

Björn Herrmann: Grammar and Perception: Dissociating of Early Auditory Processes in the Brain. Leipzig: Max Planck Institute of Cognitive Neuroscience, 2011 (MPI Series in Cognitive Neuroscience; 134)

Grammar and perception:
Dissociation of early auditory processes
in the brain

Impressum

Max Planck Institute for Human Cognitive and Brain Sciences, 2011



Diese Arbeit ist unter folgender Creative Commons-Lizenz lizenziert:
<http://creativecommons.org/licenses/by-nc/3.0>

Druck: Sächsisches Druck- und Verlagshaus Direct World, Dresden

ISBN 978-3-941504-18-9

Grammar and perception: Dissociation of early auditory processes in the brain

Von der Fakultät für Biowissenschaften, Pharmazie und Psychologie

der Universität Leipzig

genehmigte

DISSERTATION

zur Erlangung des akademischen Grades

doctor rerum naturalium,

Dr. rer. nat.,

vorgelegt

von Diplom-Kommunikationspsychologe (FH)

Björn Herrmann, geboren am 29. April 1981 in Berlin

Dekan: Prof. Dr. Matthias M. Müller

Gutachter: Prof. Dr. Angela D. Friederici
Prof. Dr. Erich Schröger

Tag der Verteidigung: Leipzig, den 27. Oktober 2011

Bibliographic details

Herrmann, Björn

Grammar and perception: Dissociation of early auditory processes in the brain

Fakultät für Biowissenschaften, Pharmazie und Psychologie

Universität Leipzig

Dissertation

147 pages, 252 references, 16 figures, 6 tables

Auditory language processing is considered a cognitive function that is different from pure perceptual processing. Recent findings from visual sentence processing studies, nevertheless, showed early modulations of visual sensory cortex activations in response to syntactic violations, i.e. in cortical regions commonly associated with perceptual processes. The present dissertation focuses on early syntactic processes in the auditory modality and their relation to perceptual processing regions in the brain. Magnetoencephalography and functional magnetic resonance imaging was used to measure the neural activity elicited by early syntactic and auditory perceptual processes. It was asked whether early syntactic processes in the auditory modality affect auditory sensory cortices; whether these areas overlap with regions modulated by auditory perceptual processes; and how parallel processing of early syntactic and auditory perceptual information is conducted in the brain. The results showed activations in auditory cortex (AC) regions in response to perceptual processes, while the most consistent activity changes caused by early syntactic processes were found in the anterior superior temporal gyrus (STG), with additional activations in the inferior frontal gyrus, superior temporal sulcus, and posterior middle temporal gyrus. Furthermore, the results indicate that processing syntactic and auditory perceptual information in parallel activates the anterior STG and posterior STG/AC simultaneously. No syntax-related modulations of auditory sensory cortices were found. Thus, the present results provide different pieces of evidence for a dissociation of cortex activations associated with early syntactic processes and auditory perceptual processes in the temporal cortex. The findings are consistent with the view of different processing streams in the auditory system.

Acknowledgements

My work on this thesis was supported by many people over the last three years. First of all, I am grateful to Prof. Dr. Angela D. Friederici for giving me the opportunity to study the neuropsychology of syntactic processes and for inspiring theoretical discussions at times where self-thinking was not sufficient anymore. These always led to new ideas and directions.

I am especially thankful to Dr. Burkhard Maeß to whom I owe much of the scientific knowledge I have learned over the last years. Not only would this endeavor have failed without the fruitful discussions about how to deal with MEG data, but, moreover, his pleasant and open-minded character enriched my time in the MEG group professionally and socially.

I thank Prof. Dr. Erich Schröger for his help and discussions at the beginning of the three years and also for warmly welcoming me as a member of his group at the University of Leipzig. Many fruitful thoughts have started to grow in this environment.

I am thankful to Christian Kalberlah and Prof. Dr. John-Dylan Haynes for introducing me to the multivariate pattern analysis methodology and helping me with the first steps. I thank Dr. Jonas Obleser for the help and enriching discussions about fMRI-related topics. Furthermore, I am grateful to Dr. Anja Hahne for providing the sentence materials that I used in the MEG experiments and for the discussions at the beginning of this three year project.

I am also thankful to Clíodhna Quigley, Philipp Ruhnau and Christian Keitel from the graduate program for the productive discussions we had about a variety of scientific topics and beyond. I thank Yvonne Wolff, Anke Kummer and Simone Wipper for their help with the MEG and fMRI data acquisition.

I further thank the people from the MEG group at the Max Planck Institute for the nice social environment over the last three years as well as the people from the neuropsychology department for the nice months I spent there writing many of the following pages.

Last, but similarly important, I thank the DFG (German research foundation) for their financial support within the graduate program "Function of Attention in Cognition" at the University of Leipzig.

Table of Contents

1	Introduction.....	9
1.1	Introduction into grammar	9
1.2	The link to the brain	13
2	Methods to study brain functions.....	15
2.1	Electromagnetic measures of brain activity.....	15
2.2	Event-related potentials and fields.....	16
2.3	Functional magnetic resonance imaging	19
2.4	Multivariate pattern analysis	21
3	Auditory perception and syntactic processing in the brain	25
3.1	Auditory perception in the brain	25
3.2	Syntactic processing in the brain	27
4	The current framework	35
4.1	Contributions to the ELAN	35
4.2	Consistency of brain responses elicited by syntactic processes	36
4.3	Location of syntax-modulated brain regions	37
4.4	Perspective	38
5	Experiment I: Contributions to the ELAN.....	41
5.1	Introduction	41
5.2	Methods	42
5.3	Results	47
5.4	Discussion.....	50
5.5	Conclusions	51
6	Experiment II: Decoding syntactic errors from single trial activations	53
6.1	Introduction	53
6.2	Methods	54
6.3	Results	61
6.4	Discussion.....	66
6.5	Conclusions	68
7	Experiment III: Dissociation of grammar and perception	69
7.1	Introduction	69

7.2	Methods.....	70
7.3	Results.....	76
7.4	Discussion	83
7.5	Conclusions	86
8	Experiment IV: Localizing early syntactic and auditory spatial processes	87
8.1	Introduction	87
8.2	Methods.....	89
8.3	Results.....	95
8.4	Discussion	101
8.5	Conclusions	106
9	General discussion	107
9.1	The fastness of the syntax-related neural responses.....	108
9.2	Sensory cortices and early syntactic processes.....	110
9.3	The inferior frontal cortex	111
9.4	The anterior temporal cortex	112
9.5	Syntax and the left hemisphere	113
9.6	Summary.....	114
10	Future directions.....	115
10.1	Further insight – Location.....	115
10.2	Further insight – Function	116
11	Conclusions.....	119
	References	121
	List of Figures	143
	List of Tables.....	145
	List of Abbreviations	147

1 Introduction

One of the most marvelous human abilities is the use of language. Just by taking a broad perspective, one can focus on the importance of speech to constitute inter-subjective reality (Habermas, 1981), or on the relevance of communication to form and maintain human identity (Krappmann, 1971; Mead, 1973), or even on the fact that people spend a lot of time speaking to themselves (in their minds) to find the right words for communications ahead or to reformulate sentences of situations already passed (Goffman, 1980, p. 592). Independent of a particular perspective, such endeavors are conducted very automatically by individuals every day. It emphasizes that sentences or fractions of sentences are processed constantly. What the fundamental mechanisms of processing sentences are, is a question best asked at the interface of psychology, linguistics and neuroscience. At the core of these mechanisms stands the concept of grammar. This first chapter of the current dissertation provides an introduction into different grammatical concepts relevant for processing sentences.

1.1 Introduction into grammar

In order to understand and make sense of a sentence a person is hearing, this person has to conduct various processing operations. A spoken sentence consists of a sound pressure wave, i.e. the acoustic signal. From this signal, the speech sounds (so called phonemes) are obtained. They provide the basis to form words, and the meaning of the words is extracted from the "mental lexicon". These aspects encoded in the signal can be referred to as segmental information due to their confined character. The acoustic signal also encodes su-

prasegmental information (i.e., beyond single words) such as the speech melody which is linguistically referred to as prosody.¹

However, recognizing the phonemes as well as the meaning of the single words is not sufficient to understand a sequence of words independent of the amount of prosodic information available. For example, a native English speaking person listening to sequence (1) is not able to make sense of the word string as a whole, even when familiar with the meaning of the single words. Example (2), on the other hand, can be understood easily by this person.

(1) * in apple a eats garden woman the delicious the²

(2) The woman in the garden eats a delicious apple.

The sentences (3) and (4) provide examples given by Chomsky (1957, p. 15), for which a native speaker of English has no trouble judging sentence (3) as grammatically correct and sentence (4) as grammatically incorrect, although the meaning of the sentences as a whole is senseless (at least for everyday situations).

(3) Colorless green ideas sleep furiously.

(4) * Furiously sleep ideas green colorless.

These sentences give a few examples which support the basic idea that language is strongly rule-governed. The formalization of rules that allow telling whether or not an arbitrary string is a well-formed sentence is referred to as grammar (Sag & Wasow, 1999, p. 23). Related to the term "grammar" is the term "syntax". Both are often used interchangeable. In linguistics, nevertheless, grammar is also used in a broader sense including all aspects of language structure, while syntax is used for descriptions of how words are combined (Sag & Wasow, 1999, p. 3). In order to produce a well-formed sentence, words cannot be combined randomly, but need to be structured according to the language-specific syntactic rules. Syntactic parsing, in this context, refers to the syntactic analysis of a given speech phrase or sentence.

One interesting aspect regarding the individual words of a given language is that some of them behave syntactically very similar. Because of this property,

¹ Note that some prosodic aspects are also rather confined (e.g., the stress pattern of a word).

² The asterisk * denotes an ungrammatical sentence.

individual words are categorized into classes of words. Examples of those so-called word categories and their abbreviations are: noun (N; e.g., "ball"), verb (V; e.g., "kick"), adjective (A; e.g., "old"), preposition (P; e.g., "on"), determiner (D; e.g., "the"). Combinatorial syntactic rules and their behavior are then described based on the word categories rather than on the individual words (Sag & Wasow, 1999, p. 26).

A further categorization subsumes word categories into phrases, where a phrase itself can be embedded in another phrase. Phrase structure rules describe which elements are allowed within a specific phrase and how phrases are combined to form a well-formed sentence (Jackendoff, 2002, p. 57; Sag & Wasow, 1999, p. 30). An example of a noun phrase (NP) and a determiner phrase (DP) along with the corresponding linguistic notations is given in (5) and (6).³

- | | |
|---------------|-------------------------------|
| (5) ball; | $NP \rightarrow N^{\circ}$ |
| (6) the ball; | $DP \rightarrow D^{\circ} NP$ |

Other phrases are prepositional phrases (PP) and verb phrases (VP).⁴ An Example of the former is given in (7), and (8) shows an example of the latter. A sentence (9) then reflects the highest level of such structures which can be referred to as hierarchical (Sag & Wasow, 1999, p. 30). It has been proposed that this hierarchical structuring of a sentence (or phrase) is the most significant aspect about syntax (Bickerton, 2009), which might be uniquely human (Fitch & Hauser, 2004).

- | | |
|---------------------------------|-------------------------------|
| (7) on the ball; | $PP \rightarrow P^{\circ} DP$ |
| (8) kick the ball; | $VP \rightarrow V^{\circ} DP$ |
| (9) The children kick the ball. | $S \rightarrow DP VP$ |

Furthermore, a set of phrase structure rules does not only enable describing well-formed sentence or phrases. In addition, phrase structure rules are used as a basis to describe syntactic violations within a specific sentence or phrase. This is relevant for psycholinguistic research investigating how individuals process syntactic rules, where behavioral performance to a syntactically correct utter-

³ The $^{\circ}$ marks the head of the phrase.

⁴ The current list of phrases is not exhaustive.

ance is commonly compared with the performance to a syntactically incorrect utterance, e.g. the examples (10) and (11).

(10) the player

(11) * he player

The phrase "the player" is a determiner phrase that contains a determiner and a noun, while the phrase "he player" includes the personal pronoun "he" that requires a verbal element to follow, and is thus violated at the noun "player". Such violations are called phrase structure violations or word category violations because the encountered word category does not match the predicted one derived from the phrase structure rules.

In addition, the syntactic relations within an utterance can be further described in terms of the distance between the relevant elements. In this sense, local dependencies can be differentiated from non-local dependencies (Kaan, 2009, Tallerman et al., 2009). Example (12) is a sentence that includes a non-local dependency, where distanced elements (highlighted) relate syntactically to one another.

(12) **A man** with stomach ache **came** into the office.

In contrast, the dependency between the two words of example (10) is referred to as local because the two elements are close to each other in the hierarchical syntactic structure (Kaan, 2009; Tallerman et al., 2009), and example (11) can therefore be considered a local syntactic violation. It has been suggested that frequently used local dependencies might already be precomputed and stored in memory (Kaan, 2009) in form of syntactic templates (Bornkessel & Schlesewsky, 2006).

Another important aspect of local dependencies refers to the morphological marking of words by an affix. One of the most common cases is the marking of a verb (e.g., "play") by the suffix "-s" when it is preceded by a third person singular pronoun (e.g., "he"). In linguistics, this is part of morphology rather than syntactic structure (Grewendorf et al., 1989; Kaan, 2009). Nevertheless, while attaching the suffix "-s" to a word stem "play" in isolation might be category ambiguous ("plays" could be either a finite verb or a plural noun), attaching the suffix "-er" to the word stem transforms it into the unambiguous noun "player". Thus, morphological marking can also be relevant for structural aspects of syntax (as it

can change the word category), and it has been argued recently that such overt morphological marking is the basis of fast syntactic processes (Dikker et al., 2009).

1.2 The link to the brain

The relation between language and the brain has gained much attention in the last decades. The link was initially established in the influential work of Paul Broca (1863) and Carl Wernicke (1874). They showed that lesions in specific regions of the brain lead to substantial language impairment in those individuals affected. Building upon their work and based on recent methodological advances in imaging brain functions in healthy individuals, different language models that relate speech and language processes to neuroanatomical structures have emerged (e.g., Friederici, 2002; Hagoort, 2005; Hickok & Poeppel, 2007). Despite the progress from Broca/Wernicke to the current models, today's neuropsychology of speech and language is far from understanding how the brain and its neuronal cell populations accomplish different aspects of language processing.

For example, the current models provide detailed information about where in the brain different aspects of speech and language processing is accomplished (Bornkessel & Schlesewsky, 2006; Friederici, 2002; Hagoort, 2005; Hickok & Poeppel, 2007). However, not all of them characterize the time course in which these aspects are processed. A detailed description about the temporal dynamics of language comprehension is given in the models of Friederici (2002) and Bornkessel and Schlesewsky (2006). Both models suggest processes to be conducted in successive phases in order to comprehend a sentence. The first phase is associated with initial syntactic structure building processes independent of relational information. It is assumed that processing in this phase draws upon syntactic templates that are precompiled and stored in memory, and thus allow fast and automatic processes. Within the second phase, processes which are based on semantic and morpho-syntactic information take place. In the model of Bornkessel and Schlesewsky's (2006), this phase is very elaborated where relational processes applied to arguments and verbs are conducted. Friederici (2002) speaks of thematic roles that are assigned within this phase. The third phase is associated with the integration of additional information from other domains and the evaluation of the well-formedness of a sentence as well as re-

vision/repair processes when necessary (Friederici, 2002; Bornkessel & Schlesewsky, 2006).

While there is no agreement on whether syntactic processes precede other language comprehension processing steps, i.e. whether semantic processes are carried out in parallel or affect syntactic processes at the earliest stage (Hagoort, 2003; Pulvermüller, 2010), it is generally agreed on that syntactic processes are conducted within the early time interval.

The present work investigates the neural correlates of syntactic processes that are accomplished very fast and automatically, i.e. within the initial phase of processing. The research mainly builds on the processing of local dependencies within natural spoken utterances and aims to elucidate on the brain regions that are involved in these processes. To this end, different methodological approaches are applied in order to address these questions.

2 Methods to study brain functions

The investigation of brain functions correlated with speech-related processes requires appropriate methods beyond behavioral measures (e.g., reaction times or hit rates). In the following sections, the methodological approaches frequently used in neuroscientific research of language and speech are described. First, electromagnetic measures of brain activity will be outlined, followed by the steps to analyze such recordings. Then, the basics of functional imaging of brain activations are described. In the last section, the analysis of multivariate patterns is characterized, a method that has recently gained much attention as it provides a very sensitive tool for the analysis of brain activity patterns.

2.1 Electromagnetic measures of brain activity

Electroencephalography (EEG) refers to the measurement of electric potentials that originate from the brain. These potentials are recorded using electrodes which are placed on the scalp of a participant. Magnetoencephalography (MEG), on the other hand, measures the magnetic fields originating from the brain by using highly sensitive sensors placed in close proximity to the participant's head. Both methods measure the brain activity directly and non-invasively with a temporal resolution in the range of milliseconds (Baillet et al., 2001; Hämäläinen et al., 1993; Jäncke, 2005; Vrba & Robinson, 2001). Thus, EEG and MEG are especially sensitive when the timing of neural processes is the main research focus.

In more detail, stimulation of a neuronal cell causes the cell to depolarize (or hyperpolarize) based on changes of the cellular membrane potential. This depolarization (or hyperpolarization) leads to a current flow within the cell (intracellular current or primary current) and to return currents outside of the cell (extracellular current or volume current). While EEG is highly sensitive to the effects of volume currents, MEG mainly measures the magnetic fields induced by the primary currents. Most of the EEG/MEG signal originates from the cortical

pyramidal neurons that are orientated perpendicular to the cortical surface. However, it is not the neuronal activity of a single neuron, but rather the summed activity of neuronal populations (often referred to as current dipoles) that is measured by EEG/MEG (Baillet et al., 2001; Jänke, 2005; Lopes da Silva, 2010; Vrba & Robinson, 2001).

Importantly, the cortical folding as well as the volume conduction needs to be considered in order to interpret the EEG/MEG signals observed outside the participant's head. The human cortex is highly convolved with sulci and gyri, and the pyramidal cells that produce the measured brain signal are orientated perpendicular to the cortical surface. As a consequence, current dipoles in different cortical areas vary in their orientation to the head surface. While EEG is most sensitive to signals that have a radial or tangential component (such as gyri and sulci, respectively), MEG strongly measures signals that have a tangential component. EEG and MEG are considered to be complementary in their sensitivity (Ahlfors et al., 2010a; Hämäläinen et al., 1993; Vrba & Robinson, 2001).⁵

Furthermore, the EEG signal observed at the scalp is strongly affected (and thus smeared) by the tissue conductivity of the head (e.g., cerebro-spinal fluid, skull, scalp), whereas the magnetic field is mostly unaffected by the head tissue it passes. This has implications for the localization of the neural generators of the measured signal. EEG requires detailed information about the tissue conductivity, while a single compartment volume conductor is sufficient to model the underlying sources of the MEG signal (Hämäläinen & Sarvas, 1989). Hence, MEG is commonly considered to be superior to EEG when it comes to source localization (Baillet et al., 2001; Hämäläinen et al., 1993; Jäncke, 2005; Vrba & Robinson, 2001).⁶

2.2 Event-related potentials and fields

In order to gain insight about a brain function associated with a specific event or stimulus, the method of event-related potentials (ERPs; EEG) or event-related

⁵ This can be observed from the potential distribution of EEG and the field distribution of MEG from a single dipole (for a comprehensive visualization see Vrba & Robinson, 2001).

⁶ Recent advances in modern electromagnetic recording hardware and analysis methods provide the practical instruments to combine EEG and MEG, which has been shown to improve the localization of the neural sources and the inferences that can be drawn (e.g., Ahlfors et al., 2010a, 2010b; Goldenholz et al., 2009; Molins et al., 2008).

fields (ERFs; MEG) is commonly applied (Key et al., 2005; Picton et al., 2000). ERPs/ERFs are potentials/fields that can be measured before, during or after a psychological or physical input is given to a participant. These potentials/fields do not reflect the activity of a single neuron, but rather the simultaneous activation of a larger population of neurons.⁷ Usually, they are very small in comparison to the ongoing oscillations of the raw EEG/MEG which are considered to be background activity and therefore noise. The application of appropriate filters, the extraction of EEG/MEG data from a time window (so-called epoch) that is time-locked to a stimulus type which is repeatedly presented, and averaging several of these epochs allows the observation of stimulus-specific brain responses (Figure 2.1).⁸ Averaging the EEG/MEG data builds on the assumption that repeating the stimulus several times elicits the same brain activation in each presentation.⁹ The background activity, on the other hand, is assumed to be independent of the stimulus presentation and will therefore be averaged out.¹⁰ Thus, increasing the number of epochs that are averaged leads to an improvement of the signal associated with the stimulus, i.e. the signal-to-noise ratio (SNR) increases (Jäncke, 2005).

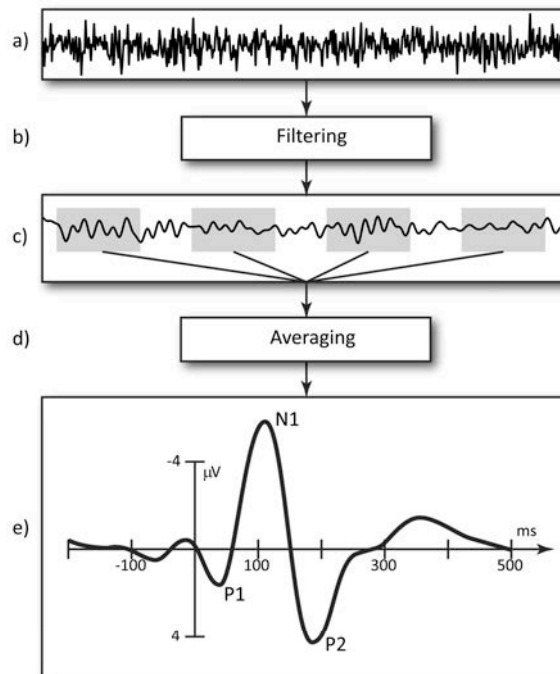
⁷ Alternative views on how ERPs/ERFs emerge are discussed in Klimesch et al. (2007; event-related phase reorganization) and Mazaheri & Jensen (2008, 2010; amplitude asymmetry mechanism).

⁸ A different term in this respect is a "trial" which refers to the whole entity of a stimulus presentation. This includes the stimulus itself, possible button presses as a response to the stimulus, as well as the time between the stimulus and the response. Depending on the context, a trial could additionally refer to the brain signal associated with the stimulus presentation.

⁹ While this assumption does not hold true on an absolute level as evidenced by habituation effects (e.g., McGee et al., 2001), it has proven valid on a practical level shown by numerous studies over the last decades (for general ERP reviews see Key et al., 2005; Picton et al., 2000).

¹⁰ Note, however, that ongoing brain oscillations carry important information as well (e.g., Makeig et al., 2002; Mazaheri & Jensen, 2008, 2010).

Figure 2.1: From the EEG raw data to the ERP. a) EEG raw data of one electrode. b) Filtering is applied on the raw data. c) Epochs time-locked to the stimuli are extracted. d) These epochs are averaged. e) Result: ERP, including the P1, N1 and P2 components. Negativity is plotted upwards by convention.



After averaging the epochs, a brain activation waveform showing positive and negative deflections is observed. A deflection is called ERP/ERF component when it can be measured repeatedly or when a specific cognitive function is associated with it. For EEG measurements, ERP components are labeled by a capital letter and a number. The letter refers to the polarity (P – positivity; N – negativity) of the ERP component, while numbers chronologically identify the first, second and so forth positivity or negativity (Figure 2.1). Alternatively, the number may indicate the latency of the component explicitly (e.g., N100, for a negativity that peaks at around 100 ms after the stimulus onset). Apart from the polarity and latency, ERP components can be differentiated by the topography measured from an electrode array at the scalp, with some components showing an anterior maximum and others showing a posterior maximum, for example. These topographical differences are taken as indicator for different underlying neural generators (Jäncke, 2005; Key et al., 2005).

The notation of the ERF components measured with MEG is slightly different as the polarity of the components cannot be interpreted in the same way as for the ERP components. In some cases the labeling of an ERF component is related to the associated component observed in EEG by adding an "m" to the

label (e.g., N100m). In other cases, an independent label is assigned to the observed deflection (e.g., M100, magnetic component at about 100 ms) (Jäncke, 2005).

Localizing the underlying neural generators of an ERP/ERF component involves solving two problems. The first is the so-called forward problem which refers to the calculation of the potential/field distribution outside of the head from a given current distribution in the brain (Baillet et al., 2001, Hämäläinen & Hari, 2002). It requires a source model, at best the individual brain anatomy, and a volume conductor model that includes information about the tissue passed by the signal. Solving the forward problem (i.e., to compute fields/potentials for a set of sensors and a certain forward model) has a unique solution. The second is the so-called inverse problem which refers to the estimation of the brain sources that produced the observed signal. The inverse problem has no unique solution as it involves the estimation of sources in 3D space based on a potential/field distribution measured in 2D. Thus, EEG/MEG source reconstruction requires making assumptions about the underlying mechanisms in order to find a solution to the otherwise not solvable problem (Hari et al., 2000). In general, estimating the underlying sources means comparing the measured data with the signal predicted by the forward model (Baillet et al., 2001; Hämäläinen & Hari, 2002).

Source reconstruction models can roughly be divided into dipole models (point-like source modeling) and distributed models (extended sources) (Hämäläinen et al., 1993; Hari et al., 2000). Dipole models usually have fewer parameters than the available data, which makes the solution of the inverse modeling a solution of an optimization problem. Distributed source models, however, have much more parameters than the data, which allows selecting one of an infinite number of solutions by adding another restriction – the minimum norm criterion. These algorithms can be made experimenter-independent, whereas dipole modeling massively relies on the choices made by the analyzing person.

2.3 Functional magnetic resonance imaging

When the spatial localization (as opposed to the exact timing) of a brain function or operation is in the center of a research question, functional magnetic resonance imaging (fMRI) is commonly applied.

The MRI signal is based on the magnetic moments of protons of atomic nuclei (often hydrogen atoms). These protons spin randomly, but align parallel (or anti-parallel) within the strong external magnetic field of an MR scanner, and thus give rise to a macroscopic magnetization. The MR signal is then measured during the relaxation time that is needed for the spins (and their magnetization) to realign with the external magnetic field after a high-frequency pulse has tilted the magnetization vector. T_1 relaxation refers to the longitudinal relaxation time, and is usually measured in structural/anatomical MRI, while T_2/T_2^* relaxation refers to the transverse relaxation time, and is measured in functional MRI (Deichmann et al., 2010; Jäncke, 2005).

In functional MRI, the neuronal activity is not measured directly. It is rather the hemodynamic-metabolic changes that occur in close proximity to an activated neuronal population which are measured. The three relevant contrast mechanisms are the cerebral blood flow (CBF), the cerebral blood volume, and the concentration of oxygen. Most of the fMRI studies exploit the latter by using the blood-oxygen-level-dependent (BOLD) contrast mechanism to measure the brain activity (Jäncke, 2005; Logothetis, 2008).

The BOLD signal is linked to an increase in the regional CBF (rCBF) and thus to an increase in fresh oxyhemoglobin close to an activated neuronal population. As the consumption of oxyhemoglobin is lower than the supply of rCBF, the relative concentration of deoxyhemoglobin decreases. Deoxyhemoglobin is paramagnetic and the reduction of its concentration leads to less signal loss caused by spin dephasing. Consequently, the signal intensity increases in a voxel (volumetric picture element) of the T_2 - or T_2^* -weighted MR image sensitized to the BOLD contrast, leading to higher functional brain "activation" (Howseman & Bowtell, 1999; Kim, 2005).

The maximal BOLD reaction is observed at about 5 – 10 s after stimulus presentation. The time resolution is considered at around 1 s at best (Deichmann et al., 2010; Horwitz et al., 2000). Consequently, brain operations separated by only a few hundreds of milliseconds cannot be differentiated based on the signal itself.

The relation between the BOLD contrast and the neuronal activity is rather complex. Nevertheless, it has been shown that local field potentials (LFPs) correlate positively with the BOLD signal (Logothetis et al., 2001), and provide a more reliable predictor than multi-unit activity related to neuronal output (Goense & Logothetis, 2008). LFPs predominantly reflect synaptic events related to synaptic

inputs from local neurons and synchronized afferent inputs (Shmuel, 2010). Thus, it has been argued that the BOLD signal is strongly linked to incoming neuronal signals, but not as much to the neuronal output signals (Goense & Logothetis, 2008; Kim, 2005; Logothetis et al., 2001; Shmuel, 2010).

2.4 Multivariate pattern analysis

When it comes to analyzing the recorded data, multivariate pattern analysis (MVPA) as compared to univariate analyses has recently gained much attention in neuroscience research (Haynes & Rees, 2006; Kriegeskorte & Bandettini, 2007; Mur et al., 2009; Norman et al., 2006). Univariate analyses usually focus on the mean activation strength associated with experimental conditions, which allows inferences about the involvement of brain regions in a specific mental function. MVPA, on the other hand, focuses on the information contained in the activation patterns related to the experimental conditions. It is sensitive to any changes in the patterns of two conditions, including the activation mean as well as changes in patterns where mean activity does not vary. This allows inferences about the representational content of a brain region (Haynes & Rees, 2006; Kriegeskorte & Bandettini, 2007; Mur et al., 2009; Norman et al., 2006), and has been shown sensitive to small effects not detectable with conventional univariate measures (Formisano et al., 2008; Haynes & Rees, 2005, 2006).

In particular, multivariate patterns are analyzed using classification algorithms that separate two experimental conditions based on the activation patterns associated with them (Figure 2.2). Before analyzing the data, independent data sets are needed that allow separating between training a classifier and testing whether the classification generalizes to a different (independent) data set. For example, the independence of data sets can be guaranteed by scanning independent runs in fMRI or by using non-overlapping epochs of EEG/MEG single trial recordings (Besserve et al., 2007; Guimaraes et al., 2007; Mur et al., 2009; Norman et al., 2006).

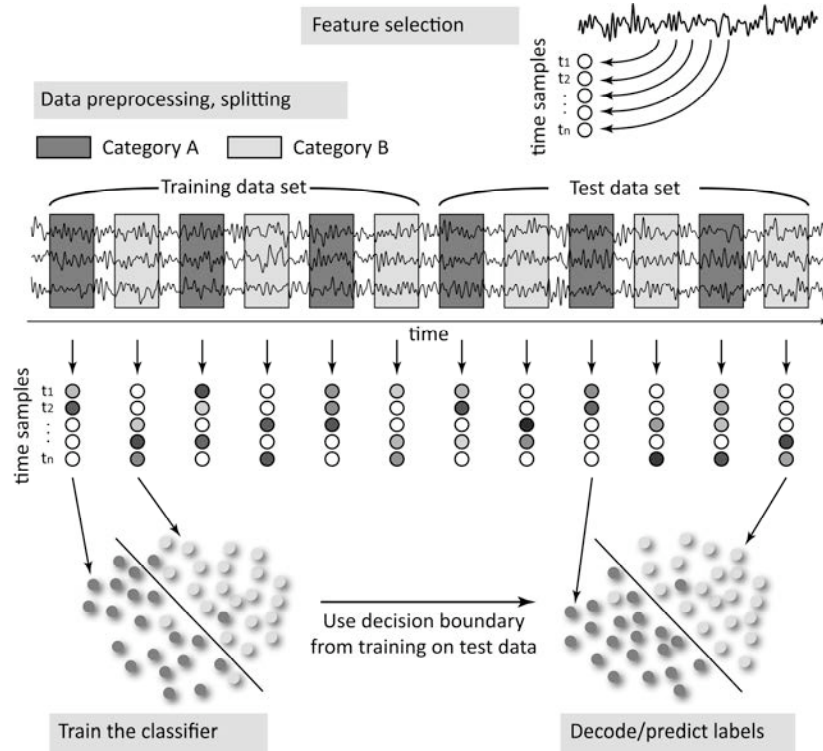


Figure 2.2: Multivariate pattern analysis example for EEG/MEG recordings. The analysis consists of data preprocessing and splitting the data into training and test data sets. Features are selected as time samples of the EEG/MEG recordings. Feature values are extracted from each epoch (dark gray and light gray marking of the recordings) of each category (e.g., different types of stimuli). The classifier is then trained on the training data set and the resulting decision boundary is used to decode/predict the labels of the epochs of the test data set (inspiration for the graphic from Norman et al., 2006 and Besserve et al., 2007).

Feature selection, in the context of MVPA, refers to the decision which aspect of the data is used for classification. In fMRI, all brain voxels or a subset of those could be used as features (Kriegeskorte et al., 2006; Poldrack et al., 2009). In EEG/MEG, features could comprise time samples or an electrode/sensor array. For the classification analysis, activation measures are then typically used as feature values. Relevant for the present work, fMRI brain activation can be estimated using a general linear model (GLM), while in MEG the magnetic field strength provides an appropriate brain activation measure. In principle, additional measures such as EEG/MEG frequency estimates or behavioral performance rates could also be used as feature values in a classification analysis.

After selecting the features used for classification and estimating the corresponding brain activity as feature values, the data points of the training data set are used to train a classifier. In the present work, a linear support vector machine (SVM; Chang & Lin, 2001, LIBSVM matlab-toolbox v2.89) classifier was used in two experiments to analyze MEG and fMRI recordings (Experiments II and III). The linear SVM classifier separates training data points of the feature vector \mathbf{x} for two different conditions by fitting a hyperplane $\mathbf{w}^T \mathbf{x} + b = 0$, defined by the weight vector \mathbf{w} and an offset b . The application of a linear SVM classifier is motivated by recent studies in cognitive neuroscience reporting high classification performance (e.g., Ethofer et al., 2009; Formisano et al., 2008; Haynes et al., 2007) as well as by studies evaluating different classifiers directly (Misaki et al., 2010; Mitchell et al., 2004). The result of training a classifier is a trained model that is then used on an independent test data set to decode the experimental conditions. The accuracy of decoding is estimated by the percentage of correctly decoded experimental conditions and reflects the generalization performance of the classifier. In order to evaluate whether the generalization performance is statistically significant, decoding accuracies are tested against chance level (Mur et al., 2009; Pereira et al., 2009).

3 Auditory perception and syntactic processing in the brain

With the methodological background acquired in the preceding chapter, this chapter aims to provide a review of previous neurophysiological evidence of auditory and syntactic processes in the brain. The first section gives an introduction into the basics of auditory processing and auditory perception. Subsequently, evidence regarding syntactic processes is reviewed.

3.1 Auditory perception in the brain

Basics of the auditory system

Before speech-specific processing in the brain is performed, the auditory sensory information passes through several nuclei of the auditory processing pathways, and complex signal processing operations are conducted at each level. Within the classical framework, the acoustic signal is initially conveyed from the cochlea in the inner ear to the cochlear nucleus. Subsequently, the information is distributed via multiple processing streams to the superior olivary complex and the lateral lemniscal nuclei, and converges at the inferior colliculus. Information is then communicated further to the medial geniculate body of the thalamus. From there it reaches the primary (core) auditory cortex (PAC; Hackett, 2011; Lee & Sherman, 2010; Nelken, 2008; Shamma & Micheyl, 2010) as well as non-core regions in the belt and parabelt (Hackett, 2011; Recanzone, in press; Recanzone & Cohen, 2010).

The frequency decomposition of the acoustic signal performed at the cochlea in the inner ear is preserved throughout the auditory pathways up to the PAC. This organization is referred to as tonotopy (Kandler et al., 2009; Lee & Sherman, 2010). Accordingly, a specific frequency of the acoustic signal spec-

trum preferable activates a specific part of the PAC (Formisano et al., 2003; Humphries et al., 2010). This suggests rather general signal processing operations at the level of the PAC, but not yet speech-specific operations (Scott & Johnsrude, 2003).¹¹

Beyond the primary auditory cortex

The core auditory cortex regions (i.e., the PAC) are anatomically surrounded by belt and parabelt regions. These regions are serially connected from core to belt to parabelt (Hackett, 2011; Kaas & Hackett, 2000; Recanzone & Cohen, 2010). It has been suggested that core regions respond strongly to simple stimuli, whereas belt and parabelt regions are most sensitive to stimuli that are more complex (Kaas & Hackett, 2000; Rauschecker et al., 1995; Tian & Rauschecker, 2004; Wessinger et al., 2001). This concept of hierarchical processing of simpler to more complex auditory stimuli has its basis in the connectivity pattern between the thalamus and the auditory cortex, where belt regions are innervated by core areas and by thalamic connections that are not shared with the core (Recanzone & Cohen, 2010).

Beyond the auditory cortex regions, two major streams have been proposed in the temporal cortex. One, the anterior-ventral stream, projects from the auditory cortex into the anterior temporal cortex, while the other, the posterior-dorsal stream, projects from the auditory cortex into the posterior parietal cortex. This model originates from an evolutionary and anatomical background, but has been extended to cover language functions as well. The anterior-ventral stream has been linked to operations relevant for speech perception, whereas the posterior-dorsal stream is associated with auditory spatial and motion processing, but also with other functions relevant in speech. Processing along these streams is considered to be accomplished in parallel (for a review see Rauschecker & Scott, 2009).¹²

¹¹ Very recent findings in animals, nevertheless, show that specific tasks or expectations about the timing of a sound can modulate the neural activity in the PAC (Jaramillo & Zador, 2011; Lee & Middlebrooks, 2011), thereby indicating the influence of "higher" brain areas on sensory cortices.

¹² Nevertheless, the functions assigned to the two streams are still under discussion. A model that particularly deals with the role of both streams in processing speech has been proposed by Hickok & Poeppel (for the most recent version see 2007).

Auditory perceptual processing

A tool to investigate auditory perceptual processing and the processing of perceptual rules established online is the mismatch negativity (MMN; Näätänen et al., 1978). The MMN is an ERP component that is elicited in an oddball sequence, where an auditory event is infrequently presented among a series of frequently repeated auditory events. For processing these sequences, a sensory memory storage unit is assumed to track the sensory input and extract the regularity (i.e., rule) potentially hidden in the input. The MMN elicitation then reflects a memory comparison process between the rule-based prediction and the violating input stimulus (Schröger, 2007; Winkler et al., 2009). Among other aspects, the MMN and its magnetic counterpart (MMF, mismatch field) has been used to investigate the discrimination of tones of different frequencies (e.g., Maess et al., 2007; Näätänen et al., 1978), intensities (e.g., Schröger, 1996; Tervaniemi et al., 1999), durations (e.g., Jacobsen & Schröger, 2003; Tervaniemi et al., 1999), or auditory locations (e.g., Deouell et al., 2006; Schröger, 1996).¹³ The MMN has been localized to auditory cortex regions (e.g., Alho et al., 1995; Maess et al., 2007) with an additional source sometimes observed in the right frontal cortex (for a review see Deouell, 2007).

3.2 Syntactic processing in the brain

The timing of syntactic processes

In order to investigate brain processes in a time-sensitive manner, ERP/ERF experiments are commonly conducted.¹⁴ In the language domain, the earliest studies using brain potentials investigated the neural correlates of semantic processing. It was shown that semantically incongruent sentences (i.e., sentences including a semantically inappropriate word) elicit the N400 component when compared to congruent sentences (Kutas & Hillyard, 1980, 1982). This effect has been replicated extensively since then (for a recent review see Lau et al., 2008).

¹³ The MMN paradigm has also been adapted that it allows the investigation of syntactic processes (for a review see Shtyrov & Pulvermüller, 2007).

¹⁴ For recent approaches using time-frequency measures to investigate syntactic processes see Davidson & Indefrey (2003) or Bastiaansen et al. (2010).

Soon, the research was extended to also investigate syntactic aspects of language and differentiate between the neural correlates of syntactic and semantic processes (Friederici et al., 1993; Kutas & Hillyard, 1983; Hagoort, 2003; Münte et al., 1993). Common in most of these studies is that a violation paradigm is applied where correct sentences are contrasted with incorrect/incongruent sentences.¹⁵ This is motivated by the assumption that those cortical regions involved in regular sentence processing respond more strongly when a violation occurs. To date, a number of components were related to syntactic processes distinguishing between different processing stages (for a neuro-cognitive model see Friederici, 2002).

One component frequently related to syntactic processes is an early negativity that peaks at around 100 – 200 ms after the onset of a syntactic violation.¹⁶ It was first reported by Neville et al. (1991), where visually presented sentences including a word category violation (e.g., *"The man admired Don's of sketch the landscape."*) were compared to correct sentences. A similar component was observed for word category violations in the auditory modality. The component showed a left anterior maximum and was therefore labeled early left anterior negativity (ELAN; Friederici et al., 1993). In subsequent studies it was observed that the early syntax-related effect could also be distributed bilaterally rather than showing a left-hemispheric predominance, especially when sentence materials were presented auditorily (C. S. Herrmann et al., 2000; Knösche et al., 1999; Kubota et al., 2003).

The ELAN has been linked to initial syntactic parsing difficulties (Friederici, 2002, 2004) and was most often found for local violations within a phrase (Dikker et al., 2009; Friederici et al., 1993; Kubota et al., 2003, 2005). This interpretation has been extended recently showing that the fastness of the effect is due to form properties associated with the syntactic category (e.g., perceptually overt category marking by an affix) that violate the expected ones (Dikker et al., 2009, 2010). This is in line with ELAN effects found for sentences containing pseudo-

¹⁵ Alternative approaches to violation paradigms comprise the comparison of (1) syntactically complex sentences to simple sentences, (2) normal sentences to unrelated word lists, or (3) sentences containing pseudowords to normal sentences (Kaan & Swaab, 2002).

¹⁶ In some studies the event-related brain signals are time-locked to the onset of the critical word rather than to the onset of the syntactic violation. This can lead to a temporal shift of the observed negativity (e.g., Hagoort et al., 2003; van den Brink & Hagoort, 2004).

words, where only closed-class morphemes/words important for the syntactic structure were conserved (Hahne & Jescheniak, 2001; Yamada & Neville, 2007).

Furthermore, the syntax-related early negativity is not tied to a specific language. It has been observed in English (Neville et al., 1991; Yamada & Neville, 2007), German (Friederici et al., 1993; Hahne & Friederici, 1999), Dutch (Hagoort et al., 2003), French (Isel et al., 2007) and Spanish (Hinojosa et al., 2003). In addition, an early syntax-related effect has not only been found in EEG but has been reported in MEG studies as well (Dikker et al., 2009, 2010; Friederici, et al., 2000a; Knösche et al., 1999; Kubota et al., 2004, 2005). The ELAN is considered to be very automatic because it was shown to be unaffected by expectations of a violation (Hahne & Friederici, 1999) or attentional factors induced by different tasks (Hahne & Friederici, 2002).

A different early negativity that is elicited in response to syntactic violations is the syntactic mismatch negativity (sMMN; Pulvermüller & Shtyrov, 2006; Shtyrov & Pulvermüller, 2007). The sMMN has been observed for word category violations as well as for morpho-syntactic violations (Hasting et al., 2007; B. Herrmann et al., 2009; Pulvermüller & Shtyrov, 2003; Shtyrov et al., 2003). Whether the sMMN and the ELAN are related or whether they even have the same neural generators has been speculated on in the past (Pulvermüller & Shtyrov, 2006). The sMMN is usually measured in an auditory oddball paradigm, whereas the ELAN is observed in sentence processing paradigms (Friederici et al., 1993; Shtyrov et al., 2003). Hence, the comparison of the two components is rather descriptive than direct. Nevertheless, both components show similarities with respect to the time window, topographical distribution and automaticity (Pulvermüller & Shtyrov, 2006).

Recently, the early syntax effect has been further subdivided into a very early component at around 40 – 80 ms and a subsequent component at around 100 – 200 ms (C. S. Herrmann et al., 2000; B. Herrmann et al., 2009). The very early effect has been linked to a stimulus filtering brain mechanism allocating resources to the sensory input (B. Herrmann et al., 2009). A different interpretation for the early effect might be that violation detection is accomplished along multiple stages as suggested by effects elicited by simple rule violations (Grimm et al., 2011; Slabu et al., 2010).

In a time window following the early effects, a positive deflection associated with syntactic processes has been frequently observed in sentence processing paradigms. This centro-parietal distributed positivity has its maximum at around

600 ms and was labeled P600 or slow positive shift (SPS; Hagoort & Brown, 2000; Kaan & Swaab, 2003; Osterhout & Holcomb, 1993). It was originally interpreted as a structural revision process that is induced by syntactically ambiguous sentences (so-called "garden path" sentences; Osterhout & Holcomb, 1993). Apart from such sentences, the P600 is also observed as a response to syntactic violations, for example by sentences containing a word category violation (Friederici et al., 1996; van den Brink & Hagoort, 2004) or a morpho-syntactic violation (Hinojosa et al., 2003; Rossi et al., 2005). This has led to the interpretation that the P600 is involved in syntactic repair processes as well. An additional interpretation was based on sentences that were varied with respect to the level of difficulty of word integration (Kaan et al., 2000), thus, linking the P600 to a syntactic integration mechanism. More recently, P600 effects could be observed for other types of violations, e.g. by a prosodic incongruity (Mietz et al., 2008; Schmidt-Kassow & Kotz, 2009) or for rule violations in arithmetic tasks (Núñez-Peña & Honrubia-Serrano, 2004). In consideration of these different aspects of processes, a more general integration mechanism has been proposed to be correlated with the P600 (Schmidt-Kassow & Kotz, 2009).

Importantly for the current framework, most of the studies that observed an early syntax-related negativity also found a P600 in a subsequent time window (Friederici et al., 1993, 1996; Hahne & Friederici, 2002; Hahne & Jescheniak, 2001; Hinojosa et al., 2003; Isel et al., 2007; Rossi et al., 2005; Yamada & Neville, 2007). Thus, initial syntactic parsing difficulties are commonly followed by syntactic revision/repair processes (Friederici, 2002).¹⁷

The location of syntactic processes

In order to localize the brain regions correlated with syntactic processes, three main sources of evidence may be considered. The first approach towards the underlying neural mechanisms of syntactic processes comes from lesion studies. For quite some time, lesion studies were the main source of evidence that provided insights about the relationship between behavioral measures and the underlying brain regions. Most relevant for the current framework are studies that used ERPs in EEG to examine whether specific lesions in the brain affect the components associated with syntactic processes. In these studies, the ELAN was

¹⁷ However, a P600 is not observed when the majority of the sentences in a given experimental set are syntactically incorrect (see Hahne & Friederici, 1999).

observed in healthy participants, while it was absent in patients with lesions in the left frontal cortex (Friederici et al., 1999) or in the left anterior temporal cortex (Kotz et al., 2003). Furthermore, the ELAN could be observed in patients with lesions in the right anterior temporal cortex (Kotz et al., 2003) or the basal ganglia (Friederici et al., 1999, 2003a). Although, these results have been taken as indicator that the inferior frontal cortex as well as the anterior temporal cortex is involved in early syntactic processes, lesion studies itself give only insight about regions relevant to support a function, but do not provide areas sufficient for the function (Caplan, 2009).¹⁸

The advances of functional imaging (fMRI) provide the technology to gain insight about syntax-related neural activations in healthy human participants. In sentence processing studies, regions in the anterior superior temporal gyrus (aSTG), the posterior STG (pSTG) and the inferior frontal gyrus (IFG) were found to be correlated with conducting syntactic operations (Friederici et al., 2003b, 2009; Humphries et al., 2005; Newman et al., 2003). One line of research focuses on how the brain processes sentences that are correct, but syntactically complex (e.g., *"The reporter that the senator attacked admitted the error."*; Just et al., 1996). Such studies frequently report activations in the pars opercularis of the inferior frontal cortex and in the posterior superior temporal cortex when syntactically complex sentences are compared to less complex sentences (Dapretto & Bookheimer, 1999; Friederici et al., 2009; Just et al., 1996; Makuuchi et al., 2009). Studies that investigated syntactic phrase structure processes reported activations in the anterior STG, the posterior STG and in the frontal operculum of the inferior frontal cortex in response to sentences containing a word category violation (Brauer & Friederici, 2007; Friederici et al., 2003b). The dissociation between the pars opercularis associated with processing syntactic complexity (e.g., sequences with hierarchically embedded structures; or non-local dependencies) and the frontal operculum associated with processing local transitions or linear sequences has also been observed using functional and dif-

¹⁸ This is due to neuronal reorganization that alters the brain after the lesion occurs, which makes the comparison to brain functions in healthy participants inconclusive. Additionally, the absence of an ERP effect in patients with a specific lesion cannot be taken as evidence for a direct role of this region in the brain function under investigation. The damaged region might "just" be part of a network that supports the function (for a recent proposal of modulators and drivers in the auditory pathways see Lee & Sherman, 2010).

fusion-weighted MRI data (Friederici et al., 2006).¹⁹ In addition, the anterior STG has been suggested to play a crucial role in syntactic processes (Friederici et al., 2003b; Humphries et al., 2005; Meyer et al., 2000). The aSTG was interpreted to be most relevant for combinatorial processes in sentence comprehension (Rogalsky & Hickok, 2009; Friederici, submitted), including syntactic structure building operations (Brauer & Friederici, 2007; Brennan et al., in press; Friederici et al., 2003b).

In the recent past, MEG methodology has become more and more sophisticated enabling the time-sensitive localizing of brain regions involved in a specific task. In the auditory modality for example, sentences that contained a word category violation elicited a magnetic ELAN (ELANm) at around 100 – 200 ms after the violation onset (Friederici et al., 2000a; Knösche et al., 1999). The main neural generator of the ELANm has been localized in the superior temporal cortex (Groß et al., 1998; Knösche et al., 2000; Kubota et al., 2003), while Friederici et al. (2000a) specified the localization by showing that regions more anterior in the superior temporal gyrus (STG) are involved. The ELANm was additionally linked to activations in the inferior frontal cortex (Friederici et al., 2000a). In the visual modality, sentences including an unexpected syntactic word category have been shown to modulate brain activations in visual sensory cortices (Dikker et al., 2009, 2010). While the exact location of these effects could not be pinpointed (i.e., whether primary or secondary sensory cortices were modulated), the results challenge previous findings in the auditory modality. The fastness of the ELAN(m) has led to the so-called "sensory hypothesis" proposing that early syntactic processes modulate brain regions at a sensory level, rather than regions in further distance (Dikker et al., 2009). Whether or not auditory sensory cortices are affected by syntactic manipulations is one of the main questions of the current dissertation.

Using MEG to localize the underlying neural mechanisms of the P600 has proven to be quite challenging, possibly due to MEG's insensitivity to radial sources. So far, only two studies related their MEG localization effects to the

¹⁹ Nevertheless, the specific role of the pars opercularis (BA44) is still heavily discussed (Rogalsky & Hickok, 2011). Furthermore, two studies reported activations in the pars opercularis rather than in the frontal operculum in response to word category violations (Friederici et al., 2010; Kang et al., 1999).

P600, reporting the middle temporal gyrus and posterior temporal cortex regions as possible candidates (Kwon et al., 2004; Service et al., 2007).

4 The current framework

As was outlined in the preceding chapter, neuroimaging and ERP/ERF studies have led to important advances over the last decades regarding the neural mechanisms underlying syntactic processes. In particular, recent findings have shed new light on early syntactic processes and the brain regions that might be involved. Some of these results not only extend previous knowledge, but, moreover, challenge findings and ideas proposed in the past. In the following three sections, a detailed description of the issues that need further elaboration is provided. The fourth section gives the general idea of the current framework and a brief outlook on the experiments conducted to elucidate on early syntactic processes in the brain.

4.1 Contributions to the ELAN

One of the main goals of the present dissertation is to localize the brain regions involved in early syntactic processes. However, as a prerequisite it needs to be examined whether different aspects of speech processing might contribute to the ELAN effect which is associated with those early syntactic processes. This question relates to the acoustic signal itself.

In Hahne & Friederici (1999; see also Sabisch et al., 2009) it was extensively described how syntactically incorrect sentences that elicit the ELAN are commonly constructed for the auditory modality. To avoid acoustic or prosodic cues prior to the critical (i.e., violating) word which might unavoidably occur if the speaker is required to voice an incorrect sentence, these sentences are initially recorded as syntactically correct sentences. Subsequently, a carefully conducted cross-splicing procedure is used to delete a single word from the correct sentence, while leaving the coarticulation intact. This results in a sentence that includes a word category violation. However, deleting a word within a sentence also leads to a slightly larger change in the fundamental frequency (F_0) contour

of the incorrect sentences compared to the correct sentences (Figure 5.1; see also Sabisch et al., 2009). Although participants perceived those incorrect sentences as natural (apart from the syntactic error; see Hahne & Friederici 1999), small changes in the F_0 contour can already lead to an enhanced early negativity in the ERPs (Mietz et al., 2008; Schön et al., 2004).

As a result, it is necessary to investigate whether a change in the F_0 contour of syntactically incorrect sentences contributes to the syntactic ELAN effect observed in EEG/MEG. This question is especially important considering previous studies using similar sentences materials (e.g., Friederici et al., 2000a; Hahne & Friederici, 1999), and it needs to be tested whether the ELAN can be considered a marker for early syntactic processes.

4.2 Consistency of brain responses elicited by syntactic processes

A common approach to investigate stimulus-specific brain responses is averaging multiple trials to a mean brain response (i.e., ERP/ERF). Averaging is motivated by the assumption that each presentation of the same stimulus type elicits the same brain response. Although this has proven to be a fruitful approach to investigate syntactic processes, some of the information contained in single trial recordings is lost in this procedure.

The advances in multivariate pattern analysis (MVPA) provide a recent approach that enables the investigation of single neural responses (Guimaraes et al., 2007), and has been shown to be very sensitive to activity changes elicited by the human brain (Haynes & Rees, 2005, 2006; Formisano et al., 2008). Using MVPA, it has been observed that the mental state associated with a specific task can be decoded from an individual's brain based on the brain activation of different individuals engaged in the same task, thereby indicating consistent neural processes across individuals (Poldrack et al., 2009).

It is an open question whether single neural recordings allow the dissociation of different syntactic states of the brain, i.e. whether the grammaticality of a presented sentence can be decoded from the brain signals. Furthermore, there is need to examine whether single neural responses associated with early syntactic processes are consistent across participants, in order to infer that the culturally learned syntactic rules underlying these processes are represented similarly in the brains of different individuals.

4.3 Location of syntax-modulated brain regions

The timing of syntax-related brain responses has been extensively investigated over the last years (e.g., Dikker et al., 2009; Friederici et al., 1993; Hahne & Friederici, 2002; Kubota et al., 2003). The underlying neural sources, on the other hand, are still under discussion (Dikker et al., 2009, 2010; Friederici, 2002). Based on studies conducted in the auditory modality, the IFG and the aSTG have been proposed to play a crucial role in early syntactic processing (Friederici, 2002). In the visual modality, early modulations of sensory cortex activations have been recently reported when participants encountered a syntactic word category violation. These effects were shown to rely on form properties associated with the syntactic category, e.g. overt perceptual marking by an affix (Dikker et al., 2009, 2010). Accordingly, previous findings diverge on whether (primary) sensory regions or brain areas at distinct levels in the processing hierarchy are modulated by early syntactic processes. In this context, some of the observations taken as evidence for the involvement of the IFG and aSTG in early syntactic processes have been challenged, while others have been related to auditory sensory cortex modulations (Dikker et al., 2009).

In detail, auditory fMRI sentence processing studies showed activations in the anterior STG, the posterior STG and the frontal operculum in the IFG as a response to sentences that included a word category violation (Brauer & Friederici, 2007; Friederici et al., 2003b). Unfortunately, fMRI provides an insufficient temporal resolution to separate brain processes that are in close temporal proximity. In other words, fMRI activations typically represent a mixture of early syntactic processes (as reflected in the ELAN) and processes occurring later such as P600 assigned revision/repair processes. Therefore, exploiting the high resolution of fMRI requires a setting that explicitly allows relating the observed brain activations to early syntactic processes.

In addition, an MEG study using auditory sentence materials suggested the involvement of the lateral inferior frontal cortex and the aSTG in early syntactic processes, i.e. as neural generators of the ELAN (Friederici et al., 2000a). In this study, dipole modeling was constrained by previous fMRI results (Meyer et al., 2000), that is, the dipoles were seeded in the IFG and aSTG using the coordinates obtained from the fMRI findings. It has been argued that this approach might lead to misinterpretations as fMRI lacks the temporal resolution to derive solid assumptions about early syntactic processes (Dikker et al., 2009). In addi-

tion, an earlier MEG study using similar stimulus materials as in Friederici et al. (2000a) and no dipole constraints reported strongest activation in the vicinity of the auditory cortex and in left frontal regions (Groß et al., 1998). Thus, further evidence is needed using a different methodological approach in MEG in order to elucidate on the underlying brain regions and to assess whether or not early syntactic processes modulate sensory cortices in audition.

Moreover, a direct comparison of early syntactic processes with auditory perceptual processes was carried out in the EEG study of Hahne et al. (2002), where a syntactic word category violation within a sentence elicited the ELAN, whereas infrequent auditory spatial deviations led to the MMN. The topographical resemblance of the ELAN and MMN has been emphasized in the context of syntax-related sensory cortex activations, and consequently taken as an indicator that both processes might modulate the same (sensory) cortex regions (Dikker et al., 2009). However, this cannot be conclusively inferred from the ERP scalp distribution as differences at the cortical level might be smeared at the scalp EEG. The ELAN and MMN would have to be localized at the cortical level to study the neural mechanisms directly. Furthermore, it remains an open question which cortical regions are modulated when the brain processes a syntactic violation and an auditory perceptual violation in parallel (Hahne et al., 2002).

To summarize, the inferior frontal cortex and the aSTG have been suggested to be involved in early syntactic processes in the auditory modality, but methodological constraints might have concealed relevant evidence. Thus, different approaches (using fMRI as well as MEG) are required in order to elucidate on the brain regions modulated by early syntactic processes, and on the role the auditory sensory cortices play in these processes.

4.4 Perspective

As a general idea in the current work, responses to syntactic violations are compared to responses elicited by auditory perceptual conditions to investigate whether the same brain regions are involved in processing these conditions. Basic auditory perceptual processes are associated with activations in sensory cortices. Whether this also holds true for early syntactic processes is a question that needs examination. The research questions can be summarized as follows:

- (1) Is the ELAN a syntactic effect or does a pitch change in the sentence prosodic contour contribute to its emergence?

- (2) Are the neural responses related to syntactic rule processing similarly decodable from the brain within and across individuals?
- (3) What is the role of auditory sensory cortices in processing syntactic violations, leading to early syntactic effects (i.e., the ELAN)?
- (4) Do early syntactic processes (reflected in the ELAN) recruit different brain regions than "simple" perceptual rule processes (reflected in the MMN), and what are the cortical underpinnings of processing both aspects in parallel?

The first experiment aimed to answer question (1) by comparing syntactically incorrect sentences with sentences that include a change in the prosodic contour. This MEG experiment will provide the basis to answer questions (4).

In the second experiment, a multivariate pattern classification approach in MEG was conducted to answer question (2). The grammaticality of auditorily presented sentences was decoded from single trial brain signals, first within participants, and then across participants. For comparative purposes, the same analysis was carried out on auditory perceptual responses.

The purpose of third experiment was to answer question (3) by comparing regions showing fMRI activations in a syntactic contrast with regions activated in an auditory perceptual contrast (realized as the absence vs. presence of a suffix that perceptually marks the syntactic word category). In order to relate the fMRI activations to early syntactic processes, two-word utterances were used that have been shown to elicit early but no late syntax-related responses (Hasting & Kotz, 2008).

Question (4) was sought to be answered in the fourth and final experiment. MEG was used to localize the ELAN and MMN without an additional prior regarding the cortical regions involved in the associated processes. Furthermore, sentences including a syntactic violation (ELAN) and an auditory perceptual violation (MMN) at the same time were presented to investigate the cortical regions involved in parallel processing effects.

5 Experiment I: Contributions to the ELAN

The text was largely derived from the study published in *Neuroscience Letters* by B. Herrmann et al. (2011).

5.1 Introduction

As outlined in chapter 4, early negativities have been observed for syntactic (Hahne & Friederici, 1999, 2002) as well as for prosodic processes (Mietz et al., 2008; Schön et al., 2004). In natural speech, syntactic and prosodic information are intertwined within the acoustic signal, and it has been advocated that processing of prosodic information can affect syntactic processes (Frazier et al., 2006). To investigate the relative contributions of syntactic and prosodic information, auditory sentence materials are frequently manipulated by cross-splicing procedures (Hahne & Friederici, 1999; Mietz et al., 2008) or by changing prosodic parameters such as the F_0 contour (Schön et al., 2004). Although applying a cross-splicing procedure already controlled for possible prosody effects in the studies reporting an ELAN (e.g., Hahne & Friederici, 1999, 2002; Hahne et al., 2002), a change in the F_0 contour occurred together with the syntactic violation.

This MEG experiment was designed to investigate whether such a prosodic change contributes to the ELAN effect. On this basis, the neural responses elicited by sentences containing a syntactic word category violation (ELAN) were compared with the neural responses elicited by sentences that included a prosodically incongruent F_0 contour. The hypotheses were as follows:

- (1) Sentences including a syntactic word category violation were expected to elicit stronger activations than syntactically correct sentences (reflecting the ELANm).

- (2) In case a prosodic incongruency contributes to the ELANm effect, similar or larger brain activity was expected to be elicited by prosodically incongruent sentences than syntactically incorrect sentences, as the former include the largest change in the F_0 contour (see Figure 5.1).
- (3) In contrast, stronger neural activity was expected for syntactically incorrect sentences than prosodically incongruent ones if the prosodic incongruency has only a small or no impact on the brain activation associated with the ELANm.

The first 200 ms after the onset of the violating word were of specific interest because previous studies investigating early syntactic and early prosodic processing have found related effects within this time window (e.g., Hahne & Friederici, 1999; Schön et al., 2004).

5.2 Methods

Participants

Eleven female and ten male (aged 20 – 32) adults took part in the MEG experiment. All were right-handed German native speakers and had no known hearing deficit or neurological diseases in their history. Right-handedness was measured using the Edinburgh Handedness Inventory (Oldfield, 1971), with a median laterality quotient of 100 (range: 77 – 100). Participants gave written consent prior to testing and were paid for their participation.

Stimulus materials

Participants were auditorily presented with 201 sentences throughout the experiment, of which 67 were syntactically correct, 67 syntactically incorrect and 67 prosodically incongruent. Syntactically correct and incorrect sentences were taken from a previous EEG experiment (Hahne et al., 2002). The sentences were spoken by a trained female native speaker of German and digitized at 44.1 kHz (16 bit, mono, normalized to peak intensity).

Syntactically correct sentences consisted of a "determiner-noun-auxiliary-past participle" sequence (e.g., "Die Küche wurde geputzt.", *Engl. "The kitchen was cleaned."*), whereas syntactically incorrect sentences consisted of a "determiner-noun-auxiliary-preposition-past participle" sequence (e.g., "Das Fenster wurde im geputzt.", *Engl. "The window was in-the cleaned."*). The syntactically incorrect sentences included a word category violation at the participle, because

in German a preposition is not permitted to be directly followed by a verb. These sentences were created from correct sentences where the preposition was directly followed by a noun. Subsequently, the noun was carefully removed from the sentence. Unnatural acoustic transitions due to coarticulation were avoided by using a noun that had the same onset phoneme as the past participle and the same offset phoneme as the preposition. In consequence of the removal of the noun, these sentences comprised a slight change in the F_0 contour as the preposition was followed by a sentence final intonation instead of a sentence prefinal intonation (Hahne and Friederici, 1999; Sabisch et al., 2009).

To analyze the sentence materials, the F_0 contour for each sentence was extracted using the software Praat (v5.1.29, <http://www.praat.org>). In Figure 5.1a, the F_0 contours centered at the onset of the participle are depicted for syntactically correct and incorrect sentences. The size of the F_0 change at the onset of the participle was quantified as the difference between a pre-onset (-20 – 10 ms) and post-onset F_0 value (10 – 20 ms; see Figure 5.1). A t-test for independent samples revealed a larger F_0 change in syntactically incorrect (55 Hz) than correct sentences (36 Hz; $t_{132} = 7.77$, $P < 0.001$).

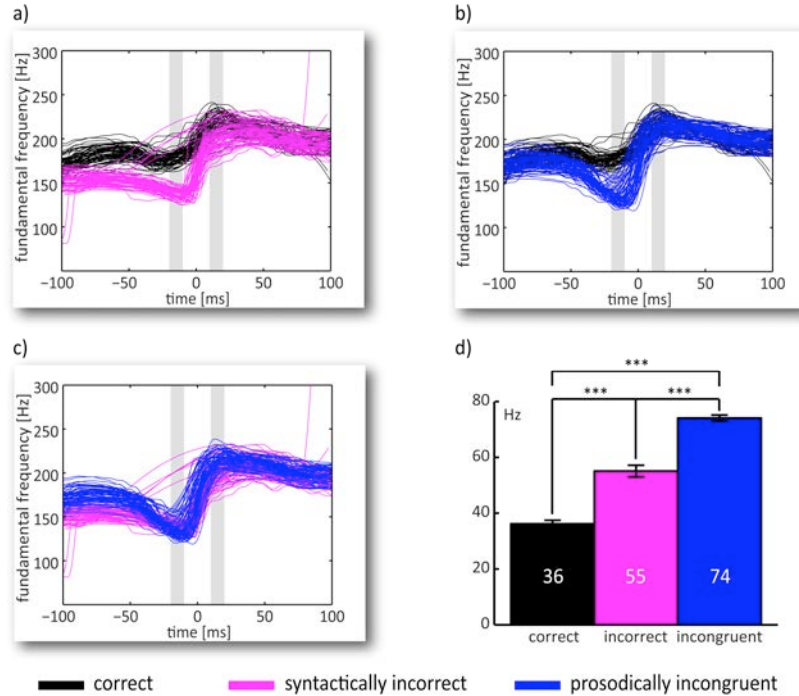


Figure 5.1: Fundamental frequency (F_0) contours for each sentence type. a-c) F_0 contours are centered at the onset of the past participle (correct – black; syntactically incorrect – magenta; prosodically incongruent – blue). Gray bars highlight the time windows used to estimate the F_0 change. d) Mean F_0 change values (Hz) for each sentence type and statistical comparisons (***) $P \leq 0.001$. The error bars reflect the standard error of the mean.

Prosodically incongruent sentences were created using Praat, whereby the F_0 contour of the correct sentences was altered within the 100 ms prior to the onset of the participle (Figure 5.1b). This was done such that the form of the F_0 contour approximated the F_0 contour of the incorrect sentences, while keeping the contour smooth (Figure 5.1c). The size of the change was then quantified as described above. The F_0 change in prosodically incongruent sentences (74 Hz) was significantly larger than in correct and in incorrect sentences ($t_{132} = 22.54$, $P < 0.001$; $t_{132} = 8.09$, $P < 0.001$, respectively). In fact, all prosodically incongruent sentences included a change that was larger than the mean change of the incorrect sentences (which was 55 Hz). Figure 5.1d shows the size of the mean F_0 change for each sentence type and the results of the statistical comparisons.

In addition to these experimental conditions, two filler conditions were included (Hahne et al., 2002). One filler condition consisted of 67 correct sen-

tences, in which the preposition was followed by a noun to ensure that participants could not determine the sentence grammaticality at the preposition. The second filler condition comprised 67 different syntactically incorrect sentences to increase the probability of sentences including a syntactic violation (60% correct, 40 % incorrect sentences).

Design and Procedure

Sentences were presented auditorily via in-ear headphones at an intensity of 55 dB above the participant's individual hearing threshold. They were randomly distributed over three blocks with equal within-block probability for each condition. Randomization within each block was constrained by maximal three sentences of the same condition in direct succession.

During auditory stimulation, a small fixation square was presented in the middle of a screen to minimize participants' eye movements. 1500 ms after the sentence ended a happy and a sad smiley were visually presented next to each other. The positions (left vs. right) of the happy and sad smiley were randomized uniformly within each block and across conditions, in order to avoid motor preparation. Participants were instructed to press the button corresponding to the happy smiley when the sentence was syntactically correct, and to press the button corresponding to the sad smiley when the sentence was syntactically incorrect. An IBM-compatible computer running with Presentation (Neurobehavioral Systems Inc., Albany, CA, USA) controlled the stimulation.

MEG data recording and processing

Participants sat in an electromagnetically shielded room (Vacuumschmelze, Hanau, Germany). MEG signals were recorded with a 306-channel MEG device (Vectorview, Elekta-Neuromag, Helsinki, Finland) at 500 Hz and online filtered with a band-pass of 0.1 – 160 Hz. Two pairs of electrodes recorded bipolar electrooculograms (EOG). Triggers marked the onset of the participle within all sentences. During blocks, the position of the participant's head was quasi-continuously measured by five HPI (head position indicator) coils to allow a correction of the magnetic fields for head movements. Head movement correction, bad channel interpolation and external interference suppression were obtained by applying the signal space separation method (Taulu et al., 2004). The MEG recordings were offline filtered with a band-pass of 2 – 10 Hz. The 2 Hz high-pass filter was specifically designed for a strong DC suppression (>150 dB at DC) to replace baseline correction. The 10 Hz low-pass filter was applied to maximize

the signal-to-noise-ratio. Such filter settings have proven useful when instigating language- or perception-related processes, by leaving the broad deflections untouched (Friederici et al., 2000a; C. S. Herrmann et al., 2000; Maess et al., 2006; Tervaniemi et al., 1999). The filtered MEG data were divided into epochs from -100 ms to 400 ms that were time-locked to the onset of the participle and excluded from averaging if they contained a signal change of more than 200 pT/m (gradiometer), 5 pT (magnetometer) or 200 μ V (EOG).

Source localization

Forward and inverse solutions were computed using a spherical model as volume conductor and individual triangularized representations of the inner skull surface as individual source models with two tangential, orthogonal dipoles at each of the 2562 locations (for a comparable approach see Mattout et al., 2007). Individual condition-specific brain activity was computed by means of the standardized low resolution electromagnetic tomography method (sLORETA; Pascual-Marqui, 2002). A global mean normalization was applied to reduce differences in overall brain activation strength between participants, which involved dividing individual condition-specific activations by the activation mean over all conditions of that participant. In order to isolate syntax-specific and prosody-specific violation effects, brain activations elicited by correct sentences were subtracted from the activations elicited by syntactically incorrect sentences and from the activations elicited by prosodically incongruent sentences. Only these brain activation differences were analyzed statistically.

Statistical analysis

For each violation effect, individual activation time courses were extracted from a region of interest (ROI) in the left and right superior temporal cortex (STC; Figure 5.3). These regions were selected because previous studies using similar sentence materials showed strongest activations in superior temporal areas (Friederici et al., 2000a; Knösche et al., 1999). Statistical analyses were conducted for the 40 – 80 ms and for the 110 – 160 ms time windows (Figure 5.2 and Figure 5.3) based on previous MEG data showing two syntax-related effects within the first 200 ms after violation onset (C. S. Herrmann et al., 2000; B. Herrmann et al., 2009).

The presence of violation-specific effects (syntax; prosody) was tested independently for each time window and hemispheric ROI using a one-sample t-test against zero. Subsequently, a repeated measures analysis of variance (rmANO-

VA) was conducted to test for differences between the violation effects. The rmANOVA included the factors Violation (syntax; prosody) and Hemisphere (left; right), and was carried out for each time window separately. Planned comparisons were conducted to resolve interaction effects. Effect sizes are provided as generalized eta-squared (η^2_G ; Bakeman, 2005).

5.3 Results

Behavioral performance

Mean percentage of hit rates (\pm SEM, standard error of the mean) were as follows: correct 97.3 % (\pm 0.5), prosodically incongruent 97.3 (\pm 0.6), syntactically incorrect 94.7 % (\pm 1.1). Hit rates were significantly higher for correct sentences and for prosodically incongruent sentences than for syntactically incorrect sentences ($F_{1,20} = 6.66$, $P = 0.018$, $\eta^2_G = 0.107$; $F_{1,20} = 7.97$, $P = 0.011$, $\eta^2_G = 0.098$; respectively). No difference was found between correct sentences and prosodically incongruent sentences ($F_{1,20} < 0.10$, $P = 0.998$).

At the same time, mean reaction times (\pm SEM) were the following: correct 716 ms (\pm 32.5), prosodically incongruent 700 ms (\pm 31.0), syntactically incorrect 683 ms (\pm 27.4). Reaction times for the syntactically incorrect sentences and for prosodically incongruent sentences were significantly faster than for correct sentences ($F_{1,20} = 13.11$, $P = 0.002$, $\eta^2_G = 0.015$; $F_{1,20} = 5.38$, $P = 0.031$, $\eta^2_G = 0.003$; respectively). A marginally significant difference was found between syntactically incorrect sentences and prosodically incongruent sentences ($F_{1,20} = 3.37$, $P = 0.081$, $\eta^2_G = 0.004$).

In other words, participants responded faster, but made more errors when judging syntactically incorrect sentences, while they responded more accurate, but slower when judging correct sentences. These significant effects may, however, reflect a speed–accuracy trade off rather than a genuine effect (Hahne et al., 2002).

MEG source estimates

In the very early time window (40 – 80 ms), a significant syntax violation effect was revealed in both hemispheres (left: $t_{20} = 3.29$, $P = 0.004$; right: $t_{20} = 3.34$, $P = 0.003$), whereas no prosody violation effects were found (left: $t_{20} = 0.48$, $P = 0.635$; right: $t_{20} = -0.73$, $P = 0.472$).

The rmANOVA confirmed these results by revealing a significant main effect of Violation ($F_{1,20} = 23.60$, $P < 0.001$, $\eta^2_G = 0.186$), but no main effect of Hemis-

phere or Violation \times Hemisphere interaction ($F_{1,20} = 2.23$, $P = 0.151$; $F_{1,20} = 2.13$, $P = 0.160$; respectively).

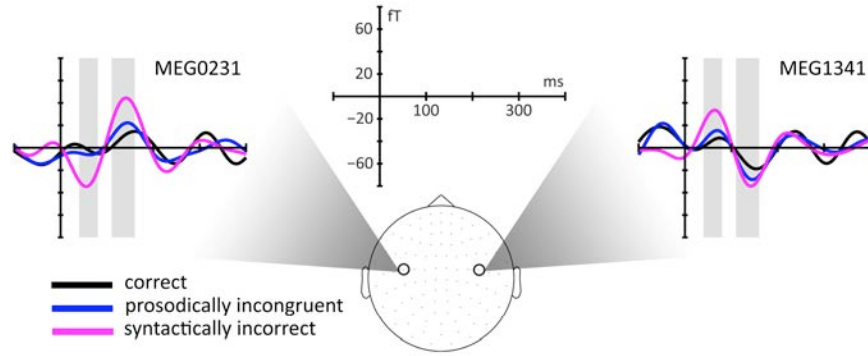


Figure 5.2: Grand average ERFs time-locked to the participle onset. One magnetometer channel over the left (MEG0231) and right (MEG1341) hemisphere is depicted. Gray bars highlight the time windows used for the statistical analysis (correct – black; syntactically incorrect – magenta; prosodically incongruent – blue).

The analyses of the violation-specific effects in the 110 – 160 ms time window revealed a significant syntax violation effect in both hemispheres (left: $t_{20} = 4.23$, $P < 0.001$; right: $t_{20} = 3.37$, $P = 0.003$) and a significant prosody violation effect in both hemispheres (left: $t_{20} = 2.11$, $P = 0.048$; right: $t_{20} = 2.75$, $P = 0.012$).

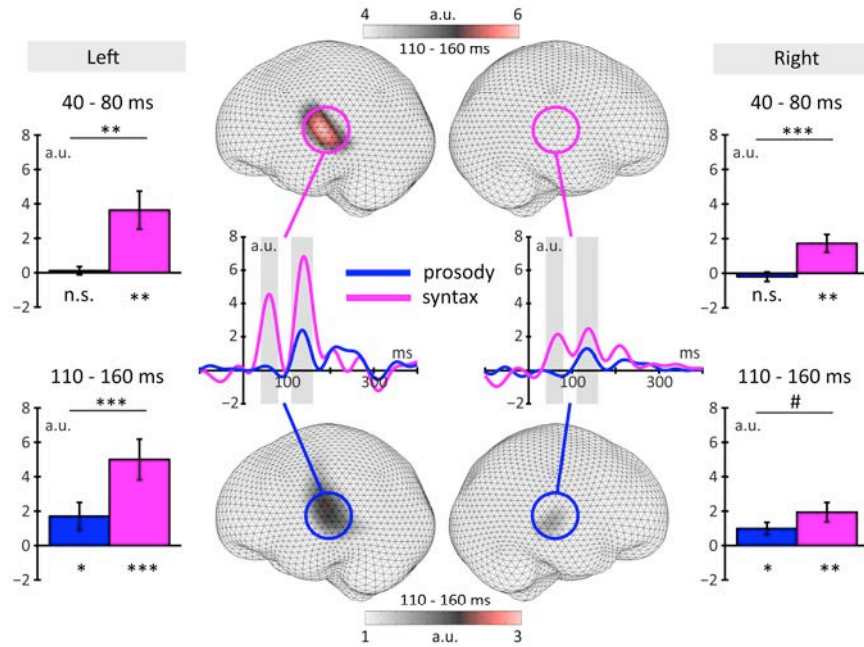


Figure 5.3: Time course of grand average brain activity. The syntax violation effects are depicted in magenta and the prosody violation effects in blue. Gray bars highlight the time windows used for the statistical analysis. Statistical comparisons for the superior temporal cortex regions are presented at the left and right, respectively (a.u. – arbitrary units; n.s. – not significant; # $P \leq 0.1$; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$).

The rmANOVA conducted to examine differences between the violation effects revealed a main effect of Violation ($F_{1,20} = 20.43$, $P < 0.001$, $\eta^2_G = 0.083$) and a marginally significant main effect of Hemisphere ($F_{1,20} = 3.26$, $P = 0.086$, $\eta^2_G = 0.067$). These effects were further specified by the significant Violation \times Hemisphere interaction ($F_{1,20} = 5.27$, $P = 0.033$, $\eta^2_G = 0.027$). Planned comparisons revealed a significantly larger syntax than prosody violation effect in the left hemisphere ($F_{1,20} = 15.04$, $P = 0.001$, $\eta^2_G = 0.118$) and a marginally greater syntax violation effect in the right hemisphere ($F_{1,20} = 3.67$, $P = 0.070$, $\eta^2_G = 0.047$). Furthermore, the syntax violation effect was significantly larger in the left than in the right hemisphere ($F_{1,20} = 4.98$, $P = 0.037$, $\eta^2_G = 0.120$), whereas no difference between hemispheres was found for the prosody violation effect ($F_{1,20} = 0.61$, $P = 0.444$).

5.4 Discussion

The current MEG experiment investigated whether a change in the F_0 contour contributes to the ELAN effect associated with syntactic processing. On this basis, neural responses elicited by syntactically incorrect sentences were contrasted with the responses elicited by prosodically incongruent sentences.

The analysis of the 110 – 160 ms time window revealed significant syntax and prosody violation effects, which is in line with previous EEG studies (Hahne & Friederici, 1999, 2002; Mietz et al., 2008; Schön et al., 2004) as well as MEG studies (Friederici et al., 2000a; Knösche et al., 1999; Kubota et al., 2003, 2004). Most relevant for the current experiment, the direct comparison of the syntax with the prosody violation effect showed a significantly larger effect elicited by the syntactic violation in the left STC and a marginally larger effect in the right STC.

Before interpreting these findings, however, it is important to note that the prosody violation effect introduced by the F_0 pitch change in prosodically incongruent sentences very likely overestimates the prosodic effect in the syntactically incorrect sentences. This is because the difference in the stimulus F_0 change between correct and prosodically incongruent sentences was almost twice as large as the difference in the stimulus F_0 change between correct and syntactically incorrect sentences (see Figure 5.1). It has been observed in previous studies that decreasing the pitch change in an auditory stimulation leads to decreasing neural activity in the 100 – 200 ms time window (Berti et al., 2004; Horváth et al., 2008; Pakarinen et al., 2007).

As a consequence, the contribution of the F_0 change in the syntactically incorrect sentences to the ELAN effect can be considered insignificant. Hence, the syntax violation effect found in the current and also in previous EEG/MEG studies (e.g., Friederici et al., 2000a; Hahne & Friederici, 1999; C. S. Herrmann et al., 2000) cannot be attributed to the detection of an unexpected prosodic contour, but rather reflects initial syntactic parsing difficulties. This finding is in perfect agreement with studies reporting an ELAN for naturally recorded syntactically incorrect sentences (Friederici et al., 1993, 1996).

Moreover, the syntax violation effect showed a left-hemispheric bias in the 110 – 160 ms time window, which supports models that emphasize regions in the left hemisphere to be involved in syntactic operations (Friederici, 2002; Pulvermüller, 2010; but see also C. S. Herrmann et al., 2000; Kubota et al., 2004).

The prosody violation effect, on the other hand, showed a bilateral distribution. Previous studies which investigated the processing of prosodic information reported a bias towards right-hemispheric cortical areas (Eckstein & Friederici, 2006; Meyer et al., 2002). However, it is noteworthy that a grammaticality judgment task was used in the current experiment. This may have led to a more bilateral distribution of the prosody effect. Other studies closely related to the current experiment in terms of the stimulus manipulation reported left-lateralized or widely distributed early effects at around 100 – 200 ms, consistent with the present findings (Mietz et al., 2008; Schön et al., 2004).

In addition to the findings in the ELAN(m) time window, a syntax violation effect was also observed in a preceding time window (40 – 80 ms), but was absent for prosodically incongruent sentences. Although this syntax-related effect occurs very early after the onset of the violating word, accumulating evidence points to different substages of early syntactic processes, separating a very early effect within the first 100 ms and a subsequent effect between 100 – 200 ms (C. S. Herrmann et al., 2000; B. Herrmann et al., 2009). Originally, this very early effect has been linked to a resource allocation mechanism assigned to modulations of the P50 component (B. Herrmann et al., 2009). A different explanation might be based on recent studies investigating the detection of simple rule violations (Grimm et al., 2011; Slabu et al., 2010). In those studies, brain activations were modulated by deviancy-related processes as early as 30 – 40 ms, suggesting a hierarchical organization of mismatch detection expanding along multiple levels.

Nevertheless, the present results cannot decide whether the very early syntax-related effect reflects an independent process or one of multiple rule violation detection levels. The null finding here regarding a very early prosodic violation effect might be due to the overall weak effect elicited by the prosodic incongruency.

5.5 Conclusions

To summarize, the current MEG experiment disentangled the neural responses elicited by the detection of a prosodic incongruency from responses elicited by a syntactic violation. The effects related to syntactic processing are not only larger in amplitude, but additionally show a left-hemispheric bias at around 110 – 160 ms and an effect in a preceding time window. Thus, the findings of the current

experiment clearly show that early syntactic processes reflected in the ELAN primarily reflect initial syntactic parsing difficulties.

6 Experiment II: Decoding syntactic errors from single trial activations

6.1 Introduction

One ERP component associated with syntactic rule processes is the ELAN which peaks at around 100 – 200 ms as a response to a syntactic violation (Friederici et al., 1993; Hahne & Friederici, 1999). Another ERP component that reflects auditory perceptual rule processes and peaks in the same time window is the MMN (Alho, 1995; Näätänen et al., 1978).

In order to obtain an ERP wave, the neural responses to single trials are averaged within a participant to increase the signal-to-noise ratio. Such an ERP for a number of participants is then used for the statistical analysis. Although, this has been shown to be a fruitful approach, indicating that the neural responses to syntactic and auditory perceptual manipulations are consistent enough for this type of analysis, it has not been shown directly whether the neural responses to single syntactic violations are consistent across participants. A direct analysis could indicate whether the culturally learned rules are represented similarly in the brains of different individuals.

Recent studies investigating the information encoded in human brain signals applied multivariate pattern classification to decode certain brain states from brain activation patterns (Haynes & Rees, 2005, 2006; Rieger et al., 2008; Suppes et al., 1997; van Gerven & Jensen, 2009). MVPA does not only allow detecting small effects in the observed neural patterns of fMRI activations (e.g., Formisano et al., 2008), but enables the decoding of brain states from single trial MEG recordings, information which is usually lost due to averaging (Guimaraes et al., 2007; Rieger et al., 2008). Furthermore, it has also been demonstrated in fMRI and MEG that multivariate neural patterns contain sufficient information to ac-

curately decode the mental state of new individuals (Chan et al., 2011; Mourao-Miranda et al., 2005; Poldrack et al., 2009), thus, providing a technique which is qualified to test the consistency of single neural responses across participants.

Here, the MMN to deviances in auditory space was used as a tool to specify the neural basis of the detection of syntactic rule violations (reflected in the ELAN) in relation to basic auditory deviance detection (reflected in the MMN).

The current auditory MEG experiment used a multivariate pattern classification approach to investigate whether single trial neural activations allow the decoding of basic auditory deviants and more interestingly violations of syntactic phrase structure rules in the temporal cortex. Importantly, the experiment aimed to explicitly test whether neural responses to single violations are inter-subjectively consistent by decoding these brain states from the activation patterns of one participant based on the single trial activation patterns of an independent subset of participants. Hypotheses were the following:

- (1) Single trial neural activations were expected to provide sufficient information to decode whether the participant's brain was processing a correct sentences or a sentence containing a syntactic violation (or an auditory perceptual violation).
- (2) In case of inter-individual comparable neural responses to syntactic rule violations, decoding accuracies were expected to be similar for classifications conducted within participants and across participants (i.e., using the data of different individuals for decoding).

6.2 Methods

Participants

Twenty-four German native speakers aged 21 to 32 (eleven female; mean age: 25.3) participated in the experiment. They were all right-handed as measured by the Edinburgh Handedness Inventory (Oldfield, 1971). The 20th percentile of the laterality quotient was 100 (range: 83 – 100). Written informed consent was obtained from each participant prior to testing. Participants had no known hearing deficit or history of neurological diseases and were paid for their participation.

Stimulus material

The experimental stimuli comprised 96 syntactically correct and 96 syntactically incorrect sentences previously used in an EEG study (Hahne et al., 2002; see Table 6.1). Correct sentences consisted of a "determiner-noun-auxiliary-past participle" sequence (e.g., "Das Buch wurde gedruckt.", *Engl. "The book was printed."*), while syntactically incorrect sentences consisted of a "determiner-noun-auxiliary-preposition-past participle" structure (e.g., "Der Roman wurde im gedruckt.", *Engl. "The novel was in-the printed."*). Incorrect sentences contained a word category violation at the participle, as a verb is not allowed to follow a preposition in German. These sentences were constructed following the description given by Hahne & Friederici (1999; see also Experiment I) and have been evaluated for unwanted acoustic or prosodic effects (Hahne & Friederici, 1999; see also Experiment I).

Two filler conditions from the above-mentioned EEG study (Hahne et al., 2002) were presented along with the experimental stimuli. One filler condition comprised 96 sentences in which the preposition was followed by a noun to ensure that participants could not determine the sentence grammaticality at the preposition. In addition, 96 syntactically incorrect sentences with a different participle were presented in order to balance the number of correct and incorrect sentences. All sentences were spoken by a trained female native speaker of German and digitalized at 44.1 kHz (16 bit, stereo, normalized to peak intensity).

A condition that elicits a MMN was created by presenting sentences with infrequent changes in the interaural time difference (ITD), a binaural cue important for localizing sound sources in the horizontal plane (Middlebrooks & Green, 1991). On this account, two versions for each of the 384 sentences were created: (A) a standard condition, in which the complete sentence was presented binaurally without an acoustic deviation, and (B) a deviant condition, in which an infrequent ITD change was included. In the latter, the left channel was delayed by 0.2 ms starting at the onset of the participle within the sentence, which gives a right-lateralized impression. Based on the number of words, an ITD change occurred in only 10 % of the words, while 90 % of the words did not include a lateralization effect. The standard and the deviant condition were identical up to the participle. Correct sentences without an ITD change are henceforth called "correct standard condition", syntactically incorrect sentences without an ITD change "incorrect standard condition", correct sentences including an ITD change "correct deviant condition" and syntactically incorrect sen-

tences containing an ITD change "incorrect deviant condition". The experimental design is summarized in Table 6.1.

Classification	Sentence, e.g.:	
Syntax cor/sta vs. inc/sta	Das Buch wurde gedruckt.	* Der Roman wurde im gedruckt.
	<i>The book was printed.</i>	* <i>The novel was in-the printed.</i>
	correct standard	incorrect standard
Auditory space cor/sta vs. cor/dev	Das Buch wurde gedruckt.	Das Buch wurde <u>gedruckt</u> .
	<i>The book was printed.</i>	<i>The book was printed.</i>
	correct standard	correct deviant
Double feature cor/sta vs. inc/dev	Das Buch wurde gedruckt.	* Der Roman wurde im <u>gedruckt</u> .
	<i>The book was printed.</i>	* <i>The novel was in-the printed.</i>
	correct standard	incorrect deviant

Table 6.1: Sentence materials and classifications. Syntactically incorrect sentences are marked with an asterisk. Underlined participles highlight the interaural time difference (ITD) change of 0.2 ms (cor/sta – correct standard; inc/sta – incorrect standard; cor/dev – correct deviant; inc/dev – incorrect deviant).

Design and Procedure

Participants were presented with all 384 sentences, whereby one half was randomly selected as standard and the other half as deviant. Sentences were randomly distributed over four blocks, with equal probability for each condition. Within each block, sentences were randomized with the constraint that no more than three stimuli of same type (standard, deviant, correct or incorrect) were presented in a row.

During auditory stimulation, participants looked at a small fixation square at the center of the screen. A picture showing a happy and a sad smiley side by side was presented 1500 ms after the sentence ending. The positions (left vs. right) of the happy and sad smiley were randomized uniformly within each block and across conditions, and participants were instructed to press either the button for the happy (correct sentence) or sad smiley (incorrect sentence). All steps of randomization were conducted individually. Sentences were presented with an intensity of 55 dB above the participant's individual hearing threshold using in-

ear headphones. An IBM compatible computer running with Presentation (Neurobehavioral Systems Inc., Albany, CA, USA) controlled the stimulation.

MEG data recording and processing

MEG signals were recorded in an electromagnetically shielded room (Vacuum-schmelze, Hanau, Germany) using a 306-channel MEG device (Vectorview, Elekta-Neuromag, Helsinki, Finland) at a sampling rate of 500 Hz and online band-pass filtered with 0.1 – 160 Hz. Two pairs of electrodes recorded bipolar EOGs. During blocks, the position of the participant's head was quasi-continuously measured by five HPI (head position indicator) coils to allow for head movement correction of the magnetic fields. Head movement correction, bad channel interpolation and external interference suppression were obtained by applying the signal space separation method (Taulu et al., 2004). Individual data were transformed to a common sensor space that allows statistical comparisons between participants (Taulu et al., 2004).

For the analysis, only the 204 orthogonal planar gradiometers in 102 locations were used as they are most sensitive to magnetic fields coming directly from below them (Hämäläinen et al., 1993). MEG signals were offline filtered with a high-pass of 1.7 Hz to avoid baseline correction (>130 dB suppression at DC) and with a low-pass of 10 Hz to further increase the signal-to-noise-ratio (Friederici et al., 2000a; Maess et al., 2006; Tervaniemi et al., 1999). Epochs of 800 ms (-100 ms to 700 ms) that were time-locked to the onset of the participle were extracted from the MEG signals and down-sampled to 100 Hz. Epochs were screened for blinks and other artifacts and excluded from the analysis if they contained signal changes by more than 200 pT/m (gradiometer) or 100 μ V (EOG).

Pattern classification and empirical guessing level

A linear SVM classifier was used to analyze MEG single trial recordings (Chang and Lin, 2001, LIBSVM matlab-toolbox v2.89). For each trial, a feature vector \mathbf{x} with the length of samples \times channels was obtained using the magnetic field strength as feature values.

The generalization of the classification was tested in each participant using a leave-one-out cross validation (LOOCV). On this account, one trial was held out, while the remaining $n - 1$ trials were used to train the classifier. The model derived from classification was then used in decoding the label of the independent test trial that was kept out. The decoding accuracy was computed by comparing

the decoded label with the experimental label of that trial. This procedure was repeated for each of the n trials. Subsequently, the n accuracies were averaged, resulting in a mean decoding accuracy value. Although the application of LOOCV can be computationally expensive, it allows using the maximum number of training samples while strictly separating training and test data (Pereira et al., 2009). Decoding accuracies were compared to an empirical guessing level derived from a permutation procedure to evaluate the reliability of the results. To this end, the experimental labels were permuted among the training data set. Then, a full cross-validation was applied. Permutation and LOOCV were repeated 500 times and then averaged to extract mean empirical guessing levels for each participant and classification.

In this experiment, the following three classifications were investigated: (1) syntax: correct standard condition vs. incorrect standard condition, (2) auditory space: correct standard condition vs. correct deviant condition, (3) double feature: correct standard condition vs. incorrect deviant condition. Hence, all three violation conditions were separately classified as pairwise classifications with the correct standard condition. Table 6.1 shows the classifications of interest together with examples of the corresponding sentence material.

Time course pattern analysis – intra-subject decoding

Using the information of all 204 gradiometers, classification and LOOCV was computed for a sliding time window of 30 ms (three samples) that moved sample by sample (10 ms) in order to obtain a time course of decoding accuracies for each participants and classification. Based on previous studies investigating early syntactic and auditory spatial processing (e.g., Friederici et al., 1993; Hahne et al., 2002; Schröger, 1996), the time window of 110 – 170 ms was selected for further analysis. It included the peak of highest decoding accuracies at 140 ms (see Figure 6.1). For each classification, mean decoding accuracies were extracted from this time window and compared to the corresponding mean empirical guessing levels using a pairwise t-test. Subsequently, a one-way rmANOVA including the factor Classification (syntax; auditory space; double feature) was carried out to test for differences in decoding accuracies between the three classifications. Post-hoc tests were applied using Bonferroni correction for multiple comparisons. Effect sizes are provided as η^2_G (Bakeman, 2005).

Local spatial pattern analysis – intra-subject decoding

In previous MEG pattern classification studies, the information contained in the weight vector \mathbf{w} of the trained classifier was used to obtain a topographical distribution of the most discriminative patterns (Besserve et al., 2007; Rieger et al., 2008). The features with higher absolute values indicate stronger impact on the class separation decision. The right column of Figure 8.4 depicts such a topographical map for each classification type using the normalized absolute values of the weight vector \mathbf{w} . Normalization was computed by dividing the absolute values of the weight vector by its norm. Nevertheless, the information contained in the weight vector of a linear SVM also depends on the correlations between features. High correlations might lead to lower absolute values in the weight vector and thus to misinterpretations (Pereira et al., 2009). Usually, neighboring channels in MEG correlate highly with each other, especially when a strong source dominates the measured signal.

To avoid this potential bias, a multivariate searchlight approach was applied to investigate the topographical distribution of informative patterns (Haynes et al., 2007; Kriegeskorte et al., 2006). On this account, classification and LOOCV was conducted at each sensor position for the 110 – 170 ms time interval (Friederici et al., 1993; Hahne et al., 2002; Schröger, 1996) using eight to twelve gradiometer channels in a radius of 40 mm from that sensor position. The resulting decoding accuracy distribution in sensor space displays the local separability of the experimental conditions. Decoding accuracies were compared to an empirical guessing level derived from the permutation procedure described above. Permutations of the experimental labels and LOOCV were repeated 500 times for each searchlight. A t-test was conducted for each sensor position to test for differences between decoding accuracies and the empirical guessing levels. Additionally, a t-test was conducted to compare decoding accuracies at each sensor position to the overall mean of the other sensor positions. Although more conservative, this procedure is especially sensitive for significant peaks in the decoding accuracy maps, and resembles the localization test proposed for ROI-based classifications in fMRI (Etzel et al., 2009). Significance levels (P) were corrected using the Bonferroni procedure.

Local spatial pattern analysis – inter-subject decoding

The preceding analysis sections described the intra-subject generalization of the classification on the training data. To investigate the inter-subject generalization

of the classifications, the following procedure was applied. Similar to the intra-subject local spatial pattern analysis, multivariate pattern classifications were conducted at each sensor position for the 110 – 170 ms time window using a searchlight radius of 40 mm. However, here the magnetic field patterns of each trial of $n - 1$ participants were used to train the classifier. Subsequently, the experimental labels of the trials of the participant which was held out were decoded based on the model derived from the training. Decoding accuracies were obtained by comparing the decoded labels to the experimental labels of each trial, which were then averaged to a mean decoding accuracy value at each sensor position. This procedure was repeated for each of the twenty-four participants, resulting in a topographical map of decoding accuracy values for each participant and classification. An empirical guessing level was obtained by permuting the experimental labels among the training data set. Permutations were repeated 500 times and then averaged to extract mean empirical guessing levels for each participant and classification. A t-test was carried out to compare the decoding accuracies to the empirical guessing levels. In addition, decoding accuracies at each sensor position were compared to the overall mean of the other sensor positions. Significance levels (P) were corrected for multiple comparisons according to Bonferroni. In addition to these topographical maps, spatial distributions for each classification type derived from the normalized weight vector \mathbf{w} are provided for comparison purposes in the right column of Figure 6.3 (but see potential drawbacks described above).

Statistical analyses of intra- vs. inter-subject decoding

A ROI was selected over the left and right temporal cortex (see Figure 6.4) based on previous syntax and memory-related studies (Alho, 1995; Friederici et al., 2000a; B. Herrmann et al., 2009). For each participant and classification, mean decoding accuracies of the topographical maps (110 – 170 ms) were extracted from these ROIs. Hemispheric differences as well as magnitude differences between the classification generalization types were tested in a three-way rmANOVA including the factors Classification (syntax; auditory space; double feature), Hemisphere (left; right) and Generalization type (intra-subject decoding; inter-subject decoding) was conducted. Greenhouse-Geisser correction was applied when the assumption of sphericity was violated (Greenhouse & Geisser, 1959). The original degrees of freedom are reported along with the Epsilon correction coefficient and the corrected probability. Post-hoc tests were carried out

using Bonferroni correction for multiple comparisons. Effect sizes are provided as η^2_G (Bakeman, 2005).

Topographical differences between generalization types driven by location changes (the rmANOVA only accounts for decoding accuracy magnitude differences between the generalization types) were obtained using the relative difference measure (RDM; Lew et al., 2009). The RDM is defined as:

$$\text{RDM}(\%) = 100 \cdot \left\| \frac{\mathbf{a}}{\|\mathbf{a}\|_2} - \frac{\mathbf{b}}{\|\mathbf{b}\|_2} \right\|_2 / 2,$$

where \mathbf{a} reflects the decoding accuracy topography of the intra-subject analysis and \mathbf{b} the decoding accuracy topography of the inter-subject analysis. RDM is zero for identical topographies (irrespective of their amplitudes). $\|\cdot\|_2$ is the Euclidian norm. In order to examine RDM differences between classifications, a one-way rmANOVA was conducted that included the factor Classification (syntax; auditory space; double feature). Post-hoc tests were applied using Bonferroni correction for multiple comparisons. Effect sizes are provided as η^2_G (Bakeman, 2005)

6.3 Results

Behavioral performance

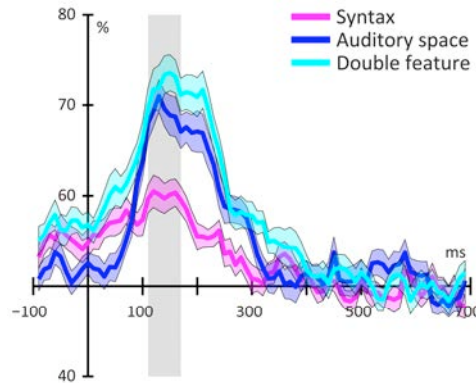
Mean percentage of hit rates (\pm SEM) were as follows: correct standard 97.6 % (\pm 0.8), incorrect standard 96.3 % (\pm 0.8), correct deviant 97.4 % (\pm 0.9), incorrect deviant 96.7 % (\pm 0.6). A rmANOVA including the factors Grammaticality (correct; incorrect) and Auditory space (standard; deviant) was conducted. There was no main effect of Grammaticality ($F_{1,23} = 3.30$, $P = 0.082$), no main effect of Auditory Space ($F_{1,23} = 0.02$, $P = 0.890$) and no interaction ($F_{1,23} = 0.30$, $P = 0.589$).

Time course pattern analysis – intra-subject decoding

Using a sliding window of 30 ms, a time course of decoding accuracies for each of the three classification types (syntax; auditory space; double feature) was obtained. After about 140 ms following the onset of the participle, highest decoding accuracies were found (Figure 6.1). Comparison of the mean decoding accuracies with the corresponding mean empirical guessing levels for the 110 – 170 ms time window revealed a significant difference for each classification

(syntax: $t_{23} = 7.23$, $P < 0.001$; auditory space: $t_{23} = 10.98$, $P < 0.001$; double feature: $t_{23} = 11.41$, $P < 0.001$).

Figure 6.1: Grand average decoding accuracy time courses (SEM in rent). The gray bar highlights the time window used for the statistical analysis and the spatial pattern analysis. Syntax: correct standard vs. incorrect standard (magenta); Auditory space: correct dard vs. correct deviant (blue); Double feature: correct standard vs. incorrect deviant (cyan).



The rmANOVA conducted to test for differences between the decoding accuracies of the three classification types for the time window of highest decoding performance (110 – 170 ms), the rmANOVA revealed a main effect of Classification ($F_{2,46} = 21.86$, $P < 0.001$, $\eta^2_G = 0.273$, $\epsilon = 0.69$). The double feature classification resulted in higher decoding accuracies than the syntax classification and the auditory space classification ($F_{1,23} = 28.94$, $P < 0.001$, $\eta^2_G = 0.345$; $F_{1,23} = 8.27$, $P = 0.026$, $\eta^2_G = 0.030$; respectively). Furthermore, the auditory space classification led to higher decoding accuracies compared to the syntax classification ($F_{1,23} = 17.58$, $P = 0.001$, $\eta^2_G = 0.249$).

Local spatial pattern analysis – intra-subject decoding

Using a multivariate searchlight approach for the 110 – 170 ms time window, a spatial distribution of decoding accuracy values was obtained for each type of classification. Highest decoding accuracies were found over temporal cortex areas for all classification types (Figure 6.2, left column). Comparison of decoding accuracies with an empirical guessing level showed significant differences over temporal areas for the syntax classification and an even more extended distribution for the auditory space classification and the double feature classification (Figure 6.2, center left column). Furthermore, comparison of decoding accuracies with the overall mean revealed most significant patterns over temporal cortices for all classification types. For the syntax classification, however, the most significant patterns were found in the left hemisphere slightly more anterior than for the other classification types (Figure 6.2, center right column).

Interestingly, the spatial distribution derived from the normalized weight vector \mathbf{w} revealed comparable patterns over temporal cortices (Figure 6.2, right column).

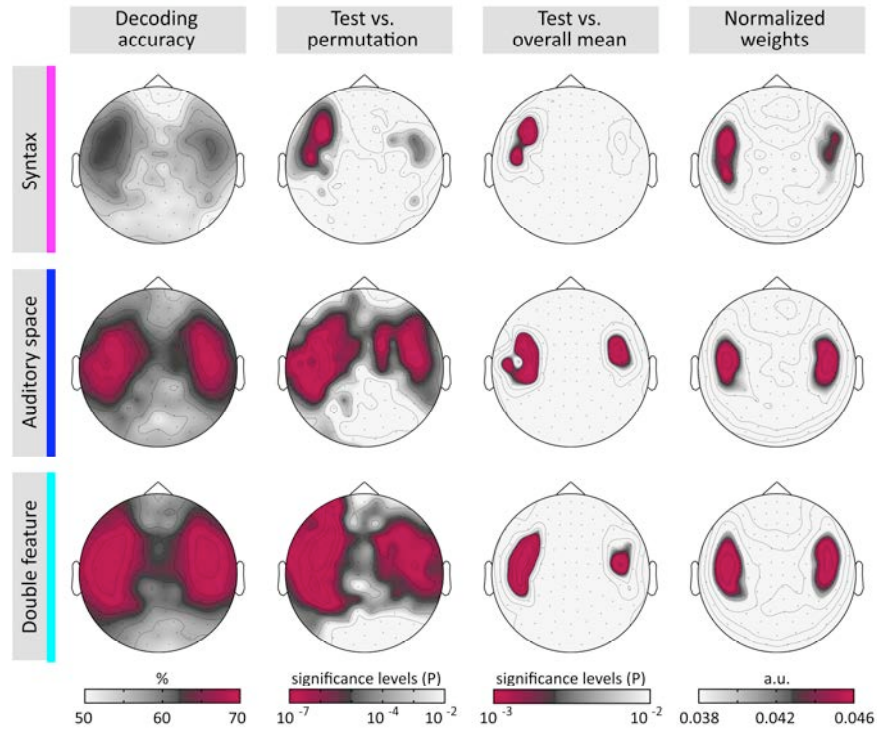


Figure 6.2: Grand average topographical maps of the intra-subject analysis for the 110 – 170 ms time window. Left column: Decoding accuracy maps for each classification (syntax; auditory space; double feature). Center left column: Bonferroni corrected significance probability maps for each classification against their corresponding guessing levels. Center right column: Bonferroni corrected significance probability maps for each classification against the overall mean of all other sensor positions. Right column: Topographical maps of the normalized weights for each classification.

Local spatial pattern analysis – inter-subject decoding

Similar to the intra-subject decoding, the spatial distribution of decoding accuracies for the 110 – 170 ms time window revealed highest values over temporal cortex areas for all classification types (Figure 6.3, left column). Comparing the decoding accuracies to the empirical guessing levels showed significant patterns over temporal cortices for the syntax classification and a more extended distribution for the auditory space and the double feature classification (Figure 6.3,

center left column). Comparisons of decoding accuracies to the overall mean revealed the most significant patterns in the left hemisphere for the syntax and the auditory space classification, whereas the most significant patterns for the double feature classification were distributed bilaterally. Here, however, the significant patterns for the syntax classification were not as anterior as for the intra-subject syntax classification (Figure 6.3, center right column). In addition, the spatial distributions derived from the normalized weight vector \mathbf{w} showed sensors with the highest impact on the class separation over bilateral temporal cortices (Figure 6.3, right column).

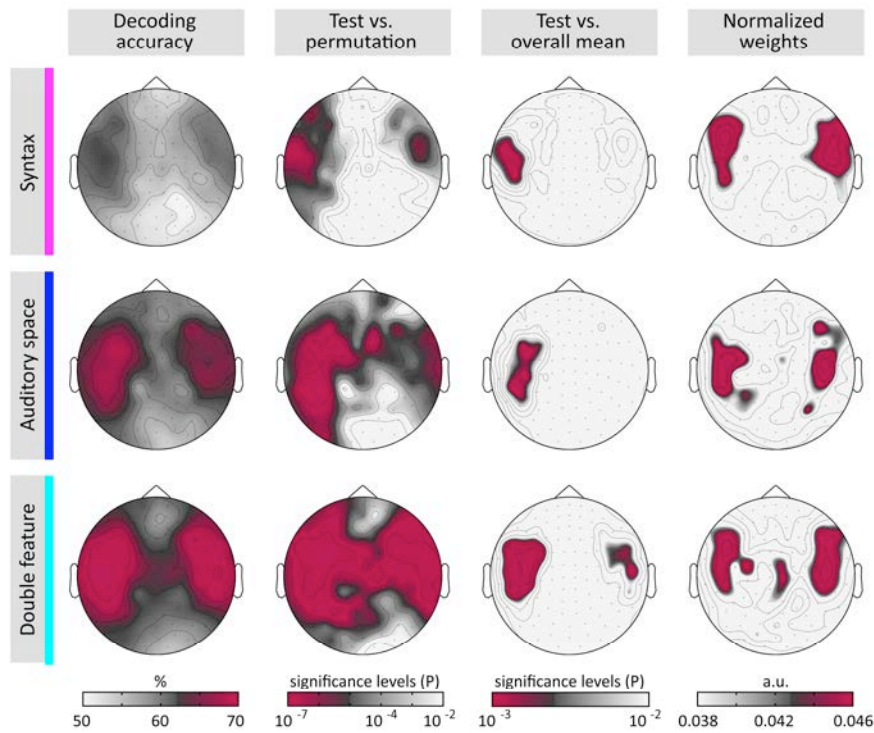
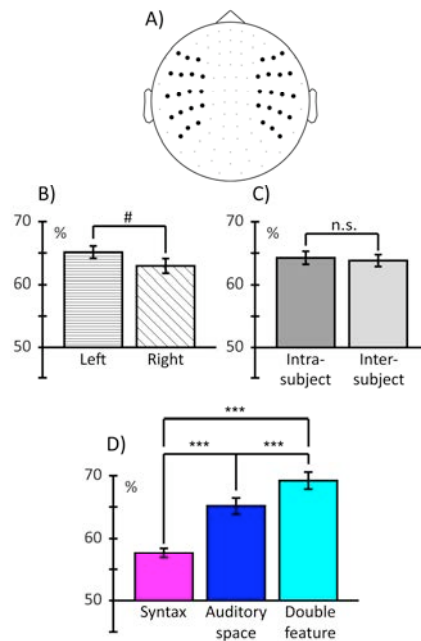


Figure 6.3: Grand average topographical maps of the inter-subject analysis for the 110 – 170 ms time window. Left column: Decoding accuracy maps for each classification (syntax; auditory space; double feature). Center left column: Bonferroni corrected significance probability maps for each classification against their corresponding guessing levels. Center right column: Bonferroni corrected significance probability maps for each classification against the overall mean of all other sensor positions. Right column: Topographical maps of the normalized weights for each classification.

Statistical analyses of intra- vs. inter-subject decoding

The rmANOVA conducted for the spatial pattern analyses revealed a main effect of Classification ($F_{2,46} = 49.94$, $P < 0.001$, $\eta^2_G = 0.311$, $\epsilon = 0.65$). Decoding the brain states from single trial brain patterns revealed higher accuracies for the double feature classification compared to the syntax classification and the auditory space classification ($F_{1,23} = 76.00$, $P < 0.001$, $\eta^2_G = 0.540$; $F_{1,23} = 43.56$, $P < 0.001$, $\eta^2_G = 0.093$; respectively). Furthermore, decoding accuracies for the auditory space classification were higher than for the syntax classification ($F_{1,23} = 28.20$, $P < 0.001$, $\eta^2_G = 0.358$). In addition, the main effect of Hemisphere was marginally significant ($F_{1,23} = 4.10$, $P = 0.055$, $\eta^2_G = 0.023$), with slightly larger decoding accuracies in the left than right hemisphere, whereas no difference was found between the intra-subject and the inter-subject decoding (main effect of Generalization type: $F_{1,23} = 0.49$, $P = 0.49$). None of the interactions was significant (for all $F < 2$, $P > 0.15$). Figure 6.4 summarizes the main effects of the rmANOVA.

Figure 6.4: Grand average decoding accuracies from the ROI analysis. A: The sensors used in the rmANOVA cover the left and right temporal cortices (marked in black). The bar graphs display the results of the rmANOVA main effects of Hemisphere (in B), Generalization type (in C) and Classification (in D) together with corresponding grand average decoding accuracies. (***) $P < 0.001$; # $P < 0.10$; n.s. – not significant). The error bars reflect the standard error of the mean. Syntax: correct standard vs. incorrect standard (magenta); Auditory space: correct standard vs. correct deviant (blue); Double feature: correct standard vs. incorrect deviant (cyan).



Differences in location between the intra-subject and the inter-subject topographical decoding accuracy maps were assessed by the RDM. For all classification types the RDM was smaller than 8 %. Additionally, the rmANOVA showed a

main effect of Classification ($F_{2,46} = 15.20$, $P < 0.001$, $\eta^2_G = 0.262$), caused by higher RDM values for the syntax classification (RDM = 7.49 %) than for the auditory space (RDM = 6.27 %) and the double feature classification (RDM = 5.82 %; $F_{1,23} = 11.80$, $P = 0.007$, $\eta^2_G = 0.206$; $F_{1,23} = 23.82$, $P < 0.001$, $\eta^2_G = 0.303$; respectively). No difference was found between the auditory space and the double feature classification ($F_{1,23} = 3.88$, $P = 0.18$). In other words, the topographical distributions of the intra-subject and the inter-subject syntax decoding accuracy values differed to a larger extent compared to the other classification types, although the overall differences between intra- and inter-subject decoding were rather small.

6.4 Discussion

The current MEG experiment investigated whether syntactic violations just as auditory spatial violations can be decoded from MEG single trial recordings intra- as well as inter-subjectively. To this end, three two-paired classifications were obtained using a linear SVM classifier: syntax (correct sentences vs. incorrect sentences), auditory space (correct sentences vs. correct sentences with ITD change) and double feature (correct sentences vs. incorrect sentences with ITD change).

Regarding the time course pattern analysis, generalization performance for the syntax and auditory space classifications was highest at around 110 – 170 ms after the onset of the deviating word. This finding is consistent with the ELAN component associated with early syntactic processes at around 100 – 200 ms (Friederici et al., 1993; Hahne & Friederici, 1999; Hahne et al., 2002) as well as with previous studies reporting MMN effects in this time window (Hahne et al., 2002; Schröger, 1996; Schröger & Wolff, 1996). The spatial distribution of informative patterns revealed highest decoding accuracies over temporal cortices for all classification types, which is in line with previous studies localizing the neural generators underlying the ELAN and the MMN (Alho, 1995; Friederici et al., 2000a; Kaiser et al., 2000; Knösche et al., 1999). The current approach additionally shows that even single trial patterns of the human brain provide sufficient information to decode violations of syntax and auditory space.

Importantly, classification performance generalized within and across participants as no difference in the magnitude of the decoding accuracies was found between the intra- and the inter-subject pattern analysis, and only small

differences in the topographical decoding accuracy distributions. Hence, these results provide strong evidence that early modulations of single trial neural activity patterns elicited by basic auditory spatial deviations and, more interestingly, by syntactic violations are largely consistent over different individuals.

At the same time, the topographical distribution of the intra-subject syntax classification showed a left anterior peak, in agreement with reports on anterior superior temporal cortex regions involved in syntactic processing (Friederici et al., 2000a, 2003b; Humphries et al., 2005), while significant patterns in the inter-subject syntax-classification was less anteriorly distributed (see Figure 6.2 and Figure 6.3, center right column).

Furthermore, a general tendency towards higher accuracies over the left temporal cortices was found. Regarding the topographical distribution of the auditory space classification, it is still an open issue whether spatial processing is mainly processed in the right hemisphere (e.g., Kaiser et al., 2000) or whether regions contralateral to the stimulation are primarily involved (e.g., Richter et al., 2009). Based on the current auditory space manipulation (i.e., an ITD change giving a right lateralized impression), the overall tendency towards a left-hemispheric predominance would be consistent with the "contralateral hypothesis". However, the current paradigm does not allow to estimate what influence sentence processing might have on the hemispheric lateralization. The distribution for the significant syntax-related patterns, on the other hand, was clearly left-lateralized as evidenced by a significant difference from chance level (and the overall mean). This finding relates to previous results highlighting the importance of the left hemisphere in syntactic operations (Friederici et al., 2000a; B. Herrmann et al., 2009; Humphries et al., 2005).

The present experiment additionally shows that double feature violations can be decoded with higher accuracy than correctly decoding syntactic violations or auditory space violations alone. Such a finding has also been reported previously, where parallel processing of syntactic and auditory spatial information at around 125 – 175 ms has been proposed (Hahne et al., 2002). Thus, the present findings provide further evidence for parallel processing of basic auditory and syntactic information decodable from single trials, with largely consistent neural responses across participants.

6.5 Conclusions

The current MEG experiment shows that the brain states correlated with auditory and with linguistic processes can be decoded from human brain single activation patterns. In particular, decoding of syntactic and auditory spatial processing states revealed highest accuracies at around 110 – 170 ms over temporal cortices. Moreover, early neural patterns elicited by single syntactic and spatial deviations were largely consistent over different participants, thereby providing evidence that the neural responses underlying culturally learned syntactic rules are represented very similar in the brains of different individuals.

7 Experiment III: Dissociation of grammar and perception

The text was largely derived from the study published in Human Brain Mapping by B. Herrmann et al. (in press-a).

7.1 Introduction

Recent MEG studies investigating the nature of early syntax-related processes reported modulations of sensory cortex activations in response to syntactic violations (Dikker et al., 2009, 2010; B. Herrmann et al., 2009). In this context, the resemblance between early auditory syntax-related responses and auditory perceptual responses has been highlighted (Dikker et al., 2009) and taken as indication that early syntactic and auditory perceptual processes share neural mechanisms. The spatial resolution of MEG, however, is limited and some effects might not be observable due to source orientation or cancellation effects (Ahlfors et al., 2010a, 2010b; Vrba & Robinson, 2001).

Thus, in this experiment the high spatial resolution of fMRI was used to shed light on the neural mechanisms underlying early syntactic processes in the auditory modality. The experiment aimed at elucidating on the role of auditory sensory cortices in these processes.

In order to relate fMRI activation findings to early syntactic processes, a setting was chosen in which two-word utterances were presented that elicited only an early negativity for incorrect utterances, but no P600 in a previous EEG study (Hasting & Kotz, 2008). If the authors' interpretation is correct that no P600 assigned revision/repair processes were initialized in these utterances because they do not suffice to form a sentence, then the syntax-related findings of the current experiment should be attributed to early syntactic processes.

Furthermore, the two-word utterances were constructed in a 2×2 fashion. One factor varied the grammaticality (correct vs. syntactically incorrect), while the second factor varied the perceptual markedness of the utterances (absence vs. presence of a perceptually overt category marking suffix). This was done in order to include an auditory perceptual contrast. The hypotheses were as follows:

- (1) Perceptually marked utterances contrasted with perceptually unmarked utterances were hypothesized to elicit auditory sensory cortex activations only.
- (2) In contrast, syntactically incorrect utterances were expected to elicit stronger activation than correct utterances in the anterior STG and the IFG.
- (3) In case of syntax-related sensory cortex modulations, the syntactically incorrect vs. correct contrast should additionally (or instead) show activations that correspond to the regions activated in the auditory perceptual contrast.

Methodologically, a conventional univariate subtraction analysis was applied as well as a multivariate pattern classification approach (Haynes & Rees, 2006; Norman et al., 2006). MVPA has been shown very sensitive to small activation changes, thus, providing a method that is potentially able to detect small syntax-related sensory effects which might be concealed in the conventional analysis.

7.2 Methods

Participants

Twenty-five German native speakers participated in the experiment (12 female, age: 22 – 32). They were all right-handed as measured by the Edinburgh Handedness Inventory (Oldfield, 1971). The 40th percentile of the laterality quotient was 100 (range: 76 – 100). Participants did not report any hearing deficit or neurological diseases in their history. They gave informed consent prior to the experiment and were paid for their participation.

Stimulus materials

182 syntactically correct and 182 syntactically incorrect German two-word utterances were auditorily presented. The ending of the second word was perceptually overtly marked in half of the syntactically correct and incorrect utterances, whereas the other half was unmarked, thereby constituting the Grammaticality–Perceptual Markedness 2×2 stimulus design.

In detail, two-word utterances were created based on 24 different monosyllabic word stems (e.g., "knie", *Engl. "knee"*) that were either perceptually overtly marked by the suffix "-t", giving 24 different verbs (e.g., "kniet", *Engl. "kneels"*), or unmarked, giving 24 different nouns ("Knie", *Engl. "knee"*). These verbs and nouns were preceded once by a personal pronoun ("er", *Engl. "he"*) and once by a preposition ("im", *Engl. "in-the"*), resulting in 96 different two-word utterances, which were each spoken by four different trained German native speakers (two female), leading to the 384 two-word utterances used in the experiment. Recordings were digitized at 44.1 kHz (16 bit, mono, normalized by peak intensity). Table 7.1 shows the 2×2 stimulus design.

Grammaticality	Perceptual markedness	
	unmarked	marked
correct	e.g., "im Knie" (<i>in-the knee</i>)	e.g., "er kniet" (<i>he kneels</i>)
incorrect	e.g., "er Knie" (<i>he knee</i>)	e.g., "im kniet" (<i>in-the kneels</i>)

Table 7.1: Stimulus materials in a 2×2 design (Transcripts of the auditory utterances).

Syntactically correct utterances were either a combination of a preposition and a noun (e.g., "im Knie", *Engl. "in-the knee"*) or of a personal pronoun and a verb (e.g., "er kniet", *Engl. "he kneels"*). Syntactically incorrect utterances consisted of a preposition-verb combination (e.g., "im kniet", *Engl. "in-the kneels"*) or of a personal pronoun-noun combination (e.g., "er Knie", *Engl. "he knee"*). The former combination included a word category violation at the verb, because in German, a noun phrase needs to follow a preposition. The latter combination, on the other hand, is not absolutely incorrect in German, because within a sentence, a noun is allowed to follow a personal pronoun (e.g., "Er vermutete, dass

sie Knie und Arm verletzt hatte.", *literal translation*: "He assumed, that she knee and arm had injured."). In isolation without sentence context, however, such a combination is perceived as absolutely incorrect (B. Herrmann et al., 2009) and is therefore taken as syntactically incorrect. Furthermore, these combinations would require an intonational phrase boundary (with a pause) after "er" ("he") when used in audition, which was not present in the current stimulus material.

Henceforth, the term "unmarked conditions" is used for syntactically correct and syntactically incorrect utterances including a bare word stem, while utterances including a perceptually overt marking are called "marked conditions". Accordingly, four different conditions were used in the experiment: correct unmarked, correct marked, incorrect unmarked and incorrect marked (see Table 7.1).

Design and Procedure

Imaging was conducted using a 3-T Siemens TRIO scanner (Erlangen, Germany) with a 12-channel head-coil. Participants were comfortably positioned in the bore and wore air-conduction headphones (Resonance Technology, Los Angeles, USA). Echo-planar imaging (EPI) scans were acquired in 30 axial slices covering temporal, inferior frontal and visual cortices. The sequence was set up with echo time (TE) 30 ms, flip angle 90°, repetition time (TR) 2.0 s, and acquisition bandwidth 116 kHz. The matrix was 64 × 64 pixels with a field of view of 192 mm², resulting in an in-plane resolution of 3 × 3 mm². A slice thickness of 2 mm plus an interslice gap of 1 mm was measured. Scans were obtained in six independent runs separated by a 30 to 60 s break in which scanning was discontinued. In addition, individual field maps were obtained, providing an estimate of local field inhomogeneities used in the spatial preprocessing of the functional data.

In each of the six independent runs, sixty-four two-word utterances (16 of each condition; see *Stimulus materials*) were auditorily presented. The inter-trial-interval was 7 s and the onset of the utterance was jittered by 0 ms, 400 ms, 800 ms and 1200 ms equally distributed over conditions. Utterances were randomized within each run and constrained by maximal three presentations of the same type (word stem, speaker's gender, grammaticality) in direct succession. A variable response key assignment was used by presenting a picture with a happy and a sad smiley side by side 2600 ms after the utterance ended. The positions (left; right) of the happy and sad smiley were randomized uniformly within each run and across conditions. In order to judge the grammaticality of

the utterance, participants pressed the button corresponding to the happy (correct utterance) or sad smiley (incorrect utterance). The response pictures were projected through an LCD projector (PLC-XP50L, Sanyo) onto the back of a screen. Participants viewed the pictures on the screen above their heads through a mirror attached to the head-coil. An IBM-compatible computer running with Presentation (Neurobehavioral Systems Inc., Albany, CA, USA) controlled the stimulation.

Univariate data analysis

Functional images were preprocessed for each run separately using Statistical Parametric Mapping (SPM8, Wellcome Imaging Department, University College, London, UK, <http://www.fil.ion.ucl.ac.uk/spm>). Functional time series were realigned, and corrected for field inhomogeneities using individual field maps (Cusack et al., 2003; Jezzard & Balaban, 1995) ("unwarped"), slice scan time corrected, normalized to the standard SPM8 EPI template using a transformation matrix calculated from the mean EPI image generated during realignment, and spatially filtered using a Gaussian filter with 6 mm FWHM. The first five images of the functional time series of each run were discarded to allow for magnetic saturation effects. The time series were filtered with a high pass of 0.01 Hz and corrected for first-order autocorrelation. A general linear model (GLM) was estimated for each participant including all six runs with four conditions (correct unmarked; correct marked; incorrect unmarked; incorrect marked) using a canonical hemodynamic response function (Friston et al., 1995). Responses to the syntactically incorrect conditions were contrasted against those to the syntactically correct conditions (Grammaticality contrast), and responses to the marked conditions were contrasted against those to the unmarked conditions (Perceptual Markedness contrast). Importantly, both contrasts controlled for any acoustic differences introduced by the personal pronoun and the preposition due to the 2×2 stimulus design. Individual contrast images were then entered into a second-level random-effects analysis using a one-sample t-test to test whether the observed differences between conditions are significantly different from zero. Subsequently, t-values were transformed into z-scores. In order to correct for multiple comparisons, activations were cluster extent thresholded ($P \leq 0.05$) using Monte Carlo simulations as described in Slotnick et al. (2003; Slotnick & Schacter, 2004). Regions were considered statistically significant if z-scores were

equal or greater than 3.719 ($P = 0.0001$) in a volume equal or greater than 216 mm³ (8 voxels).

Differences between conditions were further explored in a ROI analysis. The MarsBaR toolbox (v0.42; Brett et al., 2002) was used to estimate mean beta weights from peak-voxel-centered spheres of 4 mm radius extracted from the random-effects contrasts. Motivated by the study of B. Herrmann et al. (2009), two additional ROIs in the PAC were extracted. For this purpose, the mean coordinates of the PAC provided by Rademacher et al. (2001) were transformed into MNI space (Montreal Neurological Institute; Lancaster et al., 2007) and then entered into the analysis: left PAC (TE 1.0): -44 -20 6; right PAC (TE 1.0): 51 -11 5. Mean beta weights were transformed to percentage signal change (PSC). Subsequently, a two-way rmANOVA including the factors Grammaticality (correct; incorrect) and Perceptual Markedness (unmarked; marked) was conducted for each ROI, using the PSC as dependent measure. Effect sizes are provided as η^2_G (Bakeman, 2005). Note that such a post-hoc ANOVA is potentially biased in the subset of ROIs which has been extracted from the group SPM results of the same data set and should thus be used with caution. Strictly speaking, the statistical results of this analysis do not adhere to the same stringency as those obtained from the whole-brain analysis where a correction for multiple comparisons was applied. Nonetheless, this approach has been considered valid to further explore patterns of activity across conditions (Poldrack, 2007) and has been pursued as such previously (e.g., Altmann et al., 2008; Bornkessel-Schlesewsky et al., 2009; Shtyrov et al., 2008). For the PAC ROIs, however, no such potential bias is present because they were based on independent, previously published data (B. Herrmann et al., 2009). The SPM Anatomy toolbox (v1.6) was used to derive the cortical labels associated with the peak voxels (Eickhoff et al., 2005).

Multivariate pattern analysis

In addition to the univariate analysis, a MVPA was conducted in order to evaluate the data with a method known to also be sensitive to small changes in activity patterns (Formisano et al., 2008; Haynes & Rees 2005, 2006). The univariate fMRI analysis described in the previous section is based on spatially smoothed fMRI signals focusing on overall differences in activation strength associated with the experimental conditions. This allows inferences about the involvement of a region in a specific mental function. Pattern analysis, by contrast, focuses on the information contained in the region's local activity pattern

changes related to the experimental conditions, which allows inferences about the representational content of a region (Haynes & Rees, 2006; Kriegeskorte & Bandettini, 2007; Mur et al., 2009; Norman et al., 2006).

Preprocessing of the functional images was conducted using SPM8, whereby functional time series of each run were realigned, and corrected for field inhomogeneities using individual field maps (Cusack et al., 2003; Jezzard & Balaban, 1995) ("unwarped"), slice scan time corrected, and spatially filtered using a Gaussian filter with 3-mm FWHM. Applying spatial smoothing prior to the multivariate pattern classification has previously been shown to improve the classification performance (Ethofer et al., 2009). As in the univariate analysis, the first five images of the functional time series of each run were discarded to allow for magnetic saturation effects. The time series were filtered with a high pass of 0.01 Hz and corrected for first-order autocorrelation. For each run, a GLM was estimated at the single-participant level with the four conditions (correct unmarked; correct marked; incorrect unmarked; incorrect marked) using a canonical hemodynamic response function (Friston et al., 1995). The individual brain activity patterns used for the MVPA were then estimated as $\text{spm}\{T\}$ condition-specific main contrasts (condition vs. global baseline) for each run separately.

To analyze the brain activation patterns, a linear SVM classifier was applied (Chang & Lin, 2001, LIBSVM matlab-toolbox v2.89). For each condition and run, a feature vector \mathbf{x} with the length of voxels was obtained using the $\text{spm}\{T\}$ estimates as feature values. Classification performance generalization was tested using a leave-one-out cross validation (LOOCV), in which the data of one run was kept out while the data of the other five runs was used to train the classifier. The trained classifier was then tested in decoding the labels from the brain activation pattern of the run which had been left out in training. Decoding accuracies were obtained by comparing the decoded labels with the experimental labels and averaged afterwards. This procedure was repeated six times (i.e., using each of the six runs as test run once). Subsequently, the six accuracies were averaged, resulting in a mean decoding accuracy value.

In order to estimate the local discriminative pattern over the whole brain, a multivariate "searchlight" approach was used (Haynes et al., 2007; Kriegeskorte et al., 2006). On that account, multivariate pattern classification was conducted at each voxel position. The searchlight feature vector \mathbf{x} contained $\text{spm}\{T\}$ estimates for that voxel and its close neighbors. A searchlight radius of two voxels (6 mm) was selected, which comprised about 33 voxels per searchlight position.

Decoding accuracies were computed by applying a full LOOCV for each searchlight.

For the group analysis, individual 3-D decoding accuracy maps were spatially normalized to the standard SPM8 EPI template using a transformation matrix calculated from the mean EPI image generated during realignment, and spatially smoothed using a Gaussian filter with 6-mm FWHM. The reliability of the decoding performance was tested by conducting a t-test for each voxel comparing the decoding accuracy of that voxel to the overall mean decoding accuracy of all the other gray and white matter voxels (i.e., an effective chance level). This procedure resembles the localization test proposed for ROI-based classification approaches (Etzel et al., 2009), which is more conservative than comparing to the 50 % chance level. Subsequently, t-values were transformed into z-scores. To correct for multiple comparisons, a cluster extent threshold, ensuring a whole-brain type I error control of $\alpha \leq 0.05$, was determined in a Monte Carlo simulation, and consecutively applied (Slotnick et al., 2003; Slotnick & Schacter, 2004). Regions were considered statistically significant if z-scores were equal or greater than 3.719 ($P = 0.0001$) in a volume equal or greater than 216 mm^3 (8 voxels), similar to the univariate analysis.

The following two pairwise classifications were obtained: Grammaticality (correct conditions vs. incorrect conditions) and Perceptual Markedness (unmarked conditions vs. marked conditions).

7.3 Results

Behavioral performance

Mean percentage of hit rates (\pm SEM) were as follows: correct unmarked 88.3 % (± 3.4), correct marked 93.8 % (± 2.3), incorrect unmarked 92.7 % (± 2.1), incorrect marked 93.8 % (± 2.1). Individual hit rates were analyzed using a two-way rmANOVA including the factors Grammaticality (correct; incorrect) and Perceptual Markedness (unmarked; marked). The rmANOVA revealed a main effect of Grammaticality ($F_{1,24} = 4.62$, $P = 0.042$, $\eta^2_G = 0.008$) and a main effect of Perceptual Markedness ($F_{1,24} = 11.72$, $P = 0.002$, $\eta^2_G = 0.018$). These effects were further specified by a significant Grammaticality \times Perceptual Markedness interaction ($F_{1,24} = 9.78$, $P = 0.005$, $\eta^2_G = 0.008$), which was caused by significantly lower hit rates for the syntactically correct unmarked condition compared to each of

the other three conditions (for all, $F_{1,24} > 7.5$, $P < 0.05$, $\eta^2_G > 0.023$; all other comparisons $F_{1,24} < 2.5$, $P > 0.10$).

Reaction times were not analyzed as the participants were required to make a delayed grammaticality judgment 2.6 s after the full utterance was presented.

Univariate fMRI analysis

As depicted in Figure 7.1, the whole brain grammaticality analysis revealed stronger activations for syntactically incorrect versus syntactically correct two-word utterances in the left middle superior temporal sulcus (mSTS) extending into the posterior STS (pSTS), in the left IFG (BA44), the left aSTG as well as in the right STS/STG extending into anterior and posterior areas. Moreover, perceptually marked conditions led to stronger hemodynamic responses compared to unmarked conditions in the mSTG and the auditory cortices (AC) of both hemispheres. For each peak voxel within a z-map cluster, corresponding z-score values, MNI coordinates and voxel extent are displayed in Table 7.2.

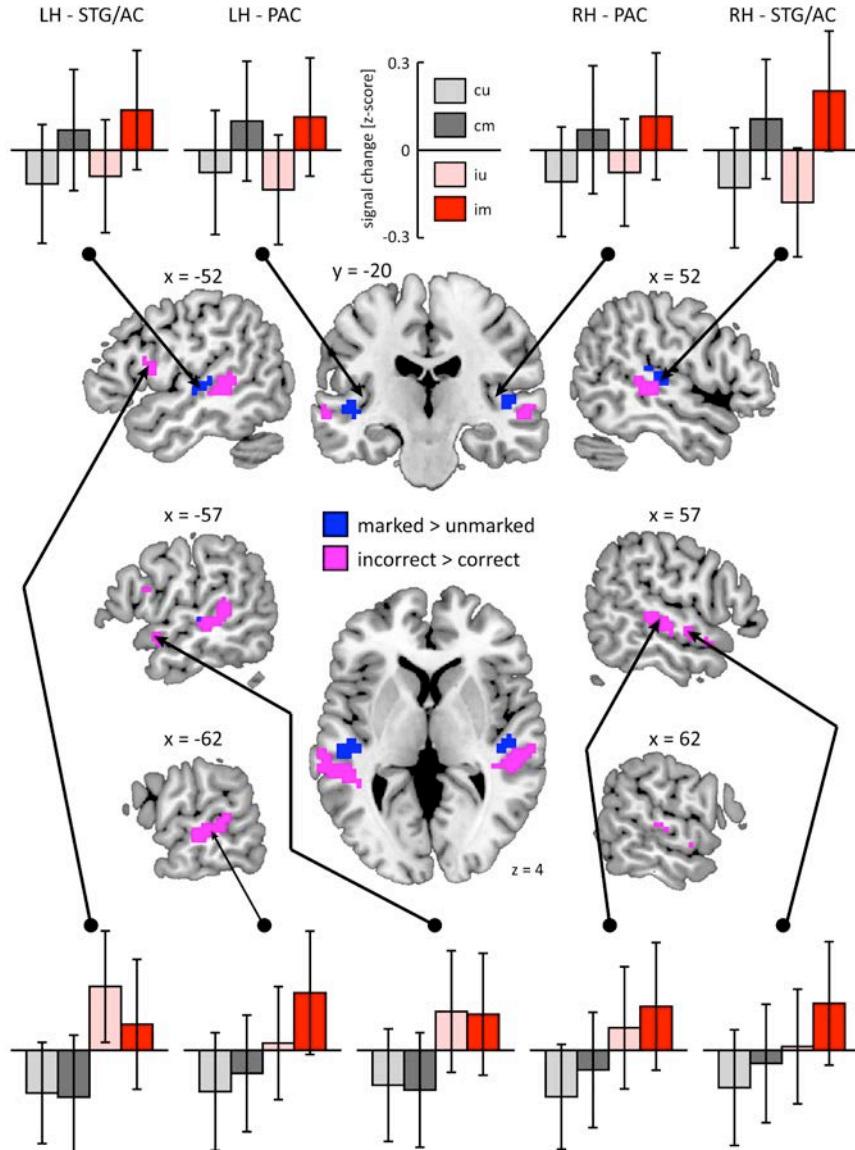


Figure 7.1: Group activation maps for the univariate contrasts. Center: syntactically incorrect > correct (magenta, Grammaticality contrast), perceptually marked > unmarked (blue, Perceptual markedness contrast), z-maps thresholded at $P \leq 0.0001$ and a cluster extent of $k \geq 8$ voxels. Top and Bottom: z-normalized percent signal change for each ROI and condition (cu – correct unmarked, cm – correct marked, iu – incorrect unmarked, im – incorrect marked) (LH – left hemisphere, RH – right hemisphere, STG – superior temporal gyrus, STS – superior temporal sulcus, IFG – inferior frontal gyrus, PAC – primary auditory cortex, AC – auditory cortex, a – anterior). The error bars reflect the standard error of the mean.

For each cluster peak voxel (sphere) presented in Table 7.2, condition-specific effects were evaluated conducting a ROI analysis. With respect to the ROIs of the Grammaticality contrast in the left hemisphere, the IFG (BA44) and the aSTG both revealed a main effect of Grammaticality exclusively ($F_{1,24} = 28.70$, $P < 0.001$, $\eta^2_G = 0.024$; $F_{1,24} = 39.02$, $P < 0.001$, $\eta^2_G = 0.017$; respectively), which was caused by higher signal change in syntactically incorrect conditions. In the left STS, a main effect of Grammaticality ($F_{1,24} = 49.04$, $P < 0.001$, $\eta^2_G = 0.012$) and a main effect of Perceptual Markedness ($F_{1,24} = 7.09$, $P = 0.014$, $\eta^2_G = 0.004$) was found. Syntactically incorrect conditions elicited higher PSC compared to syntactically correct conditions and perceptually marked conditions led to higher PSC than unmarked conditions. The same pattern of effects was found for the right STG and STS regions, showing a main effect of Grammaticality ($F_{1,24} = 40.20$, $P < 0.001$, $\eta^2_G = 0.008$; $F_{1,24} = 34.00$, $P < 0.001$, $\eta^2_G = 0.013$; respectively) as well as a main effect of Perceptual Markedness ($F_{1,24} = 6.76$, $P = 0.016$, $\eta^2_G = 0.003$; $F_{1,24} = 5.29$, $P = 0.031$, $\eta^2_G = 0.002$; respectively). None of the other main effects or interactions was significant.

Region	Contrast	MNI peak [mm]	Extent in voxels	z-score
left IFG (BA44)	G	-54 8 10	19	4.41
left STS	G	-60 -22 -2	144	5.06
left aSTG	G	-54 5 -14	13	4.85
right STS	G	57 -28 1	89	4.68
right STG	G	60 -4 -8	21	4.75
left STG/AC (TE 1.1)	P	-45 -22 1	42	4.58
right STG/AC (TE 1.1)	P	48 -22 7	61	4.80

Table 7.2: Univariate analysis: Brain regions activated in the Grammaticality and in the Perceptual Markedness contrast and peak voxel information (TE – temporal area "E", STG – superior temporal gyrus, STS – superior temporal sulcus, IFG – inferior frontal gyrus, AC – auditory cortex, a – anterior, G – Grammaticality contrast, P – Perceptual Markedness contrast).

Regarding the ROIs of the Perceptual Markedness contrast, only a main effect of Perceptual Markedness was revealed in the left and right STG/AC, due to higher PSC for the marked conditions ($F_{1,24} = 27.70$, $P < 0.001$, $\eta^2_G = 0.011$; $F_{1,24} = 28.96$,

$P < 0.001$, $\eta^2_G = 0.024$; respectively). None of the other main effects or interactions was significant.

The hypothesis-driven investigation of the PAC revealed a main effect of Perceptual Markedness in the left and right hemisphere ($F_{1,24} = 13.84$, $P = 0.001$, $\eta^2_G = 0.011$; $F_{1,24} = 5.45$, $P = 0.028$, $\eta^2_G = 0.009$; respectively). Higher PSC was elicited for the marked than unmarked conditions. No significant main effects of Grammaticality or interactions were found. Figure 7.1 shows the mean PSC for each ROI and condition.

Multivariate fMRI analysis

With respect to the Grammaticality classification, decoding performance revealed a strong left-hemispheric bias, showing accuracies significantly above chance level in the left inferior and superior IFG (BA44), the left aSTG, the left STS and the left posterior middle temporal gyrus (pMTG). That is, neural activation imprints in these subregions of the frontal and temporal cortices allowed the correct decoding of the grammatical correctness of the utterances heard (see Figure 7.2).

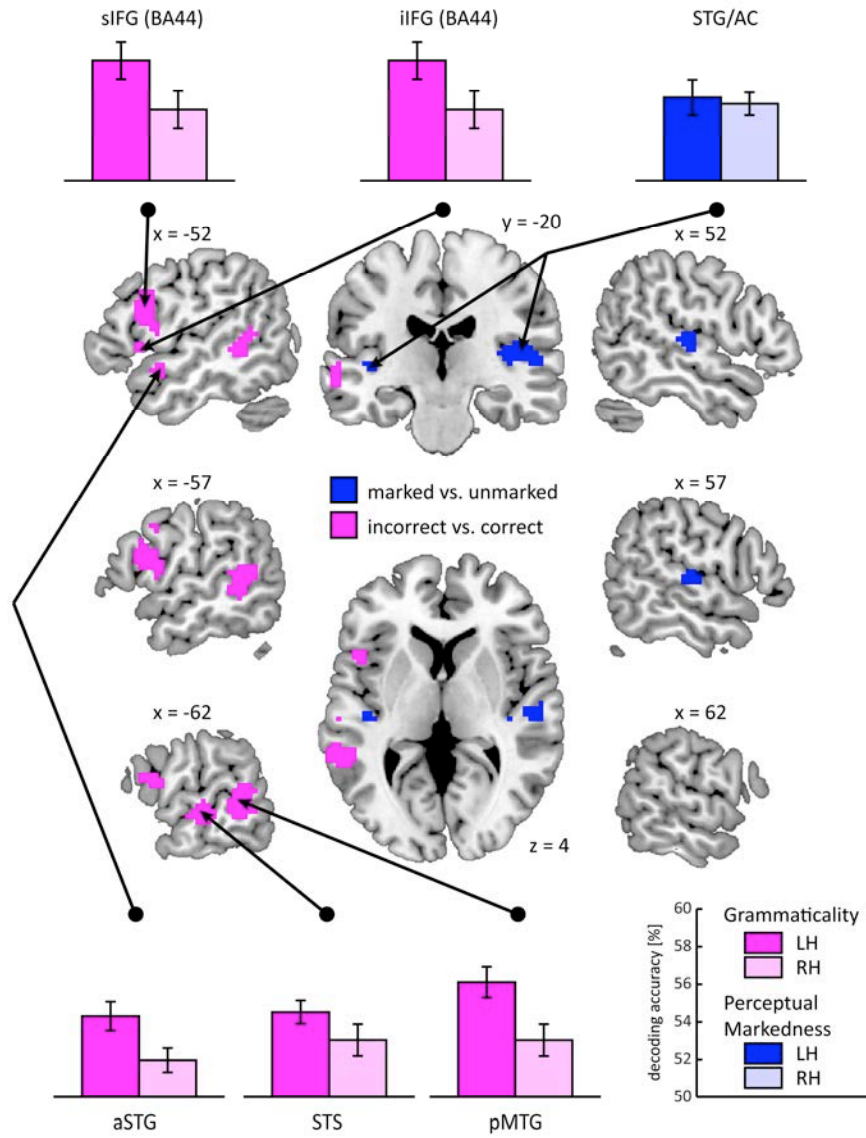


Figure 7.2: Group decoding accuracy maps for the multivariate classifications. Center: syntactically incorrect vs. correct (magenta, Grammaticality classification), perceptually marked vs. unmarked (blue, Perceptual markedness classification), z-maps thresholded at $P \leq 0.0001$ and a cluster extent of $k \geq 8$ voxels. Top and Bottom: decoding accuracies for the left hemispheric regions and their homologue regions in the right hemisphere (LH – left hemisphere, RH – right hemisphere, STG – superior temporal gyrus, STS – superior temporal sulcus, MTG – middle temporal gyrus, IFG – inferior frontal gyrus, AC – auditory cortex, a – anterior, p – posterior, i – inferior, s – superior). The error bars reflect the standard error of the mean.

The statistical significance of the leftward bias in the Grammaticality classification was tested using the following post-hoc procedure. For each peak voxel in a cluster of the z-score map (see Table 7.3), a homologue voxel in the opposite hemisphere was selected by inverting the sign of the x-coordinate of that cluster voxel. A sphere of 4 mm radius was centered on each of these voxels and the mean decoding accuracy for each participant and ROI was extracted. Subsequently, a rmANOVA including the factors Hemisphere (left; right) and ROI (inferior IFG; superior IFG; aSTG; STS; pMTG) was conducted. Importantly, the rmANOVA revealed a main effect of Hemisphere ($F_{1,24} = 34.67$, $P < 0.001$, $\eta^2_G = 0.093$), caused by higher decoding accuracies in the left hemisphere, whereas the main effect of ROI and the Hemisphere \times ROI interaction were not significant ($F_{4,96} = 2.15$, $P > 0.05$; $F_{4,96} = 0.82$, $P > 0.50$; respectively) (see Figure 7.2). To assure that these results were not caused by the left-right asymmetry of the brain, the decoding accuracy maps were also spatially normalized to a symmetrical template (built from the SPM8 EPI template described in the *Methods* by mirroring the left hemisphere to the right). As before, the rmANOVA revealed a main effect of Hemisphere ($F_{1,24} = 47.63$, $P < 0.001$, $\eta^2_G = 0.114$), due to higher decoding accuracies in the left hemisphere, whereby the main effect of ROI and the Hemisphere \times ROI interaction were not significant ($F_{4,96} = 2.14$, $P > 0.05$; $F_{4,96} = 0.40$, $P > 0.70$; respectively).

Region	Classification	MNI peak [mm]	Extent in voxels	z-score
left iIFG (BA44)	G	-45 14 4	18	4.35
left sIFG (BA44)	G	-51 11 22	131	4.61
left aSTG	G	-51 5 -11	10	4.01
left STS	G	-63 -22 -2	28	4.90
left pMTG	G	-60 -43 -2	132	4.72
left STG/AC	P	-39 -22 1	9	3.87
right STG/AC (TE 1.0)	P	54 -19 4	116	4.71

Table 7.3: Multivariate analysis: Brain regions discriminating between conditions in the Grammaticality and in the Perceptual Markedness classification and peak voxel information (TE – temporal area "E", STG – superior temporal gyrus, STS – superior temporal sulcus, MTG – middle

temporal gyrus, IFG – inferior frontal gyrus, AC – auditory cortex, a – anterior, p – posterior, i – inferior, s – superior, G – Grammaticality classification, P – Perceptual Markedness classification)

For the Perceptual Markedness classification, a bilateral pattern was observed, revealing decoding accuracies significantly above chance level in the rather medial left and right STG. Thus, bilateral areas most likely belonging to belt and parabelt areas of the auditory cortex (and being relatively low in the language processing hierarchy) allowed the correct identification of perceptually overtly marked stimuli.

Although the cluster in the right hemisphere was much larger than the one in the left hemisphere, a one-way rmANOVA including the factor Hemisphere (left; right) did not show a significant difference between decoding accuracies for peak-centered spheres in the left and right hemisphere ($F_{1,24} = 0.19$, $P > 0.60$) (see Figure 7.2).

7.4 Discussion

The present fMRI experiment aimed to test whether activation in auditory sensory cortices is modulated by initial syntactic processes, and – if so – to which processing step they specifically contribute. In the following, the results are discussed in detail starting at the behavioral level, followed by the perceptually-based processes and grammar-based processes.

Behavioral performance

On the behavioral level, participants made more errors when judging the grammaticality of the correct yet unmarked utterances (e.g., "im Knie", *Engl. "in-the knee"*) compared to the other conditions. Such a finding has also been reported in a previous rating study (B. Herrmann et al., 2009), and might be due to the slight category ambiguity of the noun (e.g., "Knie", *Engl. "knee"*). In speech, it could also serve as the seldom-used imperative form of a verb (e.g., "knie nieder", *Engl. "kneel down"*). With respect to the current fMRI findings, no distinct modulations of brain activation were observed for the correct unmarked condition, indicating automatic processing of these stimuli.

Neural imprints of perceptually-based processes

Perceptually-based brain activations were observed bilaterally in the AC, with stronger responses for two-word utterances that were perceptually overtly marked by the suffix "-t". The MVPA showed compatible results. Regions in the

STG/AC were most informative for separating the unmarked from the perceptually marked conditions, with no hemispheric differences in decoding accuracies. Hence, the present findings are in perfect agreement with the observations that core and (para)belt auditory regions are most sensitive to basic acoustic features of the auditory signal, and that the sensitivity to more complex stimuli increases with increasing distance to core regions (Kaas & Hackett, 2000; Rauschecker & Tian, 2004; Wessinger et al., 2001).

It is noteworthy that the perceptual markedness contrast (marked vs. unmarked conditions) in the present experiment also reflects a verb vs. noun contrast, because only verbs were overtly marked by the suffix. The observed AC activation patterns, however, are unlikely to reflect verb vs. noun processes, as similar contrasts previously revealed regions in the left IFG, middle frontal gyrus, MTG and STG elicited by such processes (e.g., Perani et al., 1999; Tyler et al., 2004). Furthermore, in order to perform the grammaticality judgment task, participants were required to focus on the presence or absence of the suffix which rendered the utterances syntactically correct or incorrect.

Neural imprints of grammar-based processes

With respect to grammar-based processes, the current experiment revealed dissociable neural activations for syntactically incorrect vs. correct utterances in the left IFG, the left aSTG, the left STS and in the right STS/STG, but no such difference in the AC.

Hasting & Kotz (2008) previously showed in their EEG study that two-word utterances of the kind used in the present experiment only elicits an early syntactic effect (between 100 – 300 ms) but no additional effect in a later time window. If their interpretation is correct that such stimuli do not lead to P600 assigned revision processes, then this implies that although fMRI lacks the fine-grained temporal resolution in the range of milliseconds, the observed activations can be attributed to early and automatic syntactic parsing difficulties alone (Friederici et al., 1993; Hahne & Friederici, 1999, 2002), rather than to both early processes and processes associated with revision/repair (Friederici, 2002; Friederici & Kotz, 2003).

Recent MEG studies investigating early syntactic processes reported modulations of sensory cortex activations in response to syntactic violations (Dikker et al., 2009, 2010; B. Herrmann et al., 2009). In contrast, the current results rather indicate that syntax as such leads to activations outside the auditory cortic-

es, and that the activations patterns of the auditory cortices only allow distinguishing the subtle acoustic differences between the two speech signals, i.e. the presence or absence of a suffix. This finding is in line with the view that the primary auditory regions are not yet involved in speech-specific processes (Scott & Johnsrude, 2003).

Instead, a wide neural network was involved in syntactic processes (i.e., initial syntactic parsing and possible difficulties at this stage), with stronger neural activations to syntactically incorrect than correct two-word utterances in the left IFG (BA44), the left aSTG, the left STS and the right STS/STG. Processing syntactic word category violations has previously been shown to activate the left frontal operculum adjacent to BA44 rather than BA44, in addition to the STG (Brauer & Friederici, 2007; Friederici et al., 2003b). However, the left BA44 is commonly activated in studies manipulating the syntactic complexity of sentences (Lee & Newman, 2010; Makuuchi et al., 2009), or when the demands on syntactic processes increase due to participants' inproficiency in the language (Brauer & Friederici, 2007; Rüschmeyer et al., 2005), or when sentences including a word category violation are randomly mixed with unintelligible sentences (Friederici et al., 2010). Furthermore, visually presented two-word phrases that included a syntactic word category violation also led to activations in left BA44 (Kang et al., 1999). Thus, the current findings are consistent with these previous results showing the involvement of the inferior frontal cortex in syntactic operations. It remains, nevertheless, an open question under which conditions the frontal operculum as opposed to the pars opercularis (BA44) is engaged in phrase structure processes.

Activations were also observed in the left aSTG and the left STS as well as in the right STS/STG. Moreover, the MVPA revealed similar regions carrying syntax-relevant information in the left hemisphere, with an additional cluster extending from the pSTS into the pMTG. The multivariate patterns in the right hemisphere did not carry sufficient information to significantly distinguish syntactically incorrect from correct utterances. This is in line with the notion of a left-lateralized network involved in conducting syntactic operations (Friederici, 2002; Friederici & Kotz, 2003). Interestingly, in the ROI analysis, the left STS and the right STS/STG showed a perceptual markedness effect in addition to the syntactic effect. Activation in the STS has been linked to a variety of processes (for a review see Hein & Knight, 2008). In the language domain, it has been associated with processing phonetic information (Liebenthal et al., 2005; Obleser et al.,

2007) and, in more posterior regions, with syntactic processing in general (Friederici et al., 2009, 2010). The STS in conjunction with the MTG has also been associated with accessing the mental lexicon (Kotz et al., 2002; Obleser & Kotz, 2010). The left aSTG, on the other hand, showed activations only to syntactic processes, confirming previous findings that emphasize the importance of the aSTG in syntactic operations (Brauer & Friederici, 2007; Brennan et al., in press; Friederici et al., 2003b; Humphries et al., 2005).

With respect to the current analysis approaches, the most prominent difference between the univariate and the multivariate analysis was the left-hemispheric lateralization revealed by the syntax-related multivariate patterns. Methodologically, the MVPA was based on the activation estimates derived from a single GLM for each run. The GLM for each single run evidently provides a lower signal-to-noise ratio than the GLM including all runs that was conducted in the univariate approach. Nevertheless, this in turn highlights the consistency of the left-hemispheric neural network involved in syntactic processes (Friederici, 2002; B. Herrmann et al., 2009; Kaan & Swaab, 2002; Shtyrov et al., 2003).

7.5 Conclusions

In summary, neural imprints of initial syntactic processes were found in the left IFG, the left aSTG, the left STS and the right STS/STG, with some indications of a left-hemispheric predominance. Auditory cortices were not sensitive to syntactic manipulations, but were engaged in perceptual processes associated with the word category's suffix. Thus, the current data speak against syntax-inflicted sensory cortex modulations, while providing clear evidence for a distinction between regions involved in pure perceptual processes and regions involved in initial syntactic processes.

8 Experiment IV: Localizing early syntactic and auditory spatial processes

In this experiment, the data of Experiment II were reanalyzed. A chapter on its own was conceded, nevertheless, as the investigation focused on an entirely different aspect of the data.

The text was largely derived from the study published in *NeuroImage* by B. Herrmann et al. (in press-b).

8.1 Introduction

The review of previous findings in chapter 4 has unveiled diverging neuromagnetic evidence regarding the underlying mechanisms of early syntax-related responses in the brain (Dikker et al., 2009; Friederici et al., 2000a). While previous results suggested the IFG and aSTG as underlying sources of the ELAN (Friederici et al., 2000a), recent MEG findings showed early modulations of sensory cortices elicited by syntactic violations in the visual modality (Dikker et al., 2009, 2010). In this context, localization results of the ELAN in the auditory modality have been challenged (Friederici et al., 2000a). Moreover, the resemblance of neural responses to syntactic violations and neural responses to auditory perceptual violations (Hahne et al., 2002) has been taken as indication of similar (sensory) brain regions affected by the respective processes.

Furthermore, previous findings revealed that syntactic rule violations and auditory perceptual rule violations (in auditory space) are processed in parallel at around 100 – 200 ms when a double violation is encountered (Hahne et al., 2002; see also Experiment II). These effects were observed at the scalp (EEG) or in close distance to the head (MEG). What parallel processing means in terms of

cortical activations cannot be inferred from these findings. It might be the case that both types of single violations recruit the same brain regions and that a double violation leads to stronger activation in the very same regions (i.e., the ELAN and MMN share neural sources). On the other hand, different brain regions might be involved in processing syntactic versus auditory perceptual violations and that these regions are activated simultaneously when a combined violation is encountered.

According to dual stream auditory processing models (Rauschecker & Scott, 2009) spatial information is processed in the dorsal stream involving the posterior portion of the superior temporal cortex, while speech (intelligibility of speech) processes recruit regions anterior to Heschl's gyrus in the ventral stream. It could, therefore, be hypothesized that partly different regions are activated when speech-related and auditory spatial features are processed in parallel. This would be in line with previous localization studies of the ELAN and MMN (Deouell et al., 2006; Friederici et al., 2000a; Groß et al., 1998; Kaiser et al., 2000; Knösche et al., 1999).

In addition to the ELAN effect in the 100 – 200 ms time window, previous studies were able to disentangle the "early syntax effect" into different sub-stages, observing an additional very early syntax-related effect that modulated the M50 component (C. S. Herrmann et al., 2000; B. Herrmann et al., 2009; see also Experiment I). Furthermore, the detection of simple rule violations in an auditory oddball paradigm has not only been shown to elicit the MMN, but also to modulate the brain's activity very early, starting at around 30 ms (Boutros & Belger, 1999; Ermutlu et al., 2005; Grimm et al., 2011; Slabu et al., 2010).

In the present experiment, anatomically constrained magnetoencephalography (MEG) was used to further investigate the early syntactic and auditory perceptual parallel processing effect in the brain. For the source analysis, a distributed source model was used without any priors regarding the location of the underlying cortical regions modulated by syntax and auditory space. The hypotheses were formulated as follows:

- (1) The localization of the neural responses elicited by syntactic violations allowed testing previous localizations of the ELANm (Friederici et al., 2000a), and to examine whether auditory sensory cortices are sensitive to syntactic manipulations (Dikker et al. 2009). The former study predicts activations in the anterior STG with additional weaker frontal activations,

whereas the latter view predicts the ELANm to be localized in auditory sensory cortices.

- (2) Another goal was to localize the neural sources of the MMF elicited by infrequent ITD changes within naturally spoken sentences in order to have a condition which reflects auditory perceptual rule processing (Schröger, 1996, 2005). The posterior STG/AC was expected to be sensitive to auditory spatial deviations (Deouell et al., 2006; Kaiser et al., 2000). Based on the dual pathways in the auditory system (Rauschecker & Scott, 2009), the neural sources of the ELANm and MMF were expected to differ in location.
- (3) By localizing the neural responses to sentences including a double violation, the experiment aimed to investigate how processing a syntactic violation and an auditory spatial violation in parallel is accomplished by different regions in the temporal cortex (Rauschecker & Scott, 2009). Brain regions involved in processing the single syntactic violations and those involved in processing the auditory spatial violations were expected to be activated simultaneously for sentences containing both violations.

Apart from the effects in the 100 – 200 ms time window (i.e., the ELANm and MMF), the experiment sought to further elucidate on the very early syntax and simple rule violation effects that precede the ELANm and MMF, and ask whether parallel processing can be observed already at this processing stage.

8.2 Methods

The methods and materials regarding the current data set have been described extensively in Experiment II. Overlapping aspects are therefore provided as a summarized version.

Participants

Twenty-four right-handed German native speakers participated in the experiment (mean age: 25.3).

Stimulus materials

In order to improve the signal-to-noise ratio which is most important for source reconstruction, the experimental sentences as well as sentences originally considered as fillers were included in the analysis. Note, that the design is still con-

trolled in that the critical word in all conditions was a participle marked with the prefix "ge-" and a suffix (e.g., "-t").

Thus, syntactically correct sentences consisted either of a "determiner-noun-auxiliary-past participle" sequence (e.g., "Das Obst wurde geerntet.", *Engl. "The fruit was harvested."*) or of a "determiner-noun-auxiliary-preposition-noun-past participle" sequence (e.g., "Das Gemüse wurde im Herbst geerntet.", *Engl. "The vegetable was in-the autumn harvested."*). Syntactically incorrect sentences consisted of a "determiner-noun-auxiliary-preposition-past participle" sequence (e.g., "Die Gerste wurde im geerntet.", *Engl. "The barley was in-the harvested."*).

The auditory perceptual conditions were realized by an infrequent ITD change within the sentences which is known to elicit the MMN for auditory space/lateralization deviancy (Middlebrooks & Green, 1991; Schröger, 1996; Schröger & Wolff, 1996). Correct sentences without an ITD change are labeled "correct standard condition", syntactically incorrect sentences without an ITD change "incorrect standard condition", correct sentences including an ITD change "correct deviant condition" and syntactically incorrect sentences containing an ITD change "incorrect deviant condition". Table 8.1 shows the sentence materials and corresponding conditions.

Sentence, e.g.:	Grammaticality	Auditory space
Das Obst wurde geerntet. (48) + <i>The fruit was harvested. +</i>	correct	standard (0.0 ms)
Die Gerste wurde im Herbst geerntet. (48) <i>The barley was in-the autumn harvested.</i>		
*Die Gerste wurde im geerntet. (96) <i>*The barley was in-the harvested.</i>	incorrect	standard (0.0 ms)
Das Obst wurde <u>geerntet</u> . (48) + <i>The fruit was harvested. +</i>	correct	deviant (0.2 ms)
Die Gerste wurde im Herbst <u>geerntet</u> . (48) <i>The barley was in-the autumn harvested.</i>		
*Die Gerste wurde im <u>geerntet</u> . (96) <i>*The barley was in-the harvested.</i>	incorrect	deviant (0.2 ms)

Table 8.1: Sentence materials. The asterisk marks syntactically incorrect sentences and the underlined participle highlights the interaural time difference change of 0.2 ms within the sentence. The number of sentences presented to the participants is provided in parentheses.

Design and Procedure

Sentences were presented auditorily, with one half selected as standards, while the other half was selected as deviants. Participants judged each sentence's grammaticality 1500 ms after the sentence ended. They were instructed to ignore lateralization effects in the auditory stimulation.

MEG data recording and processing

MEG signals were recorded with a 306-channel MEG device at 500 Hz. The signal space separation method was applied to correct for head movements, interpolate bad channels and suppress external interferences (Taulu et al., 2004). MEG recordings were filtered with a high-pass of 2 Hz to avoid baseline correction and a low-pass of 10 Hz to maximize the signal-to-noise-ratio (Friederici et al., 2000a; C. S. Herrmann et al., 2000; Maess et al., 2006, 2007; Tervaniemi et al., 1999). The data was divided into epochs of 700 ms (-200 ms to 500 ms) that were time-locked to the onset of the participle and to the sentence onset. Epochs were screened for blinks and other artifacts and excluded from averaging.

ing if they contained a signal change of more than 200 pT/m (gradiometer), 4 pT (magnetometer) or 100 μ V (EOG).

Source reconstruction

A T1-weighted structural MRI image was obtained in each participant with a 3 Tesla MRI scanner (Magnetom Trio, Siemens AG, Germany). The software Free-surfer (<http://surfer.nmr.mgh.harvard.edu/>) was applied to construct individual topological representations of the cortical surface for each hemisphere using the individual MRI images.

The MNE package provided by M. Hämäläinen, MGH, Boston, MA, USA (<http://www.nmr.mgh.harvard.edu/martinos/userInfo/data/>) was used to compute forward and inverse solutions. On this basis, inner skull surfaces were extracted using the above-mentioned T1-weighted MRI images in order to construct individual boundary element models (BEM) for the volume conductor. Such a single compartment volume conductor has been shown to be sufficient for solving the MEG forward problem (Hämäläinen & Sarvas, 1989). The MRI coordinate system was transformed into the MEG coordinate system using the HPI coils and about 50 additional points on the head surface estimated by a Polhemus FASTRAK 3D digitizer. As source space, the individual white matter surface was adopted.

For the inverse solution, the approximately 130,000 vertices needed to describe single hemispheres were reduced to approximately 5000 dipoles, resulting in approximately one dipole per 10 mm². The standardized low resolution brain electromagnetic tomography (sLORTEA) method was used to compute individual brain activations (Pascual-Marqui, 2002). In order to average solutions across participants, the individual cortical representations were transformed to a sphere representation, providing a unique coordinate system for all participants (Fischl et al., 1999a). For visualization purposes, this representation was morphed to the inflated cortical surface of one participant (Fischl et al., 1999b).

Statistical analysis

Based on the visual inspection of the grand average data displayed in Figure 8.1 and Figure 8.3, two time windows were selected for the statistical analyses. The first time window (40 – 90 ms) was centered at the peak of the very early deflection. The second time window (110 – 180 ms) included the peak of the ELANm/MMF at around 135 ms. These time windows are in perfect agreement with previous studies (Friederici et al., 2000a; B. Herrmann et al., 2009;

Schröger, 1996). Additionally, a third component, peaking at around 220 ms, is visible in Figure 8.1. This possibly reflects the MEG correlate of the P2 response (for a review see Crowley & Colrain, 2004) and appears to be sensitive to both auditory and grammatical manipulations. The focus of the current experiment, however, was on the ELANm/MMF time window and the preceding M50 time window. Effects occurring after 200 ms were therefore not further analyzed.²⁰

Statistical analysis of activation strength

For each condition, mean individual activation time courses were extracted from a ROI in the left and right hemisphere. The ROI covered the STG from the planum polare to the planum temporale including the lower wall of the Sylvian fissure and the upper wall of the superior temporal sulcus (see Figure 8.3). These cortical regions have also been shown previously to be involved in early syntactic and auditory spatial processing (Deouell et al., 2006; Friederici et al., 2000a). Here, only one ROI was applied in each hemisphere because grand average activations of the conditions overlapped in the STG (see Figure 8.2). Inferior frontal regions did not display independent local maxima and were therefore not included in the analysis.

Differences in the STG activations between conditions were examined using a three-way rmANOVA that included the factors Grammaticality (correct; incorrect), Auditory space (standard; deviant) and Hemisphere (left; right), and was conducted for both time windows separately. Effect Sizes are provided as η^2_G (Bakeman, 2005). Post-hoc tests were conducted whenever significant effects occurred. False discovery rate (FDR) was applied in order to prevent false positives among significant post-hoc comparisons (Benjamini & Hochberg, 1995; Genovese et al., 2002).

Statistical analysis of local maxima

Previous studies investigating early syntactic (e.g., Friederici et al., 2000a) or auditory spatial processing (e.g., Deouell et al., 2006) as well as the present grand average data show activations along the anterior – posterior gradient of the STG (see Figure 8.2). In order to evaluate the condition-specific differences

²⁰ It is noteworthy, nevertheless, that visual inspection of the amplitudes in the P2 time window (see Figure 8.3) suggests the effects of the auditory manipulation to be unaffected by the syntax manipulation, i.e. that there are only effects of syntax in cases of no additional auditory manipulation.

of the local activation maxima in the temporal cortex, the following procedure was applied. First, a region covering most of the temporal cortex was selected in each hemisphere. Second, for each time window (40 – 90 ms; 110 – 180 ms) individual local maxima were extracted from the temporal cortex regions for the incorrect standard condition, the correct deviant condition and the incorrect deviant condition. Third, individual local maxima extracted from the temporal cortex regions for the time window of 20 – 50 ms following the onset of the sentence were used as an auditory cortex reference for the violation conditions in the other two time windows (see Figure 8.4; for a similar approach see e.g. Huotilainen et al., 1998). Acoustic stimulation after a period of silence is known to elicit the M50 component, which has been repeatedly localized to the auditory cortex (e.g., Huotilainen et al., 1998; Mäkelä et al., 1994; Thoma et al., 2003, 2008). As brain activations were distributed parallel to the Sylvian fissure and not along one of the Cartesian axes of the source space, the final step consisted of feeding these extracted individual coordinates into a principal component analysis (PCA). A PCA identifies a coordinate system whose axes follow the most prominent spreadings of the data distribution. This allowed us to replace the 3D statistical analysis of the locations by a 1D analysis of the axis which corresponded to the anterior – posterior gradient of the temporal cortex. The correct standard condition was not included in this analysis as only weak activations were observed (see Figure 8.3).

Location differences were tested using a two-way rmANOVA that included the factors Condition (incorrect standard; correct deviant; incorrect deviant; sentence onset) and Hemisphere (left; right). The rmANOVA used the coordinates of the axis corresponding to the anterior – posterior gradient of the temporal cortex as dependent measure and was conducted for each time window separately. The Greenhouse-Geisser correction was applied when the assumption of sphericity was violated (Greenhouse & Geisser, 1959). The original degrees of freedom are reported along with the Epsilon correction coefficient and the corrected probability. Effect Sizes are provided as η^2_G (Bakeman, 2005). In the case of significant effects, post-hoc tests using FDR were conducted.

8.3 Results

Behavioral performance

See Experiment II for a detailed description of the statistical comparisons. No differences between conditions were found.

Source localization – activation strength

Event-related magnetic fields and corresponding topographical maps are shown in Figure 8.1. For each time window, the grand average activations of the violation conditions are depicted in Figure 8.2. The corresponding STG activation time courses as well as a summary of the statistical comparisons for each time window are displayed in Figure 8.3.

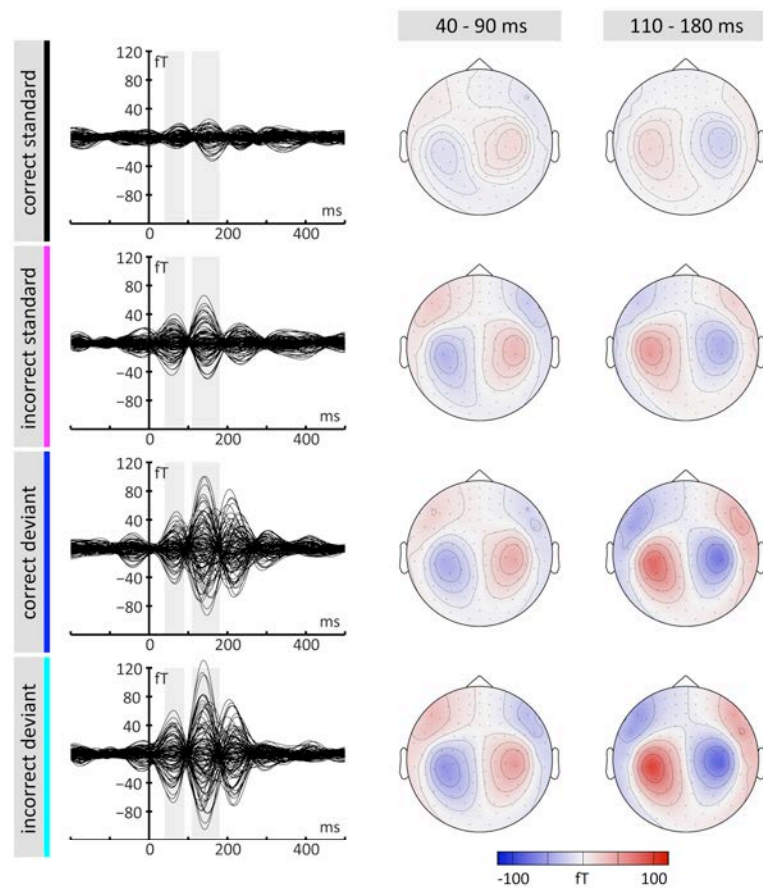


Figure 8.1: Grand average ERFs time-locked to the onset of the participle are displayed for each condition. The gray bars highlight the time windows (40 – 90 ms, 110 – 180 ms) used for the

statistical analyses. The corresponding topographical distributions are provided on the right-hand side. Only magnetometer channels were used in this figure.

In the very early time window from 40 to 90 ms, the rmANOVA revealed a main effect of Grammaticality ($F_{1,23} = 33.82$, $P < 0.001$, $\eta^2_G = 0.150$) and a main effect of Auditory space ($F_{1,23} = 48.83$, $P < 0.001$, $\eta^2_G = 0.123$). Additionally, the Grammaticality \times Auditory space interaction was significant ($F_{1,23} = 4.67$, $P = 0.041$, $\eta^2_G = 0.005$). Post-hoc tests showed stronger activation for each violation condition when compared to the correct standard condition (incorrect standard: $F_{1,23} = 50.71$, $P_{FDR} < 0.001$, $\eta^2_G = 0.298$; correct deviant: $F_{1,23} = 46.01$, $P_{FDR} < 0.001$, $\eta^2_G = 0.292$; incorrect deviant: $F_{1,23} = 64.44$, $P_{FDR} < 0.001$, $\eta^2_G = 0.433$). Furthermore, the incorrect deviant condition elicited stronger activation compared to the incorrect standard and the correct deviant condition ($F_{1,23} = 32.90$, $P_{FDR} < 0.001$, $\eta^2_G = 0.082$; $F_{1,23} = 18.04$, $P_{FDR} = 0.001$, $\eta^2_G = 0.111$; respectively). No difference was found between the incorrect standard and the correct deviant condition ($F_{1,23} = 0.32$, $P_{FDR} > 0.05$). In other words, effects to the violation conditions were highly significant, but the effect to the double violation was smaller than the sum of the effects to the single violations, thereby causing the interaction. There was no main effect of Hemisphere ($F_{1,23} = 0.92$, $P = 0.35$). None of the other interactions was significant (for all, $P > 0.15$).

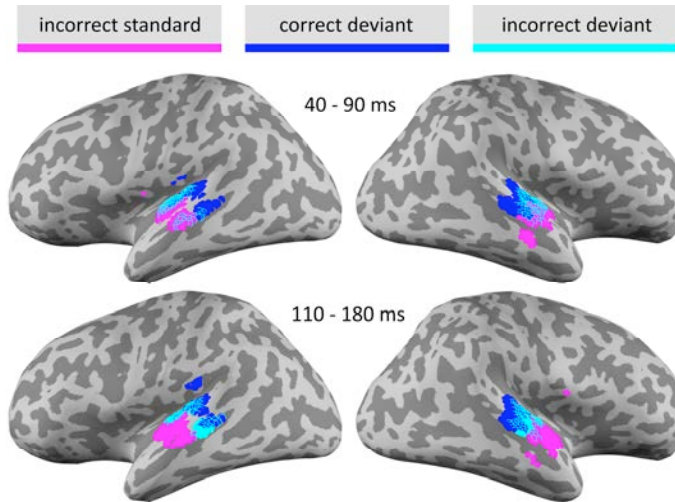


Figure 8.2: Grand average brain activations displayed as the 100 vertices in each hemisphere that show the strongest brain responses for the incorrect standard condition (magenta circles), the correct deviant condition (blue circles) and the incorrect deviant condition (cyan circles).

Brain activity is displayed on the inflated surface, with dark gray representing sulci and light gray representing gyri.

In the time window of the ELANm/MMF (110 – 180 ms), the rmANOVA revealed a main effect of Grammaticality ($F_{1,23} = 32.53$, $P < 0.001$, $\eta^2_G = 0.088$) as well as a main effect of Auditory space ($F_{1,23} = 99.59$, $P < 0.001$, $\eta^2_G = 0.409$). These main effects were specified by a significant Grammaticality \times Auditory space interaction ($F_{1,23} = 27.19$, $P < 0.001$, $\eta^2_G = 0.021$). Post-hoc tests revealed that the correct standard condition elicited significantly weaker activation compared to each of the three violation conditions (incorrect standard: $F_{1,23} = 58.30$, $P_{FDR} < 0.001$, $\eta^2_G = 0.378$; correct deviant: $F_{1,23} = 118.92$, $P_{FDR} < 0.001$, $\eta^2_G = 0.637$; incorrect deviant: $F_{1,23} = 108.36$, $P_{FDR} < 0.001$, $\eta^2_G = 0.642$). Thus, the effects to the violation conditions were highly significant. Moreover, the correct deviant condition and the incorrect deviant condition elicited significantly stronger activation than the incorrect standard condition ($F_{1,23} = 34.84$, $P_{FDR} < 0.001$, $\eta^2_G = 0.262$; $F_{1,23} = 63.50$, $P_{FDR} < 0.001$, $\eta^2_G = 0.332$; respectively). In addition, the incorrect deviant condition led to greater activation than the correct deviant condition ($F_{1,23} = 6.98$, $P_{FDR} = 0.05$, $\eta^2_G = 0.023$), although this difference was much smaller than for the other comparisons, causing the significant interaction. There was no main effect of Hemisphere ($F_{1,23} = 0.14$, $P = 0.71$). None of the other interactions was significant (for all, $P > 0.15$).

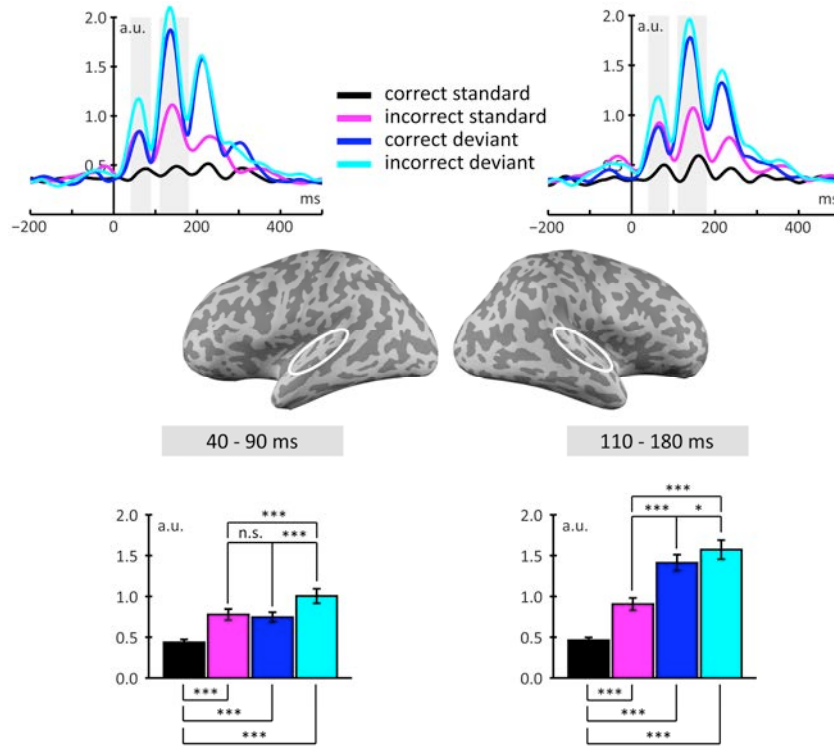


Figure 8.3: Time course of STG grand average brain activity (in a.u. – arbitrary units) for the correct standard condition (black), the incorrect standard condition (magenta), the correct deviant condition (blue) and the incorrect deviant condition (cyan). Bar graphs display the statistical comparisons between conditions for each time window (* $P_{FDR} \leq 0.05$, *** $P_{FDR} \leq 0.001$, n.s. – not significant). The error bars reflect the standard error of the mean.

Source localization – local maxima

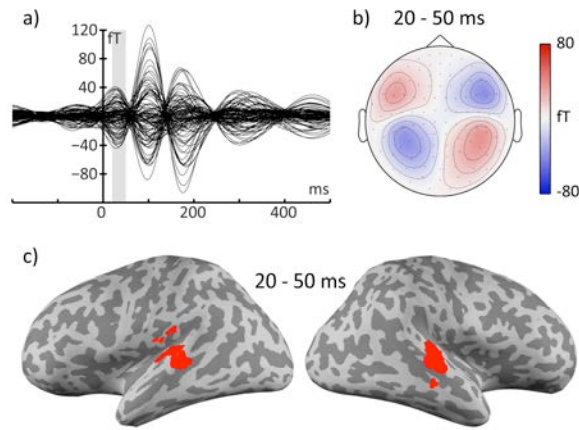
Talairach coordinates for the mean of the 100 most activated vertices of the grand average activations for each violation condition and the sentence onset M50 component are provided in Table 8.2 (Talairach and Tournoux, 1988). These were obtained using the icbm2tal transformation (Lancaster et al., 2007). An approximation to the corresponding Brodmann areas was obtained using the Talairach Client (Lancaster et al., 2000). In Figure 8.4, the neural responses to the sentence onset are displayed. Figure 8.5 depicts the results of the statistical analysis of the local maxima along the anterior – posterior gradient of the temporal cortex for each time window.

Time window	Condition	Left hemisphere		Right hemisphere	
		Region	x y z	Region	x y z
40 – 90 ms	inc/sta	STG	-49 -18 2	BA22	52 -12 3
	cor/dev	BA41	-47 -28 8	BA41	51 -23 7
	inc/dev	BA22	-45 -22 4	BA22	52 -16 7
110 – 180 ms	inc/sta	BA22	-52 -16 2	BA22	52 -6 2
	cor/dev	BA41	-49 -32 10	BA41	53 -24 9
	inc/dev	BA41	-46 -28 7	BA41	53 -19 8
20 – 50 ms	sent. onset	BA41	-54 -30 8	BA41	55 -24 8

Table 8.2: Talairach coordinates and corresponding Brodmann areas for the incorrect standard condition (inc/sta), the correct deviant condition (cor/dev), the incorrect deviant condition (inc/dev) and the sentence onset (sent. onset) M50 component. The coordinates reflect the mean of the 100 most activated vertices of the grand average source localizations (BA – Brodmann area; STG – superior temporal gyrus).

The rmANOVA conducted for the 40 – 90 ms time window showed a significant main effect of Condition ($F_{3,69} = 8.72$, $P < 0.001$, $\epsilon = 0.760$, $\eta^2_G = 0.078$). Post-hoc tests revealed that the incorrect standard condition was significantly more anterior compared to the correct deviant condition, the incorrect deviant condition and the sentence onset ($F_{1,23} = 18.11$, $P_{FDR} < 0.001$, $\eta^2_G = 0.198$, 10 mm; $F_{1,23} = 26.62$, $P_{FDR} < 0.001$, $\eta^2_G = 0.147$, 7 mm; $F_{1,23} = 12.39$, $P_{FDR} = 0.01$, $\eta^2_G = 0.187$, 9 mm; respectively). No significant differences were found between the correct deviant condition, the incorrect deviant condition and the sentence onset (for all, $P_{FDR} > 0.05$). There was no main effect of Hemisphere and no Condition x Hemisphere interaction ($F_{1,23} < 0.01$, $P = 0.94$; $F_{3,69} = 0.23$, $P = 0.87$; respectively).

Figure 8.4: Sentence onset brain responses. a) Grand average ERF (gray bar: 20 – 50 ms). b) Topographical distribution for the 20 – 50 ms time window. c) Display of the location of the 100 vertices in each hemisphere that show the strongest grand average activations (20 – 50 ms). Brain activity is displayed on the inflated surface, with dark gray representing sulci and light gray representing gyri.



In the ELANm/MMF time window (110 – 180 ms), a main effect of Condition was found ($F_{3,69} = 15.04$, $P < 0.001$, $\eta^2_G = 0.167$). Post-hoc tests showed that the incorrect standard condition was significantly more anterior compared to the correct deviant condition, the incorrect deviant condition as well as the sentence onset ($F_{1,23} = 41.01$, $P_{FDR} < 0.001$, $\eta^2_G = 0.448$, 16 mm; $F_{1,23} = 20.65$, $P_{FDR} < 0.001$, $\eta^2_G = 0.205$, 11 mm; $F_{1,23} = 13.91$, $P_{FDR} < 0.01$, $\eta^2_G = 0.235$, 10 mm; respectively). In addition, the correct deviant condition was significantly more posterior compared to the incorrect deviant condition and the sentence onset ($F_{1,23} = 8.34$, $P_{FDR} < 0.05$, $\eta^2_G = 0.064$, 5 mm; $F_{1,23} = 7.45$, $P_{FDR} < 0.05$, $\eta^2_G = 0.107$, 6 mm; respectively), whereas no difference was found between the incorrect deviant condition and the sentence onset ($F_{1,23} = 0.06$, $P_{FDR} > 0.05$). There was no main effect of Hemisphere and no Condition \times Hemisphere interaction ($F_{1,23} = 0.02$, $P = 0.90$; $F_{3,69} = 1.22$, $P = 0.31$; respectively).

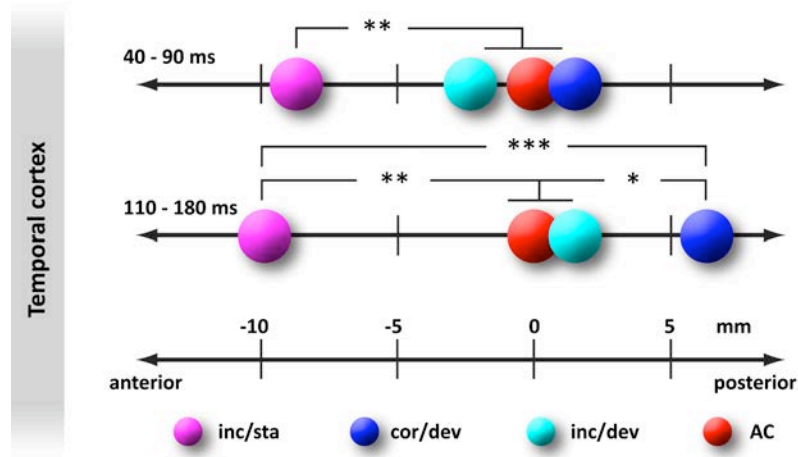


Figure 8.5: Results of the local maxima analysis in the temporal cortex for each the time windows (incorrect standard, inc/sta, magenta; correct deviant, cor/dev, blue; incorrect deviant, inc/dev, cyan; sentence onset M50 as reference to the auditory cortex, AC, red; * $P_{FDR} \leq 0.05$; ** $P_{FDR} \leq 0.01$; *** $P_{FDR} \leq 0.001$).

8.4 Discussion

The goal of the present MEG experiment was to investigate the underlying neural mechanisms of the parallel processing effect observed for early syntax-related and auditory perceptual-related responses, and to test previous localizations of early activations to syntactically incorrect sentences. The results revealed neural activations anterior to the auditory cortex elicited by syntactic violations (ELANm), whereas infrequent ITD changes led to activations more posterior in the STG (MMF). Sentences containing both violations led to activations between the activation maxima of the single violations. Moreover, very early modulations of STG activations were observed at around 60 ms which preceded the ELANm and MMF. The results are discussed in detail below.²¹

Very early effects (40 – 90 ms)

After approximately 60 ms, syntactically incorrect sentences and sentences including an ITD change led to stronger neural activations in the STG compared to correct standard sentences. Moreover, STG activations were even further increased for sentences containing both a syntactic violation and an ITD change.

²¹ The absence of syntax-related inferior frontal activations and the absence of syntax-related hemispheric differences are discussed in the general discussion in chapter 9.

These findings suggest parallel processing of syntactic and auditory spatial information already within the first 100 ms after violation onset.

Very early syntax-related effects were also observed in previous studies (C. S. Herrmann et al., 2000; B. Herrmann et al., 2009) as well as in Experiment I. Furthermore, very early effects to deviances of auditory perceptual regularities have been reported as well (Boutros & Belger, 1999; Ermutlu et al., 2005). A recently proposed interpretation of very early responses to rule violations argues for multiple stages of deviancy detection which might be organized hierarchical (Grimm et al., 2011; Slabu et al., 2010).

Furthermore, it has been put forward that early syntactic processing draws on syntactic templates, where local syntactic dependencies are preprocessed and stored in memory in form of templates (Bornkessel and Schlesewsky, 2006; Kaan, 2009). Thus, the fastness of early syntax-related responses might be due to this precompilation of phrase structure representations. If predictions during sentence comprehension are the basis of the early syntax effects (Dikker et al., 2009), then such predictions could be driven by the head of the phrase, which would then activate the respective templates, thereby allowing for fast neural responses.

One finding of the present experiment, however, needs further discussion. The present localization of the very early syntax-related effect was observed anterior to the AC, while the other violation conditions as well as previous studies investigating the M50 showed activations in AC (B. Herrmann et al., 2009; Huotilainen et al., 1998; Mäkelä et al., 1994; Thoma et al., 2003, 2008). This difference might be due to different stimulus designs, with the present experiment conducting a sentence processing paradigm, while the very early syntax-related effect in B. Herrmann et al. (2009) was observed in an auditory oddball paradigm. As this very early effect needs further elaboration in general, it is preferred not to speculate any further.

Auditory space processing: MMF – ITD change (110 – 180 ms)

In the present study, naturally spoken sentences that included an infrequent ITD change elicited a magnetic mismatch response at around 110 – 180 ms. This is compatible with previous studies investigating the MMN/MMF to infrequent ITD changes using simpler stimuli (Kaiser et al., 2000; Nager et al., 2003; Schröger, 1996; Schröger & Wolff, 1996).

In addition, the local activation maximum in the temporal cortex elicited by the ITD change was found about 6 mm more posterior to the local activation maximum of the sentence onset M50 component serving as reference to the auditory cortex. In line with the present observation, activations in posterior parts of the STG have been reported in EEG/MEG studies localizing the MMN/MMF to infrequent auditory location changes (Deouell et al., 2006; Kaiser et al., 2000; Sonnadara et al., 2006; Tata & Ward, 2005) as well as in fMRI studies varying the stimulus's ITD (Altmann et al., 2008; Krumbholz et al., 2005; Warren & Griffiths, 2003).

Importantly, the estimated local maxima in the temporal cortex showed significant differences between the ELANm elicited by the syntactic violation and the MMF to infrequent ITD changes. Syntactically incorrect sentences elicited a local maximum in the temporal cortex about 16 mm more anterior than sentences containing an ITD change. This difference of processing spatial vs. non-spatial sounds along the superior temporal cortex has been found in fMRI studies as well (Altmann et al., 2008; Warren and Griffiths, 2003) and might relate to the dual processing pathways proposed in the auditory domain (for a recent review see Rauschecker and Scott, 2009).

Regarding the hemispheric distribution of the MMN to ITD changes, it has already been discussed in the context of Experiment II that the current sentence processing paradigm might have influenced the hemispheric lateralization in the ITD change condition, which in turn does not allow drawing firm conclusions on a potential hemispheric predominance (Kaiser et al., 2000; Krumbholz et al., 2005; Nager et al., 2003; Richter et al., 2009).

Syntactic processing: ELANm (110 – 180 ms)

Regarding the ELANm component, the present results replicate previous EEG and MEG findings in which syntactically incorrect sentences led to larger brain activation compared to syntactically correct ones (Friederici et al., 1993, 2000a; Hahne & Friederici, 1999, 2002; C. S. Herrmann et al., 2000; Knösche et al., 1999; Kubota et al., 2003).

Furthermore, the present STG activations elicited by syntactically incorrect sentences were localized anterior to the M50 auditory cortex reference, which is consistent with previous reports on the ELANm showing strongest activation in the anterior STG (Friederici et al., 2000a) and the superior temporal cortex (Groß et al., 1998; Knösche et al., 1999). Recently, sentence processing experiments in

the visual domain have led to a "sensory hypothesis" for early syntactic effects (Dikker et al., 2009) by showing early modulations of visual sensory cortex activations caused by syntactic anomalies (Dikker et al., 2009, 2010). However, Dikker et al.'s localization approach did not allow them to further elaborate on the exact location of their visual sensory effect, i.e. whether activation was modulated in primary visual areas or outside of those (Dikker et al., 2009, 2010). The current findings show for the auditory domain that it is not the auditory core regions which are modulated by syntactic violations, but rather cortical regions anterior to it. This is in line with Experiment III showing regions outside sensory cortices to be involved in early syntactic processing. The present observations are also in general agreement with the view that more complex auditory stimulus processing is accomplished in belt and parabelt regions of the auditory system rather than in its core areas (Kaas & Hackett, 2000; Rauschecker & Tian, 2004).

By introducing the "sensory hypothesis" in the visual domain, Dikker et al. (2009) not only reported visual sensory cortex activations in response to syntactic word category violations, but moreover showed that the early syntax-related effects rely on phonological form properties associated with the syntactic category, e.g. an affix marking the syntactic category (Dikker et al., 2009, 2010). In the auditory sentence materials used in the current experiment, the word category was indeed overtly marked by the prefix "ge-" and a suffix (e.g., "-t"). Thus, overt phonological marking of the word category may cause the detection of word category violations and leads to early syntax effects. The present results could, therefore, be seen in relation to a study of Ahveninen et al. (2006) showing that anterior parts of the STG are tuned to phonetic/phonological information, whereas posterior parts are tuned to spatial information, and that this difference is already present at around 70 – 150 ms, partly overlapping with the current time window of the syntax effect (110 – 180 ms). Thus, in the auditory domain it appears that both the phonological effect observed by Ahveninen et al. (2006) and the present syntax effect are not localized in the auditory cortex, but rather more anteriorly to it.

Processing syntax and auditory space in parallel (110 – 180 ms)

The current experiment aimed to further investigate parallel processing of syntactic and auditory perceptual information in the 110 – 180 ms time window (Hahne et al., 2002). Here, MEG source localization was used to investigate the

underlying neural mechanisms. Local neural activations in the temporal cortex elicited by sentences including the combination of a syntactic violation and an ITD change were found significantly more anterior compared to the MMF maximum and significantly more posterior to the ELANm maximum. No difference was found to the M50 reference to the auditory cortex. Three alternative explanations of this finding are considered.

First, the intermediate location between the activation maxima of the single violations could in principle be due to averaging across participants, in which a few participants were processing only the syntactic part of these double violation sentences (i.e., more anterior), and the remaining participants only the ITD change (i.e., more posterior). However, this would have led to reduced activation strength for the double violation compared to the correct deviant condition, while the opposite was found. Hence, the present observations cannot be explained by this argument.

A second explanation might be that a completely independent mechanism underlies the processing of such a double violation compared to the single violations. According to such an explanation, activations in cortical regions different from the regions activated by single violations could be assumed. However, the current analysis did not reveal a difference between the location of the M50 auditory cortex reference and the local maximum elicited by the double violation, whereas single violations recruited cortical regions more anterior and posterior in the STG. As previous studies showed that the AC responds strongly to simple stimuli (Kaas & Hackett, 2000; Rauschecker & Tian, 2004), an even more complex violation than the single violations should have led to activations in distinct areas as well. For this reason, this explanation very unlikely accounts for the present results.

A third alternative, however, might be that the double violation simultaneously elicited activations in those temporal cortex regions that were independently activated by the single violations. Within one condition, it is fairly difficult to separate two very close sources activated at the same time using distributed source models. As a result, source reconstruction would reveal one source for the corresponding condition somewhere between the true activations, consistent with the present observations. Thus, the current data can be taken as indirect evidence that the auditory system is able to process these syntactic and auditory spatial violations in parallel by activating different brain regions simultaneously.

While this is the most likely explanation of the intermediate temporal cortex maximum to the double violations, such an activation shift due to two (or more) truly activated regions in close proximity could in principle also account for the present syntactic and auditory spatial localizations. However, this is very unlikely the case because previous fMRI studies also showed anterior STG activations for syntactic processing (Friederici et al., 2003b; see also Experiment III) and posterior STG activations for auditory spatial processing (Altmann et al., 2008; Krumbholz et al., 2005; Warren & Griffiths, 2003).

Taken together, the present findings strongly indicate that processing the combination of a syntactic violation and an auditory spatial violation simultaneously recruits brain regions in the anterior STG as well as in the posterior STG.

8.5 Conclusions

The current MEG experiment revealed a number of similarities and differences in processing syntactic and auditory spatial information. Approximately 60 ms after stimulus onset, processing of syntactic and auditory spatial deviations led to modulations in the STG, showing that both deviations are processed in parallel when encountered in combination. Following these very early effects, clear evidence of a dissociation of speech-related processes and auditory spatial processes was observed in the superior temporal cortex. Syntactically incorrect sentences elicited activations in the anterior STG at around 110 – 180 ms, while auditory spatial deviations elicited activations in the posterior STG. The current observations, moreover, suggest that brain regions independently activated by single violations are activated simultaneously in case of a combined violation. These findings are compatible with the view of different processing streams in the temporal cortex involved in syntactic and auditory spatial processing.

9 General discussion

The present dissertation investigated early syntax-related processes in the brain. These effects occur within the first 200 ms after a syntactic violation. As this time window is also known for auditory perceptual processes activating sensory cortices, and recent findings reported sensory cortex activations caused by syntactic violations, the dissertation aimed at elucidating on the role sensory cortices play in syntactic processes and whether early syntactic and auditory perceptual responses diverge in the brain.

By presenting sentences that were either syntactically incorrect or prosodically incongruent, the first experiment aimed to investigate whether a prosodic incongruency contributes to the ELAN effect associated with early syntactic processes. The experiment was designed in order to test whether the ELAN can be considered a marker for early syntactic processes. The results clearly show that a prosodic incongruency (change in F_0 contour) cannot explain the ELAN effect. Hence, the ELAN can be considered a marker for early syntactic processes primarily reflecting initial syntactic parsing difficulties.

In the second experiment, it was tested whether single neural responses allow decoding the brain states associated with early syntactic processes. Furthermore, it was tested whether the neural activations to single syntactic violations were consistent across participants. Decoding of the syntactic brain states was found to be equally good for within-participant and across-participant decoding. This showed that the neural mechanisms underlying early syntax-related processes in the brain are largely consistent across participants, which indicates that the culturally learned rules reflecting these processes are represented very similar in the brains of different individuals.

The third experiment aimed to elucidate on the cortical regions modulated by early syntactic processes and regions modulated by pure perceptual processes. An fMRI setting was chosen that allowed attributing the syntax-

related findings to an early processing stage. The results revealed syntax-related neural imprints in the IFG, aSTG, STS, whereas pure perceptual processing of a suffix that overtly marked the syntactic category elicited activations in auditory sensory cortices. Thus, activations in brain regions outside the auditory cortices were modulated by syntactic violations, while auditory cortices were sensitive to perceptual processes only.

In the fourth and final experiment, parallel processing of syntactic and auditory perceptual rule violations was investigated. While early syntactic processes were localized in anterior STG regions, auditory spatial violations lead to activations more posterior in the STG. Furthermore, this experiment provided strong indication that the anterior and posterior regions in the STG were activated simultaneously for violations in both dimension, i.e. syntax and auditory space. In addition, parallel processing of syntactic and auditory perceptual violations was observed already in a very early time window at around 60 ms.

In the following, these findings are discussed more generally. The Discussion will address: the fastness of the syntax-related neural responses; the role of sensory cortices; the absence of inferior frontal activations in the MEG experiments; the importance of the anterior STG in syntactic operations; and the notion of a left-hemispheric predominance for syntactic processes.

9.1 The fastness of the syntax-related neural responses

One question that has recently gained attention regards the fastness of the neural responses elicited by syntactic violations (Dikker et al., 2009, 2010; Lau et al., 2006). In the current MEG experiments (Experiments I and IV), syntax-related neural responses were observed already within the first 100 ms after the onset of the violating word, followed by the ELANm component at around 110 – 180 ms. The timing of the neural responses to auditory perceptual rule violations was comparable to those elicited by syntactic violations. This resemblance has also been emphasized before, thereby suggesting sensory cortex regions to be involved in both of these processes (Dikker et al., 2009). In order to explain the fastness of the syntax-related effects not only anatomically but also functionally, Dikker et al. (2009, 2010) conducted a series of sentence processing experiments in the visual modality. The authors observed that phonological form properties associated with the syntactic category play a crucial role in the fast detection of a syntactic violation. In their first study for example, only those syntax-violating

words led to an early effect which were overtly marked by closed-class morphology such as an affix (Dikker et al., 2009). From these results it appears that perceptually overt category marking enables the fast syntax-related neural responses. Consistently, the syntactic category of the violating word in the current MEG experiments was overtly marked by the prefix "ge-" and a suffix (e.g., "-t"). In addition, Dikker et al. (2010) could also observe an early syntax-related effect for words that lack an affix, but where the characteristic form of the syntactic category was violated. In the auditory modality, such a sophisticated analysis of characteristic features associated with a syntactic category has not been conducted. Nevertheless, Dikker et al.'s (2010) findings might explain the syntax-related effects observed for syntactically incorrect utterances without a category marking suffix in the current fMRI experiment (Experiment III).

Furthermore, Lau et al. (2006) as well as Dikker et al. (2009, 2010) suggested prediction-based processes to be involved in sentence comprehension.²² In particular, the authors argued that predictions take place before the syntax-violating word is encountered, which tightly constrain the expectations about the upcoming syntactic word category (Dikker et al., 2010; Lau et al., 2006). It was suggested that phonological form properties associated with the syntactic category are predicted which then allow the fast detection of a violation at the respective word. Other authors proposed that local dependencies are already preprocessed and stored in memory (Bornkessel & Schlesewsky, 2006; Kaan, 2009). Bornkessel and Schlesewsky (2006) refer to local phrases structure representations as syntactic templates, and the fastness of the early syntax effects might be due to their precompilation. In this context, local predictions about the upcoming syntactic word category could be driven by the head of a phrase, i.e. at the point where the syntactic template is opened.

Previous studies discussing top-down predictive processes with respect to visual cortex regions suggested areas in the prefrontal cortex to be involved in prediction-related representations (Bar et al., 2006; Bar, 2007; Summerfield et al., 2006). For the auditory modality, Rauschecker (2011) recently discussed the role of efferent connections in speech processes projecting from frontal cortices

²² While these studies reported early syntactic effects for unexpected rather than outright syntactic structures (Dikker et al., 2009, 2010; Lau et al., 2006), other studies failed to show early syntax-related effects for unexpected local dependencies (Friederici et al., 1996; B. Herrmann et al., 2009; Pulvermüller & Assadollahi, 2007).

to parietal and posterior auditory cortices that might provide the anatomical basis for such predictions. The current fMRI experiment provides evidence that the IFG is activated when a syntactic violation is detected. Whether it is also involved in prediction-related processes is a question that needs further attention in future research.

9.2 Sensory cortices and early syntactic processes

The current localization experiments (Experiments III and IV) explicitly aimed to investigate the role of auditory sensory cortices in syntactic processes. On this account, the stimulus materials of the experiments were not only varied in grammaticality, but moreover with respect to auditory perceptual features. The manipulation of auditory perceptual features was hypothesized to elicit activations in auditory sensory cortices allowing the comparison to those brain activations associated with syntactic processes.

The findings from the MEG and fMRI experiments revealed a dissociation in the temporal cortex between the brain regions activated in response to syntactic manipulations and those activated in response to auditory perceptual manipulations. Both experiments showed the anterior STG to be involved in syntactic processes rather than the auditory sensory cortices, which in turn were activated by auditory perceptual processes. In addition, the fMRI experiment revealed regions in the IFG, STS and partially the MTG to be affected by syntactic processes.

These findings add to the discussion about syntax-related sensory cortex modulations (Dikker et al., 2009, 2010), and show that it is not the core or primary regions that are affected but rather brain regions outside of those. This is in line with the findings that primary regions in the auditory cortex are largely involved in frequency-specific computations of the acoustic signal, while regions that are more distant to the core regions are sensitive to complex stimulus features (for a review see Hackett, 2011). Thus, although the acoustic signal of syntactically incorrect utterances is spectrally decomposed, and the primary auditory cortices process these features, modulations of brain activations in response to syntactic violations occur at subsequent stages in the auditory processing stream.

9.3 The inferior frontal cortex

In the present MEG experiments (see Experiments I and IV), no frontal activation maximum was found for syntactically incorrect sentences, while the fMRI experiment (Experiment III) revealed activations in the IFG. At first glance, the MEG experiments are in line with the idea that the IFG might be involved in predicting upcoming word categories or form features associated with it rather than in detecting word category violations (Dikker et al., 2009, 2010).

This interpretation, however, is not only contradicted by the present fMRI findings, but also by previous localizations of the ELANm reporting the IFG and anterior STG as neural generators (Friederici et al., 2000a). Furthermore, two additional MEG studies using similar sentence materials also revealed statistical differences in frontal regions (Groß et al., 1998; Knösche et al., 1999). In these studies, however, it is not clear whether the observation of higher amplitude in frontal areas for syntactically incorrect sentences is due to the spread of the source in the STG or whether it reflects a local maximum independent of the STG activations. Apart from this, the absence of a local activation maximum in inferior frontal areas in the present MEG experiments, while Friederici et al. (2000a) observed a frontal generator, might be due to the different methodological approaches applied.

In the present MEG experiments, a distributed source model was used, which accounts for activations over the whole cortical surface. No prior assumptions about source locations on the cortical surface were made. In contrast, in the study by Friederici et al. (2000a), two dipoles were explicitly seeded in each hemisphere (one in the inferior frontal cortex and one in the anterior STG) using the results of an fMRI study as prior (Meyer et al., 2000). The finding that dipole strength was significantly weaker in the inferior frontal cortex than in the anterior STG (Friederici et al., 2000a) can be related to the present MEG findings, suggesting that MEG responds strongly to the temporal source of the ELANm component, but not as much to a frontal source. EEG studies, on the other hand, suggest strong involvement of frontal areas in the detection of syntactic violations (Pulvermüller & Shtyrov, 2003), as the distribution of the ELAN was not only found very focal in frontal electrodes (Friederici et al., 1996; Hahne & Friederici, 2002), but was moreover absent in patients with selective lesions in the left inferior frontal cortex (for a review see Friederici & Kotz, 2003).

From this point of view, EEG and MEG may measure different parts of the same phenomenon, due to the orientation of the dipoles (Ahlfors et al., 2010a; Vrba & Robinson, 2001; see also chapter 2). Explicitly fitting a dipole into the frontal cortex could account for the explanation of additional variance (Friederici et al., 2000a) which might be concealed when using distributed source models without such a prior. Therefore, with MEG alone, the question about a frontal source of the ELAN/ELANm component is not conclusive.

On the other hand, the fMRI activations in the inferior frontal gyrus observed in Experiment III can be linked to early syntactic processes as the stimuli used elicited only an early but no later syntax-related effect in a previous EEG study (Hasting & Kotz, 2008). Thus, there are strong indications that the IFG is involved in detecting syntactic structure violations. This is also consistent with previous studies showing inferior frontal activation to local syntactic violations (Brauer & Friederici, 2007; Friederici et al., 2003, 2010; Kang et al., 1999), although there are differences with respect to the exact location.

9.4 The anterior temporal cortex

The most reliable finding observed in the current experiments using MEG and fMRI was the anterior STG activation in response to syntactically incorrect utterances. This finding is consistent with previous studies reporting the anterior temporal cortex to be involved in syntactic processes (Bemis & Pykkänen, 2011; Brennan et al., in press; Friederici et al., 2000a, 2003b; Humphries et al., 2005; Noppeney & Price, 2004; Rogalsky & Hickok, 2009).

In particular, activations in the anterior STG have been found for local syntactic structure violations (Friederici et al., 2003b), revealing a comparable time course as the current MEG activations (Friederici et al., 2000a). Another line of research reports anterior temporal cortex activations for sentences when compared to word lists, i.e. strings without syntactic structure (Friederici et al., 2000b; Humphries et al., 2006; Vandenberghe et al., 2002). Furthermore, the left anterior temporal cortex has been shown to be involved in syntactic structure building (Brennan et al., in press), syntactic priming (Noppeney & Price, 2004) and combinatorial processes (Bemis & Pykkänen, 2011; Pallier et al., 2011).

However, the study of Pallier et al. (2011) showed that combinatorial processes in the anterior temporal cortex require words to be semantically

meaningful, while activations in the IFG and the posterior temporal cortex were independent of the meaning of the words. This led to the conclusion that the IFG and posterior temporal cortex are involved in syntactic combinatorial processes, while the anterior temporal cortex processes semantic combinatorial aspects (Pallier et al., 2011; for a similar argument see Vandenberghe et al., 2002). Another study, nevertheless, showed activations in the anterior temporal cortex in relation to syntactic and semantic processes (Rogalsky & Hickok, 2009). With respect to the timing of combinatorial processes in the anterior temporal cortex, Bemis and Pylkkänen (2011) revealed activations starting at around 180 ms, i.e. relatively early after the visual input was provided.

Although all these studies found syntax-related activations in anterior parts of the temporal cortex, the exact location of the activations varied considerably. While some studies observed activations in the anterior STG (Friederici et al., 2000a; 2003b), others reported activations in the very anterior temporal cortex (temporal pole) covering the STG and MTG (Bemis & Pylkkänen, 2011; Noppeney & Price, 2004; Rogalsky & Hickok, 2009). The current anterior STG activations relate to the studies conducted by Friederici et al. (2000a, 2003b) in which syntactically incorrect utterances were compared with correct ones. It appears that the detection of local syntactic violations based on preprocessed syntactic templates affects brain regions posterior to the very anterior temporal cortex (temporal pole), i.e. regions closer to the auditory cortices. Overall, the current findings are consistent with the view of Friederici (submitted), suggesting the anterior STG to support rule-based combinatorial processes of adjacent elements.

9.5 Syntax and the left hemisphere

It has long been noted that syntactic operations are mainly conducted by brain regions in the left hemisphere, and neurocognitive models have emphasized this aspect (e.g., Friederici, 2002; Pulvermüller, 2010). The current dissertation provides compatible but also diverging findings. A left-hemispheric predominance was found for early syntactic processes in Experiments I, II and III, whereas the direct comparison between left- and right-hemispheric activations failed to be significant in Experiment IV.

Among previous studies, some reported stronger activations in the left than right hemisphere for processing syntactic violations (Friederici et al., 2000a; B.

Herrmann et al., 2009; Shtyrov et al., 2003), while other studies observed a bi-hemispheric involvement in early syntactic processing (C. S. Herrmann et al., 2000; Knösche et al., 1999; Kubota et al., 2003).²³ Taking these previous studies as well as the findings of Experiments I and III into account it seems that there is a tendency towards left-hemispheric regions being most important for syntactic processing. This preference has also been shown in an EEG study reporting a bilateral ELAN distribution in healthy adults and a left-lateralized one in patients with right anterior temporal lesions, whereas no ELAN was observed in patients with lesions in the left anterior temporal cortex (Kotz et al., 2003). These findings suggest that the right hemisphere has a supportive role in syntactic processes, whereas left-hemispheric brain regions are much more crucially involved in brain functions related to syntactic processes.

9.6 Summary

The findings of the current dissertation can be summarized as follows. The ELAN was shown to be a marker of syntactic rather than prosodic processes. The neural responses to syntactic structure violations were largely consistent across different individuals, suggesting that the underlying syntactic rules are represented very similar in the brains of these individuals. Modulations of neural activity caused by syntactic violations were observed within the first 200 ms after the onset of the syntax-violating word. The fastness of the observed syntax-related effects were interpreted in the context of preprocessed local syntactic dependencies (syntactic templates) that might allow local predictions about the upcoming syntactic structure. The underlying brain regions involved in early syntactic processes were localized in regions outside of the auditory cortices, most consistently in the anterior STG, with additional activation in the IFG. These findings speak against syntax-inflicted sensory cortex modulations, but show that regions in close proximity (approx. 10 mm) can be affected by syntactic violations.

²³ Importantly in this context, the absence of a statistic effect is not very informative as it can be caused by a number of reasons not known. Furthermore, there is no evidence for a right-hemispheric predominance in early syntactic operations.

10 Future directions

The present dissertation provides insight on which regions in the brain are modulated by early syntax-related processes. The most consistent localization finding across studies was the involvement of the anterior part of the STG in syntactic processes. Nevertheless, a few questions remain unanswered. In the following, the discussion will be twofold. In the first section, approaches to gain further insight about the brain regions involved in the early detection of syntactic violations will be discussed. Subsequently, the discussion will focus on how the understanding of the functional meaning of the early syntax-related effects can be further elaborated.

10.1 Further insight – Location

One piece of evidence that the current MEG studies fail to provide regards the contribution of the inferior frontal cortex in detecting a local syntactic violation. Previous studies suggested the inferior frontal cortex as one generator of the ELAN (Friederici et al., 2000a; Friederici & Kotz, 2003), thus to be involved in early syntactic processes. The discussions in the sections above, however, also showed that this topic is under heavy debate. What is missing in the literature is the localization of the ELAN using EEG, which is sensitive to sources oriented radial to the skull, as compared to MEG. For example, the sMMN, another component associated with early syntactic processes, has revealed frontal activations in an EEG localization study (Pulvermüller & Shtryov, 2003). The most obvious approach, nevertheless, is to use EEG + MEG to localize the neural generators of the early neural responses elicited by syntactically incorrect sentences. The combination of EEG and MEG has been suggested on several occasions to show superior source localization sensitivity (Ahlfors et al., 2010a, 2010b; Molins et al., 2008; Sharon et al., 2007).

Another approach to systematically track down the regions modulated by early syntactic processes is to design further studies in fMRI that allow attributing the observed activations to early processes. Although the relationship between the neural activity measured in EEG and the hemodynamic response measured in fMRI is rather complex, linking these two methods is essential in order to understand the functions that underlie language processes with respect to their timing as well as their spatial distribution in the brain. Experiment III of the current dissertation provides one approach that uses the specific configuration of ERP components in EEG to link the two measures. A different and probably more direct approach could be based on the findings of Hahne & Friederici (1999). In this study, syntactically correct and incorrect sentences were presented. In one of the two sessions the incorrect sentences occurred with a probability of 20 %, while the probability in the other session was 80 %. The authors showed that the ELAN was elicited in both sessions with similar amplitude, while the P600 amplitude was reduced in the 80 % probability session. The findings were taken as evidence that the ELAN reflects automatic syntactic processes, whereas the P600 assigned revision/repair processes are under cognitive control. This dissociation could in principle be used to localize the underlying neural mechanism of the ELAN and P600 in an fMRI setting. The brain regions that show similar activation in the two sessions would reflect the underlying sources of the ELAN, while the regions reduced in activation strength from the 20 % to 80 % probability sessions would reflect P600 assigned processes. Such a study would allow narrowing the gap between ERP components in EEG and the activated brain regions measured with the high spatial resolution of fMRI.

10.2 Further insight – Function

Functionally, it has been argued that the early syntax-related responses are the outcome of a syntactic template matching (Bornkessel & Schlesewsky, 2006; Kaan, 2009), where the encountered syntactic structure does not match the precompiled and stored local syntactic dependency of the template. Predictions have been suggested to play a crucial role in these processes, allowing for the fast neural responses observed (Dikker et al., 2009, 2010; Lau et al., 2006). The notion of syntactic templates used to process local syntactic structures implicates that predictions about the upcoming word category (or the form features associated with it) are generated only locally.

It would be interesting, nevertheless, whether the preceding sentence context has an influence on processing local syntactic dependencies. Independent studies showed that the early syntax-related effect can be observed when the violation occurs at the end of a sentence (Dikker et al., 2009; Hahne & Friederici, 1999, 2002), in the middle of a sentence (Dikker et al., 2010; Rossi et al., 2005) or even in the very reduced context of two-word utterances with no additional context preceding the local syntactic structure (Hasting & Kotz, 2008; B. Herrmann et al., 2009). Thus, it appears that this effect indeed requires mainly local information. Nevertheless, whether the amplitude is modulated as a function of the amount of information that is available at the local violation has not been directly tested. Thus, an EEG study could be conducted using sentences which either contain a syntactic violation relatively early within the sentence or relatively late. If only the local information is relevant one would predict early syntax effects for early and late occurring violations, but no difference in amplitude between the effects. On the other hand, if the preceding context influences the processing of such local violations one would predict an amplitude modulation of the early syntax effect depending on the position of the local violation (early vs. late) and whether the context is predictive or not. Such a finding would indicate that more than only local syntactic information is used in processing local syntactic dependencies.

Furthermore, local syntactic dependencies need to be learned in order to establish a syntactic template that is then applied automatically. Evidence from language acquisition comes from research conducted in children and second language (L2) learners. It has been observed that children at the age of thirteen show an adult-like ELAN (Hahne et al., 2004), which suggests that the automatic processes and thus the syntactic templates have been developed up to this age. Children younger than thirteen years of age show a later negativity, indicating more controlled processes, while such an effect is absent in six year olds (Hahne et al., 2004). With respect to second language acquisition, some studies reported the absence of early syntax-related responses for L2 learners (Hahne, 2001; Kubota et al., 2003), while other studies observed an early syntactic effect comparable to the one found in native speakers (Isel, 2007; Kubota et al., 2005; Rossi et al., 2006). The main factor influencing whether syntactic processes are conducted fast and automatically seems to be the participant's proficiency with the language (Friederici et al., 2002; Pakulak & Neville, 2010; Rossi et al., 2006). Thus, a syntactic template for local syntactic dependencies is acquired with the

extensive use of language. How this acquisition takes place, however, needs further elaboration. There are some indications that children compared to adults use a wider neural network and partly different brain regions to process violations of local syntactic dependencies (Brauer & Friederici, 2007). Whether particular regions (e.g., the anterior STG) become increasingly specialized to process local syntactic dependencies when the speaker becomes more proficient with the language is a question that requires additional research. Furthermore, it is widely accepted that children are particularly able to use the information in the environment to extract structures relevant for speech comprehension (Romberg & Saffran, 2010). In principle, a variety of information could be used in this processes and it could be asked whether the non-local context helps in learning local syntactic dependencies or whether the opposite is true, i.e. non-local information reflects noise with respect to the local structure and thus interferes with the learning process.

11 Conclusions

The current dissertation investigated early syntactic processes in the brain and their relation to auditory sensory cortices. The experiments conducted in different imaging modalities (MEG, fMRI) revealed a clear dissociation of brain regions involved in auditory perceptual processes and regions involved in early syntactic processes. Perceptual processes activated auditory cortex areas, while the anterior STG was most consistently activated for early syntax-related processes, with additional activations in the IFG, STS and pMTG. Thus, the present results do not support the idea of syntax-inflicted sensory cortex activations, but rather suggest regions anterior to the auditory cortex to be involved in syntactic processes.

These findings are largely consistent with the areas described in the neuro-cognitive model for language comprehension proposed by Friederici (2002) as well as with the model of Bornkessel and Schlesewsky (2006). In these models, the anterior STG and the IFG have been proposed to be involved in initial syntactic structure building operations that are conducted within the first 200 milliseconds. Other models are less specific with respect to the temporal dynamics of different brain regions engaged in language comprehension processes, but also consider the anterior STG and IFG to be relevant for syntactic processes (Hagoort, 2005; Hickok & Poeppel, 2007).

The timing of the current syntactic effects observed with MEG relates to the first phase of the models introduced by Friederici (2002) and Bornkessel and Schlesewsky (2006). In this early phase initial syntactic structure building processes take place. It was suggested that these processes consist of activating a syntactic template that is then used in the subsequent phases. The time course of the current early syntax-related effects, nevertheless, adds further information by showing a subdivision into a very early effect within the first 100 ms and the ELAN at around 100 – 200 ms. Thus, it seems that a very early template matching brain mechanism operates already within the first 100 ms. Hence, the

sequential division of the processing phases proposed by these models remains untouched by the results of the current experiments, while the absolute timing needs modification.

References

- Ahlfors, S. P., Han, J., Belliveau, J. W., & Hämäläinen, M. S. (2010a). Sensitivity of MEG and EEG to source orientation. *Brain Topography*, *23*, 227-232.
- Ahlfors, S. P., Han, J., Lin, F.-H., Witzel, T., Belliveau, J. W., Hämäläinen, M. S., & Halgren, E. (2010b). Cancellation of EEG and MEG signals generated by extended and distributed sources. *Human Brain Mapping*, *31*, 140-149.
- Alho, K. (1995). Cerebral generators of mismatch negativity (MMN) and its magnetic counterpart (MMNm) elicited by sound changes. *Ear & Hearing*, *16*, 38-51.
- Altmann, C. F., Hennig, M., Döring, K. M., & Kaiser, J. (2008). Effects of feature-selective attention on auditory pattern and location processing. *NeuroImage*, *41*, 69-79.
- Ahveninen, J., Jääskeläinen, I. P., Raij, T., Bonmassar, G., Devore, S., Hämäläinen, M. S., Levänen, S., Lin, F.-H., Sams, M., Shin-Cunningham, B. G., Witzel, T., & Belliveau, J. W. (2006). Task-modulated "what" and "where" pathways in human auditory cortex. *Proceedings of the National Academy of Sciences*, *103*, 14608-14613.
- Baillet, S., Mosher, J. C., & Leahy, R. M. (2001). Electromagnetic brain mapping. *IEEE Signal Processing Magazine*, *18*, 14-30.
- Bakeman, R. (2005). Recommended effect size statistics for repeated measures designs. *Behavior Research Methods*, *37*, 379-384.
- Bar, M. (2007). The proactive brain: using analogies and associations to generate predictions. *Trends in Cognitive Sciences*, *11*, 280-289.
- Bar, M., Kassam, K. S., Ghuman, A. S., Boshyan, J., Schmid, A. M., Dale, A. M., Hämäläinen, M. S., Marinkovic, K., Schacter, D. L., Rosen, B. R., & Halgren, E. (2006). Top-down facilitation of visual recognition. *Proceedings of the National Academy of Sciences*, *103*, 449-454.

- Bastiaansen, M., Magyari, L., & Hagoort, P. (2010). Syntactic unification operations are reflected in oscillatory dynamics during on-line sentence comprehension. *Journal of Cognitive Neuroscience*, 22, 1333-1347.
- Bemis, D. K., & Pylkkänen, L. (2011). Simple composition: A magnetoencephalography investigation into the comprehension of minimal linguistic phrases. *The Journal of Neuroscience*, 31, 2801-2814.
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of Royal Statistical Society*, 57, 289-300.
- Berti, S., Roeber, U., & Schröger, E. (2004). Bottom-up influences on working memory: Behavioral and electrophysiological distraction varies with distractor strength. *Experimental Psychology*, 51, 249-257.
- Besserve, M., Jerbi, K., Laurent, F., Baillet, S., Martinerie, J., & Garnero, L. (2007). Classification methods for ongoing EEG and MEG signals. *Biological Research*, 40, 415-437.
- Bickerton, D. (2009). Syntax for non-syntacticians: A brief primer. In D. Bickerton & E. Szathmáry (Eds.), *Biological foundations and origin of syntax* (pp. 3-13). Cambridge, Massachusetts, USA; London, England: The MIT Press.
- Bornkessel, I., & Schlesewsky, M. (2006). The extended argument dependency model: A neurocognitive approach to sentence comprehension across languages. *Psychological Review*, 113, 787-821.
- Bornkessel-Schlesewsky, I. D., Schlesewsky, M., & von Cramon, D. Y. (2009). Word order and Broca's region: Evidence for a supra-syntactic perspective. *Brain & Language*, 111, 125-139.
- Boutros, N. N., & Belger, A. (1999). Midlatency evoked potentials attenuation and augmentation reflect different aspects of sensory gating. *Biological Psychology*, 45, 917-922.
- Brauer, J., & Friederici, A. D. (2007). Functional neural networks of semantic and syntactic processes in the developing brain. *Journal of Cognitive Neuroscience*, 19, 1609-1623.
- Brennan, J., Nir, Y., Hasson, U., Malach, R., Heeger, D.J., & Pylkkänen, L. (in press). Syntactic structure building in the anterior temporal lobe during natural story listening. *Brain and Language*. DOI:10.1016/j.bandl.2010.04.002
- Brett, M., Anton, J.-L., Valabregue, R., & Poline, J.-B. (2002). Region of interest analysis using an SPM toolbox. *Proceedings of the 8th International Conference on Functional Mapping of the Human Brain*, 16, 497.

- Broca, P. (1863). Localisation des fonctions cérébrales: Siègne du langage articulé. *Bulletin de la Société d'Anthropologie de Paris*, 4, 200-204.
- Caplan, D. (2009). Experimental design and interpretation of functional neuroimaging studies of cognitive processes. *Human Brain Mapping*, 30, 59-77.
- Chan, A. M., Halgren, E., Marinkovic, K., & Cash, S. S. (2011). Decoding word and category-specific spatiotemporal representations from MEG and EEG. *NeuroImage*, 54, 3028-3039.
- Chang, C.-C., & Lin, C.-J. (2001). LIBSVM: a library for support vector machines. Software available at <http://www.csie.ntu.edu.tw/~cjlin/libsvm>.
- Chomsky, N. (1957). *Syntactic Structures*. The Netherlands: Mouton.
- Crowley, K. E., & Colrain, I. M. (2004). A review of the evidence for P2 being an independent component process: age, sleep and modality. *Clinical Neurophysiology*, 115, 732-744.
- Cusack, R., Brett, M., & Osswald, K. (2003). An evaluation of the use of magnetic field maps to undistort echo-planar images. *NeuroImage*, 18, 127-142.
- Dapretto, M., & Bookheimer, S. Y. (1999). Form and content: Dissociating syntax and semantics in sentence comprehension. *Neuron*, 24, 427-432.
- Davidson, D. J., & Indefrey, P. (2003). An inverse relation between event-related and time-frequency violation responses in sentence processing. *Brain Research*, 1158, 81-92.
- Deichmann, R., Nöth, U., & Weiskopf, N. (2010). The basics of functional magnetic resonance imaging. In C. Mulert & L. Lemieux (Eds.), *EEG-fMRI: Physiological basis, technique and applications* (pp. 39-62). Berlin, Heidelberg: Springer-Verlag.
- Deouell, L. Y. (2007). The frontal generator of the mismatch negativity revisited. *Journal of Psychophysiology*, 31, 188-203.
- Deouell, L. Y., Pames, A., Pickard, N., & Knight, R. T. (2006). Spatial location is accurately tracked by human auditory sensory memory: evidence from the mismatch negativity. *European Journal of Neuroscience*, 24, 1488-1494.
- Dikker, S., Rabagliati, H., & Pylkkänen, L. (2009). Sensitivity to syntax in visual cortex. *Cognition*, 110, 293-321.
- Dikker, S., Rabagliati, H., Farmer, T. A., & Pylkkänen, L. (2010). Early occipital sensitivity to syntactic category is based on form typicality. *Psychological Science*, 21, 629-634.

- Eckstein, K., & Friederici, A. D. (2006). It's early: Event-related potential evidence for initial interaction of syntax and prosody in speech comprehension. *Journal of Cognitive Neuroscience*, 18, 1696-1711.
- Eickhoff, S. B., Stephan, K. E., Mohlberg, H., Grefkes, C., Fink, G. R., Amunts, K., & Zilles, K. (2005). A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *NeuroImage*, 25, 1325-1335.
- Ermutlu, M. N., Karamürsel, S., Ugur, E. H., Senturk, L., & Gokhan, N. (2005). Effects of cold stress on early and late stimulus gating. *Psychiatry Research*, 136, 201-209.
- Ethofer, T., Van De Ville, D., Scherer, K., & Vuilleumier, P. (2009). Decoding of emotional information in voice-sensitive cortices. *Current Biology*, 19, 1028-1033.
- Etzel, J. A., Gazzola, V., & Keysers, C. (2009). An introduction to anatomical ROI-based fMRI classification analysis. *Brain Research*, 1282, 114-125.
- Fischl, B., Sereno, I. M., & Dale, A. M. (1999b). Cortical surface-based analysis II: Inflation, flattening, and a surface-based coordinate system. *NeuroImage*, 9, 195-207.
- Fischl, B., Sereno, M. I., Tootell, R. B. H., & Dale, A. M. (1999a). High-resolution intersubject averaging and a coordinate system for the cortical surface. *Human Brain Mapping*, 8, 272-284.
- Fitch, W. T., & Hauser, M. D. (2004). Computational Constraints on Syntactic Processing in a Nonhuman Primate. *Science*, 303, 377-380.
- Formisano, E., De Martino, F., Bonte, M., & Goebel, R. (2008). "Who" is saying "what"? Brain-based decoding of human voice and speech. *Science*, 322, 970-973.
- Formisano, E., Kim, D.-S., Di Salle, F., van de Moortele, P.-F., Ugurbil, K., & Goebel, R. (2003). Mirror-symmetric tonotopic maps in human primary auditory cortex. *Neuron*, 40, 859-869.
- Frazier, L., Carlson, K., & Clifton Jr, C. (2006). Prosodic phrasing is central to language comprehension. *Trends in Cognitive Sciences*, 10, 244-249.
- Friederici, A. D. (2002). Towards a neural basis of auditory sentence processing. *Trends in Cognitive Sciences*, 6, 78-84.
- Friederici, A. D. (2004). Event-related brain potential studies in language. *Current Neurology and Neuroscience Reports*, 4, 466-470.
- Friederici, A. D. (submitted). The Brain Basis of Language: From Structure to Function.

- Friederici, A. D., Bahlmann, J., Heim, S., Schubotz, R. I., & Anwander, A. (2006). The brain differentiates human and non-human grammars: Functional localization and structural connectivity. *Proceedings of the National Academy of Sciences*, 103, 2458–2463.
- Friederici, A. D., Hahne, A., & Mecklinger, A. (1996). Temporal structure of syntactic parsing: early and late event-related brain potential effects. *Journal of Experimental Psychology*, 22, 1219–1248.
- Friederici, A. D., & Kotz, S. A. (2003). The brain basis of syntactic processes: functional imaging and lesion studies. *NeuroImage*, 20, 8–17.
- Friederici, A. D., Kotz, S. A., Scott, S. K., & Obleser, J. (2010). Disentangling syntax and intelligibility in auditory language comprehension. *Human Brain Mapping*, 31, 448–457.
- Friederici, A. D., Kotz, S. A., Werheid, K., Hein, G., & von Cramon, D. Y. (2003a). Syntactic comprehension in parkinson's disease: Investigating early automatic and late integrational processes using event-related brain potentials. *Neuropsychology*, 17, 133–142.
- Friederici, A. D., Makuuchi, M., & Bahlmann, J. (2009). The role of the posterior superior temporal cortex in sentence comprehension. *NeuroReport*, 20, 563–568.
- Friederici, A. D., Meyer, M., & von Cramon, D. Y. (2000b). Auditory language comprehension: An event-related fMRI study on the processing of syntactic and lexical information. *Brain and Language*, 74, 289–300.
- Friederici, A. D., Pfeifer, E., & Hahne, A. (1993). Event-related brain potentials during natural speech processing: effects of semantic, morphological and syntactic violations. *Cognitive Brain Research*, 1, 183–192.
- Friederici, A. D., Rüschemeyer, S.-A., Hahne, A., & Fiebach, C. J. (2003b). The role of left inferior frontal and superior temporal cortex in sentence comprehension: Localizing syntactic and semantic processes. *Cerebral Cortex*, 13, 170–177.
- Friederici, A. D., Steinhauer, K., & Pfeifer, E. (2002). Brain signatures of artificial language processing: Evidence challenging the critical period hypothesis. *Proceedings of the National Academy of Sciences*, 99, 529–534.
- Friederici, A. D., von Cramon, D. Y., & Kotz, S. A. (1999). Language related brain potentials in patients with cortical and subcortical left hemisphere lesions. *Brain*, 122, 1033–1047.

- Friederici, A. D., Wang, Y., Herrmann, C. S., Maess, B., & Oertel, U. (2000a). Localization of early syntactic processes in frontal and temporal cortical areas: A magnetoencephalographic Study. *Human Brain Mapping*, 11, 1-11.
- Friston, K. J., Holmes, A. P., Worsley, K. J., Poline, J.-P., Frith, C. D., & Frackowiak, R. S. J. (1995). Statistical parametric maps in functional imaging: A general linear approach. *Human Brain Mapping*, 2, 189-210.
- Genovese, C. R., Lazar, N. A., & Nichols, T. (2002). Thresholding of statistical maps in functional neuroimaging using the false discovery rate. *NeuroImage*, 15, 870-878.
- Goense, J. B. M., & Logothetis, N. K. (2008). Neurophysiology of the BOLD fMRI signal in awake monkeys. *Current Biology*, 18, 631-640.
- Goffman, E. (1980). *Rahmen-Analyse: Ein Versuch über die Organisation von Alltagserfahrungen*. Frankfurt am Main: Suhrkamp Verlag.
- Goldenholz, D. M., Ahlfors, S. P., Hämläinen, M. S., Sharon, D., Ishitobi, M., Vaina, L. M., & Stufflebeam, S. M. (2009). Mapping the signal-to-noise-ratios of cortical sources in magnetoencephalography and electroencephalography. *Human Brain Mapping*, 30, 1077-1086.
- Greenhouse, S. W., & Geisser, S. (1959). On methods in the analysis of profile data. *Psychometrika*, 24, 95-112.
- Grewendorf, G., Hamm, F., & Sternefeld, W. (1989). *Sprachliches Wissen: Eine Einführung in moderne Theorien der grammatischen Beschreibung*. Frankfurt am Main: Suhrkamp Verlag.
- Grimm, S., Escera, C., Slabu, L., & Costa-Faidella, J. (2011). Electrophysiological evidence for the hierarchical organization of auditory change detection in the human brain. *Psychophysiology*, 48, 377-84.
- Groß, J., Ioannides, A. A., Dammers, J., Maess, B., Friederici, A. D., & Müller-Gärtner, H.-W. (1998). Magnetic field tomography analysis of continuous speech. *Brain Topography*, 10, 273-281.
- Guimaraes, M. P., Wong, D. K., Uy, E. T., Grosenick, L., & Suppes, P. (2007). Single-trial classification of MEG recordings. *IEEE Transactions On Biomedical Engineering*, 54, 436-443.
- Habermas, J. (1981). *Theorie des kommunikativen Handelns (Band 1: Handlungsrationalität und gesellschaftliche Rationalisierung)*. Frankfurt am Main: Suhrkamp Verlag.
- Hackett, T. A. (2011). Information flow in the auditory cortical network. *Hearing Research*, 271, 133-146.

- Hagoort, P. (2003). Interplay between syntax and semantics during sentence comprehension: ERP effects of combining syntactic and semantic violations. *Journal of Cognitive Neuroscience*, 15, 883-899.
- Hagoort, P. (2005) On Broca, brain, and binding: A new framework. *Trends in Cognitive Sciences*, 9, 416-423.
- Hagoort, P., & Brown, C. M. (2000). ERP effects of listening to speech compared to reading: the P600/SPS to syntactic violations in spoken sentences and rapid serial visual presentation. *Neuropsychologia*, 38, 1531-1549.
- Hagoort, P., Wassenaar, M., & Brown, C. M. (2003). Syntax-related ERP-effects in Dutch. *Cognitive Brain Research*, 16, 38-50.
- Hahne, A. (2001). What's different in second-language processing? Evidence from event-related brain potentials. *Journal of Psycholinguistic Research*, 30, 251-265.
- Hahne, A., Eckstein, K., & Friederici, A. D. (2004). Brain signatures of syntactic and semantic processes during children's language development. *Journal of Cognitive Neuroscience*, 16, 1302-1318.
- Hahne, A., & Friederici, A. D. (1999). Electrophysiological evidence for two steps in syntactic analysis: Early automatic and late controlled processes. *Journal of Cognitive Neuroscience*, 11, 194-205.
- Hahne, A., & Friederici, A. D. (2002). Differential task effects on semantic and syntactic processes as revealed by ERPs. *Cognitive Brain Research*, 13, 339-356.
- Hahne, A., & Jescheniak, J. D. (2001). What's left if the Jabberwock gets the semantics? An ERP investigation into semantic and syntactic processes during auditory sentence comprehension. *Cognitive Brain Research*, 11, 199-212.
- Hahne, A., Schröger, E., & Friederici, A. D. (2002). Segregating early physical and syntactic processes in auditory sentence comprehension. *NeuroReport*, 13, 305-309.
- Hämäläinen, M. S., & Hari, R. (2002). Magnetoencephalographic (MEG) characterization of dynamic brain activation: Basic principles and methods of data collection and source analysis. In A. W. Toga & J. C. Mazziotta (Eds.), *Brain Mapping: The Methods*, 2nd Edition (pp. 227-253). San Diego, USA: Academic Press.
- Hämäläinen, M. S., Hari, R., Ilmoniemi, R. J., Knuutila, J., & Lounasmaa, O. V. (1993). Magnetoencephalography – theory, instrumentation, and applica-

- tions to noninvasive studies of the working human brain. *Reviews of Modern Physics*, 65, 413-497.
- Hämäläinen, M. S. & Sarvas, J. (1989). Realistic conductivity geometry model of the human head for interpretation of neuromagnetic data. *IEEE Transactions On Biomedical Engineering*, 36, 165-171.
- Hari, R., Levänen, S., & Raij, T. (2000). Timing of human cortical functions during cognition: role of MEG. *Trends in Cognitive Sciences*, 4, 455-462.
- Hasting, A. S., & Kotz, S. A. (2008). Speeding up syntax: On the relative timing and automaticity of local phrase structure and morphosyntactic processing as reflected in event-related brain potentials. *Journal of Cognitive Neuroscience*, 20, 1207-1219.
- Hasting, A. S., Kotz, S. A., & Friederici, A. D. (2007). Setting the stage for automatic syntax processing: The mismatch negativity as an indicator of syntactic priming. *Journal of Cognitive Neuroscience*, 19, 386-400.
- Haynes, J.-D., & Rees, G. (2005). Predicting the orientation of invisible stimuli from activity in human primary visual cortex. *Nature Neuroscience*, 8, 686-691.
- Haynes, J.-D., & Rees, G. (2006). Decoding mental states from brain activity in humans. *Nature Reviews Neuroscience*, 7, 523-534.
- Haynes, J.-D., Sakka, K., Rees, G., Gilbert, S., Frith, C., & Passingham, R. E. (2007). Reading hidden intentions in the human brain. *Current Biology*, 17, 323-328.
- Hein, G., & Knight, R. T. (2008). Superior temporal sulcus – It's my area: Or is it? *Journal of Cognitive Neuroscience*, 20, 2125-2136.
- Herrmann, B., Maess, B., & Friederici, A. D. (2011). Violation of syntax and prosody - Disentangling their contributions to the early left anterior negativity (ELAN). *Neuroscience Letters*, 490, 116-120.
- Herrmann, B., Maess, B., Hahne, A., Schröger, E., & Friederici, A. D. (in press-b). Syntactic and auditory spatial processing in the human temporal cortex: An MEG study. *NeuroImage*. DOI:10.1016/j.neuroimage.2011.04.034
- Herrmann, B., Maess, B., Hasting, A. S., & Friederici, A. D. (2009). Localization of the syntactic mismatch negativity in the temporal cortex: An MEG study. *NeuroImage*, 48, 590-600.
- Herrmann, B., Obleser, J., Kalberlah, C., Haynes, J.-D., & Friederici, A. D. (in press-a). Dissociable neural imprints of perception and grammar in auditory functional imaging. *Human Brain Mapping*. DOI:10.1002/hbm.21235

- Herrmann, C. S., Oertel, U., Wang, Y., Maess, B., & Friederici, A. D. (2000). Noise affects auditory and linguistic processing differently: an MEG study. *NeuroReport*, 11, 227-229.
- Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience*, 8, 393-402.
- Hinojosa, J. A., Martin-Loeches, M., Casado, P., Muñoz, F., & Rubia, F. J. (2003). Similarities and differences between phrase structure and morphosyntactic violations in Spanish: An event-related potentials study. *Language and Cognitive Processes*, 18, 113-142.
- Horváth, J., Czigler, I., Jacobsen, T., Maess, B., Schröger, E., & Winkler, I. (2008). MMN or no MMN: No magnitude of deviance effect on the MMN amplitude. *Psychophysiology*, 45, 60-69.
- Horwitz, B., Friston, K. J., & Taylor, J. G. (2000). Neural modeling and functional brain imaging: an overview. *Neural Networks*, 13, 829-846.
- Howseman, A. M., & Bowtell, R. W. (1999). Functional magnetic resonance imaging: Imaging techniques and contrast mechanisms. *Philosophical Transactions of the Royal Society of London*, 354, 1179-1194.
- Humphries, C., Binder, J. R., Melder, D. A., & Liebenthal, E. (2006). Syntactic and Semantic Modulation of Neural Activity during Auditory Sentence Comprehension. *Journal of Cognitive Neuroscience*, 18, 665-679.
- Humphries, C., Liebenthal, E., & Binder, J. R. (2010). Tonotopic organization of human auditory cortex. *NeuroImage*, 50, 1202-1211.
- Humphries, C., Love, T., Swinney, D., & Hickok, G. (2005). Response of anterior temporal cortex to syntactic and prosodic manipulations during sentence processing. *Human Brain Mapping*, 26, 128-138.
- Huotilainen, M., Winkler, I., Alho, K., Escera, C., Virtanen, J., Ilmoniemi, R. J., Jääskeläinen, I. P., Pekkonen, E., & Näätänen, R. (1998). Combined mapping of human auditory EEG and MEG responses. *Electroencephalography and Clinical Neurophysiology*, 108, 370-379.
- Isel, F. (2007). Syntactic and referential processes in second-language learners: event-related brain potential evidence. *NeuroReport*, 18, 1885-1889.
- Isel, F., Hahne, A., Maess, B., & Friederici, A. D. (2007). Neurodynamics of sentence interpretation: ERP evidence from French. *Biological Psychology*, 74, 337-346.
- Jackendoff, R. (2002). Foundations of language: Brain, meaning, grammar, evolution. New York: Oxford University Press.

- Jacobsen, T., & Schröger, E. (2003). Measuring duration mismatch negativity. *Clinical Neurophysiology*, 114, 1133-1143.
- Jäncke, L. (2005). *Methoden der Bildgebung in der Psychologie und den kognitiven Neurowissenschaften*. Stuttgart: Kohlhammer.
- Jaramillo, S., & Zador, A. M. (2011). The auditory cortex mediates the perceptual effects of acoustic temporal expectation. *Nature Neuroscience*, 14, 246-251.
- Jezzard, P., & Balaban, R. S. (1995). Correction for geometric distortion in echo planar images from B0 field variations. *Magnetic Resonance in Medicine*, 34, 65-73.
- Just, M. A., Carpenter, P. A., Keller, T. A., Eddy, W. F., & Thulborn, K. R. (1996). Brain activation modulated by sentence comprehension. *Science*, 274, 114-116.
- Kaan, E. (2009). Fundamental syntactic phenomena and their putative relation to the brain. In D. Bickerton & E. Szathmáry (Eds.), *Biological foundations and origin of syntax* (pp. 117-133). Cambridge, Massachusetts, USA; London, England: The MIT Press.
- Kaan, E., Harris, A., Gibson, E., & Holcomb, P. J. (2000). The P600 as an index of syntactic integration difficulty. *Language and Cognitive Processes*, 15, 159-201.
- Kaan, E., & Swaab, T. Y. (2002). The brain circuitry of syntactic comprehension. *Trends in Cognitive Sciences*, 6, 350-356.
- Kaan, E., & Swaab, T. Y. (2003). Repair, revision, and complexity in syntactic analysis: An electrophysiological differentiation. *Journal of Cognitive Neuroscience*, 15, 98-110.
- Kaas, J. H., & Hackett, T. A. (2000). Subdivisions of auditory cortex and processing streams in primates. *Proceedings of the National Academy of Sciences*, 97, 11793-11799.
- Kandler, K., Clause, A., & Noh, J. (2009). Tonotopic reorganization of developing auditory brainstem circuits. *Nature Neuroscience*, 12, 711-717.
- Kang, A. M., Constable, R. T., Gore, J. C., & Avrutin, S. (1999). An event-related fMRI study of implicit phrase-level syntactic and semantic processing. *NeuroImage*, 10, 555-561.
- Kaiser, J., Lutzenberger, W., Preissl, H., Ackermann, H., & Birbaumer, N. (2000). Right-hemisphere dominance for the processing of sound-source lateralization. *The Journal of Neuroscience*, 20, 6631-6639.

- Key, A. P. F., Dove, G. O., & Maguire, M. J. (2005). Linking brainwaves to the brain: An ERP primer. *Developmental Neuropsychology*, 27, 183-215.
- Kim, D.-S. (2005). The cutting edge of fMRI and high-field fMRI. *International Review of Neurobiology*, 66, 147-166.
- Klimesch, W., Sauseng, P., Hanslmayr, S., Gruber, W., & Freunberger, R. (2007). Event-related phase reorganization may explain evoked neural dynamics. *Neuroscience and Biobehavioral Reviews*, 31, 1003-1016.
- Knösche, T. R., Maess, B., & Friederici, A. D. (1999). Processing of syntactic information monitored by brain surface current density mapping based on MEG. *Brain Topography*, 12, 75-87.
- Kotz, S. A., Cappa, S. F., von Cramon, D. Y., & Friederici, A. D. (2002). Modulation of the lexical-semantic network by auditory semantic priming: An event-related functional MRI study. *NeuroImage*, 17, 1761-1772.
- Kotz, S. A., von Cramon, D. Y., & Friederici, A. D. (2003). Differentiation of syntactic processes in the left and right anterior temporal lobe: Event-related brain potential evidence from lesion patients. *Brain and Language*, 87, 135-136.
- Krappmann, L. (1971). *Soziologische Dimensionen der Identität*. Stuttgart: Ernst Klatt Verlag.
- Kriegeskorte, N., & Bandettini, P. A. (2007). Analyzing for information, not activation, to exploit high-resolution fMRI. *NeuroImage*, 38, 649-662.
- Kriegeskorte, N., Goebel, R., & Bandettini, P. (2006). Information-based functional brain mapping. *Proceedings of the National Academy of Sciences*, 103, 3863-3868.
- Krumbholz, K., Schönwiesner, M., von Cramon, D. Y., Rübsamen, R., Shah, N. J., Zilles, K., & Fink, G. R. (2005). Representation of Interaural temporal information from left and right auditory space in the human planum temporale and inferior parietal lobe. *Cerebral Cortex*, 15, 317-324.
- Kubota, M., Ferrari, P., & Roberts, T. P. L. (2003). Magnetoencephalography detection of early syntactic processing in humans: comparison between L1 speakers and L2 learners of English. *Neuroscience Letters*, 353, 107-110.
- Kubota, M., Ferrari, P., & Roberts, T. P. L. (2004). Human neuronal encoding of English syntactic violations as revealed by both L1 and L2 speakers. *Neuroscience Letters*, 368, 235-240.
- Kubota, M., Inouchi, M., Ferrari, P., & Roberts, T. P. L. (2005). Human magnetoencephalographic evidence of early syntactic responses to c-selection vi-

- olations of English infinitives and gerunds by L1 and L2 speakers. *Neuroscience Letters*, 384, 300-304.
- Kutas, M., & Hillyard, S. A. (1980). Reading senseless sentences: Brain potentials reflect semantic incongruity. *Science*, 207, 203-205.
- Kutas, M., & Hillyard, S. A. (1982). The lateral distribution of event-related potentials during sentence processing. *Neuropsychologia*, 20, 579-590.
- Kutas, M., & Hillyard, S. A. (1983). Event-related brain potentials to grammatical errors and semantic anomalies. *Memory & Cognition*, 11, 539-550.
- Kwon, H., Kim, J. M., Lee, Y. H., Kim, K., Park, Y. K., Nam, K., & Kuriki, S. (2004). Auditory evoked field responses in the left hemisphere to morphosyntactic violations in Korean sentence. *Neurology and Clinical Neurophysiology*, 29, 1-4.
- Lancaster, J. L., Tordesillas-Gutierrez, D., Martinez, M., Salinas, F., Evans, A. C., Zilles, K., Mazziotta, J. C., & Fox, P. T. (2007). Bias between MNI and Talairach coordinates analyzed using the ICBM-152 brain template. *Human Brain Mapping*, 28, 1194-1205.
- Lancaster, J. L., Woldorff, M. G., Parsons, L. M., Loitti, M., Freitas, C. S., Rainey, L., Kochunov, P. V., Nickerson, D., Mikiten, S. A., & Fox, P. T. (2000). Automated Talairach atlas labels for functional brain mapping. *Human Brain Mapping*, 10, 120-131.
- Lau, E. F., Phillips, C., & Poeppel, D. (2008). A cortical network for semantics: (de)constructing the N400. *Nature Reviews Neuroscience*, 9, 920-933.
- Lau, E. F., Stroud, C., Plesch, S., & Phillips, C. (2006). The role of structural prediction in rapid syntactic analysis. *Brain and Language*, 98, 74-88.
- Lee, C.-C., & Middlebrooks, J. C. (2011). Auditory cortex spatial sensitivity sharpens during task performance. *Nature Neuroscience*, 14, 108-114.
- Lee, D., & Newman, S. D. (2010). The effect of presentation paradigm on syntactic processing: An event-related fMRI study. *Human Brain Mapping*, 31, 65-79.
- Lee, C. C., & Sherman, S. M. (2010). Drivers and modulators in the central auditory pathways. *Frontiers in Neuroscience*, 4, 79-86.
- Lew, S., Wolters, C. H., Dierkes, T., Röer, C., & MacLeod, R. S. (2009). Accuracy and run-time comparison for different potential approaches and iterative solvers in finite element method based EEG source analysis. *Applied Numerical Mathematics*, 59, 1970-1988.

- Liebenthal, E., Binder, J. R., Spitzer, S. M., Possing, E. T., & Melder, D. A. (2005). Neural substrates of phonemic perception. *Cerebral Cortex*, *15*, 1621-1631.
- Logothetis, N. K. (2008). What we can do and what we cannot do with fMRI. *Nature*, *453*, 869-878.
- Logothetis, N. K., Pauls, J., Augath, M., Trinath, T., & Oettermann, A. (2001). Neurophysiological investigation of the basis of the fMRI signal. *Nature*, *412*, 150-157.
- Lopes da Silva, F. (2010). EEG: Origin and measurement. In C. Mulert & L. Lemieux (Eds.), *EEG-fMRI: Physiological basis, technique and applications* (pp. 19-38). Berlin, Heidelberg: Springer-Verlag.
- Maess, B., Herrmann, C. S., Hahne, A., Nakamura, A., & Friederici, A. D. (2006). Localizing the distributed language network responsible for the N400 measured by MEG during auditory sentence processing. *Brain Research*, *1096*, 163-172.
- Maess, B., Jacobsen, T., Schröger, E., & Friederici, A. D. (2007). Localizing pre-attentive auditory memory-based comparison: Magnetic mismatch negativity to pitch change. *NeuroImage*, *37*, 561-571.
- Makeig, S., Westerfield, M., Jung, T.-P., Enghoff, S., Townsend, J., Courchesne, E., & Sejnowski, T. J. (2002). Dynamic brain sources of visual evoked responses. *Science*, *295*, 690-694.
- Mäkelä, J. P., Hämäläinen, M. S., & McEvoy, L. (1994). Whole-head mapping of middle-latency auditory evoked magnetic fields. *Electroencephalography and Clinical Neurophysiology*, *92*, 414-421.
- Makuuchi, M., Bahlmann, J., Anwender, A., & Friederici, A. D. (2009). Segregating the core computational faculty of human language from working memory. *Proceedings of the National Academy of Sciences*, *106*, 8362-8367.
- Mattout, J., Henson, R. N., & Friston, K. J. (2007). Canonical source reconstruction for MEG. *Computational Intelligence and Neuroscience*, Article 67613.
- Mazaheri, A., & Jensen, O. (2008). Asymmetric amplitude modulations of brain oscillations generate slow evoked responses. *The Journal of Neuroscience*, *28*, 7781-7787.
- Mazaheri, A., & Jensen, O. (2010). Rhythmic pulsing: linking ongoing brain activity with evoked responses. *Frontiers in Human Neuroscience*, *4*, Article 177.
- McGee, T. J., King, C., Tremblay, K., Nicol, T. G., Cunningham, J., & Kraus, N. (2001). Long-term habituation of speech-elicited mismatch negativity. *Psychophysiology*, *38*, 653-658.

- Mead, G. H. (1973). *Geist, Identität und Gesellschaft*. Frankfurt am Main: Suhrkamp Verlag.
- Meyer, M., Alter, K., Friederici, A. D., Lohmann, G., & von Cramon, D. Y. (2002). fMRI reveals brain regions mediating slow prosodic modulations in spoken sentences. *Human Brain Mapping, 17*, 73-88.
- Meyer, M., Friederici, A. D., & von Cramon, D. Y. (2000). Neurocognition of auditory sentence comprehension: event related fMRI reveals sensitivity to syntactic violations and task demands. *Cognitive Brain Research, 9*, 19-33.
- Middlebrooks, J. C., & Green, D. M. (1991). Sound localization by human listeners. *Annual Reviews of Psychology, 42*, 135-159.
- Misaki, M., Kim, Y., Bandettini, P. A., & Kriegeskorte, N. (2010). Comparison of multivariate classifiers and response normalizations for pattern-information fMRI. *NeuroImage, 53*, 103-118.
- Mitchell, T. M., Hutchinson, R., Niculescu, R. S., Pereira, F., & Wang, X. (2004). Learning to decode cognitive states from brain images. *Machine Learning, 57*, 145-175.
- Mietz, A., Toepel, U., Ischebeck, A., & Alter, K. (2008). Inadequate and infrequent are not alike: ERPs to deviant prosodic patterns in spoken sentence comprehension. *Brain and Language, 104*, 159-169.
- Molins, A., Stufflebeam, S. M., Brown, E. N., & Hämäläinen, M. S. (2008). Quantification of the benefit from integrating MEG and EEG data in minimum l2-norm estimation. *NeuroImage, 42*, 1069-1077.
- Mourao-Miranda, J., Bokde, A. L. W., Born, C., Hampel, H., & Stetter, M. (2005). Classifying brain states and determining the discriminating activation patterns: Support Vector Machine on functional MRI data. *NeuroImage, 28*, 980-995.
- Münste, T. F., Heinze, H.-J., & Mangun, G. R. (1993). Dissociation of brain activity related to syntactic and semantic aspects of language. *Journal of Cognitive Neuroscience, 5*, 335-344.
- Mur, M., Bandettini, P. A., & Kriegeskorte, N. (2009). Revealing representational content with pattern-information fMRI - an introductory guide. *Social Cognitive and Affective Neuroscience, 4*, 101-109.
- Näätänen, R., Gaillard, A. W. K., & Mäntysalo, S. (1978). Early selective-attention effect on evoked potential reinterpreted. *Acta Psychologica, 42*, 313-329.

- Nager, W., Kohlmetz, C., Joppich, G., Möbes, J., & Münte, T. F. (2003). Tracking of multiple sound sources defined by interaural time differences: brain potential evidence in humans. *Neuroscience Letters*, 344, 181-184.
- Nelken, I. (2008). Processing of complex sounds in the auditory system. *Current Opinion in Neurobiology*, 18, 413-417.
- Neville, H., Nicol, J. L., Barss, A., Forster, K. I., & Garrett, M. F. (1991). Syntactically based sentence processing classes: Evidence from event-related brain potentials. *Journal of Cognitive Neuroscience*, 3, 151-165.
- Newman, S. D., Just, M. A., Keller, T. A., Roth, J., & Carpenter, P. A. (2003). Differential effects of syntactic and semantic processing on the subregions of Broca's area. *Cognitive Brain Research*, 16, 297-307.
- Noppeney, U., & Price, C. J. (2004). An fMRI study of syntactic adaptation. *Journal of Cognitive Neuroscience*, 16, 702-713.
- Norman, K. A., Polyn, S. M., Detre, G. J., & Haxby, J. V. (2006). Beyond mind-reading: multi-voxel pattern analysis of fMRI data. *Trends in Cognitive Sciences*, 10, 424-430.
- Núñez-Peña, M. I., & Honrubia-Serrano, M. L. (2004). P600 related to rule violation in an arithmetic task. *Cognitive Brain Research*, 18, 130-141.
- Obleser, J., & Kotz, S. A. (2010). Expectancy constraints in degraded speech modulate the language comprehension Network. *Cerebral Cortex*, 20, 633-640.
- Obleser, J., Zimmermann, J., Van Meter, J., & Rauschecker, J. P. (2007). Multiple stages of auditory speech perception reflected in event-related fMRI. *Cerebral Cortex*, 17, 2251-2257.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia*, 9, 97-113.
- Osterhout, L., & Holcomb, P. J. (1993). Event-related potentials and syntactic anomaly: Evidence of anomaly detection during the perception of continuous speech. *Language and Cognitive Processes*, 8, 413-437.
- Pakarinen, S., Takegata, R., Rinne, T., Huottilainen, M., & Näätänen, R. (2007). Measurement of extensive auditory discrimination profiles using the mismatch negativity (MMN) of the auditory event-related potential (ERP). *Clinical Neurophysiology*, 118, 177-185.
- Pakulak, E., & Neville, H. J. (2010). Proficiency differences in syntactic processing of monolingual native speakers indexed by event-related potentials. *Journal of Cognitive Neuroscience*, 22, 2728-2744.

- Pallier, C., Devauchelle, A.-D., & Dehaene, S. (2011). Cortical representation of the constituent structure of sentences. *Proceedings of the National Academy of Sciences*, 108, 2522–2527.
- Pascual-Marqui, R. D. (2002). Standardized low resolution brain electromagnetic tomography (sLORETA): technical details. *Methods & Findings in Experimental & Clinical Pharmacology*, 24, 5-12.
- Perani, D., Cappa, S. F., Schnur, T., Tettamanti, M., Collina, S., Rosa, M. M., & Fazio, F. (1999). The neural correlates of verb and noun processing: A PET study. *Brain*, 122, 2337–2344.
- Pereira, F., Mitchell, T., & Botvinick, M. (2009). Machine learning classifiers and fMRI: A tutorial overview. *NeuroImage*, 45, 199-209.
- Picton, T. W., Bentin, S., Berg, P., Donchin, E., Hillyard, S. A., Johnson Jr., R., Miller, G. A., Ritter, W., Ruchkin, D. S., Rugg, M. D., & Taylor, M. J. (2000). Guidelines for using human event-related potentials to study cognition: Recording standards and publication criteria. *Psychophysiology*, 37, 127-152.
- Poldrack, R. A. (2007). Region of interest analysis for fMRI. *Social Cognitive and Affective Neuroscience*, 2, 67-70.
- Poldrack, R. A., Halchenko, Y. O., & Hanson, S. J. (2009). Decoding the large-scale structure of brain function by classifying mental states across individuals. *Psychological Science*, 20, 1364-1372.
- Pulvermüller, F. (2010). Brain embodiment of syntax and grammar: Discrete combinatorial mechanisms spelt out in neuronal circuits. *Brain & Language*, 112, 167-179.
- Pulvermüller, F., & Assadollahi, R. (2007). Grammar or serial order?: Discrete combinatorial brain mechanisms reflected by the syntactic mismatch negativity. *Journal of Cognitive Neuroscience*, 19, 971-980.
- Pulvermüller, F., & Shtyrov, Y. (2003). Automatic processing of grammar in the human brain as revealed by the mismatch negativity. *NeuroImage*, 20, 159-172.
- Pulvermüller, F., & Shtyrov, Y. (2006). Language outside the focus of attention: The mismatch negativity as a tool for studying higher cognitive processes. *Progress in Neurobiology*, 79, 49-71.
- Rademacher, J., Morosan, P., Schormann, T., Schleicher, A., Werner, C., Freund, H.-J., & Zilles, K. (2001). Probabilistic mapping and volume measurement of human primary auditory cortex. *NeuroImage*, 13, 669-683.

- Rauschecker, J. P. (2011). An expanded role for the dorsal auditory pathway in sensorimotor control and integration. *Hearing Research*, 271, 16-25.
- Rauschecker, J. P., & Scott, S. K. (2009). Maps and streams in the auditory cortex: nonhuman primates illuminate human speech processing. *Nature Neuroscience*, 12, 718-724.
- Rauschecker, J. P., & Tian, B. (2004). Processing of band-passed noise in the lateral auditory belt cortex of the rhesus monkey. *Journal of Neurophysiology*, 91, 2578-2589.
- Rauschecker, J. P., Tian, B., & Hauser, M. (1995). Processing of complex sounds in the macaque nonprimary auditory cortex. *Science*, 268, 111-114.
- Recanzone, G. H. (in press). The biological basis of audition. *Wiley Interdisciplinary Reviews: Cognitive Science*. DOI:10.1002/wcs.118
- Recanzone, G. H., & Cohen, Y. E. (2010). Serial and parallel processing in the primate auditory cortex revisited. *Behavioural Brain Research*, 206, 1-7.
- Richter, N., Schröger, E., & Rübsamen, R. (2009). Hemispheric specialization during discrimination of sound sources reflected by MMN. *Neuropsychologia*, 47, 2652-2659.
- Rieger, J. W., Reichert, C., Gegenfurtner, K. R., Noesselt, T., Braun, C., Heinze, H. J., Kruse, R., & Hinrichs, H. (2008). Predicting the recognition of natural scenes from single trial MEG recordings of brain activity. *NeuroImage*, 42, 1056-1068.
- Rogalsky, C., & Hickok, G. (2009). Selective attention to semantic and syntactic features modulates sentence processing networks in anterior temporal cortex. *Cerebral Cortex*, 19, 786-796.
- Rogalsky, C. & Hickok, G. (2011). The Role of Broca's Area in Sentence Comprehension. *Journal of Cognitive Neuroscience*, 23, 1664-1680.
- Romberg, A. R., & Saffran, J. R. (2010). Statistical learning and language acquisition. *Wiley Interdisciplinary Reviews: Cognitive Science*, 1, 906-914.
- Rossi, S., Gugler, M. F., Friederici, A. D., & Hahne, A. (2006). The impact of proficiency on syntactic second-language processing of german and italian: Evidence from event-related potentials. *Journal of Cognitive Neuroscience*, 18, 2030-2048.
- Rossi, S., Gugler, M. F., Hahne, A., & Friederici, A. D. (2005). When word category information encounters morphosyntax: An ERP study. *Neuroscience Letters*, 384, 228-233.

- 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*, 266-286.
- Sabisch, B., Hahne, A., Glass, E., von Suchodoletz, W., & Friederici, A. D. (2009). Children with specific language impairment: The role of prosodic processes in explaining difficulties in processing syntactic information. *Brain Research, 1261*, 37-44.
- Sag, I. A., & Wasow, T. (1999). *Syntactic theory: A formal introduction*. Stanford, California, USA: CSLI Publications.
- Schmidt-Kassow, M., & Kotz, S. A. (2009). Event-related brain potentials suggest a late interaction of meter and syntax in the P600. *Journal of Cognitive Neuroscience, 21*, 1693-1708.
- Schön, D., Magne, C., & Besson, M. (2004). The music of speech: Music training facilitates pitch processing in both music and language. *Psychophysiology, 41*, 341-349.
- Sonnadara, R. R., Alain, C., & Trainor, L. J. (2006). Effects of spatial separation and stimulus probability on the event-related potentials elicited by occasional changes in sound location. *Brain Research, 1071*, 175-185.
- Schröger, E. (1996). Interaural time and level differences: integrated or separated processing? *Hearing Research, 96*, 191-198.
- Schröger, E. (2007). Mismatch negativity: A microphone into auditory memory. *Journal of Psychophysiology, 21*, 138-146.
- Schröger, E., & Wolff, C. (1996). Mismatch response of the human brain to changes in sound location. *NeuroReport, 7*, 3005-3008.
- Scott, S. K., & Johnsrude, I. S. (2003). The neuroanatomical and functional organization of speech perception. *Trends in Neurosciences, 26*, 100-107.
- Service, E., Helenius, P., Maury, S., & Salmelin, R. (2007). Localization of syntactic and semantic brain responses using magnetoencephalography. *Journal of Cognitive Neuroscience, 19*, 1193-1205.
- Shamma, S. A., & Micheyl, C. (2010). Behind the scenes of auditory perception. *Current Opinion in Neurobiology, 20*, 361-366.
- Sharon, D., Hämäläinen, M. S., Tootell, R. B. H., Halgren, E., & Belliveau, J. W. (2007). The advantage of combining MEG and EEG: Comparison to fMRI in focally stimulated visual cortex. *NeuroImage, 36*, 1225-1235.

- Shmuel, A. (2010). Locally measured neuronal correlates of functional MRI signals. In C. Mulert & L. Lemieux (Eds.), *EEG-fMRI: Physiological basis, technique and applications* (pp. 63-82). Berlin, Heidelberg: Springer-Verlag.
- Shtyrov, Y., Osswald, K., & Pulvermüller, F. (2008). Memory traces for spoken words in the brain as revealed by the hemodynamic correlate of the mismatch negativity. *Cerebral Cortex*, 18, 29-37.
- Shtyrov, Y., & Pulvermüller, F. (2007). Language in the mismatch negativity design: Motivations, benefits, and prospects. *Journal of Psychophysiology*, 21, 176-187.
- Shtyrov, Y., Pulvermüller, F., Näätänen, R., & Ilmoniemi, R. J. (2003). Grammar processing outside the focus of attention: An MEG study. *Journal of Cognitive Neuroscience*, 15, 1195-1206.
- Slabu, L., Escera, C. Grimm, S., & Costa-Faidella, J. (2010). Early change detection in humans as revealed by auditory brainstem and middle-latency evoked potentials. *European Journal of Neuroscience*, 32, 859-865.
- Slotnick, S. D., Moo, L. R., Segal, J. B., & Hart Jr., J. (2003). Distinct prefrontal cortex activity associated with item memory and source memory for visual shapes. *Cognitive Brain Research*, 17, 75-82.
- Slotnick, S. D., & Schacter, D. L. (2004). A sensory signature that distinguishes true from false memories. *Nature Neuroscience*, 7, 664-672.
- Summerfield, C., Eger, T., Greene, M., Koechlin, E., Mangels, J., & Hirsch, J. (2006). Predictive codes for forthcoming perception in the frontal cortex. *Science*, 314, 1311-1314.
- Suppes, P., Lu, Z.-L., & Han, B. (1997). Brain wave recognition of words. *Proceedings of the National Academy of Sciences*, 94, 14965-14969.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. New York: Thieme.
- Tallerman, M., Newmeyer, F., Bickerton, D., Bouchard, D., Kaan, E., & Rizzi, L. (2009). What kind of syntactic phenomena must biologists, neurobiologists, and computer scientists try to explain and replicate? In D. Bickerton & E. Szathmáry (Eds.), *Biological foundations and origin of syntax* (pp. 135-157). Cambridge, Massachusetts, USA; London, England: The MIT Press.
- Tata, M. S., & Ward, L. M. (2005). Early phase of spatial mismatch negativity is localized to a posterior "where" auditory pathway. *Experimental Brain Research*, 167, 481-486.

- Taulu, S., Kajola, M., & Simola, J. (2004). Suppression of interference and artifacts by the signal space separation method. *Brain Topography*, 16, 269-275.
- Tervaniemi, M., Kujala, T., Alho, K., Virtanen, J., Ilmoniemi, R. J., & Näätänen, R. (1999). Functional specialization of the human auditory cortex in processing phonetic and musical Sounds: A magnetoencephalographic (MEG) study. *NeuroImage*, 9, 330-336.
- Tervaniemi, M., Lehtokoski, A., Sinkkonen, J., Virtanen, J., Ilmoniemi, R. J., & Näätänen, R. (1999). Test-retest reliability of mismatch negativity for duration, frequency and intensity changes. *Clinical Neurophysiology*, 110, 1388-1393.
- Thoma, R. J., Hanlon, F. M., Moses, S. N., Edgar, J. C., Huang, M., Weisend, M. P., Irwin, J., Sherwood, A., Paulson, K., Bustillo, J., Adler, L. E., Miller, G. A., & Canive, J. M. (2003). Lateralization of auditory sensory gating and neuropsychological dysfunction in schizophrenia. *American Journal of Psychiatry*, 160, 1595-1605.
- Thoma, R. J., Hanlon, F. M., Petropoulos, H., Miller, G. A., Moses, S. N., Smith, A., Parks, L., Lundy, S. L., Sanchez, N. M., Jones, A., Huang, M., Weisend, M. P., & Canive, J. M. (2008). Schizophrenia diagnosis and anterior hippocampal volume make separate contributions to sensory gating. *Psychophysiology*, 45, 926-935.
- Tian, B., & Rauschecker, J. P. (2004). Processing of frequency-modulated sounds in the lateral auditory belt cortex of the rhesus monkey. *Journal of Neurophysiology*, 92, 2993-3013.
- Tyler, L. K., Bright, P., Fletcher, P., & Stamatakis, E. A. (2004). Neural processing of nouns and verbs: the role of inflectional morphology. *Neuropsychologia*, 42, 512-523.
- van den Brink, D., & Hagoort, P. (2004). The influence of semantic and syntactic context constraints on lexical selection and integration in spoken-word comprehension as revealed by ERPs. *Journal of Cognitive Neuroscience*, 16, 1068-1084.
- van Gerven, M., & Jensen, O. (2009). Attention modulations of posterior alpha as a control signal for two-dimensional brain-computer interfaces. *Journal of Neuroscience Methods*, 179, 78-84.
- Vandenberghe, R., Nobre, A. C., & Price, C. J. (2002). The response of left temporal cortex to sentences. *Journal of Cognitive Neuroscience*, 14, 550-560.

- Vrba, J., & Robinson, S. E. (2001). Signal processing in magnetoencephalography. *Methods*, 25, 249-271.
- Warren, J. D., & Griffiths, T. D. (2003). Distinct mechanisms for processing spatial sequences and pitch sequences in the human auditory brain. *The Journal of Neuroscience*, 23, 5799-5804.
- Wernicke, C. (1874). *Der aphasische Symptomenkomplex. Eine psychologische Studie auf anatomischer Basis*. Breslau: Cohn und Weigert.
- Wessinger, C. M., VanMeter, J., Tian, B., Van Lare, J., Pekar, J., & Rauschecker, J. P. (2001). Hierarchical organization of the human auditory cortex revealed by functional magnetic resonance imaging. *Journal of Cognitive Neuroscience*, 13, 1-7.
- Winkler, I., Denham, S. L., & Nelken, I. (2009). Modeling the auditory scene: predictive regularity representations and perceptual objects. *Trends in Cognitive Sciences*, 13, 532-540.
- Yamada, Y., & Neville, H. J. (2007). An ERP study of syntactic processing in English and nonsense sentences. *Brain Research*, 1130, 167-180.

List of Figures

Figure 2.1: From the EEG raw data to the ERP	18
Figure 2.2: Multivariate pattern analysis example for EEG/MEG recordings.....	22
Figure 5.1: Fundamental frequency (F_0) contours for each sentence type	44
Figure 5.2: Grand average ERFs time-locked to the participle onset	48
Figure 5.3: Time course of grand average brain activity	49
Figure 6.1: Grand average decoding accuracy time courses	62
Figure 6.2: Grand average topographical maps of the intra-subject analysis.....	63
Figure 6.3: Grand average topographical maps of the inter-subject analysis.....	64
Figure 6.4: Grand average decoding accuracies from the ROI analysis.....	65
Figure 7.1: Group activation maps for the univariate contrasts	78
Figure 7.2: Group decoding accuracy maps for the multivariate classifications....	81
Figure 8.1: Grand average ERFs time-locked to the onset of the participle.....	95
Figure 8.2: Grand average brain activations.....	96
Figure 8.3: Time course of STG grand average brain activity	98
Figure 8.4: Sentence onset brain responses.....	100
Figure 8.5: Results of the local maxima analysis in the temporal cortex	101

List of Tables

Table 6.1: Sentence materials and classifications.	56
Table 7.1: Stimulus materials in a 2×2 design	71
Table 7.2: Univariate analysis	79
Table 7.3: Multivariate analysis	82
Table 8.1: Sentence materials.....	91
Table 8.2: Talairach coordinates and corresponding Brodmann areas.....	99

List of Abbreviations

AC	<i>auditory cortex</i>
BA	<i>Brodmann area</i>
BOLD	<i>blood-oxygenation-level-dependent</i>
EEG	<i>electroencephalography</i>
ELAN	<i>early left anterior negativity</i>
EOG.....	<i>electrooculogram</i>
EPI.....	<i>echo planar imaging</i>
fMRI	<i>functional magnetic resonance imaging</i>
FWHM	<i>full-width-at-half-maximum</i>
GLM	<i>general linear model</i>
IFG	<i>inferior frontal gyrus</i>
LOOCV	<i>leave-one-out cross validation</i>
MEG.....	<i>magnetoencephalography</i>
MMN	<i>mismatch negativity</i>
MNI.....	<i>Montreal Neurological Institute</i>
MTG.....	<i>middle temporal gyrus</i>
PAC	<i>primary auditory cortex</i>
PSC.....	<i>percent signal change, percent signal change</i>
rCBF	<i>regional cerebral blood flow</i>
rmANOVA.....	<i>repeated measures analysis of variance</i>
ROI	<i>region of interest</i>
SEM	<i>standard error of the mean</i>
STG	<i>superior temporal gyrus</i>
STS	<i>superior temporal sulcus</i>
TE.....	<i>temporal area "E"</i>

Curriculum Vitae

Björn Herrmann

Date of birth 29th of April 1981
Place of birth Berlin, Germany

Education

2009 – 2011 Scholarship in the DFG (German Research Foundation)
graduate program "Function of Attention in Cognition"
University of Leipzig, Germany

2004 – 2008 Diploma (UAS) in Communication Psychology
University of applied sciences Zittau/Görlitz, Germany

2000 – 2002 Vocational baccalaureate diploma
Kläre-Bloch-Schule (Night school), Berlin, Germany

1997 – 2000 Industrial mechanics (for machine and system engineering)
Apprenticeship at Siemens AG, Berlin, Germany

Professional Experience

2008 – 2011 PhD student
MPI for Human Cognitive and Brain Sciences, Germany

2006 – 2007 Scientific internship
MPI for Human Cognitive and Brain Sciences, Germany

2005 – 2007 Student assistant
University of applied sciences Zittau/Görlitz, Germany

2000 – 2004 Quality management
Siemens AG (Power Generation), Berlin, Germany

Leipzig, 3rd of June 2011

Publications and submitted work

Ruhnau, P.*, Herrmann, B.*, Schröger, E. (submitted). Finding the right control: The MMN under investigation.

* Joint first authors.

Ruhnau, P., Herrmann, B., Maess, B., Schröger, E. (under revision). Maturation of obligatory auditory responses and their neural sources: Evidence from EEG and MEG.

Herrmann, B., Maess, B., Hahne, A., Schröger, E., Friederici, A. D. (in press). Syntactic and auditory spatial processing in the human temporal cortex: An MEG study. *NeuroImage*. DOI:10.1016/j.neuroimage.2011.04.034

Herrmann, B., Obleser, J., Kalberlah, C., Haynes, J.-D., & Friederici, A. D. (in press). Dissociable neural imprints of perception and grammar in auditory functional imaging. *Human Brain Mapping*. DOI:10.1002/hbm.21235

Herrmann, B., Maess, B., & Friederici, A. D. (2011). Violation of syntax and prosody - Disentangling their contributions to the early left anterior negativity (ELAN). *Neuroscience Letters*, 490, 116-120.

Herrmann, B., Maess, B., Hasting, A. S., & Friederici, A. D. (2009). Localization of the syntactic mismatch negativity in the temporal cortex: An MEG study. *NeuroImage*, 48, 590-600.

Talks

Herrmann, B. (2009). Approaching early syntactic and auditory spatial processing using MEG. Institute Colloquium at the MPI for Human Cognitive and Brain Sciences, Leipzig, Germany, November 2, 2009.

Selbstständigkeitserklärung

Hiermit erkläre ich, dass die vorliegende Arbeit ohne unzulässige Hilfe und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt wurde und dass die aus fremden Quellen direkt oder indirekt übernommenen Gedanken in der Arbeit als solche kenntlich gemacht worden sind.

Leipzig, den 03. Juni 2011

Björn Herrmann

MPI Series in Human Cognitive and Brain Sciences:

- 1 Anja Hahne
Charakteristika syntaktischer und semantischer Prozesse bei der auditiv Sprachverarbeitung: Evidenz aus ereigniskorrelierten Potentialstudien
- 2 Ricarda Schubotz
Erinnern kurzer Zeitdauern: Behaviorale und neurophysiologische Korrelate einer Arbeitsgedächtnisfunktion
- 3 Volker Bosch
Das Halten von Information im Arbeitsgedächtnis: Dissoziationen langsamer corticaler Potentiale
- 4 Jorge Jovicich
An investigation of the use of Gradient- and Spin-Echo (GRASE) imaging for functional MRI of the human brain
- 5 Rosemary C. Dymond
Spatial Specificity and Temporal Accuracy in Functional Magnetic Resonance Investigations
- 6 Stefan Zysset
Eine experimentalpsychologische Studie zu Gedächtnisabrufprozessen unter Verwendung der funktionellen Magnetresonanztomographie
- 7 Ulrich Hartmann
Ein mechanisches Finite-Elemente-Modell des menschlichen Kopfes
- 8 Bertram Opitz
Funktionelle Neuroanatomie der Verarbeitung einfacher und komplexer akustischer Reize: Integration haemodynamischer und elektro-physiologischer Maße
- 9 Gisela Müller-Plath
Formale Modellierung visueller Suchstrategien mit Anwendungen bei der Lokalisation von Hirnfunktionen und in der Diagnostik von Aufmerksamkeitsstörungen
- 10 Thomas Jacobsen
Characteristics of processing morphological structural and inherent case in language comprehension
- 11 Stefan Kölsch
*Brain and Music
A contribution to the investigation of central auditory processing with a new electrophysiological approach*
- 12 Stefan Frisch
Verb-Argument-Struktur, Kasus und thematische Interpretation beim Sprachverstehen
- 13 Markus Ullsperger
The role of retrieval inhibition in directed forgetting – an event-related brain potential analysis
- 14 Martin Koch
Measurement of the Self-Diffusion Tensor of Water in the Human Brain
- 15 Axel Hutt
Methoden zur Untersuchung der Dynamik raumzeitlicher Signale
- 16 Frithjof Kruggel
Detektion und Quantifizierung von Hirnaktivität mit der funktionellen Magnetresonanztomographie
- 17 Anja Dove
Lokalisierung an internen Kontrollprozessen beteiligter Hirngebiete mithilfe des Aufgabenwechselparadigmas und der ereigniskorrelierten funktionellen Magnetresonanztomographie
- 18 Karsten Steinhauer
Hirnphysiologische Korrelate prosodischer Satzverarbeitung bei gesprochener und geschriebener Sprache
- 19 Silke Urban
Verbinformationen im Satzverstehen
- 20 Katja Werheid
Implizites Sequenzlernen bei Morbus Parkinson
- 21 Doreen Nessler
Is it Memory or Illusion? Electrophysiological Characteristics of True and False Recognition
- 22 Christoph Herrmann
Die Bedeutung von 40-Hz-Oszillationen für kognitive Prozesse
- 23 Christian Fiebach
*Working Memory and Syntax during Sentence Processing.
A neurocognitive investigation with event-related brain potentials and functional magnetic resonance imaging*
- 24 Grit Hein
Lokalisation von Doppelaufgabendefiziten bei gesunden älteren Personen und neurologischen Patienten
- 25 Monica de Filippis
Die visuelle Verarbeitung unbeachteter Wörter. Ein elektrophysiologischer Ansatz
- 26 Ulrich Müller
Die katecholaminerge Modulation präfrontaler kognitiver Funktionen beim Menschen
- 27 Kristina Uhl
Kontrollfunktion des Arbeitsgedächtnisses über interferierende Information
- 28 Ina Bornkessel
The Argument Dependency Model: A Neurocognitive Approach to Incremental Interpretation

- 29 Sonja Lattner
Neurophysiologische Untersuchungen zur auditorischen Verarbeitung von Stimminformationen
- 30 Christin Grünewald
Die Rolle motorischer Schemata bei der Objektpräsentation: Untersuchungen mit funktioneller Magnetresonanztomographie
- 31 Annett Schirmer
Emotional Speech Perception: Electrophysiological Insights into the Processing of Emotional Prosody and Word Valence in Men and Women
- 32 André J. Szameitat
Die Funktionalität des lateral-präfrontalen Cortex für die Verarbeitung von Doppelaufgaben
- 33 Susanne Wagner
Verbales Arbeitsgedächtnis und die Verarbeitung ambiger Wörter in Wort- und Satzkontexten
- 34 Sophie Manthey
Hirn und Handlung: Untersuchung der Handlungsrepräsentation im ventralen prämotorischen Cortex mit Hilfe der funktionellen Magnet-Resonanz-Tomographie
- 35 Stefan Heim
Towards a Common Neural Network Model of Language Production and Comprehension: fMRI Evidence for the Processing of Phonological and Syntactic Information in Single Words
- 36 Claudia Friedrich
Prosody and spoken word recognition: Behavioral and ERP correlates
- 37 Ulrike Lex
Sprachlateralisierung bei Rechts- und Linkshändern mit funktioneller Magnetresonanztomographie
- 38 Thomas Arnold
Computergestützte Befundung klinischer Elektroenzephalogramme
- 39 Carsten H. Wolters
Influence of Tissue Conductivity Inhomogeneity and Anisotropy on EEG/MEG based Source Localization in the Human Brain
- 40 Ansgar Hantsch
Fisch oder Karpfen? Lexikale Aktivierung von Benennungsalternativen bei der Objektbenennung
- 41 Peggy Bungert
*Zentralnervöse Verarbeitung akustischer Informationen
Signalidentifikation, Signallateralisation und zeitgebundene Informationsverarbeitung bei Patienten mit erworbenen Hirnschädigungen*
- 42 Daniel Senkowski
Neuronal correlates of selective attention: An investigation of electro-physiological brain responses in the EEG and MEG
- 43 Gert Wollny
Analysis of Changes in Temporal Series of Medical Images
- 44 Angelika Wolf
Sprachverstehen mit Cochlea-Implantat: EKP-Studien mit postlingual ertaubten erwachsenen CI-Trägern
- 45 Kirsten G. Volz
Brain correlates of uncertain decisions: Types and degrees of uncertainty
- 46 Hagen Huttner
Magnetresonanztomographische Untersuchungen über die anatomische Variabilität des Frontallappens des menschlichen Großhirns
- 47 Dirk Köster
Morphology and Spoken Word Comprehension: Electrophysiological Investigations of Internal Compound Structure
- 48 Claudia A. Hruska
Einflüsse kontextueller und prosodischer Informationen in der auditorischen Satzverarbeitung: Untersuchungen mit ereigniskorrelierten Hirnpotentialen
- 49 Hannes Ruge
Eine Analyse des raum-zeitlichen Musters neuronaler Aktivierung im Aufgabenwechselparadigma zur Untersuchung handlungssteuernder Prozesse
- 50 Ricarda I. Schubotz
Human premotor cortex: Beyond motor performance
- 51 Clemens von Zerssen
Bewusstes Erinnern und falsches Wiedererkennen: Eine funktionelle MRT Studie neuroanatomischer Gedächtniskorrelate
- 52 Christiane Weber
*Rhythm is gonna get you.
Electrophysiological markers of rhythmic processing in infants with and without risk for Specific Language Impairment (SLI)*
- 53 Marc Schönwiesner
Functional Mapping of Basic Acoustic Parameters in the Human Central Auditory System
- 54 Katja Fiehler
Temporospatial characteristics of error correction
- 55 Britta Stolterfoht
Processing Word Order Variations and Ellipses: The Interplay of Syntax and Information Structure during Sentence Comprehension
- 56 Claudia Danielmeier
Neuronale Grundlagen der Interferenz zwischen Handlung und visueller Wahrnehmung

- 57 Margret Hund-Georgiadis
Die Organisation von Sprache und ihre Reorganisation bei ausgewählten, neurologischen Erkrankungen gemessen mit funktioneller Magnetresonanztomographie – Einflüsse von Händigkeit, Läsion, Performanz und Perfusion
- 58 Jutta L. Mueller
Mechanisms of auditory sentence comprehension in first and second language: An electrophysiological miniature grammar study
- 59 Franziska Biedermann
Auditorische Diskriminationsleistungen nach unilateralen Läsionen im Di- und Telenzephalon
- 60 Shirley-Ann Rüschemeyer
The Processing of Lexical Semantic and Syntactic Information in Spoken Sentences: Neuroimaging and Behavioral Studies of Native and Non-Native Speakers
- 61 Kerstin Leuckefeld
The Development of Argument Processing Mechanisms in German. An Electrophysiological Investigation with School-Aged Children and Adults
- 62 Axel Christian Kühn
Bestimmung der Lateralisierung von Sprachprozessen unter besondere Berücksichtigung des temporalen Cortex, gemessen mit fMRT
- 63 Ann Pannekamp
Prosodische Informationsverarbeitung bei normalsprachlichem und deviantem Satzmaterial: Untersuchungen mit ereigniskorrelierten Hirnpotentialen
- 64 Jan Derrfuß
Functional specialization in the lateral frontal cortex: The role of the inferior frontal junction in cognitive control
- 65 Andrea Mona Philipp
The cognitive representation of tasks – Exploring the role of response modalities using the task-switching paradigm
- 66 Ulrike Toepel
Contrastive Topic and Focus Information in Discourse – Prosodic Realisation and Electrophysiological Brain Correlates
- 67 Karsten Müller
Die Anwendung von Spektral- und Waveletanalyse zur Untersuchung der Dynamik von BOLD-Zeitreihen verschiedener Hirnareale
- 68 Sonja A.Kotz
The role of the basal ganglia in auditory language processing: Evidence from ERP lesion studies and functional neuroimaging
- 69 Sonja Rossi
The role of proficiency in syntactic second language processing: Evidence from event-related brain potentials in German and Italian
- 70 Birte U. Forstmann
Behavioral and neural correlates of endogenous control processes in task switching
- 71 Silke Paulmann
Electrophysiological Evidence on the Processing of Emotional Prosody: Insights from Healthy and Patient Populations
- 72 Matthias L. Schroeter
Enlightening the Brain – Optical Imaging in Cognitive Neuroscience
- 73 Julia Reinholz
Interhemispheric interaction in object- and word-related visual areas
- 74 Evelyn C. Ferstl
The Functional Neuroanatomy of Text Comprehension
- 75 Miriam Gade
Aufgabeneinhibition als Mechanismus der Konfliktreduktion zwischen Aufgabenrepräsentationen
- 76 Juliane Hofmann
Phonological, Morphological, and Semantic Aspects of Grammatical Gender Processing in German
- 77 Petra Augurzky
Attaching Relative Clauses in German – The Role of Implicit and Explicit Prosody in Sentence Processing
- 78 Uta Wolfensteller
Habituelle und arbiträre sensorimotorische Verknüpfungen im lateralen prämotorischen Kortex des Menschen
- 79 Päivi Sivenon
Event-related brain activation in speech perception: From sensory to cognitive processes
- 80 Yun Nan
Music phrase structure perception: the neural basis, the effects of acculturation and musical training
- 81 Katrin Schulze
Neural Correlates of Working Memory for Verbal and Tonal Stimuli in Nonmusicians and Musicians With and Without Absolute Pitch
- 82 Korinna Eckstein
Interaktion von Syntax und Prosodie beim Sprachverstehen: Untersuchungen anhand ereigniskorrelierter Hirnpotentiale
- 83 Florian Th. Siebörger
Funktionelle Neuroanatomie des Textverstehens: Kohärenzbildung bei Witzen und anderen ungewöhnlichen Texten

- 84 Diana Böttger
Aktivität im Gamma-Frequenzbereich des EEG: Einfluss demographischer Faktoren und kognitiver Korrelate
- 85 Jörg Bahlmann
Neural correlates of the processing of linear and hierarchical artificial grammar rules: Electrophysiological and neuroimaging studies
- 86 Jan Zwickel
Specific Interference Effects Between Temporally Overlapping Action and Perception
- 87 Markus Ullsperger
Functional Neuroanatomy of Performance Monitoring: fMRI, ERP, and Patient Studies
- 88 Susanne Dietrich
Vom Brüllen zum Wort – MRT-Studien zur kognitiven Verarbeitung emotionaler Vokalisationen
- 89 Maren Schmidt-Kassow
What's Beat got to do with ist? The Influence of Meter on Syntactic Processing: ERP Evidence from Healthy and Patient populations
- 90 Monika Lück
Die Verarbeitung morphologisch komplexer Wörter bei Kindern im Schulalter: Neurophysiologische Korrelate der Entwicklung
- 91 Diana P. Szameitat
Perzeption und akustische Eigenschaften von Emotionen in menschlichem Lachen
- 92 Beate Sabisch
Mechanisms of auditory sentence comprehension in children with specific language impairment and children with developmental dyslexia: A neurophysiological investigation
- 93 Regine Oberecker
Grammatikverarbeitung im Kindesalter: EKP-Studien zum auditorischen Satzverstehen
- 94 Şükrü Barış Demiral
Incremental Argument Interpretation in Turkish Sentence Comprehension
- 95 Henning Holle
The Comprehension of Co-Speech Iconic Gestures: Behavioral, Electrophysiological and Neuroimaging Studies
- 96 Marcel Braß
Das inferior frontale Kreuzungsareal und seine Rolle bei der kognitiven Kontrolle unseres Verhaltens
- 97 Anna S. Hasting
Syntax in a blink: Early and automatic processing of syntactic rules as revealed by event-related brain potentials
- 98 Sebastian Jentschke
Neural Correlates of Processing Syntax in Music and Language – Influences of Development, Musical Training and Language Impairment
- 99 Amelie Mahlstedt
The Acquisition of Case marking Information as a Cue to Argument Interpretation in German An Electrophysiological Investigation with Pre-school Children
- 100 Nikolaus Steinbeis
Investigating the meaning of music using EEG and fMRI
- 101 Tilmann A. Klein
Learning from errors: Genetic evidence for a central role of dopamine in human performance monitoring
- 102 Franziska Maria Korb
Die funktionelle Spezialisierung des lateralen präfrontalen Cortex: Untersuchungen mittels funktioneller Magnetresonanztomographie
- 103 Sonja Fleischhauer
Neuronale Verarbeitung emotionaler Prosodie und Syntax: die Rolle des verbalen Arbeitsgedächtnisses
- 104 Friederike Sophie Haupt
The component mapping problem: An investigation of grammatical function reanalysis in differing experimental contexts using event-related brain potentials
- 105 Jens Brauer
Functional development and structural maturation in the brain's neural network underlying language comprehension
- 106 Philipp Kanske
Exploring executive attention in emotion: ERP and fMRI evidence
- 107 Julia Grieser Painter
Music, meaning, and a semantic space for musical sounds
- 108 Daniela Sammler
The Neuroanatomical Overlap of Syntax Processing in Music and Language - Evidence from Lesion and Intracranial ERP Studies
- 109 Norbert Zmyj
Selective Imitation in One-Year-Olds: How a Model's Characteristics Influence Imitation
- 110 Thomas Fritz
Emotion investigated with music of variable valence – neurophysiology and cultural influence
- 111 Stefanie Regel
The comprehension of figurative language: Electrophysiological evidence on the processing of irony

- 112 Miriam Beisert
Transformation Rules in Tool Use
- 113 Veronika Krieghoff
Neural correlates of Intentional Actions
- 114 Andreja Bubić
Violation of expectations in sequence processing
- 115 Claudia Männel
Prosodic processing during language acquisition: Electrophysiological studies on intonational phrase processing
- 116 Konstanze Albrecht
Brain correlates of cognitive processes underlying intertemporal choice for self and other
- 117 Katrin Sakreida
Nicht-motorische Funktionen des prämotorischen Kortex: Patientenstudien und funktionelle Bildgebung
- 118 Susann Wolff
The interplay of free word order and pro-drop in incremental sentence processing: Neurophysiological evidence from Japanese
- 119 Tim Raettig
The Cortical Infrastructure of Language Processing: Evidence from Functional and Anatomical Neuroimaging
- 120 Maria Golde
Premotor cortex contributions to abstract and action-related relational processing
- 121 Daniel S. Margulies
Resting-State Functional Connectivity fMRI: A new approach for assessing functional neuroanatomy in humans with applications to neuroanatomical, developmental and clinical questions
- 122 Franziska Süß
The interplay between attention and syntactic processes in the adult and developing brain: ERP evidences
- 123 Stefan Bode
From stimuli to motor responses: Decoding rules and decision mechanisms in the human brain
- 124 Christiane Diefenbach
Interactions between sentence comprehension and concurrent action: The role of movement effects and timing
- 125 Moritz M. Daum
Mechanismen der frühkindlichen Entwicklung des Handlungsverständnisses
- 126 Jürgen Dukart
Contribution of FDG-PET and MRI to improve Understanding, Detection and Differentiation of Dementia
- 127 Kamal Kumar Choudhary
Incremental Argument Interpretation in a Split Ergative Language: Neurophysiological Evidence from Hindi
- 128 Peggy Sparenberg
Filling the Gap: Temporal and Motor Aspects of the Mental Simulation of Occluded Actions
- 129 Luming Wang
The Influence of Animacy and Context on Word Order Processing: Neurophysiological Evidence from Mandarin Chinese
- 130 Barbara Ettrich
Beeinträchtigung frontomedianer Funktionen bei Schädel-Hirn-Trauma
- 131 Sandra Dietrich
Coordination of Unimanual Continuous Movements with External Events
- 132 R. Muralikrishnan
An Electrophysiological Investigation Of Tamil Dative-Subject Constructions
- 133 Christian Obermeier
Exploring the significance of task, timing and background noise on gesture-speech integration