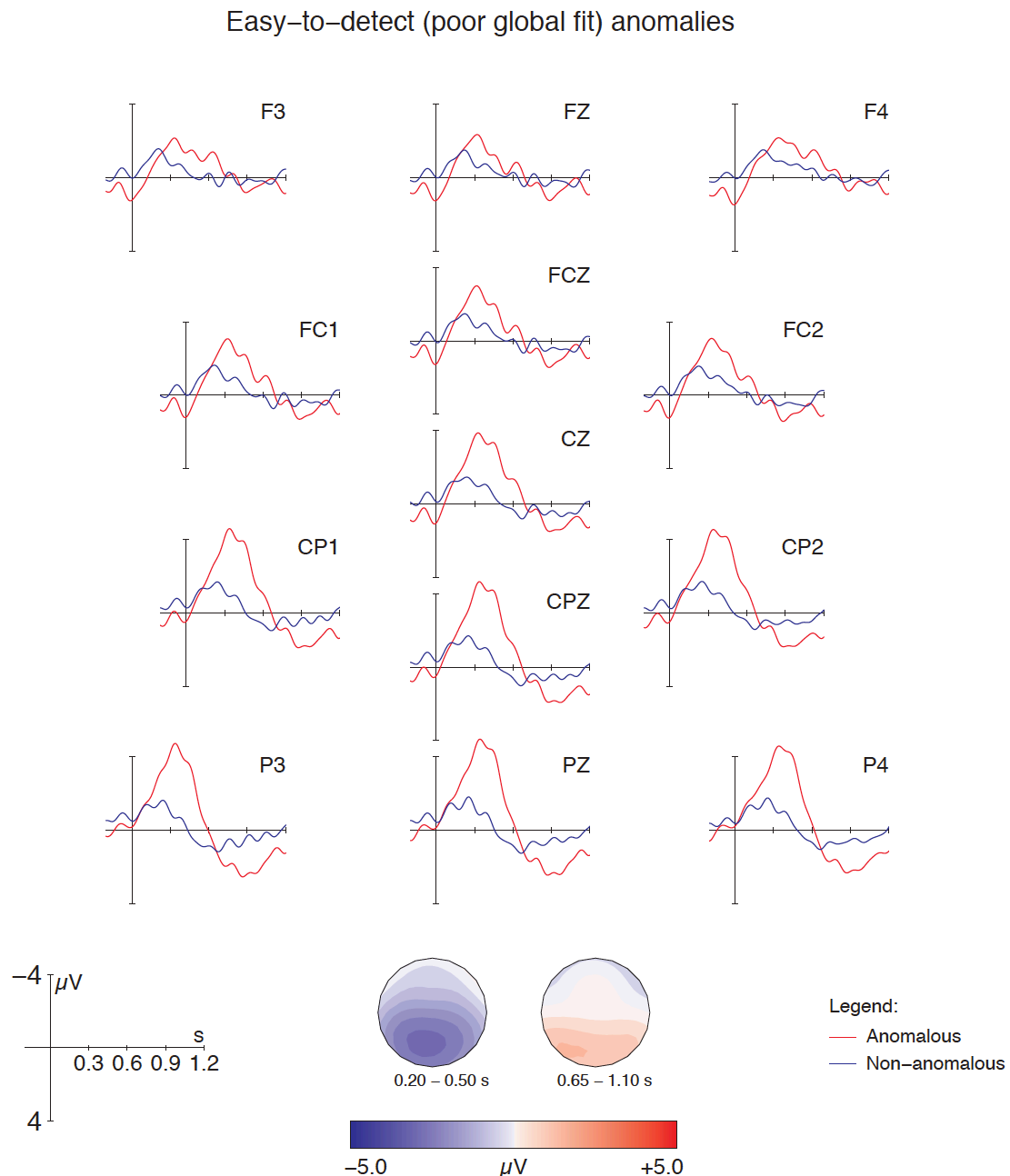

Figure 5: Grand average ERPs at the position of the critical word (onset at the vertical bar) in the borderline (good global fit) anomaly conditions at 13 selected electrodes in Experiment 2b. The figure contrasts ERP responses to detected anomalies (red traces), missed anomalies (blue traces) and plausible controls (black traces). Negativity is plotted upwards. The topographical maps show the scalp distribution for the voltage difference between detected anomalies and plausible sentences in the N400 and late positivity time windows, respectively.

For the 200-500 ms time window, neither the lateral nor the midline electrodes showed a significant effect of ANOMALY [all ps > 0.11] or an interaction of ANOMALY x ROI [all Fs < 1].

In the 650-1100 ms time window, the data showed a main effect of ANOMALY for the midline electrodes [$F(2,34) = 5.09$, $p < 0.05$]. Pairwise comparisons between the three levels of anomaly type showed a significant difference between detected and plausible borderline anomalies [$F(1,17) = 6.62$, $p < 0.05$] as well as between detected and missed borderline anomalies [$F(1,17) = 6.87$, $p < 0.05$]. There was no difference between missed anomalies and plausible controls [$F < 1$].

ERP data: Easy-to-detect anomalies

The ERP results for easy-to-detect anomalies and their plausible counterparts are shown in Figure 6. As in Experiments 1 and 2a as well as Sanford et al. (2011), these types of anomalies elicited a biphasic N400 - late positivity response in comparison to plausible controls.

In the 300-600 ms time window, the data showed a main effect of ANOMALY for the midline electrodes [$F(1,17) = 7.99$, $p < 0.05$] and an interaction ANOMALY x ROI [lateral: $F(3,51) = 11.36$, $p < 0.0001$; midline: $F(5,85) = 11.97$, $p < 0.0001$]. Analyses per ROI revealed significant effects of ANOMALY in posterior lateral ROIs [Fs > 10.4] and for midline sites CZ, CPZ, PZ and POZ [Fs > 7.7].

The analysis of the 650-1100 ms time window revealed an interaction of ANOMALY x ROI [lateral: $F(3,51) = 16.19$, $p < 0.0001$; midline: $F(5,85) = 10.05$, $p < 0.0001$]. Analyses per ROI showed that the positivity effect for anomalous versus plausible sentences reached significance only at midline sites PZ [$F(1,17) = 4.94$, $p < 0.05$] and marginal significance at POZ [$F(1,17) = 3.61$, $p = 0.07$].
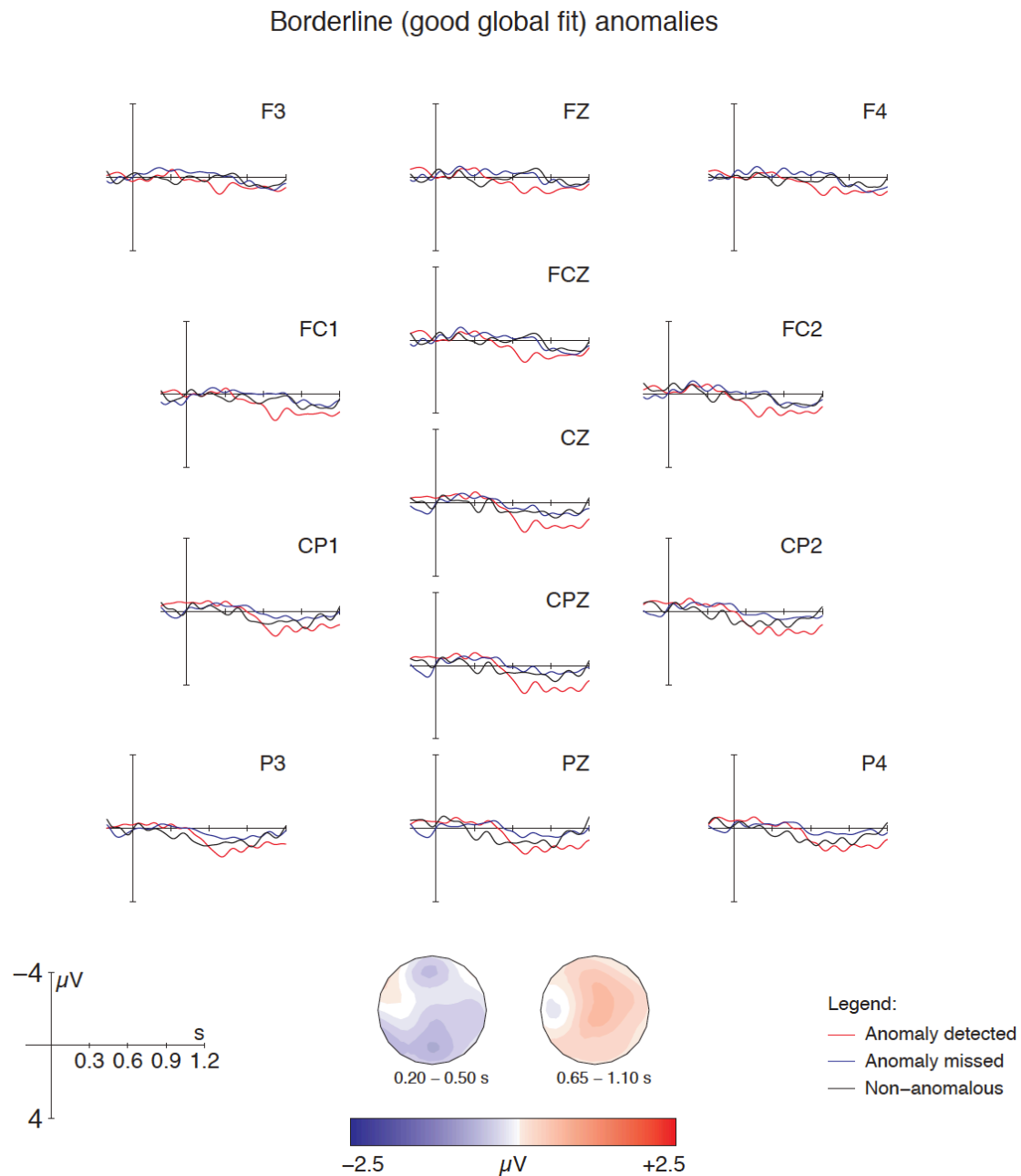
Easy–to–detect (poor global fit) anomalies
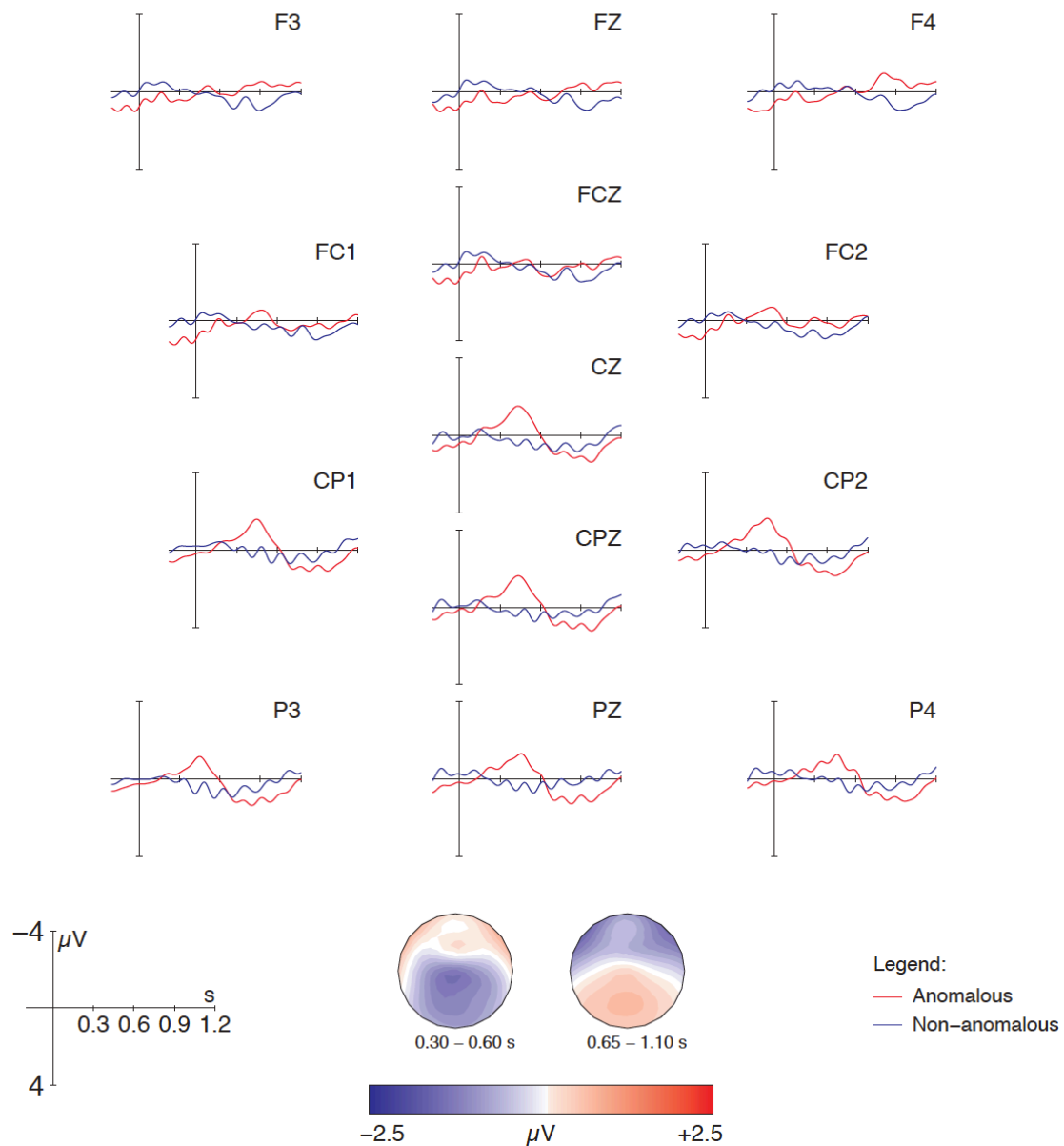
Figure 6: Grand average ERPs at the position of the critical word (onset at the vertical bar) in the easy-to-detect (poor global fit) anomaly conditions at 13 selected electrodes in Experiment 2b. The figure contrasts ERP responses to anomalous (red traces) and non-anomalous sentences (blue traces). Negativity is plotted upwards. The topographical maps show the scalp distribution for the voltage difference between anomalous and plausible sentences in the N400 and late positivity time windows, respectively.

8.3.3   Cross-experiment analysis of Experiments 2a and 2b

In order to directly compare the German and English findings in Experiments 2a and 2b, we conducted an additional cross-experiment analysis including LANGUAGE as a between-participants factor. Note that, while main effects of LANGUAGE apparent in this analysis could in principle be due to the different ERP systems used in Experiments 2 and 3 (though this appears unlikely in view of the basic methodological

foundations of event-related brain potentials), the predicted interactions between LANGUAGE and ANOMALY cannot be explained via a change in amplifier.

8.3.3.1 Borderline anomalies

In the N400 time window, the cross-experiment analysis of the borderline anomaly sentences showed an interaction of ANOMALY x LANGUAGE [lateral: $F(2,76) = 5.37, p < 0.01$; midline: $F(2,76) = 3.40, p < 0.05$].

The analysis of the late positivity time window, by contrast, did not show an ANOMALY x LANGUAGE interaction [ps < 0.3], but only main effects of ANOMALY and LANGUAGE.

8.3.3.2 Easy-to-detect anomalies

In spite of the qualitatively similar data patterns observed for the easy-to-detect anomalies in German and English, the analysis of the N400 time window showed an interaction of ANOMALY x LANGUAGE [lateral: $F(1,38) = 14.03, p < 0.001$; midline: $F(1,38) = 9.81, p < 0.01$]. This result indicates that the N400 effect for easy-to-detect anomalies was smaller in amplitude in the English experiment (Experiment 2b) as opposed to the German experiment (Experiment 2a).

In the late positivity time window, no interactions with LANGUAGE reached significance. Rather, we only observed a main effect of ANOMALY.

8.3.4   Discussion

The results of Experiment 2 replicate the findings of Experiment 1 and Sanford et al. (2011) for German and English, respectively. They thus demonstrate that the cross-linguistic difference suggested by the comparison of Experiment 1 and Sanford and colleagues' findings is indeed robust. This conclusion was supported by an additional cross-experiment analysis including the between-participants factor LANGUAGE, which revealed an interaction between ANOMALY and LANGUAGE in the N400 time window but not the late positivity time window for the borderline anomalies.

Interestingly, the cross-experiment analysis also showed an interaction with LANGUAGE in the N400 time window for the easy-to-detect anomalies, thus indicating that the magnitude of the N400 effect for this anomaly type varies across lan-

guage. Specifically, it appears to be less pronounced for English (Experiment 2b) than for German (Experiment 2a); visual inspection suggests a similar difference in magnitude between Experiment 1 and the data in Sanford et al. (2011). We shall return to this issue in the General Discussion, where we suggest that differences in N400 effect magnitude for the easy-to-detect anomalies can potentially be explained by the same mechanism that accounts for the cross-linguistic variation in the borderline anomalies.

Finally, the findings of Experiments 2a and 2b – when viewed in comparison to the results of Experiment 1 and those by Sanford et al. (2011) – suggest that the detection rates for borderline anomalies are subject to a certain degree of inter-individual variability, rather than being influenced systematically by the choice of task or the language under investigation. While the direct comparison of the behavioural findings between the two German studies (Experiment 1 and Experiment 2a) appear to suggest, at a first glance, that the methodology employed in Experiments 2a and 2b engenders higher detection rates, this assumption is not compatible with the comparison between the corresponding English experiments (Experiment 2b and Sanford and colleagues' 2011 study), which showed a reversed effect (a 55% detection rate in Experiment 2b versus a 63% detection rate in Sanford et al's experiment). Overall, these various comparisons do not show systematic differences in detection rate depending on task or language, but rather indicate that the detection rate in a give experiment depends, at least in part, on the particular sample of participants under examination.

8.4   General Discussion

The results of recent ERP studies indicate that the N400 effect elicited by semantic manipulations is subject to systematic cross-linguistic variation in some cases, as reflected in diverging electrophysiological responses to semantic reversal anomalies in English and German. Here, we investigated the processing of German and English borderline and easy-to-detect anomalies to test whether language-specific patterns would also be found in this case. We thereby aimed to provide new evidence regarding the functional mechanism(s) underlying the N400.

Three ERP experiments confirmed our predictions regarding cross-linguistic differences in the electrophysiological response to borderline anomalies. For German, Experiments 1 and 2a demonstrated a biphasic N400 - late positivity response to detected borderline anomalies in comparison to both non-detected anomalies and plaus-

ible controls. For English, by contrast, Experiment 2b replicated previous findings by Sanford et al. (2011) in showing only a late positivity effect for detected borderline anomalies versus both non-detected anomalies and controls, but no N400 effect. For classic easy-to-detect anomalies with a poor fit to the global context, all of our experiments showed a similar result (as also observed by Sanford et al., 2011), namely a biphasic N400 - late positivity pattern for anomalous versus plausible sentences.[10]

In view of these findings, the following discussion focuses mainly on the implications of the differential results found for English and German for current accounts of the lexical-semantic N400. We will propose an analysis that accounts for both the English and German patterns and also provides a potential explanation for task-dependent variation within a language. We will also touch briefly on the late positivity effects found in both German and English; however, the discussion is mainly centred around the N400, since this is the effect that differentiates the neural responses to borderline anomalies in the two languages.

8.4.1   Cross-linguistic differences in the N400

8.4.1.1 Challenges for preactivation-based (lexical) accounts of the N400

Several accounts have been put forward with respect to the underlying mechanisms of the N400. The two most prominent theories link N400 modulations to (i) the costs of integrating new information into an ongoing meaning representation (integration view) (e.g. Hagoort & van Berkum, 2007; Hagoort, 2008); or (ii) to the accessibility of a word's lexical representation as determined by its "preactivation" (lexical preactivation view) (e.g. Kutas & Federmeier, 2000; Lau et al., 2008). Recently, lexical accounts have been advocated by a number of researchers on the basis of findings such as the fact that semantic reversal anomalies typically do not engender N400 effects in English and that N400 amplitude therefore does not appear to reflect message-level plausibility (e.g. Brouwer et al., 2012; Stroud & Phillips, 2012). Since the com-

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[10] Note that, while semantic anomalies were traditionally associated with a monophasic N400 response (Kutas & Hillyard, 1980), a range of studies have now observed biphasic N400 - late positivity patterns in response to "classic" (easy-to-detect) semantic violations (e.g. Faustmann, Murdoch, Finnigan, & Copland, 2007; Gunter, Jackson, & Mulder, 1992; Roehm, Bornkessel-Schlesewsky, Rösler, & Schlesewsky, 2007; Sanford et al., 2011) and to semantic reversal anomalies (Bornkessel-Schlesewsky et al., 2011; Bourguignon et al., 2012). It has not yet been shown conclusively under which conditions semantic incongruities engender a late positivity in addition to an N400, though van de Meerendonk, Kolk, Vissers, & Chwilla (2010) recently suggested that this may be related to the strength of the incongruity.

paratively low detection rates for borderline anomalies appear to be connected to the close semantic fit of the critical word to the global context (Barton & Sanford, 1993), the absence of an N400 effect for English borderline anomalies also seemed best explained in terms of lexical preactivation. The findings of the current study, however, challenge this interpretation. As the stimuli used in the German experiments were kept as similar as possible to the English materials and the degree of contextual fit in the respective conditions was almost identical between the two languages (see section 2.1.2), the lexical preactivation perspective does not account for the presence of an N400 effect for detected borderline anomalies in German.

Moreover, the qualitative differences in the processing of German and English are further corroborated by the finding of comparable electrophysiological dissociations in two different domains: semantic reversal anomalies (Bornkessel-Schlesewsky et al., 2011) and the borderline anomalies reported in the present study. These results thus call for an account in which an N400 modulation reflects more than a purely top-down influence of contextually generated lexical preactivation.

8.4.1.2 The interplay of top-down and bottom-up information sources

We propose that the cross-linguistic differences in question are most adequately explained within accounts that emphasise the interplay of top-down and bottom-up information sources in lexical-semantic N400 modulations (e.g. Federmeier, 2007; Lotze, Tune, Schlesewsky, & Bornkessel-Schlesewsky, 2011). Lotze and colleagues, for example, observed a change in N400 amplitude due to a purely form-based, bottom-up manipulation, which modulated neither lexical preactivation nor ease of integration (i.e. capitalisation of a semantically incongruous sentence-final word). Additional evidence in favour of their "bidirectional coding account" stems from studies that have demonstrated an influence of discourse and information structure (Burkhardt, 2006; Schumacher, 2009) or prosody (Schumacher & Baumann, 2010) on the N400. From a cross-linguistic perspective, the bidirectional coding account allows for a modulation of the proposed interactive mechanism by assuming that different languages vary with regard to their (default) relative weighting of top-down and bottom-up information sources. It also provides a potential explanation for task effects, assuming that task can modulate the top-down/bottom-up balance (e.g. in the sense of a rational adaptation to current task constraints; Howes, Lewis, & Vera, 2009). In the

following, we will discuss the general assumptions of the account in more detail as well as how it applies to the processing of English and German borderline anomalies, respectively.

During sentence interpretation, language processing requires the use of various cues in the input. Top-down influences include semantic cues such as global contexts and lexical associations at a more local level. Additionally, there are grammatical cues, with position and word order having special status. Because language unfolds over time, word order is a cue that is equally accessible in all human languages, whereas availability of other grammatical cues is dependent on characteristics of the language in question (see Bornkessel-Schlesewsky et al., 2011, for discussion).

The semantic cues provided by context serve to activate potential referents and concepts. Concomitantly, grammatical cues focus the predictions for upcoming words (e.g., via category restrictions). If grammatical cues induce the anticipation of a noun, this can lead to decreased activation of verbs and consequently to stronger predictions. While this basic principle is assumed to hold for all languages, individual languages differ with respect to the balance of top-down and bottom-up influences. Specifically, the degree to which interpretation is driven by word order seems to play a crucial role: though German and English are closely related, they show substantial differences with regard to the extent of their dependency on word order in interpretation.

In English, rigid word order gives rise to a high degree of position-based predictability and to a dominant top-down influence. The importance of word order as a cue to sentence interpretation in English has been well studied, but most prominently by those within the framework of the competition model. MacWhinney et al. (1984) describe that word order clearly overrides agreement as a cue to sentence interpretation in English: "When given a sentence like 'The pencil are kicking the cows', English and Italian listeners make their decisions in entirely opposite directions" (MacWhinney et al., 1984, p. 144), i.e., English listeners choose a subject-verb-object (SVO) interpretation while Italian listeners interpret the structure as object-verb-subject (OVS). In terms of the bidirectional coding account, the pronounced positional predictability leads to strong expectations, and reduction in the probability of encountering certain words as opposed to others. The dominance of top-down information also means that the influence of potentially conflicting bottom-up information is signifi-

cantly weaker: no problem is recognized unless there is a category error or failed expectation. For borderline anomalies, neither of these occurs as the context leads to strong lexical associations and preactivation (including that of the critical, locally implausible word), with category expectations satisfied at the same time. This is reflected in the absence of an N400 effect for English borderline anomalies.

Importantly, the N400 observed for easy-to-detect anomalies can be explained by the same basic mechanism. In contrast to the borderline anomalies, the critical word in these semantic anomalies has a very poor fit to the global context and is therefore not preactivated during discourse processing. The lack of lexical preactivation leads to a conflict, and thus engenders an N400 effect for anomalous words.

German, by contrast, is a language that allows for more flexible word order, thus rendering positional predictability considerably weaker. As a result, bottom-up cues such as morphological case marking or agreement are more important for sentence interpretation (cf. MacWhinney et al., 1984, who use the terms "local" vs. "topological" cues for a similar distinction to that framed in terms of bottom-up vs. top-down cues here). Without strong top-down expectations, these bottom-up features must be matched against the sentence context to determine the relation of the current word to previous discourse. In borderline anomalies, the implausibility is introduced by a mismatch between the critical word and a preceding local context word. As a result of the stronger weighting of bottom-up information in German, this mismatch has a stronger impact as reflected by the presence of an N400 effect for detected borderline anomalies. This account further explains why the amplitude of the N400 effect is more pronounced for the easy-to-detect anomalies than for the borderline anomalies, since the former involve a stronger conflict between bottom-up and top-down information in the absence of lexical preactivation.

In summary, the interaction of top-down and bottom-up information is subject to cross-linguistic variation, with the importance of word order in interpretation constituting the crucial difference between German and English. Despite comparable preactivation for the critical word in borderline anomalies in German and English, only German requires strong focus on bottom-up information. The mismatch between the critical word and the local sentence context yields the N400 effect in German because of the grammatically motivated weighting of bottom-up information that is significant in German and negligible in English.

This account can also explain the cross-linguistic differences in the magnitude of the N400 effect for easy-to-detect anomalies. Recall that the statistical analysis comparing Experiments 2a and 2b revealed a less pronounced N400 effect for English in contrast to German, similar to the visual comparison of Experiment 1 and Sanford et al.'s (2011) findings. If the threshold for inducing a bottom-up mismatch between a word and its preceding context is higher in English than in German – even if this threshold is exceeded by the easy-to-detect anomalies in both languages – it is exceeded to a higher degree in German. Thus, in spite of comparable fit to the global context (or lack thereof) and virtually identical detection accuracy in both languages, the N400 effect for the easy-to-detect anomalies appears to be reliably larger in German in comparison to English. This could suggest that a smaller number of easy-to-detect anomaly trials engenders an N400 effect in English compared to German (i.e. the bottom-up-threshold is exceeded only in a certain number of cases). Note that this variation in the N400 is independent of detection accuracy, an issue which we will discuss in more detail in the following section.

8.4.2 **Neural correlates of anomaly detection and the late positivity**

It is important to note that the dominance of top-down influences in English does not imply that English speakers should be more susceptible to semantic illusions. The comparable anomaly detection rates for English and German (see section 3.4 for discussion) show that this is not the case. In other words, the presence or absence of an N400 effect is not directly correlated with the detectability of a distorted meaning, but reflects a language-specific interaction of the cues that drive interpretation. Depending on the importance of specific cues for interpretation, a conflict may or may not be registered during this phase of processing. Detection may, however, occur later. Accordingly, we argue that anomaly detection is reflected in the late positivity that follows the N400, but not in the N400 itself. This view is supported by the presence of a significant correlation between individual detection rates for borderline anomalies and late positivity effect in Experiment 1 measured at electrode POZ [$r(21) = .43$, $p < 0.05$], and the lack of such correlation between the mean anomaly detection rate per participant and the N400 effect [$r(21) = -.11$, $p = 0.67$]. These results are also in line with findings by Kolk, van Herten and colleagues, which suggest that conflict detection correlates with positivity effects (e.g. Kolk et al., 2003; van Herten, Kolk, &

Chwilla, 2005; van Herten, Chwilla, & Kolk, 2006). Since the presence of a late positivity for German borderline and easy-to-detect anomalies mirrors the results found in English, we refer to Sanford et al. (2011) for a more detailed discussion of this effect.

8.4.3   Outlook: Modulating the top-down/bottom-up balance

A question that arises from our interpretation of the present findings is whether and how the balance between top-down and bottom-up factors during language comprehension can be modified. As suggested by Bohan et al.'s (2012) findings, it may be possible to induce N400 effects for borderline anomalies in English with a suitable task manipulation. This indicates that the top-down/bottom-up balance is not fixed at a set level within a language, but can vary depending on the experimental environment.

Previous behavioural results suggest that manipulating sentence focus can increase detection rates of Moses-type illusions (e.g., by means of it-clefts such as "It was Moses who took two animals of each kind on the Ark. True or False?", Brédart & Modolo, 1988), as can increasing the difficulty of a font in reading (Song & Schwarz, 2008). In addition, Wang, Hagoort and Yang (2009) observed an increased N400 effect for contextually inappropriate vs. appropriate continuations in Chinese when the critical word was in focus. Taken together, these results suggest that the manipulation of (certain) structural and physical properties may lead to an increased salience of bottom-up information; a comparable manipulation could thus help induce an N400 effect for borderline anomalies in English.

Another possibility lies in manipulating the linguistic content itself. For example, if the critical word were to induce a morphosyntactic mismatch (e.g., an agreement violation), this could increase the degree of bottom-up processing. Similar outcomes can also be achieved by information at the syntax-semantics interface, e.g. verbs with non-standard mappings from form to meaning. Bourguignon et al. (2012) observed N400 rather than late positivity effects for semantic reversal anomalies in English when these were induced by Experiencer-verbs instead of standard action (Agent-Patient) verbs. This suggests that a verb which requires such a non-standard form-to-meaning mapping could lead to an increased consideration of bottom-up information.

Finally, as suggested by Bohan et al.'s (2012) findings, task demands might also

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modulate the bottom-up/top-down balance. By focusing participants' attention on judgement accuracy, the importance of bottom-up information is increased. (For further evidence regarding task-based modulations of electrophysiological activity within the N400 time window, see Haupt, Schlesewsky, Roehm, Friederici, & Bornkessel-Schlesewsky, 2008).

In summary, we propose that the cross-linguistic variation reported here (and that previously observed for semantic reversal anomalies) reflects differences in the default weighting of top-down versus bottom-up information in a given language. In this framework, these weights are not fixed, but can vary depending on the contextual environment. Importantly, however, in the majority of ecological situations, German and English call for a differential weighting of top-down and bottom-up information.

8.5   Conclusion

The present findings demonstrate that the N400 response to semantic anomalies is subject to cross-linguistic variation. We interpret this result as arising from the interplay between top-down and bottom-up factors during language processing and the importance of these different information sources in a given language. We suggest that in languages with a relatively strict word order (e.g. English) and concomitant top-down predictability, language comprehension is constrained much less by bottom-up factors than in a language in which item-based information is more directly relevant for sentence understanding (e.g. German, in which morphological case marking and animacy play important roles in interpretation). We assume that the N400 reflects the degree of match between top-down and bottom-up information sources and that this is why German shows an N400 effect for borderline anomalies while English does not.

8.6   References

Barton, S. B., & Sanford, A. J. (1993). A case-study of anomaly detection: Shallow semantic processing and cohesion establishment. *Memory and Cognition*, *21*, 477-487.

Bates, E., Devescovi, A., & Wulfeck, B. (2001). Psycholinguistics: A cross-language perspective. *Annual Review of Psychology*, *52*, 369-396.

Bohan, J., & Sanford, A. J. (2008). Anomaly detection at the borderline of consciousness: An eyetracking study. *Quarterly Journal of Experimental Psychology*, *61*, 232-239.

Bohan, J., Sanford, A. J., Glen, K., Clark, F., & Martin, E. (2008). Focus and emphasis devices modulate depth of processing as reflected in semantic anomaly detection. Poster presented at the 14th Architectures and Mechanisms for Language Conference, Cambridge, UK.

Bohan, J., Leuthold, H., Hijikata, Y., & Sanford, A. J. (2012). The processing of good-fit semantic anomalies: An ERP investigation. Neuropsychologia, 50(14), 3174-3184.

Bornkessel-Schlesewsky, I., Kretzschmar, F., Tune, S., Wang, L., Genç, S., Philipp, M. et al. (2011). Think globally: Cross-linguistic variation in electrophysiological activity during sentence comprehension. *Brain and Language*, *117*, 133-152.

Bornkessel-Schlesewsky, I., & Schlesewsky, M. (2008). An alternative perspective on "semantic P600" effects in language comprehension. *Brain Research Reviews*, *59*, 55-73.

Brédart, S., & Modolo, K. (1988). Moses strikes again: Focalisation effect on a semantic illusion. *Acta Psychologica*, *67*, 135-144.

Brouwer, H., Fitz, H., & Hoeks, J. C. J. (2012). Getting real about semantic illusions: Rethinking the functional role of the P600 in language comprehension. Brain Research, 1446, 127-143.

Bourguignon, N., Drury, J. E., Valois, D., & Steinhauer, K. (2012). Decomposing animacy reversals between agents and experiencers: An ERP study. Brain and Language, 122, 179-189.

Burkhardt, P. (2006). Inferential bridging relations reveal distinct neural mechanisms: Evidence from event-related brain potentials. *Brain and Language*, *98*, 159-168.

Büttner, A. C. (2007). Questions versus statements: Challenging an assumption about semantic illusions. *Quarterly Journal of Experimental Psychology, 60*(6), 779-789.

Daneman, M., Reingold, E. M., & Davidson, M. (1995). Time course of phonological activation during reading: Evidence from eye fixations. *Journal of Experimental Psychology: Learning, Memory and Cognition*, *21*, 884-898.

Erickson, T. A., & Matteson, M. E. (1981). From words to meaning: A semantic illusion. *Journal of Verbal Learning and Verbal Behavior*, *20*, 540-552.

Faustmann, A., Murdoch, B. E., Finnigan, S. P., & Copland, D. A. (2007). Effects of advancing age on the processing of semantic anomalies in adults: Evidence from event-related brain potentials. E*xperimental Aging Research, 3*3, 439-460.

Ferreira, F., Ferraro, V., & Bailey, K. G. D. (2002). Good-enough representations in language processing. *Current Directions in Psychological Science*, *11*, 11-15.

Gunter, T. C., Jackson, J. L., & Mulder, G. (1992). An electrophysiological study of semantic processes in young and middle-aged academics. P*sychophysiology, 2*9, 38-54.

Hagoort, P. (2008). The fractionation of spoken language understanding by measuring electrical and magnetic brain signals. *Philosophical Transactions of the Royal Society B*, *363*, 1055-1069.

Hagoort, P., & van Berkum, J. J. A. (2007). Beyond the sentence given. *Philosophical Transactions of the Royal Society B*, *362*, 801-811.

Hannon, B., & Daneman, M. (2001). Susceptibility to semantic illusions: An individual-differences perspective. *Memory and Cognition*, *29*, 449-461.

Hannon, B., & Daneman, M. (2004). Shallow semantic processing of text: An individual-differences account. *Discourse Processes*, *37*, 187-204.

Haupt, F. S., Schlesewsky, M., Roehm, D., Friederici, A. D., & Bornkessel-Schlesewsky, I. (2008). The status of subject-object reanalyses in the language comprehension architecture. *Journal of Memory and Language, 59*, 54-96.

Hoeks, J. C. J., Stowe, L. A., & Doedens, G. (2004). Seeing words in context: The interaction of lexical and sentence level information during reading. *Cognitive Brain Research*, *19*, 59-73.

Howes, A., Lewis, R. L., & Vera, A. (2009). Rational adaptation under task and processing constraints: Implications for testing theories of cognition and action. *Psychological Review, 116*, 717-751.

Huynh, H., & Feldt, L. S. (1970). Conditions under which the mean-square ratios in repeated measurement designs have exact F-distributions. *Journal of the American Statistical Association*, *65*, 1582-1589.

Jung, T. P., Makeig, S., Humphries, C., Lee, T. W., McKeown, M. J., Iragui, V., & Sejnowski, T. J. (2000). Removing electroencephalographic artifacts by blind source separation. *Psychophysiology*, 37(2), 163–178.

Keppel, G. (1991). *Design and analysis* (3rd ed.). Englewood Cliffs, NJ: Prentice Hall.

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

Kolk, H. H. J., Chwilla, D. J., van Herten, M., & Oor, P. J. (2003). Structure and limited capacity in verbal working memory: A study with event-related potentials. *Brain and Language*, *85*, 1-36.

Kuipers, J. R., & Thierry, G. (2011). N400 amplitude reduction correlates with an increase in pupil size. *Frontiers in Human Neuroscience*, *5*, 61.

Kuperberg, G. R., Sitnikova, T., Caplan, D., & Holcomb, P. (2003). Electrophysiological distinctions in processing conceptual relationships within simple sentences. *Cognitive Brain Research*, *17*, 117-129.

Kutas, M., & Federmeier, K. D. (2000). Electrophysiology reveals semantic memory use in language comprehension. *Trends in Cognitive Sciences*, *4*, 463-469.

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

Lakatos, P., Karmos, G., Mehta, A. D., Ulbert, I., & Schroeder, C. E. (2008). Entrainment of neuronal oscillations as a mechanism of attentional selection. *Science*, *320*, 110-113.

Lau, E., Phillips, C., & Poeppel, D. (2008). A cortical network for semantics: (de)constructing the N400. *Nature Reviews. Neuroscience*, *9*, 920-933.

Lotze, N., Tune, S., Schlesewsky, M., & Bornkessel-Schlesewsky, I. (2011). Meaningful physical changes mediate lexical-semantic integration: Top-down and form-based bottom-up information sources interact in the N400. *Neuropsychologia*, *49*, 3573-3582.

MacWhinney, B., Bates, E., & Kliegl, R. (1984). Cue validity and sentence interpretation in English, German and Italian. *Journal of Verbal Learning and Verbal Behavior*, *23*, 127-150.

Mathewson, K. E., Lleras, A., Beck, D. M., Fabiani, M., Ro, T., & Gratton, G. (2011). Pulsed out of awareness: EEG alpha oscillations represent a pulsed-inhibition of ongoing cortical processing. *Frontiers in Psychology*, *2*, 99.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*, 97-113.

Reder, L. M., & Kusbit, G. W. (1991). Locus of the Moses Illusion: Imperfect encoding, retrieval or match? *Journal of Memory and Language*, *31*, 385-406.

Roehm, D., Bornkessel-Schlesewsky, I., Rösler, F., & Schlesewsky, M. (2007). To predict or not to predict: Influences of task and strategy on the processing of semantic relations. *Journal of Cognitive Neuroscience*, *19*, 1259-1274.

Sanford, A. J., & Garrod, S. (1998). The role of scenario mapping in text comprehension. *Discourse Processes*, *26*, 159-190.

Sanford, A. J., & Graesser, A. C. (2006). Shallow processing and underspecification. *Discourse Processes*, *2*, 99-108.

Sanford, A. J., Leuthold, H., Bohan, J., & Sanford, A. J. S. (2011). Anomalies at the Borderline of Awareness: An ERP Study. *Journal of Cognitive Neuroscience*, *93*, 514-523.

Sanford, A. J., & Sturt, P. (2002). Depth of processing in language comprehension: not noticing the evidence. *Trends in Cognitive Sciences*, *6*, 382-386.

Schlesewsky, M., & Bornkessel-Schlesewsky, I. (2009). When semantic P600s turn into N400s: On cross-linguistic differences in online verb-argument linking. In M. Horne, M. Lindgren, M. Roll, K. Alter, & J. v. K. Torkildsen (Eds.), *Brain Talk: Discourse with and in the brain. Papers from the first Birgit Rausing Language Program Conference in Linguistics* (pp. 75-97). Lund: Birgit Rausing Language Program.

Schumacher, P. B. (2009). Definteness marking shows late effects during discourse processing: Evidence from ERPs. In S. L. Devi, A. Branco, & R. Mitkov (Eds.), *Anaphora processing and applications* (pp. 91-106). Heidelberg: Springer.

Schumacher, P. B., & Baumann, S. (2010). Pitch accent type affects the N400 during referential processing. *Neuroreport*, *21*, 618-622.

Shafto, M. & McKay, D.G. (2000). The Moses, mega-Moses, and Armstrong illusions: Integrating language comprehension and semantic memory. *Psychological Science, 11*(5), 372-378.

Song, H., & Schwarz, N. (2008). Fluency and the detection of misleading questions: Low processing fluency attenuates the Moses illusion. *Social Cognition, 26*, 791-799.

Stroud, C., & Phillips, C. (2012). Examining the evidence for an independent semantic analyzer: An ERP study in Spanish. *Brain and Language*, *120*, 108-126.

van de Meerendonk, N., Kolk, H. H. J., Chwilla, D. J., & Vissers, C. T. W. M. (2009). Monitoring in language perception. *Language and Linguistics Compass*, *3*, 1211-1224.

van de Meerendonk, N., Kolk, H. H. J., Vissers, C. T. W. M., & Chwilla, D. J. (2010). Monitoring in Language Perception: Mild and Strong Conflicts Elicit Different ERP Patterns. J*ournal of Cognitive Neuroscience, 22*, 67-82.

van Herten, M., Chwilla, D. J., & Kolk, H. H. J. (2006). When heuristics clash with parsing routines: ERP evidence for conflict monitoring in sentence perception. *Journal of Cognitive Neuroscience*, *18*, 1181-1197.

van Herten, M., Kolk, H. H. J., & Chwilla, D. J. (2005). An ERP study of P600 effects elicited by semantic anomalies. *Cognitive Brain Research*, *22*, 241-255.

Van Oostendorp, H., & DeMul, S. (1990). Moses beats Adam: A semantic relatedness effect on a semantic illusion. *Acta Psychologica*, *74*, 35-46.

Viola, F. C., Thorne, J., Edmonds, B., Schneider, T., Eichele, T., & Debener, S. (2009). Semi-automatic identification of independent components representing EEG artifact. *Clinical Neurophysiology*, *120*, 868-877.

Wang, L., Hagoort, P., & Yang, Y. (2009). Semantic illusion depends on information structure: ERP evidence. *Brain Research*, *1282*, 50-56.

9   STUDY 3

Depth of semantic processing in discourse context modulates contributions of temporal and parietal regions: fMRI evidence.

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ABSTRACT

Neuroimaging studies investigating semantic processes in language comprehension have predominantly focused on single words and sentences, leaving aside contextual influences present in natural communication. In the present study, we used contextually embedded easy to detect and more subtle borderline anomalies to examine how predictions, expectations and semantic associations impact on the depth of processing. We found that analysis and interpretation of the sentence pairs involved a complex set of brain regions in the frontal, temporal and inferior parietal lobes. In contrast to results of single sentence studies, the intensity and extent of neural activity observed in these regions were largely balanced across hemispheres. We suggest that this reflects cognitive processes like coherence establishment, inference making, and/or the matching of predictions against world knowledge required in semantic analysis at a more complex level. Borderline anomalies showed more extensive activation in areas of the prefrontal cortex, consistent with its role in domain general processes of cognitive control. In addition, anomaly types differed with respect to patterns of neural activity in temporal and inferior parietal regions observed relative to control sentences. Processing of easy to detect anomalies led to stronger responses in temporal regions, whereas detected borderline anomalies showed increased engagement of inferior parietal regions. We suggest that this distinction reflects differences in the required depth of semantic processing: whereas increased involvement of parietal regions correlates with the need for context-based inferencing, contributions of temporal regions indicate mismatches at a less complex level.

Keywords: language processing, fMRI, borderline anomalies, processing depth, prediction

9.1   Introduction

The principal goal of language comprehension in natural communicative settings is to arrive at the most meaningful interpretation of the input, such that this information can be used to guide interaction with the environment. To this end, in a very short amount of time, a plethora of flexible semantic relationships need to be analysed against a background of expectations derived from previous discourse (among other sources). The specific nature of the neural mechanisms and principles engaged in this process remains insufficiently characterized despite the fact that many neuroimaging studies have sought to examine it using functional magnetic resonance imaging (fMRI) or positron emission tomography (PET). The majority of these studies have investigated semantic processing at the word or single sentence level, where research questions have typically focused on the segregation of brain regions or networks involved in combinatorial semantic processes from those engaged in syntactic analysis. To isolate brain activity related to semantic processes, common experimental manipulations include incongruencies between a critical word and the sentence context or different degrees of intra-sentential semantic coherence. Such sentences are typically contrasted with non-anomalous sentences, syntactic violations or syntactically well-formed sentences with random content words that do not allow for a coherent semantic interpretation (e.g., Ni et al., 2000; Newman et al., 2001; Vandenberghe et al., 2002; Friederici et al., 2003; Humphries et al., 2006, 2007). Yet, the analysis of meaning in real world situations typically involves utterances that go beyond the level of isolated sentences and therefore recruit additional cognitive processes. These include integrating the information from an utterance with the background of expectations evoked through prior context and with factual knowledge about the state of affairs in the world. Consider for example the following sentence pair that was used in an English ERP study by Federmeier and Kutas (1999).

(1)   They wanted to make the hotel look more like a tropical resort.

         So along the driveway, they planted rows of <u>palms/pines/tulips</u>.

Here, the information provided by the context sentence creates a global scenario that leads to very specific expectations for the sentence final word (underlined). While all three versions of the second sentence are *per se* semantically coherent, as

their final words describe plantable entities, only the first version has a close fit to the scenario currently under discussion. In this case the sentence final word "palms" is a highly representative exemplar of plants typically found in a tropical environment. Pines and tulips both lack this specific association with the global scenario since they only share some of the most basic semantic features with the expected continuation (i.e., they belong to the category "trees" or the higher-level category "plants"). A word's fit to a described event is one major way in which language can inform us with respect to what we believe about the world, by either confirming or disproving our assumptions and predictions regarding a current scenario.

The importance of global context in semantic processing is aptly illustrated by a particular class of semantic anomalies, so-called "anomalies at the borderline of awareness" or simply "borderline anomalies" (Sanford et al., 2011), of which the "Moses illusion" is the most famous example (Erickson and Mattson, 1981). These semantic illusions are particularly hard to detect because the anomaly-inducing word has a strong semantic relationship to the meanings of the words and even to the propositional content of the context. In their seminal study on the Moses illusion, Erickson and Mattson (1981) asked participants to read and answer a number of questions, some of which were designed to elicit semantic illusions. For the anomalous question "*How many animals of each kind did Moses take on the ark?*" the authors found that fewer than 20% of the participants noticed the distortion even though they had the relevant knowledge that in the biblical story, Noah, not Moses, took animals onto the ark. Several theoretical accounts aim to explain the linguistic features and cognitive processes involved in the occurrence of the illusion (Park and Reder, 2004). One of the most widely accepted of these accounts builds on the basic assumption that language comprehension, like other higher cognitive processes, is rarely exhaustive and is more commonly guided by simple heuristics. In the case of the Moses illusion, the high degree of semantic similarity between the anomalous and correct term on the one hand, and the conceptual relatedness of the incorrect term and the surrounding context on the other lead to an incomplete but partly satisfying fulfilment of many semantic predictions, both at the immediate level and with respect to general knowledge. Crucially, processing mechanisms that rely on an incomplete match between predictions and the actual input are more economic in terms of recruiting processing resources but they also increase the susceptibility to semantic illusions (Erickson and

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Mattson, 1981; Van Oostendorp and De Mul, 1990; Van Oostendorp and Kok, 1990; Reder and Kusbit, 1991; Hannon and Daneman, 2001).

In the present study, we aimed to examine how the processing of words and concepts interacts with the expectations from local and global context to lead to deep or superficial interpretations. To this end, we employed "mini discourses" composed of two semantically related sentences, and contrasted the processing of easy to detect anomalies with the more subtle borderline anomalies. In easy to detect anomalies – perhaps comparable to intra-sentential incongruencies – the lexical meaning of the critical word leads to failed expectations both at the local context level, but also with respect to the more global scenario. Borderline anomalies, by contrast, evoke a number of associations that are semantically related to the global scenario and thus fulfil the ongoing expectations to a considerable degree. In the original Moses illusion, for example, Moses can generally be linked to a biblical context, and to various stories that involve a male character taking direction from God about leading his people, etc., in short, associations that also closely match the episode of building the ark. It is only upon closer scrutiny that the mismatch between the critical word and our background assumptions about the current event becomes apparent. Thus, for easy to detect anomalies, the global context provides clear expectations that bear on the proposition expressed by the critical sentence and facilitate detection of the anomaly. For borderline anomalies, the global context provides expectations that actually enhance the perception of a semantic illusion, which is why successful detection of an anomaly requires a more extensive evaluation of the encountered proposition.

Brain activation during the processing of sentences with readily detectable semantic violations compared to those without such violations typically involves the left hemisphere in a number of frontal, temporal and inferior parietal regions (Lau et al., 2008). Relatively few studies have explicitly aimed to disentangle the roles of local and global semantic expectations on the processing of semantic violations. With few exceptions, the relevant studies were restricted to single sentences, thus removing an important source of global expectation that has significant effects on interpretation. One fMRI study of single sentence reading used stimuli such as "*The Dutch trains are yellow/white/sour* ..." to compare brain activity in response to different types of semantic violations (Hagoort, 2004). The statement that the national trains are white allows for a coherent semantic interpretation that is nevertheless factually incorrect

since, for Dutch people, it is a well-known fact that the trains are yellow. The description of Dutch trains as sour, by contrast, is a more elementary semantic anomaly because of a mismatch between the expectation pertaining to core semantic features derived from interpretation of the noun phrase and the predicative adjective. Hagoort et al. found increased activation in the left inferior frontal gyrus (IFG), more specifically in the pars triangularis and pars orbitalis (roughly corresponding to BA 45 and 47) for each of the two anomalous conditions relative to the control condition, which they interpret as evidence for an important role of these regions in the retrieval and integration of both lexical semantic and real-world knowledge.

To further corroborate these assumptions and to investigate the interaction of local context and world knowledge, Menenti and colleagues (2009) adapted the original design by introducing a contextual manipulation. They found that by preceding an unlikely or implausible event with mitigating context, they could attenuate the activation increase for anomalous sentences compared to non-anomalous sentences. Strong statistical evidence suggested an interaction between context type (neutral vs. mitigating) and semantic anomaly (anomalous vs. correct control) in the left angular gyrus, with w evidence also implicating the right anterior IFG (pars triangularis and pars orbitalis). A similar trend was found for homologous regions of the left IFG where the comparison of neural activity in response to anomalous and non-anomalous sentences following mitigating context yielded little to no activation. In absence of an interaction, several other regions showed differential degrees of neural activity elicited by anomalous and non-anomalous sentences in a neutral context and a lack of such a difference in the brain response to sentences presented with mitigating context. These regions included the right middle temporal gyrus (BA 21) and caudate nucleus as well as the angular gyrus (BA39) and parts of the superior frontal gyrus bilaterally (BA 9). The contrast of semantic violations and control sentences embedded in neutral context replicates Hagoort et al. (2004), who also reported an increased involvement of the left pars triangularis and pars orbitalis. However, the data also suggest that several regions of the right hemisphere might play an important role in comprehension by supporting predictions based on contextual information.

While classical neurological models of language processing postulated that human language is predominantly processed in the left hemisphere, it is nowadays undisputed that the right hemisphere is engaged at least to a degree in most language-

related processes. The precise nature of language comprehension (and other higher-cognitive) circuits of the left and right hemispheres – and of their interactions – remains a topic of tremendous interest. There are accounts based on evidence from neuropsychological and neuroimaging research as well as from clinical observations that suggest higher-cognitive processes involved in reasoning, inference drawing, theme identification and discourse integration may be relatively right lateralised compared to other processes, e.g., certain phonological and syntactic processes, which tend to have a left predominance. All of these mechanisms are necessary for an analysis of semantic meaning that is informed by semantic associations and predictions based on input beyond the level of single words or sentences (for reviews see Bookheimer, 2002; Mar, 2004; Jung-Beeman, 2005; Mitchell and Crow, 2005).

In a similar spirit, Kuperberg and colleagues (2008) used fMRI to investigate whether different types of violations would engage distinct areas or networks in the brain during single sentence reading. They included stimuli that described very unlikely events such as "*Every morning at breakfast the boys would plant the flowers*" and examined the intersection of brain responses to these unexpected events, to morphosyntactic and animacy violations as well as to non-anomalous control sentences. They found that pars orbitalis of the left IFG (BA47) showed a stronger response to these unlikely scenarios than to the other sentences types. For the given example, the beginning of the sentences leads to specific expectations for activities that one typically engages in during breakfast and the increased neural activity in pars orbitalis may reflect the failure of such predictions upon encountering the non-finite verb.

Ferstl and von Cramon (2001) reported results from an fMRI study that explored semantic coherence in sentence pairs. When comparing the processing of coherent and incoherent sentence pairs, the authors found activation in a portion of the left posterior cingulate cortex (PCC) and the neighbouring inferior precuneus as well as the left superior frontal gyrus. The authors argue that higher levels of neural activity found in the PCC for coherent relative to incoherent sentences reflect a contribution of this region to processes related to the continuous integration of incoming information into an initially established situation model. With regard to the findings on the left superior frontal gyrus, they suggest that this region engages in controlled inference. This might be initiated when the most dominant (lexical-semantic) associa-

tions evoked by presented information fail to establish coherence between individual parts of discourse.

Finally, a recent fMRI study on the Moses illusion (Raposo and Marques, 2013) used cleft sentences expressing true or false statements. Among the false statements were obvious semantic anomalies and more subtle incongruencies (e.g., "*It was the terrible stepmother who tried to kill Cinderella with a poisoned apple*"). For subtle semantic mismatches compared to true statements, the authors report an increased neural response in the left precentral gyrus, posterior cingulate cortex and putamen and the right inferior parietal lobule (IPL). Because this contrast included both detected and non-detected semantic illusions, the results are not readily comparable to previous findings. A separate analysis revealed that individual detection rates correlated with an increase in activation intensity for detected compared to non-detected anomalies in some frontal-parietal regions including the right pars triangularis of IFG, orbitofrontal cortex and insula as well as the left pre- and postcentral gyrus, anterior cingulate gyrus and occipital gyrus. With respect to the first analysis, the authors suggest that the stronger response found in the right IPL for semantic illusion sentences relative to controls might reflect higher inference demands needed for semantic interpretation. Furthermore, they suggest that the stronger response elicited by detected compared to non-detected illusions in lateral prefrontal regions of the right hemisphere and the left anterior cingulate implicates a possible role of these regions in conflict monitoring processes.

In light of these previous findings we formulated a number of hypotheses for the present study. We first hypothesized that brain activation for processing sentences with detected anomalies compared to sentences without anomalies would differ depending on the specific role of contextual information and the required degree of processing depth. For easy to detect anomalies, we expected increased activation in the left IFG and middle temporal gyrus, with possible additional activity in adjacent areas of the superior and inferior temporal lobe, as well as the most anterior part of the left temporal lobe. We based this expectation on (i) the results found for semantic violations in single sentence paradigms; and (ii) regions implicated in processes of basic combinatorial processing. In accordance with accounts that propose a domain general role of the left IFG in cognitive control mechanisms (Thompson-Schill et al., 1997; 2005; Miller and Cohen, 2001; Bornkessel-Schlesewsky and Schlesewsky, 2013), we

suggest that this region should show differential degrees of activation as a reflection of task difficulty across anomaly types. Our second hypothesis relates to the processing of sentences containing borderline anomalies compared to those with easy to detect anomalies. Since the analysis and judgement of borderline anomalies impose greater processing demands, we predicted higher levels of prefrontal activation for these items than for easy to detect sentences. Furthermore, we expected processing of borderline anomalies to produce more extensive involvement of the IPL than easy to detect sentences, since this region appears to play a role in semantic processing at a more complex conceptual level (Vigneau et al., 2006; Lau et al., 2008; Binder et al., 2009; Menenti et al., 2009). Our third hypothesis relates to the difference between processing sentence pairs compared to individual sentences. Processing language in context means that the interpretation of the second sentence of a pair is crucially influenced by predictions and semantic associations evoked by the preceding (context) sentence. Establishing coherence between two or more sentences might require controlled inference processes in cases where salient semantic associations elicited by separate input elements are mismatched at a more global level. Several brain regions have been implicated in an "extended language network" involved in processing language in context (Ferstl et al., 2008). In line with results from the meta-analysis by Ferstl and colleagues, we anticipated brain activation for processing sentence pairs (compared to individual sentences) to be increased (or added) in medial portions of the frontal and parietal lobes, particularly in the frontal-medial part of the superior frontal gyrus, the inferior precuneus and the PCC. To date, it is unclear whether those regions that are additionally recruited by processes of discourse comprehension compared to single sentence comprehension also engage in a more extensive semantic analysis. In the present work, we aim to shed light on this matter.

9.2   Materials and Methods

9.2.1   Participants

Twenty-two healthy, right-handed (indicated by an adapted German version of the Edinburgh Inventory of Handedness (Oldfield, 1971)) monolingually raised, native speakers of German participated in the fMRI study (11 women, mean age 24.5, range 20-30). All participants were recruited at the University of Marburg. They had normal

or corrected-to-normal vision and no known neurological, psychiatric or auditory disorders. Prior to the scanning session, participants were screened to ensure that they met all safety and participation requirements and they gave informed written consent. Four participants had to be excluded: two due to excessive motion, one due to structural abnormalities and one because of an incomplete functional run. The study was approved by the ethics committee at the University of Marburg.

9.2.2   Stimuli

The materials in the present study were identical to those used in the German ERP experiments reported in Tune et al. (under revision). They were a translated and adapted version of the English stimuli employed in an ERP study by Sanford et al. (2011). The experimental conditions (see Table 1 for examples) belonged to two types of semantic violations: hard to detect ("borderline") anomalies and more classic easy to detect anomalies (i.e., words with a poor fit to the context). Some of the original items needed to be excluded because the strength of the semantic illusion was weakened by translation to German or because they relied on knowledge that could not be presumed for German participants. Other items were modified in the sense that British characters, places and names were replaced by German equivalents to render the materials more relevant and applicable to the targeted test subjects.

To ensure that borderline anomalies were reliably missed some of the time and that easy to detect anomalies were categorised as incorrect at least 95% of the time, all materials were pre-tested in a questionnaire study. To this end, the stimuli were distributed across ten lists, each containing 13 borderline anomalies, 16 easy to detect anomalies and equal numbers of non-anomalous control items for both anomaly types. Each pseudo-randomised list was presented to seven participants, who were asked to indicate and explain any detected anomalies. The results of the questionnaire study showed that 68% of the presented borderline anomalies were correctly judged as being implausible. Twenty borderline items detected at a rate of above 75% were excluded and replaced by newly created items. The final set of materials was further subjected to an additional questionnaire study that investigated the contextual fit of the critical word. Following the procedure used by Sanford et al. (2011), this was accomplished by asking twenty participants to judge the relevance of the critical word to the situation on a 7-point Likert scale (1 = "does not fit", 7 = "perfect fit"). Borderline

anomalies and poor fit anomalies yielded mean ratings of 5.02 and 2.20, respectively, indicating that borderline anomalies showed a significantly better contextual fit than their poor fit counterparts ($t(210.201) = 18.54$, p < 0.0001). To account for unequal variances as indicated by Levene's test for homogeneity of variance, Welch's correction for the degrees of freedom was used.

In total, 180 stimulus sets consisting of an anomalous condition and a corresponding congruent control condition were constructed, 120 pairs for the borderline anomalies and 60 pairs for the easy to detect anomalies. All stimuli were composed of two semantically connected sentences, with the first sentence providing context, and a second, critical sentence, containing a target word which determined whether the sentence was semantically anomalous or not. All critical sentences consisted of 17 words; however, sentence structures and linguistic methods of inducing the anomalies differed across anomaly types. In the following, the different layouts will be described on the basis of German and English examples listed in Table 1.

Borderline anomalies

In the borderline anomaly condition, the second sentence was a thematic continuation of the context sentence and contained two alternative local context words (highlighted in italics in Table 1) and the critical target word (set in bold print in Table 1). The target word was always in the 13th word position and separated by five words from the contextual manipulation. For most items, the local context was altered by replacing one word only, while more words needed to be changed for a few others. It is the relation between local context word/phrase and target word that determines whether the latter is perceived to be anomalous. Therefore, upon encountering the target word, the listener/reader should be able to judge whether the sentence is plausible without needing any further input. However, borderline anomalies are often missed because the target word is highly associated semantically to the overall context, despite its implausibility for the meaning of the particular sentence in which it appears.

Table 1: Example items for each of the four experimental conditions. Target words are highlighted in bold print, contextual manipulations are given in italics.

German example with word-by-word translation	English example (Sanford et al., 2011)
Ein amerikanischer Jumbo jet wurde von bewaffneten Extremisten in Kanada zu landen gezwungen, und Experten waren schnell vor Ort, um zu *vermitteln*. An american jumbo jet was by armed extremists in Canada to land forced, and experts were quickly on site, for to *mediate*.	A North American jumbo jet was forced at gunpoint to land in Canada, experts were quickly on hand to help.
Die Lage beruhigte sich durch die *Verhandlungen* der Behörden mit den verängstigten **Geiseln**, die im Flugzeug saßen. The situation calmed itself by the *negotiations* of-the authorities with the scared **hostages**, who in-the plane sat.	First of all the authorities' initial *negotiations* with the scared and desperate **hostages** helped calm the situation.
Die Lage beruhigte sich durch die *Kommunikation* der Behörden mit den verängstigten **Geiseln**, die im Flugzeug saßen. The situation calmed itself by the *communications* of-the authorities with the scared **hostages**, who in-the plane sat.	First of all the authorities' initial *communications* with the scared and desperate **hostages** helped calm the situation.
Christian und Julias gemeinsamer Abend in dem neuen Restaurant war ein richtiger Reinfall. Christian and Julia's shared evening in the new restaurant was a proper letdown.	Denise and Fred's date to the new restaurant was a complete disaster.
Zuerst servierte ihnen der **Maler** die falschen Gerichte und dann wurde ihnen auch noch zu viel berechnet. First served them the **painter** the wrong meals and then was them also still too much charged.	They were given the wrong meals by the **painter** and then they were over-charged for their meals.
Zuerst servierte ihnen der **Kellner** die falschen Gerichte und dann wurde ihnen auch noch zu viel berechnet. First served them the **waiter** the wrong meals and then was them also still too much charged.	They were given the wrong meals by the **waiter** and then they were over-charged for their meals.

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Easy to detect anomalies

Sixty sets of easy to detect anomaly sentence were used. These sentence pairs were constructed in a similar manner to the borderline anomalies, but the internal structure of the critical sentences was less standardised because in these cases the anomaly is elicited by a single word with a very poor fit to both local and global context. The critical words (highlighted in bold print in Table 1) appeared in different positions across stimulus sentences. This ensured that participants had to pay close attention to the whole sentence and could not predict the critical region in the stimuli presented.

The critical target words in all sentences were controlled for frequency (using the on-line Wortschatz corpus of the University of Leipzig) and length. The mean frequency class for the target words was 12.79 for borderline anomaly items, 13.47 for anomalous target words in easy to detect items and 12.37 for their plausible counterparts ($F < 2$). There were no significant differences in the average length of target words across anomaly types (mean length of target words: 8.1 letters for the borderline condition, 8.1 for poor fit to context anomalies and 7.5 for poor fit to context controls; $F < 2$). The duration of context sentences across conditions ranged from 3.5 to 10.5s (mean = 5.4s ±1.5s), while the critical sentence had a more standardised length with a mean of 6.4s (± 0.8s) and a range of 5-8.5s.

Auditory stimuli were recorded by a female native speaker of German who read the sentences with clear and natural intonation. To ensure equal volume levels, the stimuli were normalised digitally. On average the target word was presented 4.0s (± 0.64s) after sentence onset in borderline anomaly sentences and 3.73s (± 1.3s) in poor fit, easy to detect anomaly sentences.

The stimuli were distributed across eight lists, each composed of 180 sentence pairs, consisting of 120 borderline and 60 poor fit stimuli. While poor fit stimuli were divided evenly, of the 120 borderline items, 90 contained an anomaly and the remaining 30 were plausible controls. We employed this asymmetrical design, adopted from Sanford et al. (2011), to obtain a similar number of trials for each of the three experimental conditions (detected anomalies, missed anomalies, plausible controls) for the analysis. Within a final list, an item was presented as either an anomalous or control condition, while across all lists, each condition of a stimulus pair was presented at least once. This was accomplished by rotating the borderline materials over four lists with 120 stimuli each. Poor fit materials were divided into two lists consisting of 60

stimuli. Merging each borderline list with each poor fit list yielded the eight final lists. The order of stimuli was then pseudo-randomised.

9.2.3   Procedure

Prior to the imaging experiment, participants performed a short training session. Stimuli used for training purposes were not part of the imaging experiment. In the experimental sessions, participants listened to the auditory stimuli via MRI compatible noise-cancelling headphones. Visual cues were displayed on a monitor placed at the rear of the scanner and viewed by the participants via a mirror attached to the head coil. Each trial started with the presentation of a fixation cross in the centre of the screen, followed by the auditory presentation of the context and critical sentence. After the second sentence ended, the fixation cross was replaced by an answer screen that served as a cue for the participants to indicate via button press using their right index and middle finger whether they had detected an anomaly. A schematic description of this paradigm is shown in Figure 1. In order to avoid anticipatory motor response preparation following the processing of the critical word, we did not employ a fixed assignment of push-buttons to the "plausible" and "implausible" categorisations per participant. Rather, the assignment of the left and right buttons to "plausible" and "implausible" responses varied on a trial-by-trial basis and was signalled by two smiley faces (one laughing and one frowning). Across each session, the assignment of the "plausible" and "implausible" categories to the left and right buttons was counterbalanced. The maximal response time was set to 2000ms. Onset and timing of stimuli in the event-related design was optimised for efficiency by introducing short jittered rest periods between the presentation of the context and critical sentence, as well as between the offset of the critical sentence and the presentation of the response screen and after the 2000ms response interval and the beginning of the next trial. Jittered rest intervals had a mean duration of 1020ms ($\pm$ 622ms) and a range of 500-3000ms. Each participant was presented with one of the eight lists that were split into six 10 minute runs of 30 trials each. Between each pair of experimental runs, we collected resting state data for one minute.
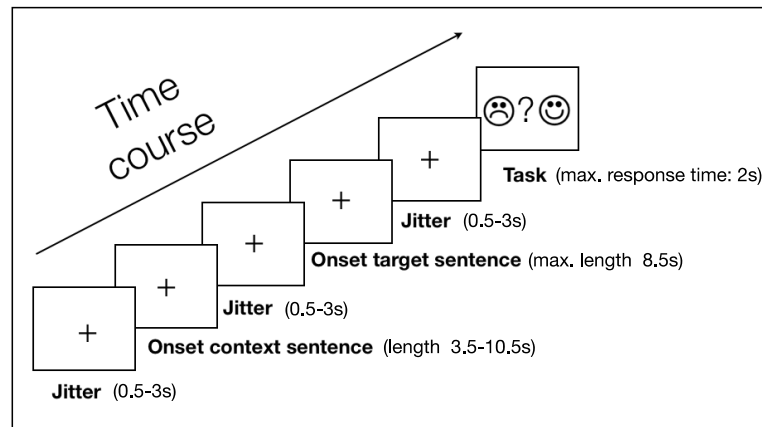
Figure 1: Schematic depiction of the fMRI paradigm for a single trial.

9.2.4   fMRI data acquisition

Functional imaging was performed on a 3T MR Magnetom Trio Tim scanner (Siemens, Erlangen, Germany). Twenty-nine axial slices were acquired using a T2-weighted gradient-echo echo-planar image (EPI) sequence optimised for blood oxygen level dependent (BOLD) effects (TR = 1500ms, TE = 21ms, flip angle = 71°, slice thickness = 4mm, in-plane resolution = 3.8 x 3.8mm, 1mm gap, FOV = 240mm, matrix dimension = 64 x 64). Four dummy scans recorded at the beginning of the functional sequence were discarded to account for magnetisation stabilisation effects. A total of 2750 functional images were acquired. In addition, a high-resolution anatomical image was collected for each participant using a T1-weighted MPRAGE GRAPPA sequence (TR = 1900ms, TE = 2.52ms, flip angle = 9°, FOV = 256mm, 176 slices, voxel size = 1.0 x 1.0 x 1.0mm).

9.2.5   fMRI data analysis

Analysis of the neuroimaging data was conducted using Analysis of Functional Neuroimages/Surface Mapping with AFNI (AFNI/SUMA; http://afni.nimh.nih.gov; Cox, 1996; 2012; Saad and Reynolds, 2012) and Freesurfer software packages (http://surfer.nmr.mgh.harvard.edu; Dale et al., 1999; Fischl, 1999; 2004).

9.2.5.1 Pre-processing

All functional time series were subjected to the following pre-processing steps in the native volume domain: de-spiking, slice-timing correction, mean normalisation, three-

dimensional affine motion correction using a weighted linear least squares cost function for the alignment of three translational (x,y,z) and three rotational (pitch, roll, yaw) parameters, registration to the middle image of the functional run and to the structural image. Time points that showed excessive motion (> 1mm) were censored and subsequently excluded from regression analysis. To assess the degree of BOLD activity against an implicit resting baseline consisting of all jittered intervals plus the resting state data collected between runs, each voxel's time series was analysed by multiple linear regression analysis with separate regressors for each experimental condition. Context sentences and behavioural response intervals were each collapsed across conditions and included in the analysis as single regressors. Since context sentences showed substantial variation in length, this regressor was convolved with a duration modulated square wave function by specifying onset and duration of each trial, while the regressor modelling the response was convolved with a fixed length (2 s) square wave function. Depending on the behavioural response, target sentences were divided into five conditions of interest (*borderline detected, borderline non-detected, borderline control, easy detected, easy control*) and a condition of no interest that included false rejections and false alarm responses. Event-related BOLD signal elicited by each of the target sentence conditions was deconvolved by linear interpolation using AFNI's tent basis function, i.e. a piecewise linear function that allows the temporal shape of the response model to vary across voxels. The hemodynamic response was modelled from the onset of the target sentence for a period of 21s to cover the entire duration of the stimulus and to allow for additional time for the BOLD signal to return to baseline. Each tent spanned an interval of 1.5s matching the length of 1 TR. In addition to the predictors representing experimental conditions, mean, linear and quadratic trend components along with the six parameters obtained from the spatial alignment procedure were included. Finally, to further minimise the influence of nuisance variance unlikely to reflect signal of interest, we regressed out signal from both lateral ventricles and bilateral white matter (Fox, 2005; Dick et al., 2010).

The analysis resulted in regression weights (reflecting percent signal change relative to the implicit resting baseline) along with an associated t statistic assessing their reliability. For regressors modelled with a fixed shape hemodynamic response function (HRF), this first-level single-subject analysis resulted in individual regres-

sion coefficients per voxel and condition, while the data-driven, deconvolution analysis used for target sentences yielded estimated impulse response functions consisting of 15 regression coefficients per voxel and condition.

Since it is well established that the characteristics of the hemodynamic response (HDR) such as amplitude, peak latency and refractory period vary across cortical regions   (see e.g., Schacter et al., 1997; Huettel and McCarthy, 2001; Handwerker et al., 2004; Inan et al., 2004), we analysed the response to target sentence conditions in two separate time windows. To this end, beta values of the impulse response function corresponding to an early time window of 1.5 to 4.5s (interval 1) and a later time window of 4.5 to 9s (interval 2) post sentence onset were averaged. The choice of these time windows was motivated by the occurrence of the target word at roughly 4s after sentence onset (see section 2.2).

Second-level group analysis was conducted on two-dimensional cortical surface representations of each participant's high-resolution anatomical volume (Dale et al., 1999; Fischl, 1999). We chose a surface-based approach over a volume-based analysis for multiple reasons: analysing functional data on the surface respects the fact that despite its complex folding, the intrinsic geometry of the cerebral cortex is essentially that of a two-dimensional sheet with a thickness of several millimetres. This means that in the folded, volumetric space two regions close enough to be sampled in neighbouring voxels might actually be much more distant in the unfolded, two-dimensional space. Substantial inter-individual variation in folding patterns that needs to be accounted for in group analysis further complicates this situation, especially when averaging is accomplished by stereotaxic normalisation. In surface-based analyses, a more accurate averaging across subjects is achieved by preserving the typology of individual brains in aligning spherical representations of individual and average brains. Improved smoothing of functional data on the surface (i.e., avoiding the risk of spreading activation across sulci or white and grey matter boundaries) has shown to increase statistical power (Desai et al., 2005; Argall et al., 2006).

As a first step, two-dimensional surface renderings of the high-resolution structural scans were constructed using Freesurfer. To this end, white and grey matter of the anatomical volumes were automatically segmented, the results inspected and manually improved when needed, separate cortical surfaces for each hemisphere were inflated and brought into registry with a common template of average gyral and sulcal

folding (Dale et al., 1999; Fischl, 1999; Fischl et al., 1999). Using SUMA, the resultant individual surface models were then imported into the AFNI three-dimensional space where the regression coefficients obtained from first-level analysis were interpolated from the three-dimensional volume domain to the two-dimensional surface model of each individual participant's anatomical volume. To compare activation patterns across the group, individual surfaces were converted to a standard indexing system (i.e., a standard mesh with identical number of nodes and correspondence between node indices and cortical regions) via icosahedral tessellation and projection (Argall et al., 2006). To decrease spatial noise due to inter-individual variation, functional data were smoothed on the surface using a 6mm full with at half maximum (FWHM) heat kernel (Chung et al., 2005).

Finally, for display purposes an average of individual cortical surface representations was created using Freesurfer. Active regions are described following the automated parcellation scheme implemented in Freesurfer (Destrieux et al., 2010). The procedure uses an algorithm based on macroanatomical landmarks that incorporates the anatomical conventions of Duvernoy (1999). Talairach coordinates for local activation maxima were extracted by projecting surface clusters back to a single subject's anatomical volume after alignment to the „Colin brain" stereotaxic anatomical template (Holmes et al., 1998, http://www.bic.mni.mcgill.ca/ServicesAtlases/Colin27) using AFNI's @auto_tlrc programme.

9.2.5.2 Whole-brain analysis

A mixed effects (repeated-measures) analysis of variance (ANOVA) with CONDITION (5) as fixed and PARTICIPANT (18) as random factor was performed on a vertex-by-vertex basis using the normalised beta weights from each individual's regression model as the dependent variable. Simple contrasts against the resting baseline were conducted for each condition and time window, and two planned comparisons among conditions (*borderline detected* versus *borderline control* and *easy detected* versus *easy control*) were specified to explore our specific research questions. Here, the comparisons between conditions for the second interval were of primary interest, motivated by the fact that, on average, the critical word appeared roughly 4s

after sentence onset.[6] A Monte Carlo simulation approach (cf. Forman et al., 1995) was used in the surface domain to identify significant clusters of activated vertices, with an individual vertex threshold of $p < 0.001$ for simple contrasts against resting baseline and $p < 0.01$ for comparisons among condition, with a family-wise error (FWE) correction at the whole-brain level at $p < 0.05$. The difference in individual vertex thresholds is motivated by results obtained from signal-to-noise analyses that indicate a power advantage for contrasts against baseline compared to contrasts between conditions (see e.g., Dick et al., 2009). FWE correction was based on estimating the minimum cluster size defined by number of contiguous nodes and the simulation determined that minimum cluster sizes of 83 and 234 nodes were needed to achieve the chosen vertex-wise thresholds.

9.3   Results

9.3.1   Behavioural results

Analysis of the behavioural data showed that the detection rate for borderline anomalies was 78.1% (± 8.5%), while easy to detect anomalies were correctly judged as implausible at a rate of 96.8% (± 4.6%). Sentences without anomalies were correctly judged as plausible at a rate of 76.9% (± 11.5%).

9.3.2   Neuroimaging results

9.3.2.1 Comparison of conditions against baseline

We first computed both increases and decreases in activation for each of the five conditions with respect to the resting baseline in both time windows. The results of these analyses are presented in Figure 2.[7] In the early interval, all five conditions show bilateral activation in frontal and superior and middle temporal regions compared to baseline. Frontal activation is most pronounced in conditions involving successful anomaly detection (borderline detected and easy detected), where it covers large parts

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[6] The activation differences observed in the early interval are presented in Figures S1 and S2 and Tables S3 and S4 in the supplementary materials.
[7] For more detailed descriptions of the observed activation patterns against baseline, please see Table S1 and S2 in the supplementary materials. These tables list Talairach coordinates and clusters sizes (number of nodes) for the local maxima of all significant clusters.

of the IFG as well as a portion of the anterior insula. Additional clusters of frontal activation are found in the inferior part of the precentral sulcus, middle frontal gyrus and inferior frontal sulcus as well as the medial portion of the superior frontal gyrus. Even though most of these activation clusters are bilateral, the activation intensity and volume tends to be greater in the left hemisphere. Activation in the superior temporal gyrus (STG) and sulcus (STS), as well as the middle temporal gyrus (MTG) is more widespread and has a higher intensity for borderline anomalies than for easy to detect ones. The analysis appears to show clusters of positive signal change in the left and right pulvinar nuclei of the thalamus, but the chosen surface-based analysis approach does not generally provide complete or reliable results in areas of subcortical grey matter. To make a more substantiated statement about the role of subcortical structures like the thalamus, amygdala or basal ganglia, a separate analysis that encompasses these regions would be necessary. Significant clusters that show a negative signal deflection relative to the resting baseline, i.e., areas in which the resting baseline is more active than the language processing task, are predominantly found in the parietal lobes – both inferior and superior lobules – and occipital lobes, encompassing lateral and medial occipital areas, with smaller clusters also located in frontal regions, all bilaterally.

For the later time window ranging from 4.5 to 9s after stimulus onset, significant clusters of positive signal increase compared to the resting baseline are found in similar frontal regions to those observed in the early time window. However, in the later interval, the difference in the extent of frontal activation between easy to detect and borderline conditions becomes more marked. In addition, all borderline conditions show activation in the left STS and this includes more of the left MTG in the borderline detected and borderline control conditions. Compared to baseline, easy detected and borderline detected conditions appear to elicit a higher degree of neural activity in the IPL than control sentences and undetected borderline anomalies. For all five conditions, a large cluster of negative signal deflection from baseline is found bilaterally in the middle and posterior portions of the superior temporal lobe, which seems also to include portions of the subcentral gyrus and sulcus and central sulcus. Additional such clusters with higher levels of activity during baseline than during language processing are found in the medial portions of the parietal and occipital lobes bilaterally.
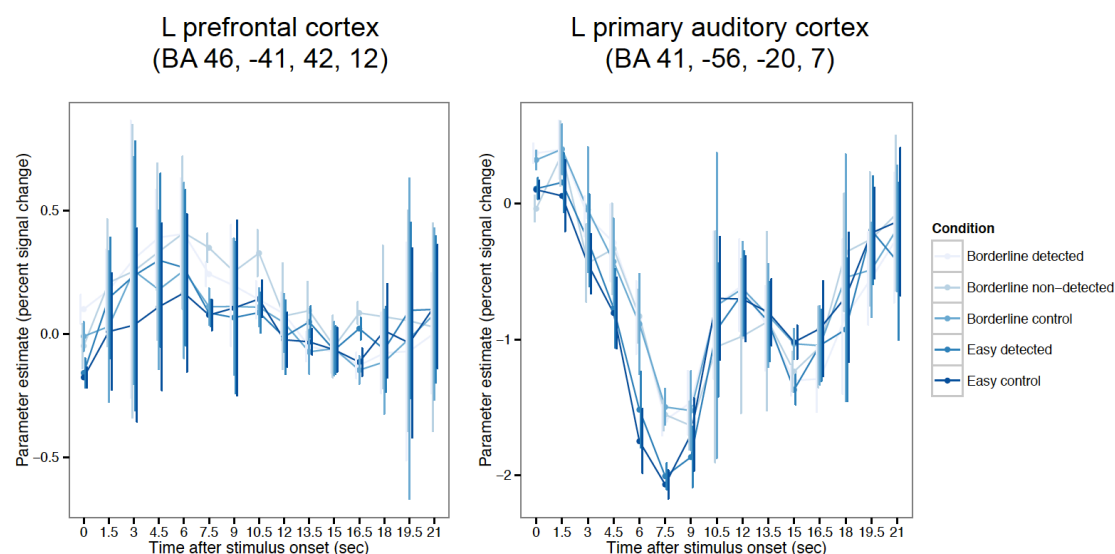
Figure 2: Whole-brain analysis results for each condition compared to baseline for two separate time windows. The individual per-vertex threshold was p < .001 (corrected FWE p < .05).

The change from positive to negative deflection in these regions during the first nine seconds (six functional acquisitions) of target sentence processing appears to relate to the complexity and persistence of the stimulus in two ways. First, primary sensory areas have an earlier and less sustained hemodynamic response than many other areas, e.g., frontal association areas (Schacter et al., 1997; Handwerker et al., 2004). Indeed a comparison of the hemodynamic response in auditory cortex and prefrontal cortex in the present data supports the importance of this difference in hemodynamic response properties. As shown in Figure 3, the estimated hemodynamic response function for a chosen voxel in the primary auditory cortex is characterised by an early interval of positive signal deflection followed by a pronounced negative undershoot starting at approximately 3s and a beginning recovery of the signal at about 7s post onset. By contrast, the estimated response function extracted from a voxel in the inferior frontal cortex (BA 46) shows a later and more sustained positive peak. Second, the experimental design itself plays a role: Because context and target sentences were separated by a short jittered inter-stimulus interval (ISI), there was a persistent auditory signal throughout the entire time of each trial, with the likelihood of habituation and concomitant repetition suppression in the BOLD signal.[8]

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[8] Importantly, the activation found for context sentences merged across all conditions (data not shown) indicates an increase in signal relative to baseline throughout the primary auditory cortex and neigh-
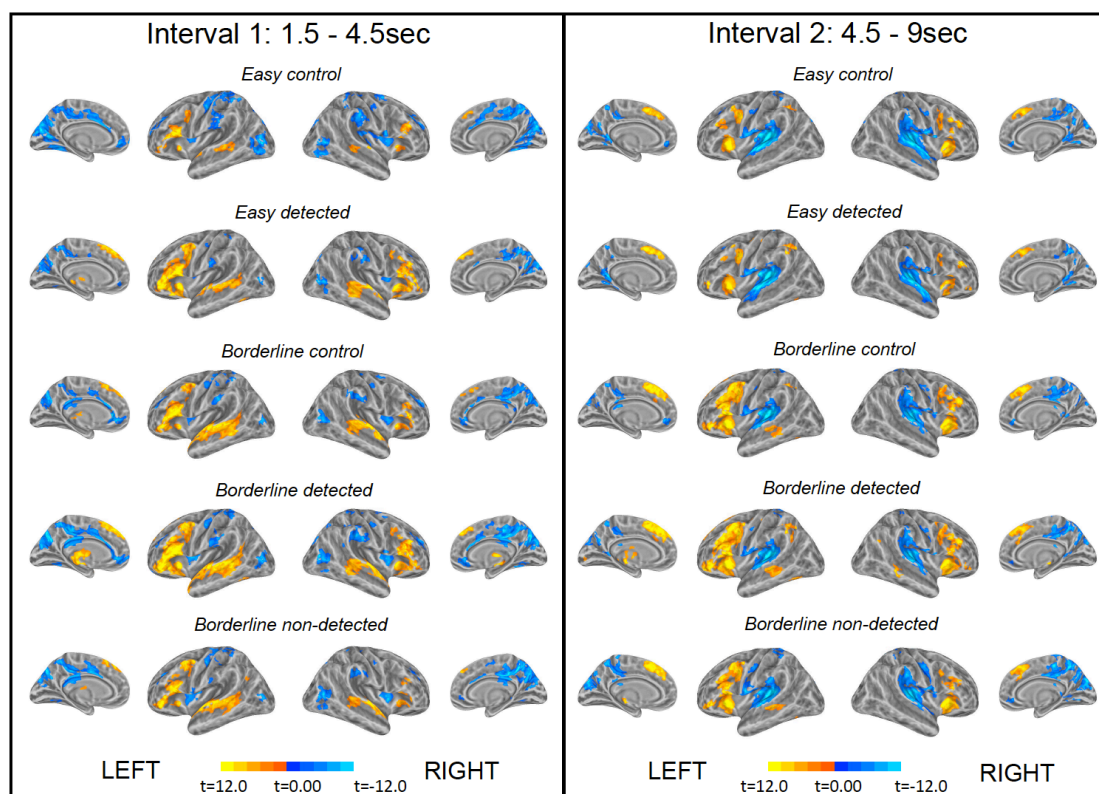
Figure 3: Comparison of estimated impulse response functions for two representative voxels in the pre-frontal cortex and primary auditory cortex, respectively. Line graphs reflect the estimated hemodynamic response to the second sentence of each experimental condition averaged across participants; error bars indicate standard error of the mean. Coordinates are in Talairach space.

9.3.2.2 Interval 1: Contrasts between conditions of interest

Easy detected versus easy control

When comparing detected easy anomalies and non-anomalous controls, significant clusters show one of four types of patterns: with respect to the relative difference in neural activity, most clusters reflect stronger responses to sentences with detected easy anomalies compared to those without, while a few clusters reveal a difference in the reverse direction. At the same time, significant clusters of both directions are based on differences in either negative or positive deflections from baseline. Clusters that show more pronounced positive deflections from baseline for easy detected anomalies than for control sentences include portions in the left inferior temporal gyrus (ITG), parahippocampal gyrus, the middle portion of the left anterior cingulate gyrus and left thalamus; and in the right lateral orbital sulcus. Higher levels of positive de-

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bouring regions, thereby ruling out that the decrease in signal during target sentences was caused by an inappropriate baseline.

flections for control compared to detected sentences were found in portions of the pars opercularis of the left IFG, in the right middle frontal gyrus and in the anterior insula bilaterally. For the majority of clusters that are based on a difference in negative deflections from baseline, control sentences led to stronger decreases in neural activity than detected easy anomalies. These clusters generally include regions described as part of the default mode network (Shulman et al., 1997). A summary of all the easy anomaly data is shown in Figure 4 and Table 2.

As noted above, for all target sentences, the STG and STS of both hemispheres show lower signal than the baseline, which includes the interval between context and target sentences. Thus, analysis of this region by target sentence condition depends not on comparing positive deflections from baseline but the relative magnitudes of negative deflections. The left transverse temporal gyrus/sulcus and the right STG and STS all elicited a positive contrast for detected easy anomalies compared to easy control sentences.

Table 2: Regions showing reliable differences for the comparison of *borderline detected* versus *borderline control* at the whole-brain level

INTERVAL 2: Borderline detected > Borderline control

	DESCRIPTION	Talairach Coordinates				Cluster Size		
		X	Y	Z	BA	Nodes	Area	MI
frontal	L. Anterior cingulate gyrus	-3	37	6	24	561	182.2	0.10
	L. Anterior insula	-21	14	-8	-	263	85.8	0.10
	L. Pericallosal sulcus	-3	27	12	24	240	119.7	0.08
	L. Precentral sulcus	-37	7	23	6	241	81.1	0.13
	R. Anterior cingulate gyrus	7	32	16	24	292	112.0	0.07
	R. Anterior insula	24	19	-6	-	241	77.3	0.13
	R. Lateral orbital sulcus/pars triangularis of the IFG	38	41	7	46	337	102.6	0.13
temporal	L. Inferior temporal gyrus/lateral occipito-temporal sulcus	-56	-39	-9	37	368	75.6	0.27
	R. Inferior temporal sulcus/gyrus	51	-51	-8	37	279	89.5	0.18
	R. Middle temporal gyrus	64	-31	-10	21	338	110.3	0.13
	R. Parahippocampal gyrus	29	-14	-10	28	599	186.3	0.35
parietal	L. Angular gyrus/intraparietal sulcus	-36	-57	47	39	318	65.1	0.10
	L. Supramarginal gyrus/intraparietal sulcus	-50	-39	48	40	803	234.4	0.16
	L. Supramarginal gyrus	-57	-22	40	40	388	70.4	0.13
	R. Angular gyrus	38	-73	30	39	319	68.7	0.17
med. wall	L. Thalamus	-1	-4	15	-	542	171.0	0.29
	R. Thalamus	2	-10	15	-	481	162.5	0.27

Notes: Individual vertex threshold $p < .01$, corrected (FWE $p < .05$). Local maximum defined by Talairach and Tournoux coordinates in the volume space. BA = Brodmann Area. Nodes = Cluster size in number of surface vertices. Area = Area of cluster calculated in square millimeters (mm^2). MI = Maximum intensity in terms of percent signal change. L = Left. R= Right. IFG = Inferior frontal gyrus.

Figure 4: Results of the whole-brain comparison between the easy detected and easy control condition for interval 2 shown on inflated average brain surfaces of the left and right hemisphere. The individual per-vertex threshold was p < .01 (corrected FWE p < .05). Warm colours indicate higher levels of activation for easy detected; cold colours reflect greater activation for the easy control sentences. Bar graphs present the difference between conditions for the local activation maximum of each cluster. Error bars depict standard error of the mean. ACC=anterior cingulate cortex, AI=anterior insula, AG=angular gyrus, CS=central sulcus, ITG=inferior temporal gyrus, LOrS=lateral orbital sulcus, MCC=middle cingulate cortex, MFS=middle frontal sulcus, MOG=middle occipital gyrus, PCC= posterior cingulate cortex, PCun=precuneus, PerCaS=pericallosal sulcus, PHG=parahippocampal gyrus, POp=pars opercularis of the inferior frontal gyrus, POS=posterior occipital sulcus, PP=planum polare, PrG=precentral gyrus, SFG=superior frontal gyrus, SMG=supramarginal gyrus, SOG, superior occipital gyrus, STS=superior temporal sulcus, STG=superior temporal gyrus, TH=thalamus, TTG=transverse temporal gyrus.

Table 3: Regions showing reliable differences for the comparison of easy detected versus easy control at the whole-brain level

INTERVAL 2: Easy detected > Easy control

	Local Maximum/Cluster Extent	Talairach Coordinates			BA	Cluster Size		MI
		X	Y	Z		Nodes	Area	
frontal	L. Anterior cingulate gyrus/superior frontal gyrus	-12	43	7	24	471	139.7	0.12
	L. Anterior/middle cingulate gyrus	-4	14	36	24	447	171.3	0.08
	L. Anterior/middle cingulate gyrus	-12	5	41	23/24	267	61.8	0.07
	L. Middle/posterior cingulate gyrus	-21	-17	31	23	285	81.7	0.09
	L. Middle frontal sulcus/gyrus	-22	46	29	46	246	99.2	0.09
	R. Central sulcus	21	-21	50	3	252	92.9	0.09
	R. Lateral orbital sulcus/pars triangularis of the IFG	38	40	3	46	327	97.1	0.14
	R. Precentral gyrus	49	-3	42	4	258	81.6	0.13
	R. Superior frontal gyrus (anterior)	12	61	14	9	908	364.9	0.24
	R. Superior frontal gyrus (middle)	15	20	49	8	330	125.0	0.11
	R. Superior frontal gyrus (posterior)	9	3	62	6	296	94.6	0.11
temporal	L. Inferior temporal gyrus/lateral occipito-temporal sulcus	-56	-39	-9	20	522	127.7	0.16
	L. Parahippocampal gyrus	-21	-15	-7	28	574	176.1	0.14
	L. Planum polare (medial portion)	-30	1	-19	38	457	83.0	0.08
	L. Transverse temporal gyrus/sulcus	-47	-18	6	41	1202	419.1	0.13
	R. Inferior temporal gyrus/lateral occipito-temporal sulcus	50	-50	-10	20	237	88.7	0.19
	R. Parahippocampal gyrus	25	1	-8	28	646	154.3	0.25
	R. Superior temporal gyrus	62	-26	3	22	623	147.7	0.12
parietal	L. Parieto-occipital sulcus/precuneus/cuneus	-8	-60	30	7/19	1435	341.4	0.12
	L. Precuneus	-13	-62	55	7	337	62.9	0.16
	L. Supramarginal gyrus	-57	-27	29	40	1418	320.4	0.16
	R. Angular gyrus/posterior superior temporal sulcus	51	-59	33	39	467	66.6	0.12
	R. Superior occipital gyrus/parieto-occipital sulcus/cuneus	7	-81	37	7/19	641	202.9	0.16
	R. Supramarginal gyrus/planum temporale	60	-32	31	40	653	238.6	0.16
	R. Supramarginal gyrus/intermediate sulcus	52	-45	23	40	468	115.6	0.17
occipital	L. Middle occipital gyrus	-43	-76	19	19	260	91.79	0.08
	L. Middle occipital gyrus	-51	-66	12	19	241	71.4	0.08
	R. Anterior/middle occipital sulcus	35	-64	12	19	257	69.5	0.08
med. wall	L. Thalamus (pulvinar)	-14	-33	4	-	344	97.7	0.10

INTERVAL 2: Easy control > Easy detected

	Local Maximum/Cluster Extent	X	Y	Z	BA	Nodes	Area	MI
frontal	L. Anterior insula	-24	22	6	-	256	80.9	0.09
	L. Pars opercularis	-44	19	16	44	324	97.5	0.12
	R. Anterior/superior insula	28	28	0	-	844	289.0	0.19
	R. Middle/inferior frontal gyrus	44	18	30	46	284	87.0	0.14
temp.	L. Superior temporal sulcus	-53	-33	9	22	436	116.1	0.10
par.	R. Patrieto-occipital sulcus	12	-53	18	7/19	290	137.1	0.09

Notes: Individual vertex threshold $p < .01$, corrected (FWE $p < .05$). Local maximum defined by Talairach and Tournoux coordinates in the volume space. BA = Brodmann Area. Nodes = Cluster size in number of surface vertices. Area = Area of cluster calculated in square millimeters (mm^2). MI = Maximum intensity in terms of percent signal change. L = Left. R= Right. IFG = Inferior frontal gyrus.
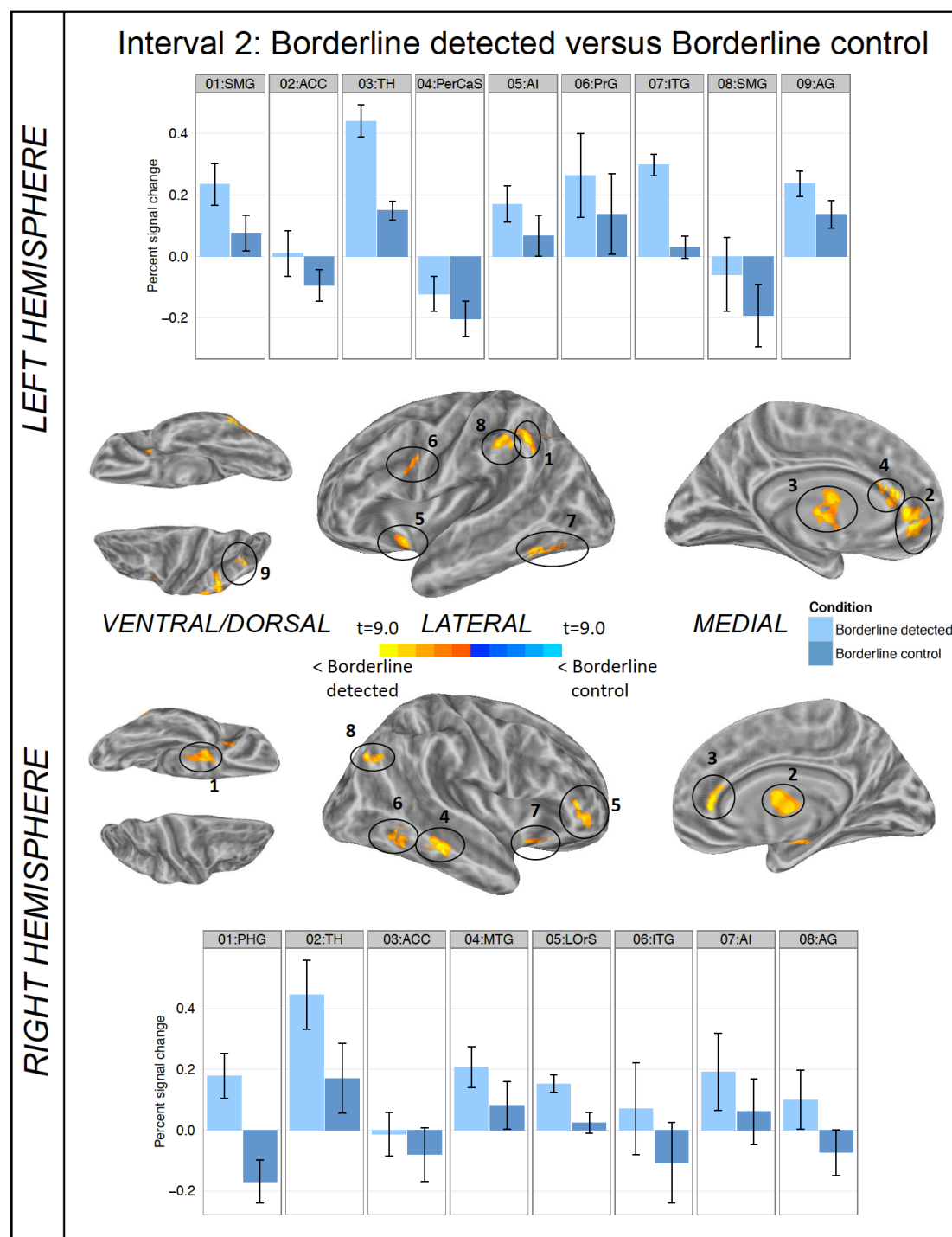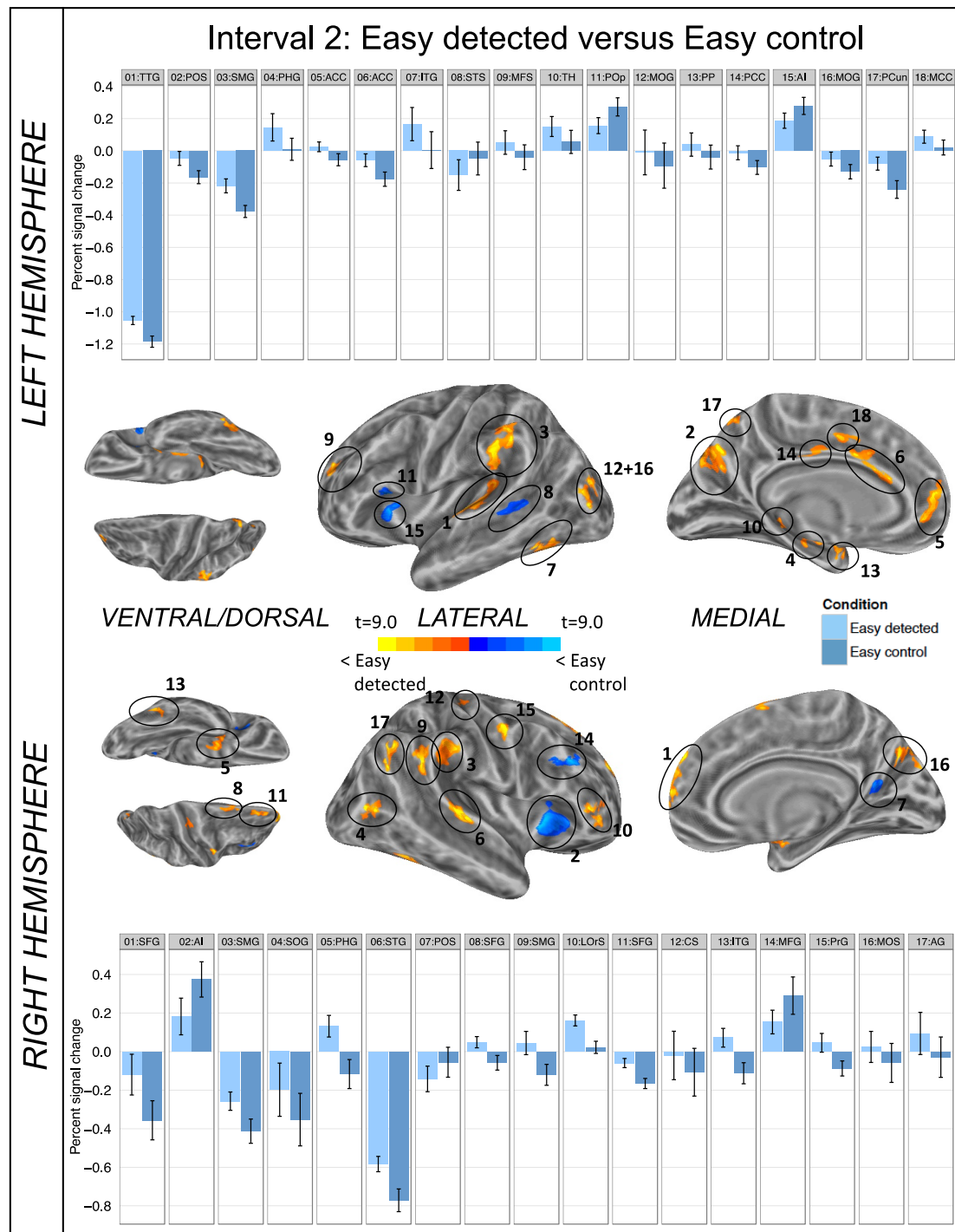
Figure 5: Results of the whole-brain comparison between the borderline detected and borderline control condition for interval 2 shown on inflated average brain surfaces of the left and right hemisphere. The individual per-vertex threshold was p < .01 (corrected FWE p < .05). Warm colours indicate higher levels of activation for borderline detected; cold colours reflect greater activation for the borderline control sentences. Bar graphs present the difference between conditions for the local activation maximum of each cluster. Error bars depict standard error of the mean. ACC=anterior cingulate cortex, AI=anterior insula, AG=angular gyrus, ITG=inferior temporal gyrus, LOrS=lateral orbital sulcus, MTG=middle temporal gyrus, PerCaS=pericallosal sulcus, PHG=parahippocampal gyrus, PrG=precentral gyrus, SMG=supramarginal gyrus, TH=thalamus.

Borderline detected versus borderline control

The comparison of *borderline detected* anomalies with their control condition produced a number of significant clusters (see Figure 5 and Table 3), and none for the reverse contrast. Clusters of bilateral activation are found in the anterior part of the insula, the IPL, and the posterior inferior temporal region. In the left hemisphere, significant clusters in the IPL are located in the supramarginal gyrus (SMG) and the adjacent (ventral) part of the intraparietal sulcus (IPS); and in the dorsal part of IPS and a portion of the adjacent angular gyrus (AG). In the right hemisphere, increased activation in the IPL occurred only in the AG. Additional frontal clusters are situated in the inferior part of the left precentral sulcus, as well as in the right lateral orbital sulcus and pars triangularis of the IFG. Medially, detected borderline anomalies elicited stronger activation in the left and right anterior cingulate gyrus and the right parahippocampal gyrus. However, the contrasts in the cingulate represent differences in negative deflections from baseline. Finally, we observed a cluster that showed higher activation in both thalami.

9.4 Discussion

The aim of the present study was to shed light on the brain regions engaged in the processing of different types of semantic anomalies, with particular attention to discourse context and depth of processing. To this end, our experimental question differed in several respects from those posed in previous studies designed to examine semantic processing in the human brain. Investigating semantic processing in the presence of discourse context set the study apart from many previous studies, which focused on context-independent processing. We hypothesized that discourse context would have a greater effect on brain activation patterns during the processing of sentences with detected borderline anomalies than sentences with undetected anomalies, other types of anomalies, or without anomalies. Borderline anomalies are purposely constructed to manifest strong associations between their key words and discourse context, and thus deeper and more thorough processing is required for the successful detection of these anomalies compared to other types of sentences.

With respect to the processing of easy to detect anomalies, our biological findings nicely match what would have been expected on the basis of single sentence

studies on semantic congruity on the one hand, and multi-sentence studies on discourse coherence on the other. We thus found contributions by the superior and inferior temporal lobe, the medial portion of the planum polare of the STG, and the IPL for the processing of easy to detect anomalies relative to their control condition. For the reverse comparison, a higher level of neural activity was found in prefrontal areas, a result that will be discussed in more detail below. While single sentence studies characteristically report left lateralised activation in regions of the frontal, temporal, and parietal lobes in response to the processing of semantic anomalies, we found similar regions in the right hemisphere to be significantly involved as well. When comparing the neural responses to *easy detected* and *easy control* sentences to the responses found for *borderline detected*, *borderline non-detected* and *borderline control* sentences, differences in extent of frontal and superior temporal activation become apparent. Whereas easy to detect anomalies and controls elicit more widespread activation across the superior and middle temporal cortex than the borderline sentences, the borderline sentences show more extensive frontal activation. In the following sections, we discuss both shared and unshared contributions of the individual regions to the processing of both anomaly types relative to their control conditions.

9.4.1   Inferior frontal gyrus

Increased activation in lateral prefrontal cortex in semantic processing – particularly the pars triangularis and pars orbitalis (BA 45 and 47) of the left IFG – is a fairly robust finding. The precise roles of each of the three major portions of the IFG in semantic processing (as well as other types of processing), is a matter of considerable debate. The roles of adjacent regions, including the anterior insula and middle frontal gyrus also enter into this debate. The spectrum of accounts ranges from suggestions that the left IFG mediates the controlled retrieval of semantic knowledge from long-term memory (Fiez, 1997; Wagner et al., 2001; Gold and Buckner, 2002), and subsequent integration (Hagoort, 2004; Kuperberg et al., 2008), to those that argue for an important function of the left IFG in domain general processes of cognitive control (Thompson-Schill et al., 1997; Moss et al., 2005). The present study shows generally higher levels of inferior frontal activity for borderline compared to easy anomaly conditions, suggesting that engagement of the prefrontal cortex (and possibly also the anterior insula) reflects the difficulty of decision making rather than semantic processing

per se. This interpretation fits well with the observation of stronger activation in the pars opercularis of the left IFG (BA44) and anterior insula for control sentences compared to those with easy to detect anomalies. Why might control sentences place higher demands on the processing system than sentences with easy to detect anomalies? Recall that the different types of sentences were presented in pseudorandom order and required an overt decision. Sentences with easy to detect anomalies can be quickly and easily categorised as anomalous upon encountering the critical word, whereas sentences with a hard to detect anomaly or no anomaly at all both require more extensive and complete processing. This assumption is corroborated by the behavioural results, in which sentences with easy to detect anomalies were correctly judged >95% of the time, whereas those with either a borderline anomaly or no anomaly were correctly judged <80% of the time (see behavioural results above). Note that only correctly judged control sentences were included in the analysis.

Overall, the pattern of results provides converging support for inferences about the roles of the left IFG (and adjacent anterior insula) in language processing that emphasise domain general functions like conflict resolution and decision making, rather than linguistic functions. Importantly, an account that implicates these frontal areas in semantic processing should predict a stimulus-based pattern of activation that produces higher levels of activity for anomalous sentences than for those without anomalies, since these call for increased semantic processing. This prediction, however, is not borne out by the results of the present study. Instead, our findings suggest that the experimental (task) environment plays a crucial role, thus supporting accounts of a more general cognitive control function of the prefrontal cortex (Thompson-Schill et al., 1997; 2005; Stowe et al., 1998; 2005; Miller and Cohen, 2001; Bornkessel-Schlesewsky and Schlesewsky, 2013).

9.4.2   Posterior and anterior temporal lobes

With respect to the pattern of activation in the anterior and mid-posterior temporal lobes, two main findings can be distinguished. First, easy anomalies led to a larger extent of temporal activation than borderline anomalies, when each was compared to its respective control condition. Second, in contrast to results reported for studies of single sentences, we observed substantial activation in the right hemisphere.

Regarding our first observation, we found the asymmetry in the degree of temporal activity across anomaly types to be most pronounced in the left hemisphere. Here, anomalous sentences of the easy to detect type elicit higher levels of activation in the posterior superior and inferior temporal gyri and the medial portion of the planum polare relative to control sentences. The reverse comparison showed increased activity in the posterior STS. By contrast, comparing sentences with borderline anomalies to control sentences yielded only a single cluster in the posterior ITG. Notably, clusters found in the inferior and middle temporal gyrus reflect differences in positive deviations from baseline (for anomalous sentences compared to control), whereas clusters in superior temporal regions reflect differences in negative deviations from baseline. As noted above, the negative deflections are likely due to habituation in primary auditory cortex and adjacent areas. Differences in attenuation of the neural response in these areas might point to a faster recovery of the signal due to selective engagement of these areas in elementary aspects of stimulus recognition and discrimination. Regarding the smaller negative signal deflection for detected easy anomalies compared to control sentences in the left transverse temporal gyrus, a possible explanation for the involvement of this region lies in the relatively high degree of predictability for the correct target word. The majority of sentences with easy to detect anomalies described very general, everyday occurrences such as the following example (Original in German; English translation given):

(2)   Fred was feeling really tired when he got home. All he wanted was to sleep after he closed his bedroom curtains and curled up in bed/crayons.

In this example, the context renders the correct sentence final word bed highly predictable. Therefore, it could be argued that the relatively high expectation for a specific continuation led to a predictability down to the level of sensory representations. The stronger activity observed for anomalous items would thus reflect the mismatch between a context-based expectation pertaining the physical form of a stimulus and the effectively encountered input. Evidence for this assumption stems from a series of visual MEG studies that showed that violation of form-related predictions led to an increased amplitude of an early event-related component localised in the visual cortex (Dikker et al., 2009; 2010; Dikker and Pylkkänen, 2011). These results demon-

strate that context-based predictions that pertain to the physical form of future input can have an impact even on the earliest sensory processing of words.

Increased engagement of the left and right inferior temporal gyri for both borderline and easy to detect anomalies relative to control sentences may point to an involvement of these regions in processes that mediate access to word meaning. Based on evidence gleaned from lesion deficit studies, the lateral portion of the ITG may play a role in some general aspects of semantic processes such the dynamic composition of word or sentence meaning that are independent of modality or stimulus properties (Sharp et al., 2004; Noppeney et al., 2006). Stronger activation for anomalous sentences might thus indicate increased processing demands due the lack of a strong semantic relationship of the anomalous word and the preceding context.

Finally, we observed a significant cluster in the medial portion of the planum polare of the STG that was active during processing of easy to detect semantic violations. Single cell recordings in non-human primates show that the anterior-lateral portion of the auditory belt – roughly corresponding to the planum polare in the human brain – responds to complex auditory stimuli such as different type of species-specific vocalisations ("monkey calls") (Tian et al., 2001). These findings are in line with previous results that suggest a functional segregation of auditory association regions into an anterior-ventral "what" and posterior-dorsal "where" stream of auditory processing that support sound recognition and sound localisation, respectively (Rauschecker, 1998a; 1998b; Hackett et al., 2001). Data from studies in humans further corroborate a possible role of the planum polare in identification and categorisation of complex auditory objects, either depending on sensory properties (Ahveninen et al., 2006; Viceic et al., 2006) or encoding representations at a more abstract perceptual level (Hasson et al., 2007). The stronger response to easy to detect anomalies than control sentences in the planum polare might therefore reflect the processing of an auditory object that is perceptually deviant from the expected continuation. To date, it remains unclear if this region of the anterior temporal lobe engages in abstract and sublexical speech processing only or if it also supports lexical-semantic analysis, basic combinatory processes or semantic integration as has been suggested for more lateral portions of the anterior temporal lobe like the anterior STS, MTG or ITG (Mazoyer et al., 1993; Stowe et al., 1998; Friederici et al., 2000; Lau et al., 2008). In the present study, we did not find differential degrees of activation in these regions of the anterior tem-

poral lobe. However, one needs to keep in mind that BOLD signal from the inferior portion of the anterior temporal lobe is frequently degraded by susceptibility artefacts. Since we analysed the data at the whole-brain level only, it is possible that further distinction might have gone unnoticed because of a lack in statistical power.

Our second main finding of more extensive right hemisphere contribution is in line with a growing body of evidence that supports an important role of the right hemisphere in ecological language comprehension. Virtually all studies of sentence comprehension and discourse comprehension that do not rely on contrasts between highly similar conditions show bilateral activation (Mazoyer et al., 1993; Indefrey and Cutler, 2004; Vigneau et al., 2006; Wilson et al., 2008; Dick et al., 2009; 2010; Straube et al., 2009). Various theories have been proposed to account for functional differentiation of the two hemispheres, but suffice it to say that an enormous network of brain activation for ecological language, encompassing many regions in both hemispheres, reflects a very large number of concurrent processes, including those at the level of sounds, words, meaning, grammar, prosody, emotion, inference, memory, and others. Some of the needed processes have been considered relatively right lateralized, e.g., emotional prosody (Weintraub et al., 1981; Brådvik et al., 1991; George et al., 1996), inference, but the overall network differences across tasks that vary in different aspects of ecological language performance remain to be elucidated. (See Jung-Beeman et al. (2005) and Ferstl et al. (2008) for contrasting theories about hemispheric contributions to language processing.)

9.4.3 Inferior parietal lobule

The inferior parietal lobule, encompassing the supramarginal gyrus (SMG; BA40) and the angular gyrus (AG; BA39), is a functionally heterogeneous region consistently implicated in neuropsychological and neuroimaging studies on semantic processing. The results of the present study show divergent patterns of activation in these regions for processing easy to detect and borderline stimuli. More precisely, detected borderline anomalies engage the AG bilaterally while easy to detect anomalies show greater activity than baseline only in the right AG. With respect to the SMG, both anomaly types show clear asymmetry in the extent of activation across hemispheres, but in opposite directions. For borderline anomalies compared with control sentences, two clusters are found in the left hemisphere and none in the right, whereas easy to detect

anomalies produce two right and one left hemisphere clusters. At the same time, the SMG clusters can be differentiated based on their location and the polarity of signal change from baseline: the more anteriorly situated clusters reflect negative deflections from baseline for both anomalous and non-anomalous conditions, whereas the more posterior clusters reflect positive deflections from baseline for the anomalous conditions and either positive or negative deflections for the control. In the following paragraphs we will separately discuss the role of the AG and SMG as these two regions might contribute differentially to processing sentence meaning.

9.4.3.1 Angular gyrus

Recent meta-analyses that aimed to shed light on the brain regions involved in semantic processing showed that the angular gyrus is one the regions most consistently reported (Lau et al., 2008; Binder et al., 2009). At the same time, an extensive body of evidence suggests the AG to be activated by a variety of different tasks that include number processing, reading and conflict resolution among others. Due to its strategic location in the heteromodal parietal association cortex and its rich structural and functional connectivity, it is considered a multimodal association area, with functional characterizations as a "convergence zone" (Damasio, 1989) or "hub" for cross-modal integration (Joseph, 1982; Hagmann et al., 2008; ; Tomasi and Volkow, 2011), that plays a role in a number of core processes, such as categorisation of events, access to semantic representations, fact retrieval and attention shifting (Seghier, 2013). In line with traditional accounts put forward by Geschwind (1965) and Joseph (1982), Binder et al. (2009) summarise the role of the AG as "*[occupying] a position at the top of a processing hierarchy underlying concept retrieval and conceptual integration (...) [that] may play a particular role in behaviours requiring fluent conceptual combination, such as sentence comprehension, discourse, problem solving, and planning*". This perspective fits well with the processing demands imposed by anomalous sentences embedded in context and more specifically with hard to detect anomalies that call for a more extensive analysis and application of world knowledge. An interpretation along these lines is supported by bilateral activation of the angular gyrus in association with detected borderline anomalies relative to control, which suggests that this region is critically involved in the detection of more subtle anomalies that only become apparent upon integration of all relevant facts. Evidence that the AG is engaged

in the computation of coherent interpretations at the sentence or discourse level stems from several fMRI studies that found increased activation in this region for anomalous sentences contrasted with either a low-level resting baseline or a condition of syntactic processing (Ni et al., 2000; Friederici et al., 2003; Newman et al., 2003; Menenti et al., 2009). We thus conclude that the AG plays an important role in cognitive processes related to the conceptual retrieval and integration of information at a complex level that are sensitive to the contextual environment and afford a more thorough evaluation and semantic analysis.

9.4.3.2 Supramarginal gyrus

As outlined above, the observed clusters in the left and right supramarginal gyrus can be distinguished based their location (anterior vs. posterior) and the polarity of neural signal changes (positive vs. negative) that underlie the observed difference between anomalous and control sentences. The fact that these pairwise differences reflect distinct levels of signal deflection from baseline might imply that two distinct neural mechanisms come into play.

As with other multimodal association cortices including the AG, the SMG has been implicated in a range of very different processes. Some accounts emphasise the contribution of this region to language-specific aspects like phonological processing, while others focus on its role as part of a parietal-premotor neural circuit engaged in action understanding or on its involvement in task-relevant and attention-related processes. With respect to phonological processing, there is a growing body of evidence from neuroimaging and TMS studies on written word recognition that suggests a selective engagement of the supramarginal gyri in tasks that require decisions based on phonological properties of the stimulus relative to those that focus on semantic relations or visual features. Neuroimaging studies typically report an upregulation of neural activity in both left and right SMG in response to tasks that focus on syllable, phoneme or rhyme judgements compared to semantic decisions, which consistently produce higher levels of neural activity in the (left) AG (Démonet et al., 1994; Price et al., 1997; Mummery et al., 1998; Devlin et al., 2003; McDermott et al., 2003). TMS studies further attest to this possible link between the SMG and phonological processes by finding phonological, but not semantic judgments to be disrupted by magnetic stimulation of the left, right or bilateral SMG (Devlin et al., 2003; Hart-

wigsen et al., 2010; Sliwinska et al., 2012; but see Stoeckel et al., 2009). It is unlikely that SMG activity in the present study reflects phonological processing, since participants performed a judgement task that clearly focused on semantic relations

On the other hand, the role of SMG in phonological processing appears to relate to its more general contribution in a temporal-frontal pathway relating sensory and motor information during action understanding (including speech) (Rauschecker and Scott, 2009). With respect to semantics, the meanings of words and sentences may not rely exclusively on abstract, conceptual representations but also in part on activation of underlying neural systems for action understanding, sensation, emotional processing, and so forth. Using a well-known example about actions, a concept like grasping is neurobiologically grounded in the sensory-motor circuit also involved in planning and executing the action of grasping (Barsalou, 1999; Gallese and Lakoff, 2005; Pulvermüller, 2005; Kemmerer and Gonzalez-Castillo, 2010). Motor simulation of actions may involve a ventral-dorsal portion of the visual-motor pathway that connects the ventral premotor cortex, the adjacent pars opercularis of the IFG and parts of the inferior parietal lobule, in particular the SMG (Rizzolatti and Matelli, 2003; Rizzolatti and Craighero, 2004). In fact, several neuroimaging studies have reported activation along this pathway including the IPL for passive language tasks (Hauk et al., 2004; Tettamanti et al., 2005; Aziz-Zadeh and Damasio, 2008). With respect to the findings of the present study, it thus seems possible that the processing of unexpected events expressed in the anomalous sentences might have relied more on this action understanding pathway, especially when they describe unusual actions. The precise role of sensory-motor-emotional processing during language comprehension remains debated (Hauk and Tschentscher, 2013), and thus further systematic investigations are needed for a more conclusive judgement on this matter.

Finally, there is an extensive body of evidence that indicates that the SMG is part of a predominantly right-lateralised ventral frontal-parietal attention network that comprises a region at the interface of the temporal and parietal lobes, the inferior frontal gyrus, anterior cingulate cortex, anterior insula, and supplementary motor area. This ventral attention network – frequently co-activated with a more dorsally located attention network – is thought to engage in the detection of salient and behaviourally relevant targets in a stimulus-driven fashion (Corbetta et al., 2008; Kristensen et al., 2013).

Shulman et al. (2003) found sustained "deactivation" (negative deflection from baseline during task compared to rest) in the temporal-parietal region bilaterally during periods in which attention was strongly focused on the search for a behaviourally relevant target stimulus until a significant target had been detected. The authors argue that suppression of activity in the ventral attention network acts as a filter to protect the attention system from distractions caused by irrelevant stimuli and thus improves task performance. In the present task environment that emphasised the detection of anomalies, the attenuation of this negative deflection observed for semantic anomalies of both types could therefore indicate that detection of an anomaly has taken place, while the usual pattern for control sentences could point to a prolonged search for a relevant target.

In summary, we suggest that the pattern of activation found in the IPL reflects cognitive processes related to semantic processing and supported by the AG on the one hand, and neural mechanisms possibly associated with motor simulation or attention- and behaviour-related processes on the other. The conclusion that these regions engage in processes that mark the final evaluation of the presented stimuli is also in line with a lack of comparable activation in these areas in the early time window (see supplementary materials). More extensive activation in the IPL for borderline anomaly sentences compared to easy to detect stimuli might therefore reflect increased processing demands and the execution a more detailed analysis.

9.4.4   Medial wall

The comparison of each condition against the resting baseline produced a large cluster of activation situated in the dorsal-medial portions of the superior frontal gyrus and in the middle and anterior cingulate cortices bilaterally. The activation was stronger and more widespread for sentences with borderline anomalies than for those with easy to detect anomalies. The frontal-median cortex, described as the medial portion of the superior frontal gyrus (and roughly corresponding to the medial portion of BA 8, 9 and 10), has been linked to processes related to coherence building in multi-sentence paradigms as well as to Theory of Mind (ToM) processing and evaluative judgements (Ferstl and Cramon, 2001; 2002; Zysset et al., 2002; Ferstl et al., 2008). Stronger activation for borderline sentences might thus reflect the overall good global fit of both anomalous and non-anomalous target sentences with the preceding context that allows

for coherent interpretation. A meta-analysis by Ferstl and von Cramon (2008) reported stronger activation in the frontal-median cortex for congruent relative to incongruent sentence pairs or sequences. The present study did, however, observe a reverse activation pattern with stronger activation along the right superior frontal gyrus for detected easy anomalies versus plausible control sentences. It is thus unlikely that the observed differential activation for easy anomaly sentences is associated with the establishment of coherence *per se* and rather with the evaluation of the extracted proposition (Zysset et al., 2002). In this respect, easy to detect anomalies should be associated with the highest level of confidence in the evaluative judgment task that asked participants to indicate whether they considered the second sentence to be plausible or not.

Both borderline and easy to detect anomalies, when compared to baseline, elicit a cluster of increased activation in the left anterior cingulate cortex and in the right parahippocampal gyrus. Overall, the comparison of detected easy anomalies with control sentences elicited activation in a much more extensive collection of limbic areas, including the parts of the parahippocampal gyrus and anterior cingulate gyrus, than the corresponding comparison for detected borderline anomalies. This finding most likely reflects the role of limbic areas in processes related to affect and emotion as easy to detect anomalies describe absurd events that could have triggered emotions like amusement, surprise or disgust in the participants.

9.5   Conclusion

The present study contrasted the processing of two types of contextually embedded semantic anomalies that call for distinct levels of processing depth. We demonstrated that the analysis of sentences presented in context led to more symmetric hemispheric activity than is typically reported in single word or even some single sentence studies, reflecting the ecological need for additional cognitive processes such as inferencing, coherence establishment, and application of world knowledge. Additionally, we identified differential activation in the prefrontal cortex across anomaly types that speaks in favour of a role for these regions in domain general processes of cognitive control. With respect to the engagement of temporal and inferior parietal regions in the processing of semantic violations, we observed important distinctions between the anomaly types that point to differences in the required depth of analysis. We found the

detection of easy anomalies to be predominantly supported by temporal regions while processing of detected borderline anomalies led to more extensive activation in inferior parietal regions. Overall, we observed a large set of regions in frontal, temporal, and parietal lobes activated in response to our experimental manipulation. Future research on brain connectivity that assesses the relevant neural networks is needed to shed more light on the functional roles of the involved regions and their interaction in complex language comprehension.

9.6   References

Ahveninen J, Jaaskelainen IP, Raij T, Bonmassar G, Devore S, Hamalainen M, Levanen S, Lin FH, Sams M, Shinn-Cunningham BG, Witzel T, and Belliveau JW. Task-modulated "what" and "where" pathways in human auditory cortex. PNAS, 103 (39): 14608–14613, 2006.

Argall BD, Saad ZS, and Beauchamp MS. Simplified intersubject averaging on the cortical surface using SUMA. Human brain mapping, 27 (1): 14–27, 2006.

Aziz-Zadeh L and Damasio A. Embodied semantics for actions: Findings from functional brain imaging. Journal of Physiology-Paris, 102 (1-3): 35–39, 2008.

Barsalou LW. Perceptual symbol systems. Behavioral and brain sciences, 1999.

Binder JR, Desai RH, Graves WW, and Conant LL. Where Is the Semantic System? A Critical Review and Meta-Analysis of 120 Functional Neuroimaging Studies. Cerebral Cortex, 19 (12): 2767–2796, 2009.

Bookheimer S. Functional MRI of Language: New Approaches to Understanding the Cortical Organization of Semantic Processing. Annual Review of Neuroscience, 25 (1): 151–188, 2002.

Bornkessel-Schlesewsky I and Schlesewsky M. Reconciling time, space and function: A new dorsal–ventral stream model of sentence comprehension. Brain and Language, 125 (1): 60–76, 2013.

Brådvik B, Dravins C, Holtås S, Rosen I, Ryding E, and Ingvar DH. Disturbances of speech prosody following right hemisphere infarcts. Acta Neurologica Scandinavica, 84 (2): 114–126, 1991.

Chang LJ, Yarkoni T, Khaw MW, and Sanfey AG. Decoding the Role of the Insula in Human Cognition: Functional Parcellation and Large-Scale Reverse Inference. Cerebral Cortex, 23 (3): 739–749, 2013.

Chung MK, Robbins SM, Dalton KM, Davidson RJ, Alexander AL, and Evans AC. Cortical thickness analysis in autism with heat kernel smoothing. NeuroImage, 25 (4): 1256–1265, 2005.

Corbetta M, Patel G, and Shulman GL. The Reorienting System of the Human Brain: From Environment to Theory of Mind. Neuron, 58 (3): 306–324, 2008.

Cox RW. AFNI: Software for Analysis and Visualization of Functional Magnetic Resonance Neuroimages. Computers and Biomedical Research, 29 (3): 162–173, 1996.

Cox RW. AFNI: What a long strange trip it's been. NeuroImage, 62 (2): 743–747, 2012.

Dale AM, Fischl B, and Sereno MI. Cortical surface-based analysis: I. Segmentation and surface reconstruction. NeuroImage, 9 (2): 179–194, 1999.

Damasio AR. Time-locked multiregional retroactivation: A systems-level proposal for the neural substrates of recall and recognition. Cognition, 33 (1-2): 25–62, 1989.

Desai R, Liebenthal E, Possing ET, Waldron E, and Binder JR. Volumetric vs. surface-based alignment for localization of auditory cortex activation. NeuroImage, 26 (4): 1019–1029, 2005.

Desai RH, Binder JR, Conant LL, Mano QR, and Seidenberg MS. The neural career of sensory-motor metaphors. Journal of Cognitive Neuroscience, 23 (9): 2376–2386, 2011.

Destrieux C, Fischl B, Dale A, and Halgren E. Automatic parcellation of human corti-

cal gyri and sulci using standard anatomical nomenclature. NeuroImage, 53 (1): 1–15, 2010.

Devlin JT, Matthews PM, and Rushworth MF. Semantic processing in the left inferior prefrontal cortex: a combined functional magnetic resonance imaging and transcranial magnetic stimulation study. Journal of Cognitive Neuroscience, 15 (1): 71–84, 2003.

Démonet JF, Price C, Wise R, and Frackowiak RSJ. Differential activation of right and left posterior sylvian regions by semantic and phonological tasks: a positron-emission tomography study in normal human subjects. Neuroscience Letters, 182 (1): 25–28, 1994.

Dick AS, Goldin-Meadow S, Hasson U, Skipper JI, and Small SL. Co-speech gestures influence neural activity in brain regions associated with processing semantic information. Human brain mapping, 30 (11): 3509–3526, 2009.

Dick AS, Solodkin A, and Small SL. Neural development of networks for audiovisual speech comprehension. Brain and Language, 114 (2): 101–114, 2010.

Dikker S and Pylkkänen L. Before the N400: Effects of lexical–semantic violations in visual cortex. Brain and Language, 118 (1-2): 23–28, 2011.

Dikker S, Rabagliati H, and Pylkkänen L. Sensitivity to syntax in visual cortex. Cognition, 110 (3): 293–321, 2009.

Dikker S, Rabagliati H, Farmer TA, and Pylkkänen L. Early Occipital Sensitivity to Syntactic Category Is Based on Form Typicality. Psychological Science, 21 (5): 629–634, 2010.

Duvernoy HM. The Human Brain. Springer, 1999.

Erickson TD and Mattson ME. From words to meaning: A semantic illusion. Journal of Verbal Learning and Verbal Behavior, 20 (5): 540–551, 1981.

Federmeier KD and Kutas M. A Rose by Any Other Name: Long-Term Memory Structure and Sentence Processing. Journal of Memory and Language, 41 (4): 469–495, 1999.

Ferstl EC and Cramon von DY. The role of coherence and cohesion in text comprehension: an event-related fMRI study. Cognitive Brain Research, 11 (3): 325–340, 2001.

Ferstl EC, Guthke T, and Cramon von DY. Text comprehension after brain injury: Left prefrontal lesions affect inference processes. Neuropsychology, 16 (3): 292–308, 2002.

Ferstl EC, Neumann J, Bogler C, and Cramon von DY. The extended language network: A meta-analysis of neuroimaging studies on text comprehension. Human brain mapping, 29 (5): 581–593, 2008.

Fiez JA. Phonology, semantics, and the role of the left inferior prefrontal cortex. Human brain mapping, 5 (2): 79–83, 1997.

Fischl B. Cortical Surface-Based Analysis II: Inflation, Flattening, and a Surface-Based Coordinate System. NeuroImage, 9 (2): 195–207, 1999.

Fischl B. Automatically Parcellating the Human Cerebral Cortex. Cerebral Cortex, 14 (1): 11–22, 2004.

Fischl B, Sereno MI, Tootell RB, and Dale AM. High-resolution intersubject averaging and a coordinate system for the cortical surface. Human brain mapping, 8 (4): 272–284, 1999.

Forman SD, Cohen JD, Fitzgerald M, Eddy WF, Mintun MA, and Noll DC. Improved Assessment of Significant Activation in Functional Magnetic Resonance Imaging (fMRI): Use of a Cluster-Size Threshold. Magnetic Resonance in Medicine, 33 (5): 636–647, 1995.

Fox MD. From The Cover: The human brain is intrinsically organized into dynamic, anticorrelated functional networks. PNAS, 102 (27): 9673–9678, 2005.

Friederici AD, Meyer M, and Cramon von DY. Auditory Language Comprehension: An Event-Related fMRI Study on the Processing of Syntactic and Lexical Information. Brain and Language, 75 (3): 465–477, 2000.

Friederici AD, Rüschemeyer S-A, Hahne A, and Fiebach CJ. The role of left inferior frontal and superior temporal cortex in sentence comprehension: localizing syntactic and semantic processes. Cerebral Cortex, 13 (2): 170–177, 2003.

Gallese V and Lakoff G. The Brain's concepts: the role of the Sensory-motor system in conceptual knowledge. Cognitive Neuropsychology, 22 (3-4): 455–479, 2005.

George MS, Parekh PI, Rosinsky N, Ketter TA, Kimbrell TA, Heilman KM, Herscovitch P, and Post RM. Understanding Emotional Prosody Activates Right Hemisphere Regions. Archives of Neurology, 53 (7): 665–670, 1996.

Geschwind N. Disconnexion syndromes in animals and man: Part 1. Brain, (88): 237–294, 1965.

Gold BT and Buckner RL. Common Prefrontal Regions Coactivate with Dissociable Posterior Regions during Controlled Semantic and Phonological Tasks. Neuron, 35 (4): 803–812, 2002.

Hackett TA, Preuss TM, and Kaas JH. Architectonic identification of the core region in auditory cortex of macaques, chimpanzees, and humans. The Journal of Comparative Neurology, 441 (3): 197–222, 2001.

Hagmann P, Cammoun L, Gigandet X, Meuli R, Honey CJ, Van J Wedeen, and Sporns O. Mapping the Structural Core of Human Cerebral Cortex. PLOS Biology, 6 (7): 1479-1493, 2008.

Hagoort P. Integration of Word Meaning and World Knowledge in Language Comprehension. Science, 304 (5669): 438–441, 2004.

Handwerker DA, Ollinger JM, and D'Esposito M. Variation of BOLD hemodynamic responses across subjects and brain regions and their effects on statistical analyses. NeuroImage, 21 (4): 1639–1651, 2004.

Hannon B and Daneman M. Susceptibility to semantic illusions: An individual-differences perspective. Memory & Cognition, 29 (3): 449–461, 2001.

Hauk O and Tschentscher N. The Body of Evidence: What Can Neuroscience Tell Us about Embodied Semantics? Frontiers in Psychology, 4, 2013.

Hauk O, Johnsrude I, and Pulvermüller F. Somatotopic representation of action words in human motor and premotor cortex. Neuron, 41 (2): 301–307, 2004.

Hartwigsen G, Baumgaertner A, Price CJ, Koehnke M, Ulmer S, and Siebner HR. Phonological decisions require both the left and right supramarginal gyri. Proceedings of the National Academy of Sciences, 107 (38): 16494–16499, 2010.

Holmes CJ, Hoge R, Collins L, Woods R, Toga AW, and Evans AC. Enhancement of MR Images Using Registration for Signal Averaging. Journal of Computer Assisted Tomography, 22 (2): 324, 1998.

Huettel SA and McCarthy G. Regional Differences in the Refractory Period of the Hemodynamic Response: An Event-Related fMRI Study. NeuroImage, 14 (5): 967–976, 2001.

Humphries C, Binder JR, Medler DA, and Liebenthal E. Syntactic and Semantic Modulation of Neural Activity during Auditory Sentence Comprehension. Journal of Cognitive Neuroscience, 18 (4): 665–679, 2006.

Humphries C, Binder JR, Medler DA, and Liebenthal E. Time course of semantic processes during sentence comprehension: An fMRI study. NeuroImage, 36 (3):

924–932, 2007.

Inan S, Mitchell T, Song A, Bizzell J, and Belger A. Hemodynamic correlates of stimulus repetition in the visual and auditory cortices: an fMRI study. NeuroImage, 21 (3): 886–893, 2004.

Indefrey P and Cutler A. Prelexical and lexical processing in listening. The cognitive neurosciences, 3: 759–774, 2004.

Joseph R. The neuropsychology of development: Hemispheric laterality, limbic language, and the origin of thought. Journal of Clinical Psychology, 38 (1): 4–33, 1982.

Jung-Beeman M. Bilateral brain processes for comprehending natural language. Trends in Cognitive Sciences, 9 (11): 512–518, 2005.

Kemmerer D and Gonzalez-Castillo J. The Two-Level Theory of verb meaning: An approach to integrating the semantics of action with the mirror neuron system. Brain and Language, 112 (1): 54–76, 2010.

Kristensen LB, Wang L, Petersson KM, and Hagoort P. The Interface Between Language and Attention: Prosodic Focus Marking Recruits a General Attention Network in Spoken Language Comprehension. Cerebral Cortex, 23 (8): 1836–1848, 2013.

Kuperberg GR, Sitnikova T, and Lakshmanan BM. Neuroanatomical distinctions within the semantic system during sentence comprehension: Evidence from functional magnetic resonance imaging. NeuroImage, 40 (1): 367–388, 2008.

Lau EF, Phillips C, and Poeppel D. A cortical network for semantics: (de)constructing the N400. Nature Reviews Neuroscience, 9 (12): 920–933, 2008.

Mar RA. The neuropsychology of narrative: story comprehension, story production and their interrelation. Neuropsychologia, 42 (10): 1414–1434, 2004.

Mashal N, Faust M, Hendler T, and Jung-Beeman M. An fMRI investigation of the neural correlates underlying the processing of novel metaphoric expressions. Brain and Language, 100 (2): 115–126, 2007.

Mazoyer BM, Tzourio N, Frak V, Syrota A, Murayama N, Levrier O, Salamon G, Dehaene S, Cohen L, and Mehler J. The cortical representation of speech. Journal of Cognitive Neuroscience, 5 (4): 467–479, 1993.

McDermott KB, Petersen SE, Watson JM, and Ojemann JG. A procedure for identifying regions preferentially activated by attention to semantic and phonological relations using functional magnetic resonance imaging. Neuropsychologia, 41 (3): 293–303, 2003.

Menenti L, Petersson KM, Scheeringa R, and Hagoort P. When elephants fly: differential sensitivity of right and left inferior frontal gyri to discourse and world knowledge. Journal of Cognitive Neuroscience, 21 (12): 2358–2368, 2009.

Miller EK and Cohen JD. An Integrative Theory of Prefrontal Function. Annual Review of Neuroscience, 24 (1): 167–202, 2001.

Mitchell RLC and Crow TJ. Right hemisphere language functions and schizophrenia: the forgotten hemisphere. Brain, 128 (5): 963–978, 2005.

Moss HE, Abdallah S, Fletcher P, Bright P, Pilgrim L, Acres K, and Tyler LK. Selecting among competing alternatives: selection and retrieval in the left inferior frontal gyrus. Cerebral Cortex, 15 (11): 1723–1735, 2005.

Mummery CJ, Patterson K, Hodges JR, and Price CJ. Functional Neuroanatomy of the Semantic System: Divisible by What? Journal of Cognitive Neuroscience, 10 (6): 766–777, 1998.

Newman AJ, Pancheva R, Ozawa K, Neville HJ, and Ullman MT. An Event-Related fMRI Study of Syntactic and Semantic Violations. Journal of Psycholinguistic

Research, 30 (3): 339–364, 2001.

Newman, SD, Just, MA, Keller, TA, Roth, J, and Carpenter, PA. Differential effects of syntactic and semantic processing on the subregions of Broca's area. Cognitive Brain Research, 16, 297–307, 2003.

Ni W, Constable RT, Mencl WE, Pugh KR, Fulbright RK, Shaywitz SE, Shaywitz BA, Gore JC, and Shankweiler D. An Event-related Neuroimaging Study Distinguishing Form and Content in Sentence Processing. Journal of Cognitive Neuroscience, 12 (1): 120–133, 2000.

Noppeney U, PATTERSON K, Tyler LK, Moss H, Stamatakis EA, Bright P, Mummery C, and Price CJ. Temporal lobe lesions and semantic impairment: a comparison of herpes simplex virus encephalitis and semantic dementia. Brain, 130 (4): 1138–1147, 2006.

Oldfield RC. The assessment and analysis of handedness: The Edinburgh inventory. Neuropsychologia, 9 (1): 97–113, 1971.

Park H and Reder LM. Moses illusion: Implication for human cognition. In Pohl RF (Ed.),Hove, UK: Psychology Press: Cognitive illusions: A handbook on fallacies and biases in thinking, judgment, and memory, 2004: 275–291.

Price CJ, Moore CJ, Humphreys GW, and Wise RJS. Segregating Semantic from Phonological Processes during Reading. Journal of Cognitive Neuroscience, 9 (6): 727–733, 1997.

Pulvermüller F. Opinion: Brain mechanisms linking language and action. Nature Reviews Neuroscience, 6 (7): 576–582, 2005.

Raposo A and Marques JF. The contribution of fronto-parietal regions to sentence comprehension: Insights from the Moses illusion. NeuroImage, 83: 431–437, 2013.

Rauschecker JP. Cortical processing of complex sounds. Current Opinion in Neurobiology, 8 (4): 516–521, 1998a.

Rauschecker JP. Parallel processing in the auditory cortex of primates. Audiology and Neurotology, 3 (2-3): 86–103, 1998b.

Rauschecker JP and Scott SK. Maps and streams in the auditory cortex: nonhuman primates illuminate human speech processing. Nature Neuroscience, 12 (6): 718–724, 2009.

Reder LM and Kusbit GW. Locus of the Moses illusion: Imperfect encoding, retrieval, or match? Journal of Memory and Language, 30 (4): 385–406, 1991.

Rizzolatti G and Craighero L. The mirror-neuron system. Annual Review of Neuroscience, 27 (1): 169–192, 2004.

Rizzolatti G and Matelli M. Two different streams form the dorsal visual system: anatomy and functions. Experimental Brain Research, 153 (2): 146–157, 2003.

Saad ZS and Reynolds RC. SUMA. NeuroImage, 62 (2): 768–773, 2012.

Sanford AJ, Leuthold H, Bohan J, and Sanford AJ. Anomalies at the borderline of awareness: An ERP study. Journal of Cognitive Neuroscience, 23 (3): 514–523, 2011.

Schacter DL, Buckner RL, Koutstaal W, Dale AM, and Rosen BR. Late onset of anterior prefrontal activity during true and false recognition: an event-related fMRI study. NeuroImage, 6 (4): 259–269, 1997.

Seghier ML. The Angular Gyrus Multiple Functions and Multiple Subdivisions. The Neuroscientist, 19 (1): 43–61, 2013.

Sharp DJ, Scott SK, and Wise RJ. Retrieving meaning after temporal lobe infarction: the role of the basal language area. Annals of Neurology, 56 (6): 836–846, 2004.

Shulman GL. Two Attentional Processes in the Parietal Lobe. Cerebral Cortex, 12 (11): 1124–1131, 2002.

Shulman GL, Fiez JA, Corbetta M, Buckner RL, Miezin FM, Raichle ME, and Petersen SE. Common Blood Flow Changes across Visual Tasks: II. Decreases in Cerebral Cortex. Journal of Cognitive Neuroscience, 9 (5): 648–663, 1997.

Shulman GL, McAvoy MP, Cowan MC, Astafiev SV, Tansy AP, d'Avossa G, and Corbetta M. Quantitative analysis of attention and detection signals during visual search. Journal of Neurophysiology, 90 (5): 3384–3397, 2003.

Sliwinska MW, Khadilkar M, Campbell-Ratcliffe J, Quevenco F, and Devlin JT. Early and sustained supramarginal gyrus contributions to phonological processing. Frontiers in Psychology, 3, 2012.

Stoeckel C, Gough PM, Watkins KE, and Devlin JT. Supramarginal gyrus involvement in visual word recognition. CORTEX, 45 (9): 1091–1096, 2009.

Stowe LA, Broere CA, Paans AM, Wijers AA, Mulder G, Vaalburg W, and Zwarts F. Localizing components of a complex task: sentence processing and working memory. NeuroReport, 9 (13): 2995–2999, 1998.

Stowe LA, Haverkort M, and Zwarts F. Rethinking the neurological basis of language. Lingua, 115 (7): 997–1042, 2005.

Straube B, Green A, Weis S, Chatterjee A, and Kircher T. Memory Effects of Speech and Gesture Binding: Cortical and Hippocampal Activation in Relation to Subsequent Memory Performance. Journal of Cognitive Neuroscience, 21 (4): 821–836, 2009.

Tettamanti M, Buccino G, Saccuman MC, Gallese V, Danna M, Scifo P, Fazio F, Rizzolatti G, Cappa SF, and Perani D. Listening to Action-related Sentences Activates Fronto-parietal Motor Circuits. Journal of Cognitive Neuroscience, 17 (2): 273–281, 2005.

Thompson-Schill SL, Bedny M, and Goldberg RF. The frontal lobes and the regulation of mental activity. Current Opinion in Neurobiology, 15 (2): 219–224, 2005.

Thompson-Schill SL, D'Esposito M, Aguirre GK, and Farah MJ. Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. Proceedings of the National Academy of Sciences, 94 (26): 14792–14797, 1997.

Tian B, Reser D, Durham A, Kustov A, and Rauschecker JP. Functional specialization in rhesus monkey auditory cortex. Science, 292 (5515): 290–293, 2001.

Tomasi D and Volkow ND. Association between Functional Connectivity Hubs and Brain Networks. Cerebral Cortex, 21 (9): 2003–2013, 2011.

Tune S, Schlesewsky M, Small SL, Sanford AJ, Bohan J, Sassenhagen J, and Bornkessel-Schlesewsky I. Cross-linguistic variation in the neurophysiological response to semantic processing: Evidence from anomalies at the borderline of awareness. Neuropsychologia, under revision.

Van Oostendorp H and De Mul S. Moses beats Adam: A semantic relatedness effect on a semantic illusion. ACTPSY, 74 (1): 35–46, 1990.

Van Oostendorp H and Kok I. Failing to notice errors in sentences. Language and Cognitive Processes, 5 (2): 105–113, 1990.

Vandenberghe R, Nobre AC, and Price CJ. The response of left temporal cortex to sentences. Journal of Cognitive Neuroscience, 14 (4): 550–560, 2002.

Viceic D, Fornari E, Thiran J-P, Maeder PP, Meuli R, Adriani M, and Clarke S. Human auditory belt areas specialized in sound recognition: a functional magnetic resonance imaging study. NeuroReport, 17 (16): 1659–1662, 2006.

Vigneau M, Beaucousin V, Herve P-Y, Duffau H, Crivello F, Houde O, Mazoyer B,

and Tzourio-Mazoyer N. Meta-analyzing left hemisphere language areas: phonology, semantics, and sentence processing. NeuroImage, 30 (4): 1414–1432, 2006.

Wagner AD, Paré-Blagoev EJ, Clark J, and Poldrack RA. Recovering meaning: left prefrontal cortex guides controlled semantic retrieval. Neuron, 31 (2): 329–338, 2001.

Weintraub S, Mesulam M, and Kramer L. Disturbances in prosody: A right-hemisphere contribution to language. Archives of Neurology, 1981.

Wilson SM, Molnar-Szakacs I, and Iacoboni M. Beyond Superior Temporal Cortex: Intersubject Correlations in Narrative Speech Comprehension. Cerebral Cortex, 2008.

Zysset S, Huber O, Ferstl E, and Cramon von DY. The Anterior Frontomedian Cortex and Evaluative Judgment: An fMRI Study. NeuroImage, 15 (4): 983–991, 2002.

10   APPENDIX

10.1   Supplementary Materials Study 1

10.1.1 Analyses involving only the trials with correct performance on the judgement task

Figures S1 and S2 show grand average ERPs at the position of the critical sentence-final word, with averages including only those trials on which participants gave expected answers for the judgement task.
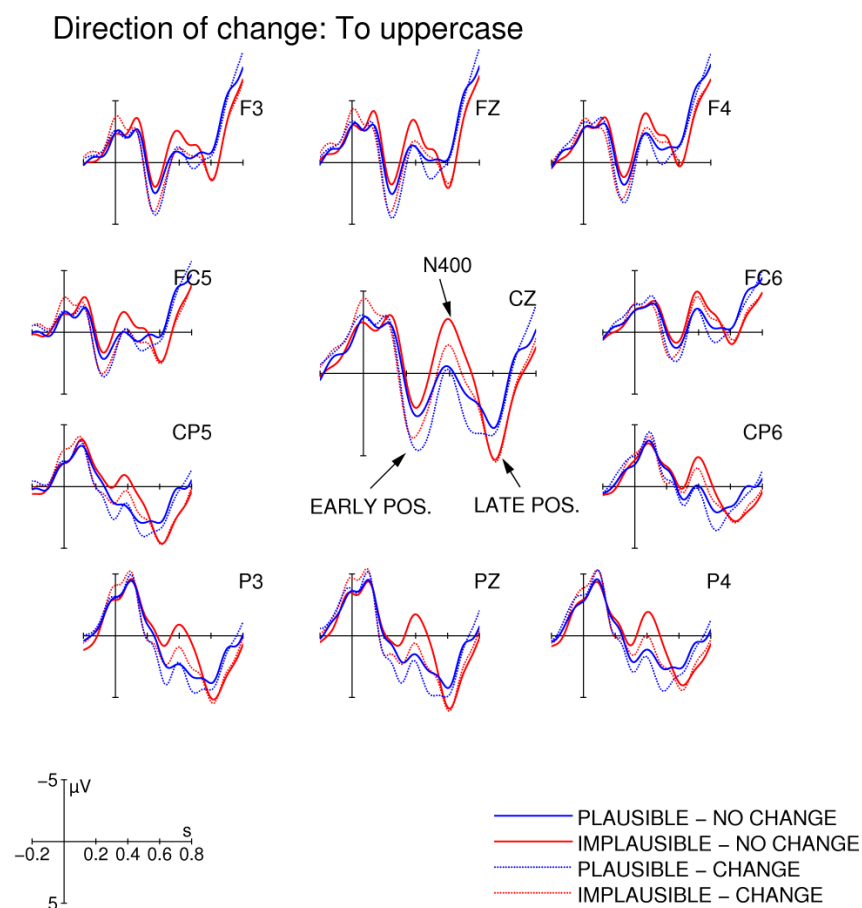
Figure S1. Grand average ERPs (N=20) at the position of the critical clause-final word (onset at the vertical bar) for the for the UP group (direction of physical change: from normal text to uppercase). Negativity is plotted upwards. Only trials for which participants gave expected responses on the plausibility judgement task were included in the averaging procedure.

Direction of change: To lowercase
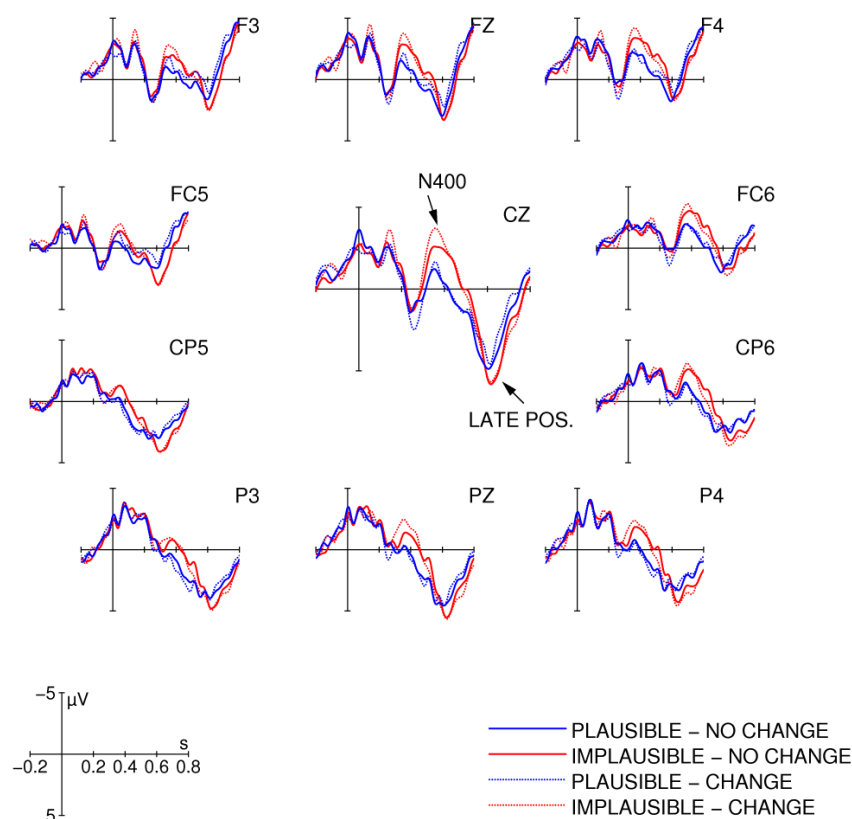
Figure S2. Grand average ERPs (N=20) at the position of the critical clause-final word (onset at the vertical bar) for the for the DOWN group (direction of physical change: from uppercase to normal text). Negativity is plotted upwards. Only trials for which participants gave expected responses on the plausibility judgement task were included in the averaging procedure

Visual inspection of Figures S1 and S2 in comparison to Figures 2 and 3 in the main text suggests that the pattern of ERP results is unaffected by whether all trials are included in the averaging procedure or only those for which participants gave expected answers on the judgement task. This descriptive impression was confirmed by statistical analyses on the data containing only correctly answered trials. The results of these analyses are visualised in Figures S3 and S4 for lateral and midline analyses, respectively.

LATERAL ELECTRODE SITES
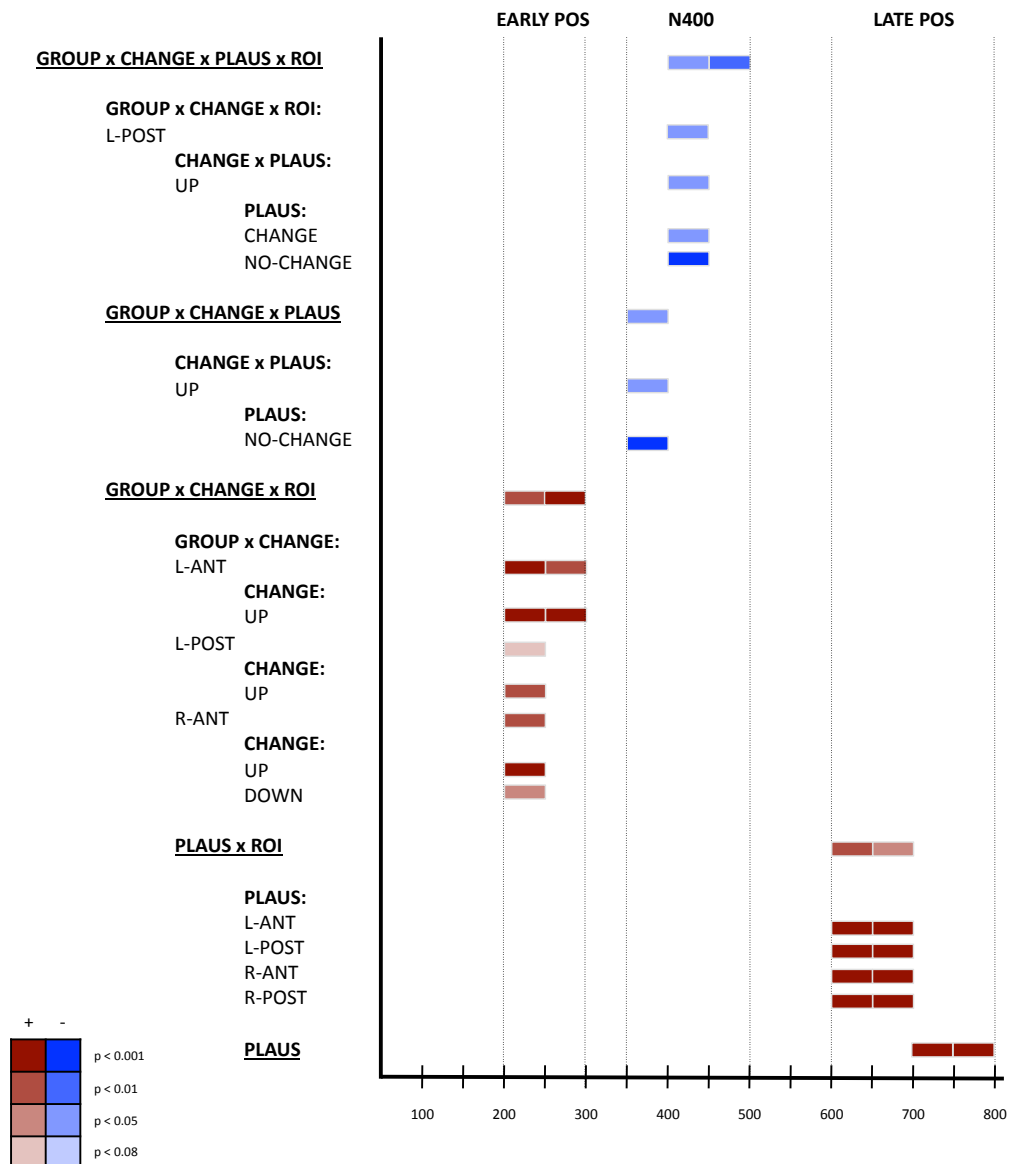
Figure S3. Summary of the statistical analysis for ERPs at lateral electrode sites when only trials for which participants gave expected responses on the plausibility judgement task were included in the averaging procedure.

MIDLINE ELECTRODE SITES
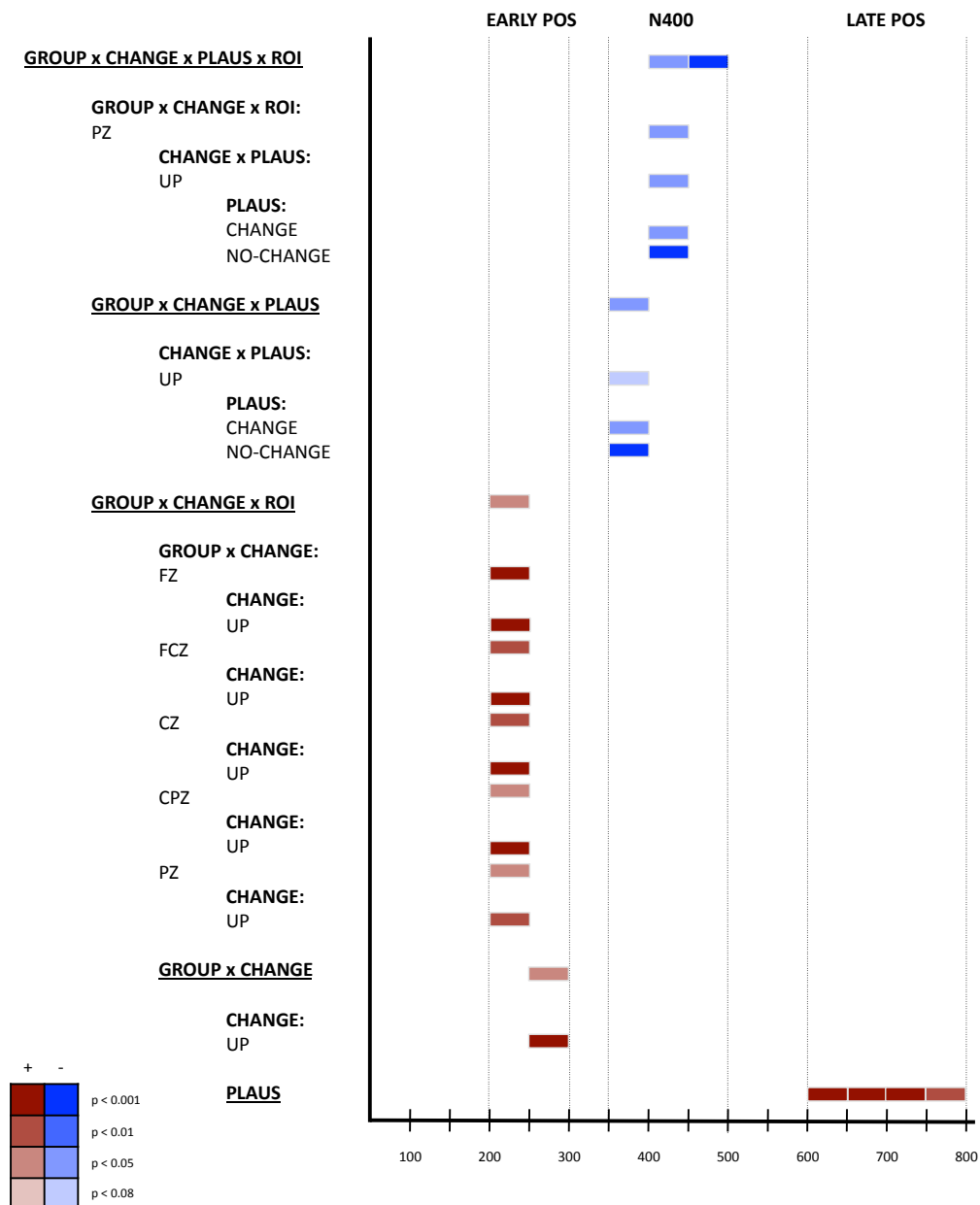
Figure S4. Summary of the statistical analysis for ERPs at midline electrode sites when only trials for which participants gave expected responses on the plausibility judgement task were included in the averaging procedure.

10.1.2 Split-half analysis of the ERP data for the UP group to rule out a floor effect in the N400

Some researchers have reported "floor effects" on the N400, i.e. observed that, under certain circumstances, N400 amplitude appears to have reached a level which cannot be reduced further. Though these effects have typically been reported for stimulus repetitions and they have not been found in all relevant studies (see Debruille & Renoult, 2009, for a recent summary), it appears possible that the interaction between PLAUS and CHANGE for the UP group in the present study may have resulted from an (uppercase-specific) floor effect in the N400 in the IMPLAUSIBLE - CHANGE condition.

In order to rule out this possibility, we conducted a split-half analysis for the data of the UP group in which we examined (a) the relative N400 amplitude for the IMPLAUSIBLE - CHANGE condition in the first and second halves of the experiment; and (b) the overall ERP pattern in the first half of the experiment.

As Figure S5 shows, N400 amplitude was reduced for half two vs. half one in the IMPLAUSIBLE - CHANGE condition, thus demonstrating that it was not at floor level in the first half of our study. In addition, Figure S6 shows that the ERP pattern reported for the entire experiment – and specifically the N400 difference between the IMPLAUSIBLE - NO CHANGE and IMPLAUSIBLE - CHANGE conditions – was already present during the first half of the experiment. Taken together, these two observations indicate that the N400 difference between the two implausible conditions in the UP group cannot have resulted from a floor effect in the IMPLAUSIBLE - CHANGE condition.
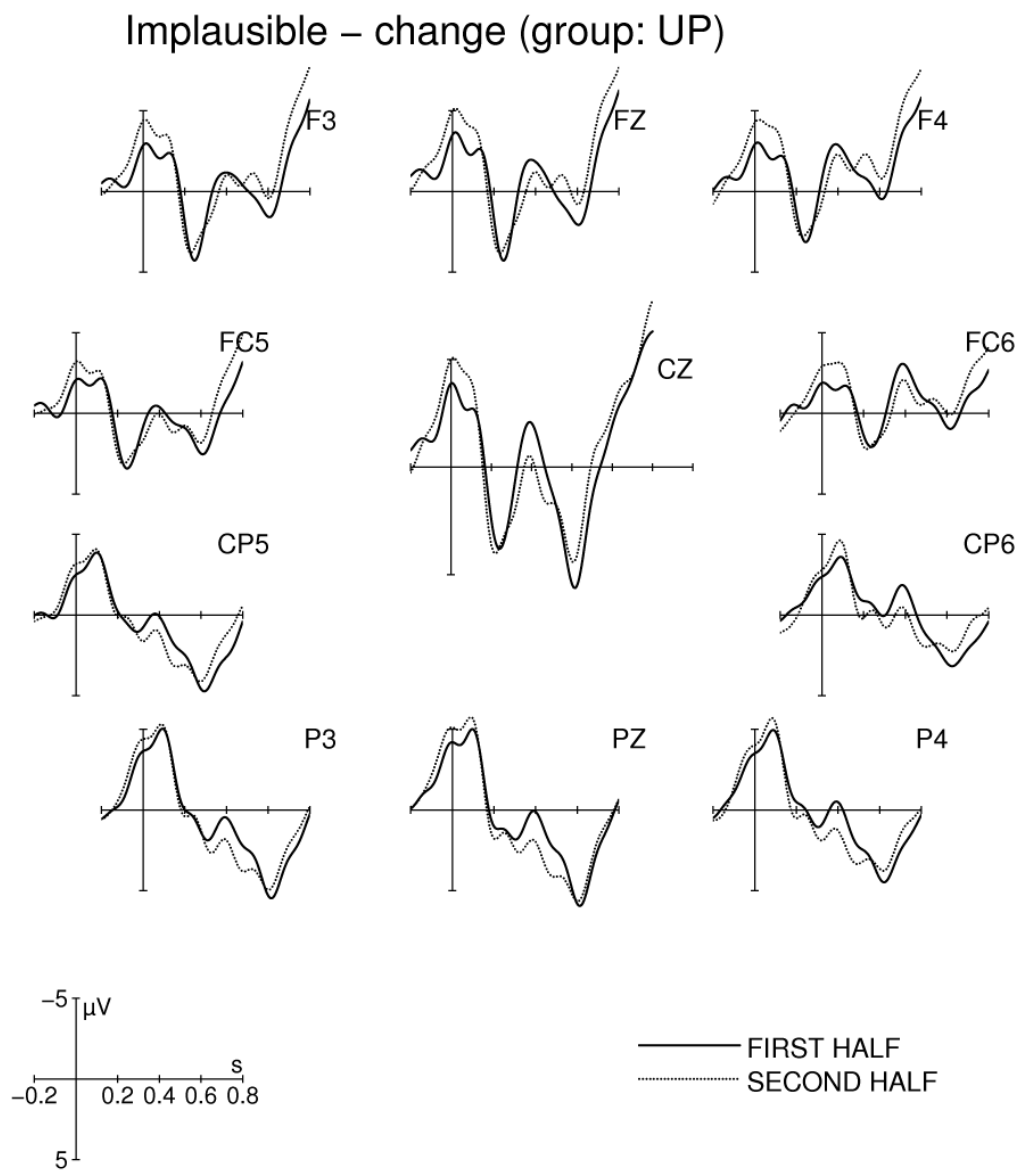
Figure S5. Split-half analysis for the IMPLAUSIBLE - CHANGE condition in the UP group.

Direction of change: To uppercase (first half)
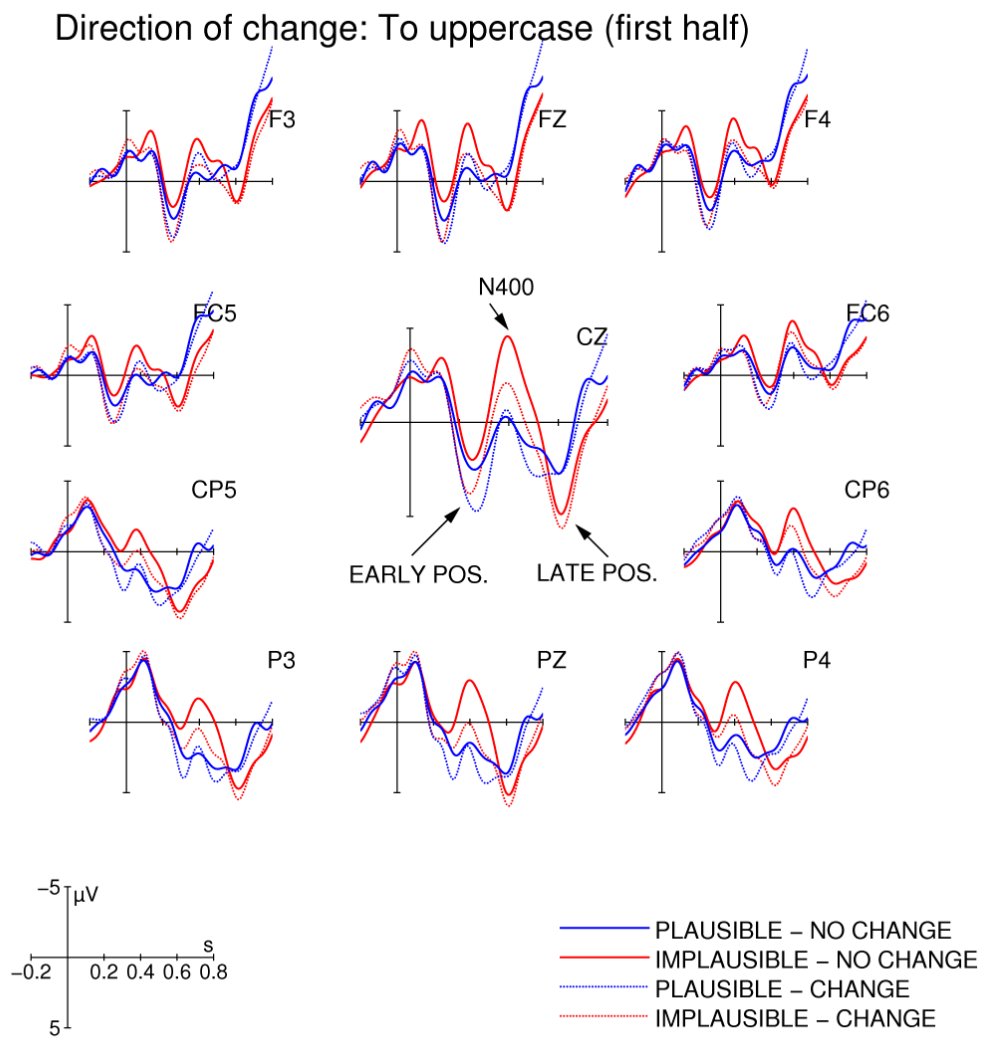
Figure S6. Grand average ERPs for the UP group in the first half of the experiment.

10.1.3 References

Debruille, J. B., & Renoult, L. (2009). Effects of semantic matching and of semantic category on reaction time and N400 that resist numerous repetitions. Neuropsychologia, 47, 506-517.

10.2   Supplementary Materials Study 2

10.2.1 Additional examples and description of sentence materials used in Experiments 1, 2a and 2b.

Tables A1 and A2 show additional examples for the borderline anomalies and easy-to-detect anomalies, respectively. A full set of experimental materials can be obtained from the corresponding author upon request.

Table A1: Additional examples for borderline anomalies in Experiments 1, 2a and 2b.

Borderline anomalies	
German (Exp. 1 and 2a)	**English (Exp. 2b)**
(1) Dorothea und Sascha hatten einige Freunde zum Abendessen eingeladen, allerdings waren sie noch nicht ganz fertig, als die ersten Gäste eintrafen. Dorothea zerdrückte schnell ein paar reife *{Artischocken/Avocados}* für die Zubereitung ihres Lieblingsdips <u>Guacamole</u>, der zuerst serviert wurde.	(1) Dorothy and Sam were having a dinner party, but their guests were arriving and they weren't quite ready. Dorothy quickly mashed up some fresh *{artichokes/avocados}* to make his favourite dip, <u>guacamole</u>, which she served first.
(2) Emma hatte Sarah schon gewarnt, dass sie beim Betreten des Zimmers jede Menge Schmutz erwarten würde. Trotzdem war sie verärgert über die *{weiße/schwarze}* Dreckschicht, die die Lieferung der <u>Kohlen</u> am Vormittag verursacht hatte.	(2) Emily warned Sarah to expect a large mess when she walked in to the living room. However, when she saw a fine *{white/black}* dust everywhere due to the <u>coal</u> delivery, she was angry.
(3) Draußen herrschten eiskalte Temperaturen und so entschied sich Jakob für s eine wärmste Winterkleidung. Als erstes zog er seine *{neuen Winterschuhe/neue Winterjacke}* an und dann noch dicke <u>Socken</u>, um nicht zu frieren.	(3) It was an icy, cold day outside and Jack decided to put on his warmest clothes. He put on his new winter *{boots/jacket}* and then his thick woolly <u>socks</u> so he'd stay warm.
(4) Es war das größte und modernste Schiff seiner Zeit und niemand hatte erwartet, was passieren würde. Auf ihrer lang ersehnten Jungfernfahrt im *{Indischen/Atlantischen}* Ozean sank die bis heute berühmte <u>Titanic</u> innerhalb von wenigen Stunden.	(4) It was the biggest ship of its day and no one expected what was about to happen. On her maiden voyage in the *{Indian/Atlantic Ocean}*, an accident sunk the <u>Titanic</u> in a few hours.
(5) Peter hörte im Radio den neusten Song von Lady Gaga und mochte ihn sehr. Er konnte einfach nicht mit dem *{Summen/Singen}* des im Grunde genommen albernen <u>Songtextes</u> ihrer neuen Single aufhören.	(5) Pete heard the new song by Lady Gaga on the radio and liked it a lot. He really could not stop himself *{humming/singing}* those quite silly and annoying <u>lyrics</u> for the whole day.

For Experiment 2b, the materials from Sanford et al. (2011) were used, of which some had to be modified for American participants. Importantly, changes were kept as minimal as possible and never affected the context words differentiating between plausible and anomalous condition of a given item or the critical target word to which ERPs were time-locked. For borderline anomalies, 23 items were adapted; for easy-to-detect anomalies, four items were changed. In some cases, changes were made to context or target sentences only, while other items required adaptation of both target and context sentence. Some examples of the modifications are provided in Table A3.

Table A2: Additional examples for easy-to-detect anomalies in Experiments 1, 2a and 2b.

Easy-to-detect anomalies	
German (Exp. 1 and 2a)	**English (Exp. 2b)**
(1) Harald wollte seiner Frau zum Hochzeitstag ein schönes Geschenk kaufen und entschied sich, ihr neue Schuhe zu schenken. Im Schuhgeschäft kaufte er ein Paar <u>Pedalen/Stiefel</u> und bat die nette Verkäuferin, sie als Geschenk zu verpacken.	(1) Harold wanted to buy his wife a lovely present and decided to buy her some shoes. In the shoe shop he bought her some <u>pedals/boots</u> and asked the assistant to gift wrap them.
(2) Sarah rief nach ihrem Ehemann, nachdem sie die Treppe im Haus heruntergestürzt war. Tom verband ihren Knöchel mit einem <u>Schrauben-schlüssel/Verband</u> aus dem Erstehilfekoffer und brachte sie anschließend ins nächste Krankenhaus.	(2) Sarah called for her husband Don to help her after she fell down the stairs. Don bandaged Sarah's ankle with the <u>spanner/bandages</u> from his first-aid box and then took her to hospital.
(3) Da er erst kürzlich einen Unfall auf dem Wasser gehabt hatte, war Johann bei seinen Segeltrip ein wenig nervös. Er lenkte sein Boot vorsichtig in das <u>Blumenbeet</u>/in den <u>Hafen</u>, und ankerte ohne Probleme am Ende des langen Steges.	(3) John was feeling nervous about sailing because he'd had an accident on the water recently. He sailed his boat carefully into the <u>flowerbed/harbour</u> and successfully moored alongside the pier without hitting anything.
(4) Johannes war es überaus wichtig, komfortabel und stilvoll zu reisen. Er zahlte zweitausend Euro für einen Flug erster Klasse nach Australien in einem nagelneuen, großen <u>Schlauchboot/Airbus</u>.	(4) Travelling in comfort and style was so important to John. He paid two thousand dollars for a premium class flight to Australia on a newly refurbished <u>dinghy/jet.</u>
(5) Die beide Wanderer waren durchgefroren und hungrig, und zu allem Übel war ihr Ziel noch weit entfernt. Sie waren offensichtlich im Kreis gelaufen, da sie wohl einen Fehler beim Lesen der <u>Diät/Karte</u> gemacht hatten.	(5) The two walkers were cold, hungry and lost. They had been walking in circles for nearly the whole day because they had misread the <u>diet/map.</u>

Table A3: Examples of the modifications undertaken in adapting Sanford et al.'s (2011) materials for American participants. Modified words are printed in bold.

Changes	British Version (Sanford et al., 2011)	American Version (Exp. 2b)
context sentence	A pay dispute between **lorry** drivers and their employer reached a crisis in negotiation, even the professional mediators seemed very dejected.	A pay dispute between **truck** drivers and their employer reached a crisis in negotiation, even the professional mediators seemed very dejected.
target sentence	Television news reports of **British** soldiers {celebrating/weeping} in response to their enemy's victory have received many complaints.	Television news reports of **US** soldiers {celebrating/weeping} in response to their enemy's victory have received many complaints.
context and target sentence	**Scotland** has chronic levels of heart disease and obesity and **Scotland's** politicians want to change this. The **Scottish Executive** is hoping to {prevent/encourage} people from adopting a healthy lifestyle to halt this trend.	**The USA** have chronic levels of heart disease and obesity and **America's** politicians want to change this. The **Surgeon General** is hoping to {prevent/encourage} people from adopting a healthy lifestyle to halt this trend.

Table A4: Comparison of the word categories of the critical words in Experiments 2a and 2b.

Condition	Exp.	Noun	Proper noun	Adjective	Verb	Total
Borderline anomalies	2a	95	10	7	18	120
	2b	83	18	6	10	120
Easy-to-detect anomalies	2a	58	-	1	1	60
	2b	56	2	1	1	60

The comparison of the stimuli used in Experiments 2a and 2b shows that, for the easy-to-detect anomaly condition, 56 of 60 items were literal translations of the same sentence pairs. For the borderline anomaly condition, Experiment 2a used 101 literal translations of the 120 items of Experiment 2b, the remaining 19 items belonged to the pool of new stimuli added to Experiment 1. An overview of the target words divided by lexical category is given in Table A4. In addition, for noun phrases, presence/absence of case marking and grammatical functions are listed in Table A5.

Table A5: For critical words that were nouns / noun phrases, overview of the number of case-marked nouns and of the grammatical functions of the critical items.

Condi-tion	Exp.	Case-marking		Grammatical function				
		Yes	No	Subject	Direct object	Indirect object	Prepositional object	Other
Border-line anoma-lies	2a	98	7	15	18	1	25	46
	2b	61	40	3	31	-	25	42
Easy-to-detect anoma-lies	2a	51	7	3	26	10	11	8
	2b	26	32	1	29	-	19	9

For English, target words were counted as case-marked when they were pronouns or part of prepositional phrases. The category *other* includes prepositional phrases, appositions, adverbial phrases and attributes.

10.2.2 Number of trials included in the ERP analysis per experiment and condition.

Table B1 provides an overview of the number of trials included in the final ERP analysis per experiment and condition.

Table B1: Trials analysed per experimental condition and experiment.

Condition		Exp. 1		Exp. 2a		Exp. 2b	
		Range	Average	Range	Average	Range	Average
Border-line Anoma-lies	detected	27-67	52.3 (10.6)	44-80	63.0 (8.9)	24-66	50.5 (10.4)
	non-detected	16-38	25.4 (5.7)	15-44	24.6 (8.0)	24-65	37.7 (10.2)
	plausible control	18-42	35.3 (6.1)	17-28	23.0 (3.0)	20-28	24.2 (2.4)
Easy-to-detect Anoma-lies	anomalous	24-42	37.2 (4.6)	22-30	28.2 (2.1)	20-30	25.6 (3.2)
	plausible control	28-40	37.0 (3.2)	24-29	27.0 (1.8)	24-29	27.3 (1.5)

10.2.3 Analysis of the pre-onset negativity found in Experiment 1 and 2a.

Figures C.1 and C.2 show grand average ERPs time locked to the critical word in the borderline anomaly conditions and the corresponding plausible controls for Experiment 1 and 2a, respectively. As is apparent from the Figures, in addition to the N400 and late positivity, a further negative effect can be observed for detected anomalies relative to non-detected anomalies and plausible controls in time windows beginning before the onset of the critical word. While the effect is broadly distributed in Experiment 1, it appears to be restricted to parietal electrodes in Experiment 2a.
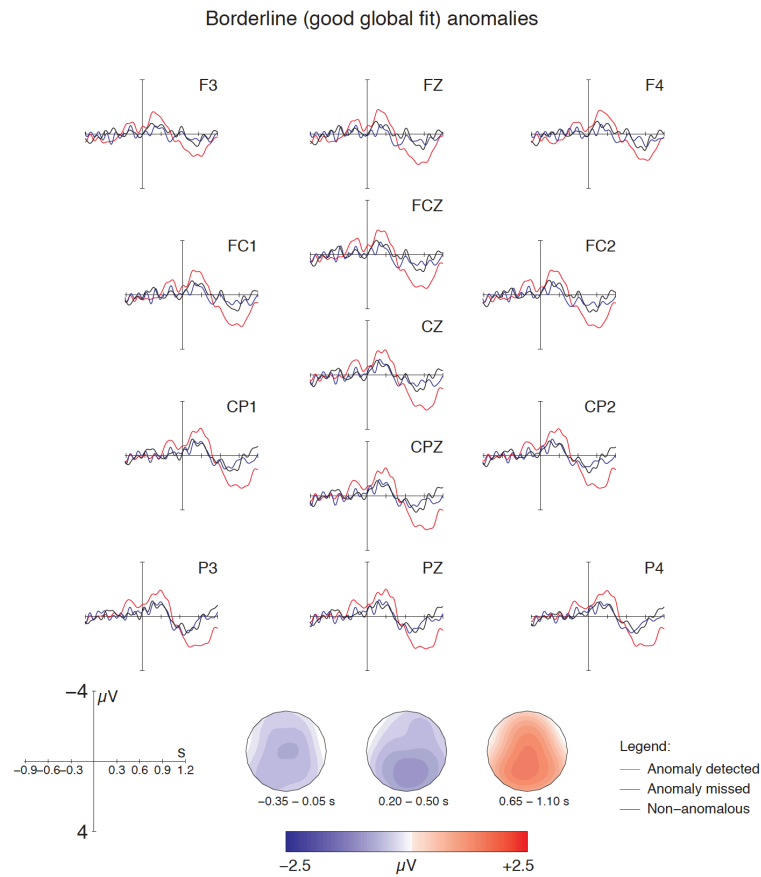
Figure C.1: Grand average ERPs at the position of the critical word (onset at the vertical bar) in the borderline (good global fit) anomaly conditions at 13 selected electrodes in Experiment 1. The figure contrasts ERP responses to detected anomalies (red traces), missed anomalies (blue traces) and plausible controls (black traces). Negativity is plotted upwards. The topographical maps show the scalp distribution for the voltage difference between detected anomalies and plausible sentences in the pre-onset negativity, N400 and late positivity time windows, respectively.

For Experiment 1, a time window of -350 to +50ms was chosen for statistical analysis of lateral and midline regions; the time window of -200 to +50ms was analysed for Experiment 2a. The results of the statistical analyses summarised below confirm the impression gained through visual inspection of the grand average ERPs: in Experiment 1, main effects of ANOMALY show that the negativity is broadly distributed across the lateral and midline regions. In Experiment 2a, on the other hand, interactions of ANOMALY x ROI were observed, with main effects of ANOMALY only significant at PZ and POZ.

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Borderline (good global fit) anomalies
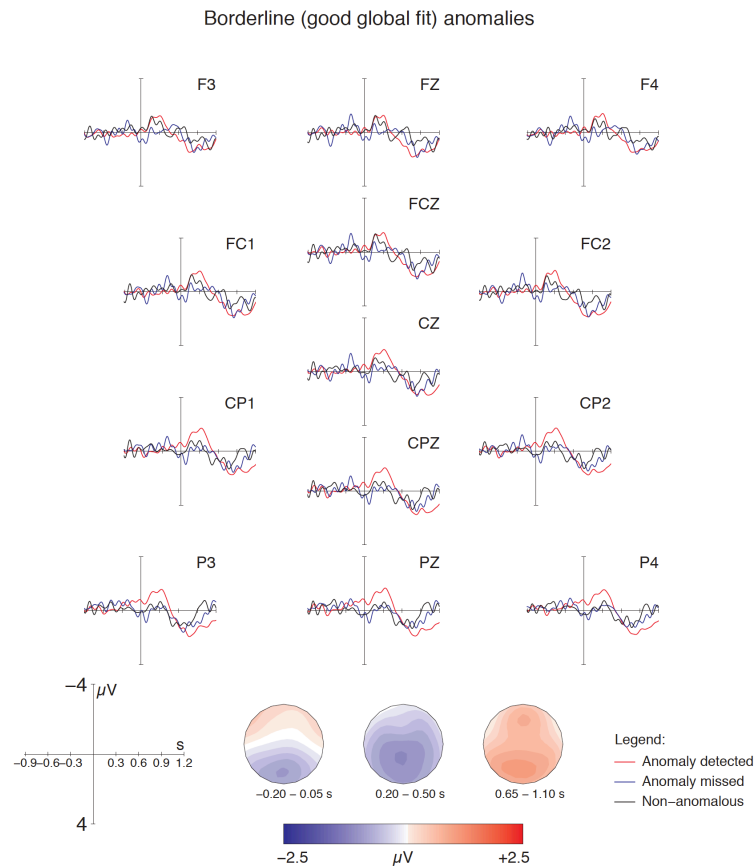
Figure C.2: Grand average ERPs at the position of the critical word (onset at the vertical bar) in the easy-to-detect (poor global fit) anomaly conditions at 13 selected electrodes in Experiment 2a. The figure contrasts ERP responses to anomalous (red traces) and non-anomalous sentences (blue traces). Negativity is plotted upwards. The topographical maps show the scalp distribution for the voltage difference between detected anomalies and plausible sentences in the pre-onset negativity, N400 and late positivity time windows, respectively.

The topographical maps provided in Figures C.1 and C.2 show that the pre-onset negativities are not only differentially distributed across the German experiments, but that their topography is also distinct from that of the respective N400 effects. Importantly, the deduction that the presence of the N400 effects is not dependant the pre-onset negativity is, on the one hand, supported by a significant negative correlation between the two negative effects at PZ [$r(20) = -.68$, $p<0.001$] and POZ [$r(20) = -.70$, $p<0.001$] in Experiment 2a and, on the other hand, by the lack of such a correlation in Experiment 1 [PZ: $r(21) = .04$, $p=0.85$; POZ: $r(21) = .08$, $p=0.71$], see also Figure C.3.
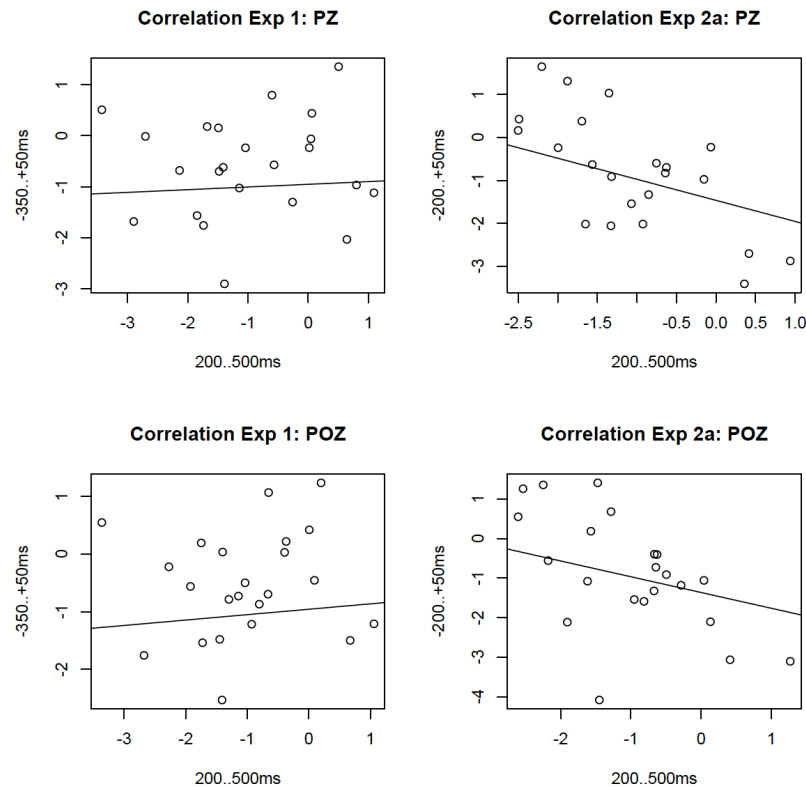
Figure C.3: Scatterplots correlating the amplitude differences of detected borderline anomalies and plausible sentences in Experiment 1 and 2a for the pre-onset negativity and the N400 time windows at PZ and POZ.

Furthermore, we tested whether the pre-onset negativity might have been caused by items in which the word preceding the critical word could have led to an early detection of the anomaly. For example, in the anomalous target sentence „First of all the authorities' initial *negotiations* with the scared and desperate hostages...“ the attributes preceding the critical word might have already rendered a plausible continuation less likely. We carefully searched the materials for items with similar characteristics and computed an additional ERP analysis excluding these items. Visual inspection of the resultant ERPs, however, showed that the pre-onset negativity as well as the N400 effect were unaffected by this procedure.

Table C1: Summary of the statistical analysis for the pre-onset negativity in Experiments 1 and 2a.

Exp. 1 (-350 - +50ms)	Exp. 2a (-200 - +50ms)
ANOMALY	**ANOMALY x ROI**
LAT: F(2,44) = 3.95, p=0.02	LAT: F(6,126) = 5.73, p=0.002
detected vs. non-detected: F(1,22)=5.10, p=0.034, mar-ginally significant	ANOMALY
	- no effect in any ROI -
detected vs. control: F(1,22) = 7.61, p=0.011	
	MID: F(10,210)= 4.97, p=0.009
	ANOMALY
MID: F(2,44)= 5.74, p=0.006	PZ: F(2,42)= 3.48, p = 0.040
detected vs. non-detected: F(1,22)=7.80, p=0.010	detected vs. control: F(1,21) = 8.13, p=0.009
detected vs. control: F(1,22) = 10.80, p=0.003	POZ: F(2,42)= 4.15, p = 0.023
	detected vs. non-detected: F(1,21), = 8.73, p=0.007
	detected vs. control: F(1,21) = 8.30, p=0.009

Only effects that reached significance are reported. Analogous to the analyses reported in the main text, a modified Bonferroni procedure was used to account for multiple testing, resulting in a corrected threshold of p= 0.033 for pair-wise comparisons.

Taken together, the results speak against an interpretation of the observed pre-onset negativities in Experiment 1 and 2a as a systematic effect that might have been caused by the stimulus materials used. Moreover, the presence of the N400 found in the German studies cannot be explained by the occurrence on this earlier negativity. While there is not yet a clear explanation for the causes underlying the pre-onset negativity, it is possible that this effect is linked to inter-subject variability in terms of physiological parameters such as arousal, attention or overall mood that might have influenced cognitive performance (e.g. Lakatos et al., 2008; Kuipers & Thierry, 2011; Mathewson et al., 2011).

10.3   Supplementary Materials Study 3

Table S1: Regions showing reliable activation or deactivation relative to baseline for interval 1 across all conditions

REGION / LOCAL MAXIMUM / ACTIVATION	Easy detected				Easy control				Borderline detected				Borderline non-detected				Borderline control			
	Talairach			CS	Talairach			CS	Talairach			CS	Talairach			CS	Talairach			CS
	Z	Y	X		Z	Y	X		Z	Y	X		Z	Y	X		Z	Y	X	
frontal																				
L. Anterior insula	6	20	-26	252	3	20	-26	333					4	19	-28	195				
L. Middle frontal gyrus	46	1	-33	1487																
L. Pars triangularis of the IFG	6	40	-46	3773	14	42	-43	2983	14	41	-44	9222	9	43	-44	177	14	41	-43	8344
L. Pars triangularis of the IFG													9	41	-45	157				
L. Pars triangularis of the IFG													10	27	-47	1593				
L. Precentral sulcus	34	7	-37	86	47	1	-35	1768					34	8	-39	711				
L. Superior frontal gryus					53	30	-4	520												
L. Superior frontal gyrus	51	13	-4	1294	51	13	-4	468	51	13	-4	2255					51	13	-4	1634
R. Anterior insula	3	32	30	494	5	27	27	452	-2	23	27	201	2	31	29	291	-10	20	26	336
R. Inferior frontal sulcus					19	28	42	129	32	17	35	100								
R. Middle frontal gyrus	27	19	45	416	25	20	43	125					26	20	45	725				
R. Orbital gyrus																	-8	41	40	133
R. Pars opercularis of the IFG	12	19	45	212									11	19	44	214				
R. Pars orbitalis of the IFG									-2	42	45	4175								
R. Pars triangularis of the IFG					4	39	44	152									6	41	45	4107
R. Pars triangularis of the IFG	6	39	48	586	9	29	47	402												
R. Precentral sulcus									32	10	48	306					32	11	48	260
R. Superior frontal gyrus	49	14	9	199	44	26	8	222	44	26	8	674	43	26	9	256	53	20	9	656
R. Superior frontal gyrus	44	37	8	109																

Table S1 (continued): Regions showing reliable activation or deactivation relative to baseline for interval 1 across all conditions

REGION / LOCAL MAXIMUM / ACTIVATION	Easy detected Talairach Z	Y	X	CS	Easy control Talairach Z	Y	X	CS	Borderline detected Talairach Z	Y	X	CS	Borderline non-detected Talairach Z	Y	X	CS	Borderline control Talairach Z	Y	X	CS
temporal																				
L. Inferior temporal gyrus					29	18	-31	169	-8	-43	-52	267					-8	-43	-52	262
L. Parahippocampal gyrus					-14	-11	-10	92												
L. Superior temporal gyrus	5	-18	-61	6590	6	-24	-61	4980	5	-21	-65	7146	-1	-1	-53	234	4	-18	-60	3058
L. Superior temporal sulcus					34	-54	-39	173												
R. Parahippocampal gyrus									-13	-17	16	539								
R. Planum temporale	8	-30	56	108																
R. Superior temporal gyrus	4	-19	62	4214	3	-20	61	2815	4	-18	61	4322	3	-18	60	137	4	-21	62	2667
R. Superior temporal gyrus																	-7	-1	53	241
R. Superior temporal gyrus																	-12	10	47	115
R. Superior temporsal sulcus													3	-33	42	625				
medial wall																				
L. Thalamus	14	-15	-1	169	14	-13	-1	150	14	-10	-1	2377					9	-19	-1	161
L. Thalamus (pulvinar)	4	-30	-6	191													2	-29	-7	420
R. Thalamus									13	-13	2	230								

Notes: Individual vertex threshold p < .001, corrected (FWE p < .05). Local maximum defined by Talairach and Tournoux coordinates in the volume space. CS = Cluster size in number of surface vertices. L = Left. R= Right. IFG = Inferior frontal gyrus

Table S1: Regions showing reliable activation or deactivation relative to baseline for interval 1 across all conditions

REGION LOCAL MAXIMUM	Easy detected				Easy control				Borderline detected				Borderline non-detected				Borderline control			
	Talairach			CS	Talairach			CS	Talairach			CS	Talairach			CS	Talairach			CS
DEACTIVATION	Z	Y	X		Z	Y	X		Z	Y	X		Z	Y	X		Z	Y	X	
parietal																				
L. Marginal branch of the cingulate sulcus									37	-32	-15	1220	42	-35	-6	1028				
L. Paracentral lobule					58	-39	-3	238	69	-35	-14	279	68	-33	-6	671				
L. Parieto-occipital sulcus	26	-64	-14	182	25	-64	-13	278					25	-63	-13	426				
L. Parieto-occipital sulcus	30	-69	-20	92																
L. Postcentral gyrus				98					61	28	-26	385								
L. Postcentral gyrus	61	-28	-26	156	67	-29	-13	1844	67	-29	-13	139					68	-29	-9	132
L. Postcentral sulcus													54	-42	-31	206				
L. Posterior cingulate gyrus	28	-34	-4	267	28	-34	-4	133												
L. Posterior cingulate gyrus, ventral													5	-42	-8	2539				
L. Posterior pericallosal sulcus	24	-30	-1	343	24	-30	-1	167	24	-30	-1	127								
L. Precuneus (inferior)																	46	-43	-5	160
L. Precuneus (posterior)	39	-69	-5	952	39	-69	-5	417	41	-69	-5	724								
L. Precuneus (superior)	60	-55	-9	1503	63	-51	-11	2742	64	-52	-11	358	63	-54	-11	324	59	-55	-9	203
L. Subcentral sulcus									12	-6	-58	1785								
L. Superior parietal lobule (anterior)	68	-43	-18	476	62	-46	-17	179					67	-46	-19	348				
L. Superior parietal lobule (lateral)													55	-48	-15	152				
L. Supramarginal gyrus (inferior)																	21	-23	-55	204
R. Marginal branch of the cingulate sulcus													37	-37	7	2421	32	-31	14	428
R. Paracentral lobule (anterior)	62	-30	4	278					62	-30	4	122								
R. Paracentral lobule (posterior)	67	-39	5	347	67	-39	5	853					67	-39	5	477				
R. Postcentral gyrus	61	-27	27	85					59	-27	32	373	60	-27	32	189				
R. Postcentral sulcus					59	-39	25	97					59	-40	24	85				
R. Postcentral sulcus					56	-32	22	98												
R. Posterior cingulate gyrus (dorsal)													19	-50	8	122				
R. Posterior cingulate gyrus (ventral)	5	-44	11	287	3	-42	12	498	5	-44	10	413	5	-43	10	1873	5	-43	10	2014
R. Posterior pericallosal sulcus	24	-32	2	96	24	-31	2	85	24	-31	2	98								

Table S1: Regions showing reliable activation or deactivation relative to baseline for interval 1 across all conditions

REGION LOCAL MAXIMUM DEACTIVATION	Easy detected				Easy control				Borderline detected				Borderline non-detected				Borderline control			
	Talairach			CS	Talairach			CS	Talairach			CS	Talairach			CS	Talairach			CS
	Z	Y	X		Z	Y	X		Z	Y	X		Z	Y	X		Z	Y	X	
parietal																				
R. Precuneus																	49	-72	8	113
R. Precuneus (inferior)	45	-71	6	337	52	-70	10	1527					33	-61	6	416	29	-63	5	183
R. Precuneus (superior)									63	-53	10	4260	63	-53	13	1123	58	-54	7	948
R. Subcentral gyrus					21	-14	62	1848												
R. Subcentral sulcus									9	-9	58	1008					9	-9	59	910
R. Superior parietal lobule (lateral)	63	-41	23	189	61	-47	22	219					58	-54	22	102				
R. Superior parietal lobule (medial)	54	-58	13	4731	54	-58	13	5514	54	-57	13	1531	52	-55	14	398	55	-58	13	192
R. Supramarginal gyrus	36	-26	59	94					36	-26	59	140					36	-26	59	104
occipital																				
L. Calcarine sulcus (inferior)																	-2	-47	-15	415
L. Calcarine sulcus (superior)									5	-44	-8	359					5	-43	-9	1748
L. Cuneus					35	-80	-9	1820	35	-81	-9	652					39	-80	-9	164
L. Lingual gyrus													5	-54	-16	199				
R. Cuneus	27	-78	3	170	33	-79	3	1611	27	-78	3	451	30	-80	3	674	25	-77	3	104
R. Lingual gyrus					0	-66	3	163					3	-64	3	336				
R. Posterior pericallosal sulcus (ventral)	8	-37	5	166	8	-36	5	245												
R. Superior occipital gyrus	40	-80	9	96									39	-80	7	97				
temporal																				
L. Parahippocampal gyrus																	-10	-33	-19	270
L. Transverse temporal gyrus	9	-19	-43	8983	8	-20	-44	9738	9	-19	-43	6941	7	-17	-45	10792	7	-17	-45	9911
R. Inferior insula													-13	-6	38	108				
R. Middle temporal gyrus													-5	-22	54	105				
R. Parahippocampal gyrus									10	-33	63	95					-10	-33	20	190
R. Superior temporal gyrus																				
R. Transverse temporal gyrus	4	-19	47	10322	4	-19	47	9716	4	-19	48	7959	4	-18	49	12651	4	-19	48	9167

Table S2: Regions showing reliable activation or deactivation relative to baseline for interval 2 across all conditions

REGION LOCAL MAXIMUM ACTIVATION	Easy detected				Easy control				Borderline detected				Borderline non-detected				Borderline control			
	Talairach			CS	Talairach			CS	Talairach			CS	Talairach			CS	Talairach			CS
	Z	Y	X		Z	Y	X		Z	Y	X		Z	Y	X		Z	Y	X	
frontal																				
L. Anterior insula					4	20	-26	7057					4	20	-26	2384	3	19	-26	2456
L. Anterior/middle cingulate sulcus	34	21	-11	124					34	21	-11	164								
L. Central sulcus (superior)									46	-18	-29	184					46	-18	-29	225
L. Inferior frontal sulcus													28	30	-37	549	28	24	-39	181
L. Middle frontal gyrus																	47	14	-40	141
L. Pars triangularis of the IFG	10	42	-43	9113	11	42	-43	604	10	42	-44	10446					1	43	-42	215
L. Precentral sulcus (inferior)													33	4	-44	1473				
L. Precentral sulcus (superior)									46	-3	-35	176					41	-3	-27	398
L. Precentral sulcus																	34	7	-46	1192
L. Superior frontal gyrus	50	12	-4	2492	50	12	-5	2121	49	12	-4	3572	50	10	-9	1118	50	10	-10	1231
L. Superior frontal gyrus	59	7	-12	178																
R. Anterior insula	4	27	26	2446	4	27	26	2419	4	26	26	5127	4	28	26	1787	5	29	27	1060
R. Lateral orbital sulcus									-1	43	38	94					-3	40	44	146
R. Middle frontal gyrus	27	19	45	2168	25	21	42	841	41	2	34	170	28	19	45	495	26	23	44	387
R. Pars opercularis of the IFG													15	23	44	144	7	19	41	266
R. Pars orbitalis of the IFG									-2	42	45	137								
R. Precentral sulcus					32	10	49	229					31	4	38	883	29	7	50	500
R. Superior frontal gyrus	49	14	9	1260	49	14	9	1089	44	27	8	1506	50	14	10	811	49	10	10	734

Table S2 (continued): Regions showing reliable activation or deactivation relative to baseline for interval 2 across all conditions

REGION LOCAL MAXIMUM	Easy detected				Easy control				Borderline detected				Borderline non-detected				Borderline control			
	Talairach			CS	Talairach			CS	Talairach			CS	Talairach			CS	Talairach			CS
ACTIVATION	Z	Y	X		Z	Y	X		Z	Y	X		Z	Y	X		Z	Y	X	
parietal																				
L. Angular gyrus									27	-45	-60	253								
L. Intraparietal sulcus (anterior)	43	-40	-28	793					47	-51	-25	1422	43	-40	-27	947	45	-49	-27	1485
L. Intraparietal sulcus (posterior)	39	-54	-32	211	39	-53	-32	504	39	-54	-32	741					37	-52	-30	547
L. Postcentral sulcus																				
L. Supramarginal gyrus (anterior)									47	-43	-52	586	53	-29	-44	89	53	-29	-48	406
L. Supramarginal gyrus (posterior)																	37	-38	-59	199
occipital																				
L. Calcarine sulcus									6	-79	-13	127								
L. Lateral occipito-temporal sulcus	0	-45	-42	87	-2	-43	-40	109									-3	-43	-39	181
L. Superior occipital sulcus					0	-30	-44	985	1	-30	-44	1386	25	-60	-33	90				
temporal																				
L. Inferior temporal gyrus									-8	-43	-52	479								
L. Middle temporal gyrus	1	-36	-63	1117																
R. Middle temporal gyrus									-4	-40	60	302								
R. Superior temporal sulcus									30	-61	37	90								
medial wall																				
L. Caudate nucleus									13	-4	-1	174								
L. Thalamus									14	-17	-1	451								
L. Thalamus									16	-12	-1	105								
L. Thalamus (pulvinar nucleus)					2	-23	-2	217	2	-32	-11	132								
R. Thalamus									-4	-24	4	88								

Table S2 (continued): Regions showing reliable activation or deactivation relative to baseline for interval 2 across all conditions

REGION LOCAL MAXIMUM DEACTIVATION	Easy detected Talairach				Easy control Talairach				Borderline detected Talairach				Borderline non-detected Talairach				Borderline control Talairach			
	Z	Y	X	CS	Z	Y	X	CS	Z	Y	X	CS	Z	Y	X	CS	Z	Y	X	CS
frontal																				
L. Anterior cingulate sulcus	4	41	-12	382									5	42	-11	245				
L. Central sulcus	38	-8	-36	95	38	-9	-35	700												
L. Precentral gyrus									41	-5	-43	103	42	-4	-45	368				
L. Superior frontal sulcus													43	24	-14	125	41	23	-16	84
L. Superior insula					17	5	-33	83												
R. Anterior cingulate sulcus	0	35	13	293	1	35	13	351	0	35	13	167	0	35	13	274				
R. Central sulcus									29	-11	60	143								
R. Precentral gyrus	36	-6	51	527					35	-6	51	492	36	-6	51	540				
R. Precentral sulcus, inferior	27	-11	62	131																
R. Superior frontal sulcus (middle)	36	23	28	92													40	29	26	109
R. Superior frontal sulcus (posterior)																	37	16	24	207
R. Superior insula	16	7	32	189	16	7	32	142												
parietal																				
L. Marginal branch of the cingulate sulcus									37	-32	-15	1220	42	-35	-6	1028				
L. Paracentral lobule					58	-39	-3	238	69	-35	-14	279	68	-33	-6	671				
L. Parieto-occipital sulcus	26	-64	-14	182	25	-64	-13	278					25	-63	-13	426				
L. Parieto-occipital sulcus	30	-69	-20	92																
L. Postcentral gyrus				98					61	28	-26	385								
L. Postcentral gyrus	61	-28	-26	156	67	-29	-13	1844	67	-29	-13	139					68	-29	-9	132
L. Postcentral sulcus													54	-42	-31	206				
L. Posterior cingulate gyrus	28	-34	4	267	28	-34	4	133												
L. Posterior cingulate gyrus, ventral													5	-42	-8	2539				
L. Posterior pericallosal sulcus	24	-30	-1	343	24	-30	-1	167	24	-30	-1	127								

Table S2 (continued): Regions showing reliable activation or deactivation relative to baseline for interval 2 across all conditions

REGION LOCAL MAXIMUM / DEACTIVATION	Easy detected				Easy control				Borderline detected				Borderline non-detected				Borderline control			
	Talairach			CS	Talairach			CS	Talairach			CS	Talairach			CS	Talairach			CS
	Z	Y	X		Z	Y	X		Z	Y	X		Z	Y	X		Z	Y	X	
parietal																				
L. Precuneus (posterior)	39	-69	-5	952	39	-69	-5	417	41	-69	-5	724								
L. Precuneus (superior)	60	-55	-9	1503	63	-51	-11	2742	64	-52	-11	358	63	-54	-11	324	59	-55	-9	203
L. Precuneus (inferior)																	46	-43	-5	160
L. Subcentral sulcus									12	-6	-58	1785								
L. Superior parietal lobule (anterior)	68	-43	-18	476	62	-46	-17	179					67	-46	-19	348				
L. Superior parietal lobule (lateral)													55	-48	-15	152				
L. Supramarginal gyrus (inferior)																	21	-23	-55	204
R. Marginal branch of the cingulate sulcus													37	-37	7	2421	32	-31	14	428
R. Paracentral lobule (anterior)	62	-30	4	278					62	-30	4	122								
R. Paracentral lobule (posterior)	67	-39	5	347	67	-39	5	853					67	-39	5	477				
R. Postcentral gyrus	61	-27	27	85					59	-27	32	373	60	-27	32	189				
R. Postcentral sulcus					59	-39	25	97					59	-40	24	85				
R. Postcentral sulcus					56	-32	22	98												
R. Posterior cingulate gyrus (dorsal)													19	-50	8	122				
R. Posterior cingulate gyrus (ventral)	5	-44	11	287	3	-42	12	498	5	-44	10	413	5	-43	10	1873	5	-43	10	2014
R. Posterior pericallosal sulcus	24	-32	2	96	24	-31	2	85	24	-31	2	98								
R. Precuneus																	49	-72	8	113
R. Precuneus (superior)	45	-71	6	337	52	-70	10	1527	63	-53	10	4260	63	-53	13	1123	58	-54	7	948
R. Precuneus (inferior)					21	-14	62	1848					33	-61	6	416	29	-63	5	183
R. Subcentral gyrus																				
R. Subcentral sulcus									9	-9	58	1008					9	-9	59	910
R. Superior parietal lobule (medial)	54	-58	13	4731	54	-58	13	5514	54	-57	13	1531	52	-55	14	398	55	-58	13	192
R. Superior parietal lobule (lateral)	63	-41	23	189	61	-47	22	219					58	-54	22	102				
R. Supramarginal gyrus	36	-26	59	94					36	-26	59	140					36	-26	59	104

Table S2 (continued): Regions showing reliable activation or deactivation relative to baseline for interval 2 across all conditions

REGION LOCAL MAXIMUM	Easy detected				Easy control				Borderline detected				Borderline non-detected				Borderline control			
	Talairach			CS	Talairach			CS	Talairach			CS	Talairach			CS	Talairach			CS
DEACTIVATION	Z	Y	X		Z	Y	X		Z	Y	X		Z	Y	X		Z	Y	X	
occipital																				
L. Calcarine sulcus (superior)									5	-44	-8	359					5	-43	-9	1748
L. Calcarine sulcus (inferior)																	-2	-47	-15	415
L. Cuneus					35	-80	-9	1820	35	-81	-9	652					39	-80	-9	164
L. Lingual gyrus													5	-54	-16	199				
R. Cuneus	27	-78	3	170	33	-79	3	1611	27	-78	3	451	30	-80	3	674	25	-77	3	104
R. Lingual gyrus					0	-66	3	163					3	-64	3	336				
R. Posterior pericallosal sulcus (ventral)	8	-37	5	166	8	-36	5	245												
R. Superior occipital gyrus	40	-80	9	96									39	-80	7	97				
temporal																				
L. Parahippocampal gyrus																	-10	-33	-19	270
L. Transverse temporal gyrus	9	-19	-43	8983	8	-20	-44	9738	9	-19	-43	6941	7	-17	-45	10792	7	-17	-45	9911
R. Inferior insula													-13	-6	38	108				
R. Middle temporal gyrus													-5	-22	54	105				
R. Parahippocampal gyrus									10	-33	63	95					-10	-33	20	190
R. Superior temporal gyrus													4	-18	49	12651				
R. Transverse temporal gyrus	4	-19	47	10322	4	-19	47	9716	4	-19	48	7959					4	-19	48	9167

Notes: Individual vertex threshold p < .001, corrected (FWE p < .05). Local maximum defined by Talairach and Tournoux coordinates in the volume space. CS = Cluster size in number of sur-face vertices. L = Left. R= Right. IFG = Inferior frontal gyrus.
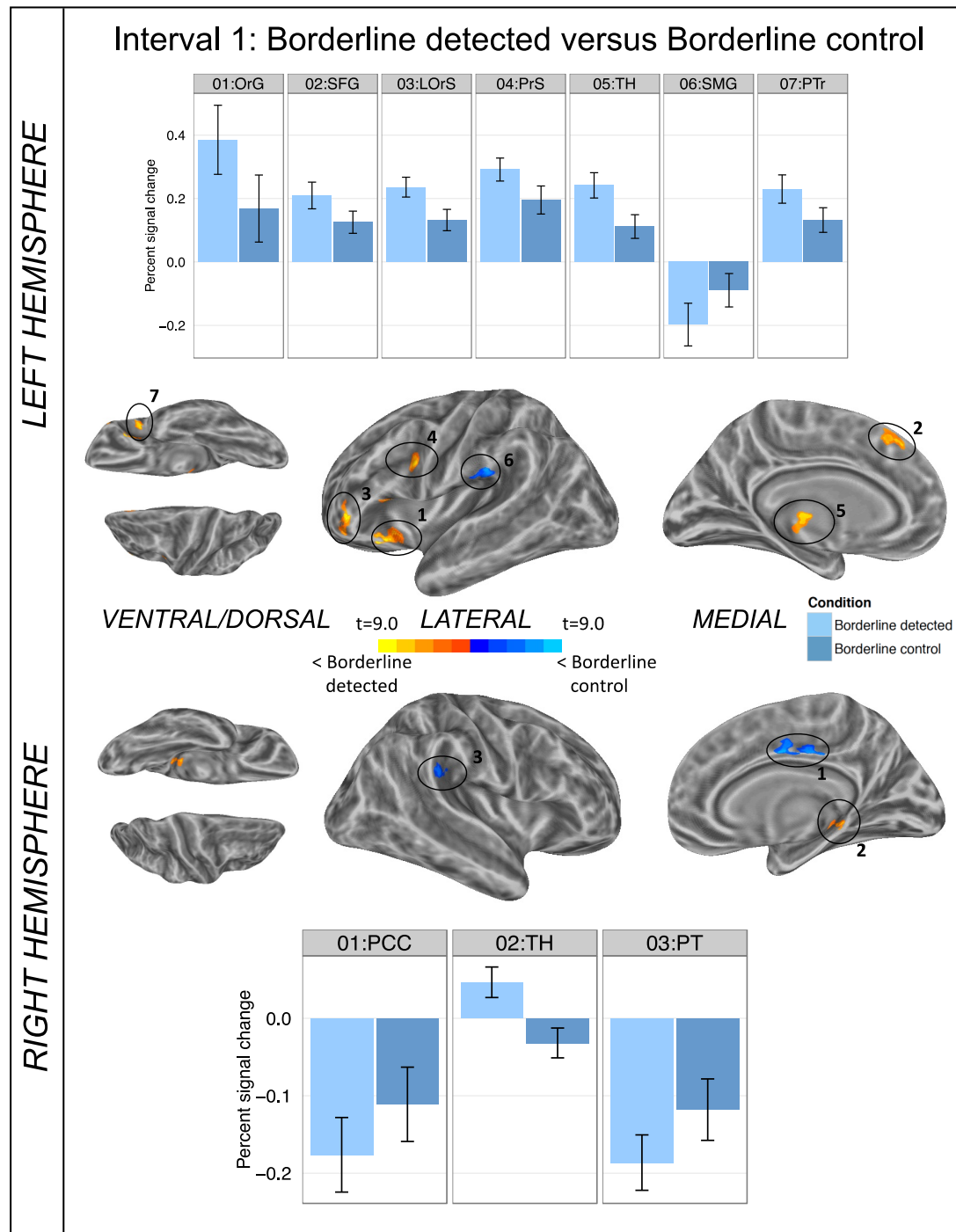
Figure S1: Results of the whole-brain comparison between the easy detected and easy control condition for interval 1 shown on inflated average brain surfaces of the left and right hemisphere. The individual per-vertex threshold was p < .01 (corrected FWE p < .05). Warm colours indicate higher levels of activation for easy detected; cold colours reflect greater activation for the easy control sentences. Bar graphs present the difference between conditions for the local activation maximum of each cluster. Error bars depict standard error of the mean. ACC=anterior cingulate cortex, CS=central sulcus, ITG=inferior temporal gyrus, LinG=lingual gyrus, OrG=orbital gyrus, PHG=parahippocampal gyrus, POp=pars opercularis of the inferior frontal gyrus, PP=planum polare, PrS=precentral sulcus, PTr=pars triangularis of the inferior frontal gyrus, SFG=superior frontal gyrus, STG=superior temporal gyrus, STS=superior temporal sulcus, TH=thalamus, TTG=transverse temporal gyrus, Un=uneus.
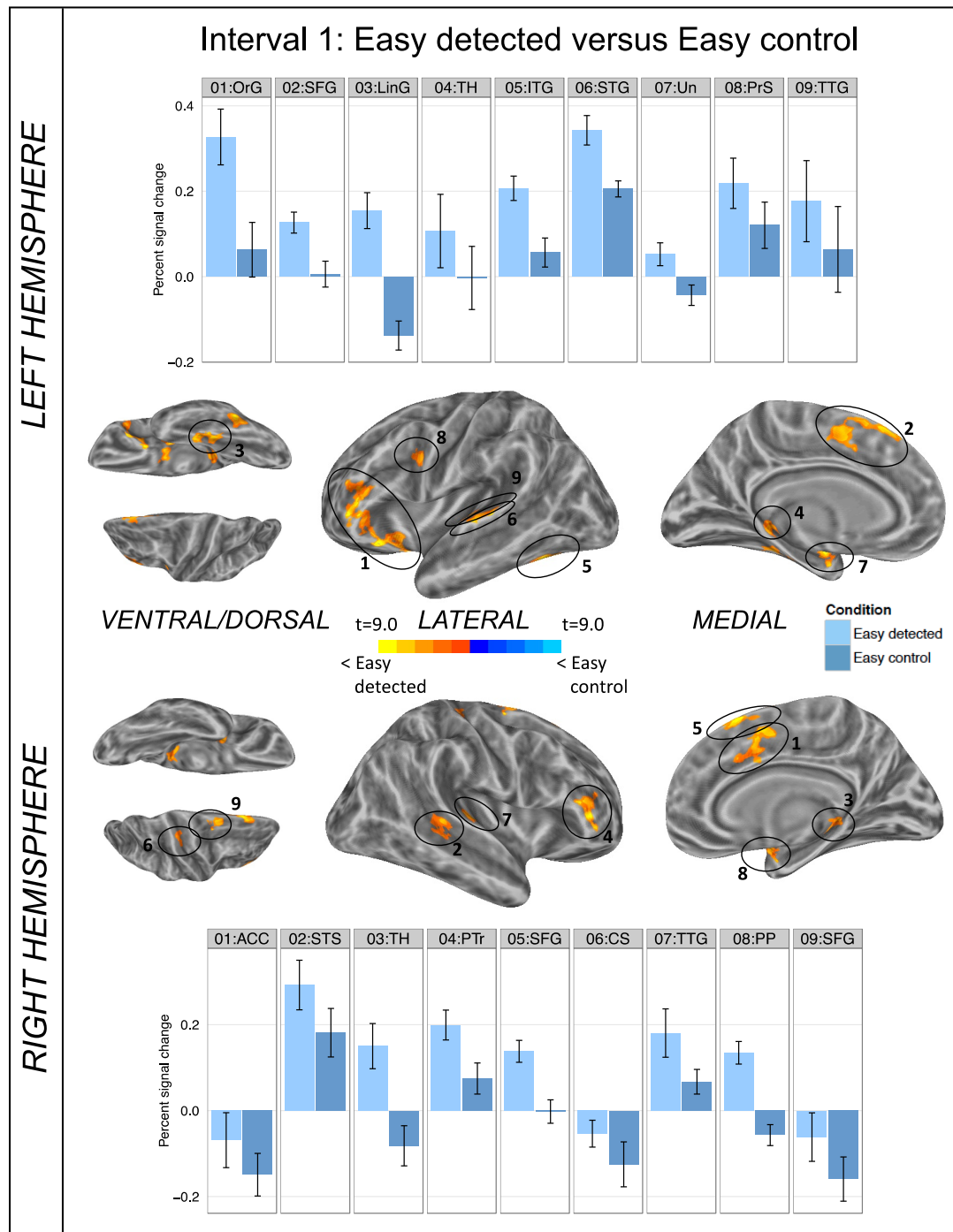
Figure S2: Results of the whole-brain comparison between the borderline detected and borderline control condition for interval 1 shown on inflated average brain surfaces of the left and right hemisphere. The individual per-vertex threshold was p < .01 (corrected FWE p < .05). Warm colours indicate higher levels of activation for borderline detected; cold colours reflect greater activation for the borderline control sentences. Bar graphs present the difference between conditions for the local activation maximum of each cluster. Error bars depict standard error of the mean. LOrS=lateral orbital sulcus, OrG=orbital gyrus, PHG=parahippocampal gyrus, PrS=precentral sulcus, PT=planum temporale, PTr=pars triangularis of the inferior frontal gyrus, PCC=posterior cingulate cortex, SFG=superior frontal gyrus, SMG=supramarginal gyrus, TH=thalamus.

Table S3: Regions showing reliable differences for the comparison of *easy detected* versus *easy control* at the whole-brain level

INTERVAL 1: Borderline detected > Borderline control

	DESCRIPTION	Talairach Coordinates				Cluster Size		
		X	Y	Z	BA	Nodes	Area	MI
frontal	L. Lateral orbital sulcus/pars triangularis of the IFG/ inferior frontal sulcus	-40	36	-7	47	271	120.7	0.10
	L. Orbital gyrus/pars orbitalis of the IFG/anterior insula	-38	16	-5	47	476	194.0	0.22
	L. Pars triangularis of the IFG	-38	24	13	45	298	52.8	0.10
	L. Precentral sulcus	-39	7	33	9	267	94.4	0.10
	L. Superior frontal gyrus	-4	26	53	6	272	125.4	0.08
medial wall	L. Thalamus	0	-21	8	-	291	86.8	0.13
	R. Thalamus	15	-31	-1	-	574	159.9	0.08

INTERVAL 1: Borderline control > Borderline detected

	DESCRIPTION	X	Y	Z	BA	Nodes	Area	MI
frontal	R. Middle/posterior cingulate sulcus/gyrus	31	-11	43	31	916	192.1	0.03
temporal	R. Planum temporale/lateral fissure	52	-40	22	40	263	102.5	0.05
parietal	L. Supramarginal gyrus	-46	-22	20	40	413	84.0	0.11

Notes: Individual vertex threshold p < .01, corrected (FWE p < .05). Local maximum defined by Talairach and Tournoux coordinates in the volume space. BA = Brodmann Area. Nodes = Cluster size in number of surface vertices. Area = Area of cluster calculated in square millimeters (mm^2). MI = Maximum intensity in terms of percent signal change. L = Left. R= Right. IFG = Inferior frontal gyrus.

Table S4: Regions showing reliable differences for the comparison of *easy detected* versus *easy control* at the whole-brain level

INTERVAL 1: Easy detected > Easy control

	DESCRIPTION	Talairach Coordinates				Cluster Size		
		X	Y	Z	BA	Nodes	Area	MI
frontal	L. Orbital gyrus/anterior insula/pars orbitalis and pars triangularis of the IFG/inferior frontal sulcus	-38	15	5	47	1931	713.1	0.26
	L. Precentral sulcus	-44	7	33	9	304	101.0	0.10
	L. Superior frontal gyrus/anterior/middle cingulate sulcus	-10	21	55	6	1185	404.0	0.12
	R. Anterior/middle cingulate sulcus/gyrus	9	4	35	24	739	229.7	0.08
	R. Central sulcus	18	-26	49	4	386	130.9	0.07
	R. Pars triangularis of the IFG/inferior frontal sulcus	40	42	5	45	572	179.3	0.12
	R. Superior frontal gyrus	11	20	57	6	486	175.1	0.14
	R. Superior frontal gyrus	12	-1	63	6	256	70.3	0.10
temporal	L. Inferior temporal gyrus/ lateral occipito-temporal sulcus	-50	-43	-8	37	518	174.2	0.15
	L. Superior temporal gyrus/planum temporale	-61	-17	5	22	381	121.4	0.14
	L. Transverse temporal gyrus	-47	-14	6	22	249	77.17	0.11
	L. Uncus/parahippocampal gyrus	-27	-3	-21	34/28	656	114.6	0.10
	R. Planum polare/parahippocampus gyrus	31	1	-13	38	591	108.1	0.19
	R. Superior temporal sulcus	49	-32	2	22	614	189.5	0.11
	R. Transverse temporal gyrus/sulcus	47	-18	4	41	425	120.5	0.11
occipital	L. Lingual gyrus/parahippocampal gyrus	-31	-14	-19	36	657	257.3	0.29
medial wall	L. Thalamus	-12	-33	3	-	858	206.4	0.11
	R. Thalamus (pulvinar nucleus)	10	-32	2	-	828	180.7	0.23

Notes: Individual vertex threshold p < .01, corrected (FWE p < .05). Local maximum defined by Talairach and Tournoux coordinates in the volume space. BA = Brodmann Area. Nodes = Cluster size in number of surface vertices. Area = Area of cluster calculated in square millimeters (mm^2). MI = Maximum intensity in terms of percent signal change. L = Left. R= Right. IFG = Inferior frontal gyrus.

10.4   List of Figures

10.5   List of Tables

10.6 Zusammenfassung und Beschreibung des Eigenanteils

Studie 1:

Lotze, N., Tune, S., Schlesewsky, M. & Bornkessel-Schlesewsky, I. (2011). Meaningful physical changes mediate lexical-semantic integration: Evidence for the interplay between top-down and bottom-up information sources in the N400. *Neuropsycholgia, 49*(13), 3573–3582.

Beteiligung an: Datenerhebung, Datenauswertung, Dateninterpretation, Vorbereitung des Manuskriptes zur Publikation

Studie 2:

Tune, S., Schlesewsky, M., Small, S. L., Sanford, A.J., Bohan, J., Sassenhagen, J., Bornkessel- Schlesewsky, I. (in revision). Cross-linguistic variation in the neurophysiological response to semantic processing: Evidence from anomalies at the borderline of awareness. *Neuropsychologica*.

Beteiligung an: Entwicklung von Stimulusmaterial und Experimentalparadigma, Implementierung des Paradigmas, Datenerhebung, Datenauswertung, Dateninterpretation, Vorbereitung des Manuskriptes zur Publikation

Studie 3:

Tune, S., Schlesewsky, M., Nagels, A., Small, S.L., Bornkessel-Schlesewsky, I. (submitted). Depth of semantic processing in discourse context modulates contributions of temporal and parietal regions: fMRI evidence. *Cortex*.

Beteiligung an: Entwicklung von Stimulusmaterial und Experimentalparadigma, Implementierung des Paradigmas, Datenerhebung, Datenauswertung, Dateninterpretation, Vorbereitung des Manuskriptes zur Publikation

Zusammenfassung

Wenn wir Texte lesen oder mit anderen Menschen kommunizieren, dann besteht eine der Hauptaufgaben darin, von dem sensorisch aufgenommenen sprachlichen Input zu einer möglichst kohärenten Interpretation zu gelangen. Die Untersuchung der neurobiologischen Grundlagen, die die effiziente und daher scheinbar mühelose Bewältigung dieser Aufgabe ermöglichen, ist ein Thema, das Wissenschaftler unterschiedlicher Disziplinen seit vielen Jahrzehnten beschäftigt. Die Verfügbarkeit moderner neurowissenschaftlicher Methoden, wie beispielsweise die Ableitung von ereigniskorrelierten Potentialen (EKP) oder bildgebende Verfahren wie die funktionelle Magnetresonanztomographie (fMRT), hat in den letzten dreißig Jahren zu einem erheblichen Erkenntnisgewinn geführt. Die Ergebnisse von neurokognitiven Studien, die sich dieser Methoden bedient haben, konnten zeigen, dass die semantische Analyse maßgeblich durch ein Zusammenspiel von externen und internen Einflüssen bestimmt wird.

Während bereits die frühesten EKP-Studien den Einfluss des Satzkontextes auf die Interpretation einen satzfinales Wortes belegten (Kutas & Hillyard, 1980), sprechen die Befunde neuerer EKP-Studien dafür, dass die Interaktion zwischen sensorischer, stimulusbasierter *bottom-up* Information und *top-down* Prozessen, wie die Generierung von Erwartungen und Prädiktionen aufgrund von kontextueller Information und Weltwissen, weitaus umfangreicher ist, als bisher angenommen (e.g. Schumacher & Baumann, 2010). In der Forschungsliteratur zu so genannten N400-Effekten, die ein wichtiges elektrophysiologisches Korrelat der semantischen Verarbeitung darstellen, findet sich darüber hinaus erste Evidenz dafür, dass die Gewichtung von top-down und bottom-up Informationsquellen unter anderem von den Eigenschaften der jeweils untersuchten Sprache determiniert wird (Bornkessel-Schlesewsky et al., 2011).

Die hier vorliegende Arbeit hat sich daher aus einer sprachübergreifenden Perspektive mit den neurokognitiven und neurobiologischen Prozessen beschäftigt, die dem dynamischen Zusammenspiel von top-down und bottom-up Informationen in der Sprachverarbeitung zu Grunde liegen. Zu diesem Zweck wurden insgesamt vier EKP-Experimente und eine fMRT-Studie durchgeführt, die die Sprachverstehensprozesse anhand von semantischen Anomalien untersuchten. Im Folgenden werden die Fragestellungen und Ergebnisse der einzelnen Studie kurz zusammengefasst.

Das erste EKP-Experiment, das zum Deutschen durchgeführt wurde, hat sich mit der Fragestellung befasst, ob die Manipulation von rein formbasierten und damit kontextunabhängigen Eigenschaften eines kritischen Wortes Einfluss auf seine Verarbeitung im Satz haben könnte. Die Ergebnisse haben gezeigt, dass die Hervorhebung eines inkongruenten satzfinalen Wortes durch Großschreibung eine Reduktion des N400-Effektes zur Folge hatte. Da dieser Befund durch keine der bestehenden Theorien zur funktionalen Interpretation der N400 vorhergesagt wurde, haben wir einen neuen Ansatz vorgeschlagen, der Modulationen der N400 Amplitude über einen Mechanismus erklärt, der Information aus bottom-up und top-down Prozessen miteinander abgleicht.

In der zweiten Studie wurden insgesamt drei EKP-Experimente durchgeführt, die sich mit der Verarbeitung von klassischen semantischen Verletzungen und schwer detektierbaren „Moses Illusionen" (Erickson & Mattson, 1981) im Deutschen und Englischen. Der Begriff Moses Illusion bezeichnet das relativ robuste Phänomen, dass semantische Anomalien häufig unentdeckt bleiben, wenn das inkongruente Wort eine enge Verbindung zum vorherigen Kontext aufweist. Die Analyse der detektierten und übersehenen semantischen Illusionen im Vergleich zu kongruenten Kontrollsätzen offenbarte qualitative Unterschiede zwischen den beiden untersuchten Sprachen. Während sich die drei Bedingungen im Englischen lediglich durch eine späte Positivierung für detektierte semantische Illusionen im Vergleich zu unerkannten Anomalien und korrekten Kontrollsätzen unterschieden, zeigten detektierte Illusionen im Deutschen ein biphasisches Muster aus einem N400-Effekt gefolgt von einer späten Positivierung.

Die englischen Daten replizierten damit auf der einen Seite das Ergebnis einer früheren EKP-Studie von Sanford und Kollegen (Sanford, Leuthold, Bohan, & Sanford, 2011); andererseits waren die sprachübergreifenden Unterschiede vergleichbar mit dem Muster, dass für semantische Verletzungen auf der Ebene von thematischen Rollen gefunden wurde (Bornkessel-Schlesewsky et al., 2011). Die beobachteten sprachübergreifenden Differenzen sprechen dafür, dass in den beiden untersuchten Sprachen eine unterschiedliche Gewichtung von top-down und bottom-up Informationsquellen vorliegt. Wir argumentieren, dass sich das Ausbleiben eines N400-Effektes im Englischen vor allem über die Dominanz von sequenzbasierten Prädiktionen auf Grund der starren Wortstellung dieser Sprache erklären lässt.

Die dritte Studie beschäftigte sich ebenfalls mit der Verarbeitung von unterschiedlichen Anomalietypen, allerdings wurden die neuronalen Korrelate der Sprachverstehensprozesse hier mittels fMRT untersucht. Während die deutschen EKP-Studien bestätigt hatten, dass einfach und schwer zu erkennende semantische Anomalien im Vergleich zu ihren jeweiligen Kontrollbedingungen ähnliche N400-Effekte auslösen, zeigte eine analoge Vergleiche in den fMRT Daten unterschiedliche Ergebnisse für die beiden Anomalietypen. Während klassische semantische Verletzungen im Vergleich zu kongruenten Sätzen erhöhte Aktivierung in temporalen Arealen auslösten, führten detektierte semantische Illusionen zu einer stärkeren Beteiligung von inferior parietalen und präfrontalen Regionen. Diese Unterschiede spiegeln vermutlich Konflikte zwischen top-down und bottom-up Informationen auf unterschiedlichen Verarbeitungsebenen wieder, da klassische Anomalien einen Konflikt auf der Ebene basaler Selektionsrestriktionen darstellen, während für die Detektion von semantischen Illusion in vielen Fällen Weltwissen hinzugezogen werden muss.

Insgesamt bestätigen die Ergebnisse der fünf durchgeführten Studie die Annahme, dass die Interpretation von sprachlichem Input nicht nur durch die stimulusinduzierte Prozesse gesteuert wird, sondern dass eingehende Informationen permanent mit bestehenden Erwartungen und Prädiktionen abgeglichen werden. Hierbei kommt es zu einer dynamischen Wechselwirkung zwischen diesen unterschiedlichen Informationsquellen, deren relative Gewichtung zueinander in Abhängigkeit von einzelsprachspezifischen Eigenschaften variieren kann.

Bornkessel-Schlesewsky, I., Kretzschmar, F., Tune, S., Wang, L., Genç, S., Philipp, M., et al. (2011). Think globally: Cross-linguistic variation in electrophysiological activity during sentence comprehension. *Brain and Language*, *117*(3), 133–152. doi:10.1016/j.bandl.2010.09.010

Erickson, T. D., & Mattson, M. E. (1981). From words to meaning: A semantic illusion. *Journal of Verbal Learning and Verbal Behavior*, *20*(5), 540–551.

Kutas, M., & Hillyard, S. A. (1980). Reading senseless sentences: Brain potentials reflect semantic incongruity. *Science*, *207*(4427), 203–205.

Sanford, Anthony J, Leuthold, H., Bohan, J., & Sanford, A. J. (2011). Anomalies at the borderline of awareness: An ERP study. *Journal of Cognitive Neuroscience*, *23*(3), 514–523.

Schumacher, P. B., & Baumann, S. (2010). Pitch accent type affects the N400 during referential processing. *NeuroReport*, *21*(9), 618–622. doi:10.1097/WNR.0b013e328339874a

10.7 Curriculum vitae

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Gifhorn

05/2010 - 01/2014   **Promotion zum Dr. phil.** im Fach „Deutsche Sprache" über das Fast Track Promotionsprogramm am Fachbereich Germanistik und Kunstwissenschaften der Philipps-Universität Marburg

10/2008 – 04/2010   **M.A. Germanistische Linguistik** bis zur Aufnahme in das Fast Track Promotionsprogramms nach drei Semestern

02/2005 – 07/2005   **Università degli studi di Trento, Italien**
Auslandssemester

10/2003 – 05/2007   **B.A. Sprache und Kommunikation** der Philipps-Universität Marburg

08/1995 – 05/2002   **Allgemeine Hochschulreife,** Kaiserin-Auguste-Viktoria-Gymnasium Celle

10.8   Ehrenwörtliche Erklärung

Hiermit versichere ich, Sarah Tune, dass ich die vorgelegte Dissertation mit dem Titel *„The neurocognitive processing of plausibility and real-world knowledge: A cross-linguistic investigation"* selbst und ohne fremde Hilfe verfasst, nicht andere als die in ihr angegebenen Quellen oder Hilfsmittel benutzt (einschließlich des World Wide Web und anderen elektronischen Text- und Datensammlungen), alle vollständig oder sinngemäß übernommene Zitate als solche gekennzeichnet sowie die Dissertation in der vorliegenden oder einer ähnlichen Form noch keiner anderen in- oder ausländischen Hochschule anlässlich eines Promotionsgesuches oder zu anderen Prüfungszwecken eingereicht habe.

Marburg, den 18. Dezember 2013   _____