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The Cortical Infrastructure of Language Processing:
Evidence from Functional and Anatomical
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Introduction

Theoretical accounts of language as a combinatorial symbolic system generally distinguish the description of the meaning of the symbols themselves and the description of the rules that govern the way in which multiple symbols may be combined, with the former constituting the field of semantics and the latter constituting the field of syntax. Crucially, the meaning of an utterance is dependent on both its syntactic structure and the semantics of the individual words that it contains. This is particularly relevant when considering on-line processes of speech comprehension in the context of grammatical anomalies: a sentence that is syntactically illegal is also harder to understand in terms of the combinatorial meaning that it is supposed to convey.

This last point is critical with regard to the interpretation of the results of psycho- and neurolinguistic experiments utilizing "violation" paradigms. The basic logic of this method of investigation is compelling: participants are presented with a number of sentences that are either correct or contain an anomaly that concerns a particular subset of linguistic rules. Assuming that the grammatical violation will selectively disrupt the corresponding cognitive processes, a comparison of the reactions to incorrect and correct sentences makes it possible to draw inferences about the mental operations that are involved - depending on the method that is used to acquire the empirical data, this can encompass the timing, the electrophysiology and the neuroanatomical localization of the underlying processes.

However, the separation of syntactic and semantic aspects of the processing of grammatical anomalies can be tricky because of the inherent entanglement of both levels of representation that was described further above. This is especially true with regard to imaging methods like functional magnetic resonance imaging (fMRI) that have a comparatively low temporal resolution. One of the goals of the current dissertation is to remedy this situation by investigating the brain response to syntactic violations both in the presence of word-level semantic information (that is, in conventional real word sentences) and in pseudo-word sentences that are deprived of lexical-semantic meaning. This will be done in both an fMRI and an event-related potentials (ERPs) experiment (see Chapter 7) in order to be able to gather

information on both the neuroanatomical localization and the processing timecourse of the relevant cognitive operations.

In order to be able to construct pseudo-word sentences that are really devoid of meaning, a first experiment will evaluate the suitability of different types of pseudo-words with regard to the blocking of lexical-semantic processes. In the existing literature on pseudo-word processing, non-lexical stimuli are often generated by only changing a small number of phonemes or letters in a real word, yielding pseudo-words that can potentially be "repaired" and may thus not be an optimal choice if word-level semantic processes are to be suppressed. Another type of pseudo-word - sometimes contrastively referred to as "non-word" - that is commonly implemented is created by combining phonemes into sequences that are phonotactically illegal in a given language. While such stimuli may be more successful in blocking lexical access than pseudo-words that are derived from real words, they may also induce additional processing costs because of their anomalous phonotactic structure, thus creating a potential confound. The experiment described in Chapter 6 will contrast the brain response to the processing of these two types of pseudo-words while at the same time introducing and testing a novel procedure for pseudo-word generation that is designed to overcome the problems described above.

The experiments that were characterized so far make use of two different methods of data acquisition (fMRI and ERPs) that will yield complementary information on the hemodynamic and electrophysiological correlates of speech comprehension, addressing a broad range of topics from lexical access to syntactic structure building and conceptual interpretation. In order to fully appreciate the architecture of the language processing network, however, information about both the neuroanatomical organization and the cortico-cortical connectivity of the brain regions that are critically involved in comprehension-related cognitive operations have to be taken into account. One of the areas that is highly relevant in this respect is the superior temporal gyrus (STG) of the left hemisphere which houses both the primary auditory cortex and a number of higher-level processing regions (the most prominent probably being Wernicke's Area). In Chapter 5, diffusion tensor imaging (DTI) will be utilized as a tool to investigate both the possibility of an anatomical parcellation of the STG into different subareas and to shed light on its connectivity to other regions of the cortex. Since such information is already available for the frontal lobe (see Anwander et al., 2007), the DTI study just described will yield important complementary information allowing a considerably refined description of the neuroanatomical and communicative infrastructure of the language processing network.

Part I

Theoretical Background

Chapter 1

Tools of the Trade

1.1 Introduction

In the following sections, the theoretical foundations of the techniques used to acquire the data presented in Part II will be discussed. While there are numerous other methods for investigating the relation between cognitive and neurobiological processes (see Section 2.3), the procedures that are described here allow the study of three important areas of inquiry in cognitive neuroscience: while electroencephalography (EEG) permits the observation of evolving brain signals on a millisecond scale, functional magnetic resonance imaging offers the opportunity to localize the sources of ongoing neural activity with an accuracy in the millimeter range. Finally, diffusion tensor imaging can supply detailed information about the anatomical connections between different regions of the brain, yielding important insights into the communicative infrastructure of the neuronal networks underlying cognition.

1.2 Event-Related Brain Potentials

1.2.1 Introduction

While evidence for nerve fibers transmitting information by means of minute electrical currents had already been discovered by Luigi Galvani as early as 1780 (first published in: Galvani, 1791), empirical indications for the existence of electricity in brain tissue were not reported until Richard Caton published his experiments on the brains of apes and dogs almost a century later (Caton, 1875). Still later, in 1924, Hans Berger was the first to demonstrate the possibility of measuring electric current flow by directly placing electrodes on the exposed cortical surface of the human brain (first published in: Berger, 1929). While initially only recording the electrical activity of the brain intracranially during surgery, Berger

quickly developed a method of measuring current flow on the scalp, laying the groundwork for modern electroencephalography.

1.2.2 The Physiological Basis of Electroencephalography

Electrochemical gradients due to different ion concentrations across cell membranes are crucial for the generation and maintenance of the bioelectrical signals that neurons use to transmit information.¹ While it is possible to measure the electrical activity of a single cell with intracranial recordings, currents that are strong enough to be picked up at the surface of the skull are only generated by larger cell assemblies.

In order to elicit a measurable EEG signal, a group of neurons must satisfy a number of conditions: all cells must have a comparable structure and have to be aligned in a parallel fashion, otherwise positive and negative charges in different directions will cancel each other out. Furthermore, the electrical activity of the cells must occur in temporal synchrony so that the small discharges of the individual neurons accumulate and generate a detectable signal. Finally, the electrical dipole that is to be measured must be aligned perpendicular to the cranial surface so that it can be picked up by electrodes placed on the scalp. The most prominent type of neuron meeting these criteria is the pyramidal cell found in layer five of the cortex. An electrical charge traveling down the apical dendrite of such a neuron leaves a shortage of positively charged ions in the extracellular space surrounding the synapse while generating a corresponding surplus at the soma (see Figure 1.1), effectively creating a dipole with the correct alignment to be measurable at the surface of the skull.

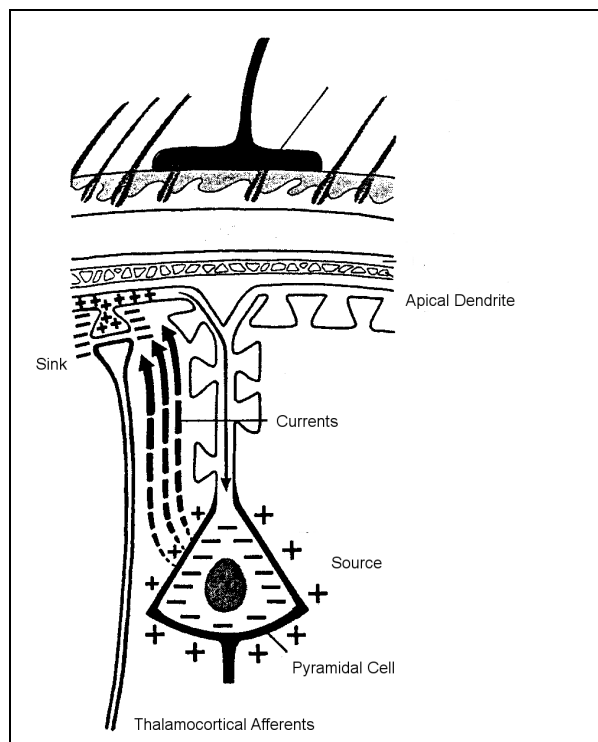
It is important to note that EEG is not suited to pick up the electrical currents generated by a number of potentially interesting sources like axonal action potentials and post-synaptic potentials traveling along basal (non-apical) dendrites. In addition to this, the spatial resolution of EEG is very low: it is not possible to uniquely determine the brain region in which a dipole generating an electrical current on the scalp is situated (this is known as the “inverse problem” in EEG research, although it should be noted that this is a rather general term that is also applied to a whole range of phenomena in other scientific fields). While these drawbacks have to be kept in mind when designing experiments and interpreting data, the EEG method is still an invaluable tool for neuroscientific investigations when temporal information on the millisecond scale is essential.

1.2.3 From the EEG to ERPs

Recording some of the electric currents generated by the brain has important uses in a clinical setting (e.g. in the diagnosis and treatment of epileptic seizures; see Smith, 2005), but a

¹The following descriptions are based on Birbaumer and Schmidt (2003) and Cacioppo et al. (2000).

Figure 1.1: Dipole Generated by a Pyramidal Cell



Current flow and dipole generated by an electrical charge travelling down the apical dendrite of a pyramidal cell. Adapted from Birbaumer and Schmidt (2003).

continuously acquired electroencephalogram as such does only allow for very coarse inferences with regard to ongoing cognitive processes. While general physiological states like sleep and wakefulness can be clearly distinguished by the overall amplitude and frequency of EEG waveforms (Niedermeyer and da Silva, 2004; Nunez, 1995), subtle variations in the signal that occur in response to external stimuli and the associated cognitive processes remain undetectable unless additional mathematical and experimental techniques are implemented. It is this observation that spawned the development of the ERP paradigm (Handy, 2004; Niedermeyer and da Silva, 2004).

The basic idea behind the aforementioned method (also see Figure 1.2) is that the signal-to-noise-ratio (SNR) of EEG data that are acquired in an experimental setting can be increased by averaging across a number of measurements that are comparable with regard to

Figure 1.2: Computing ERPs from Raw EEG Data

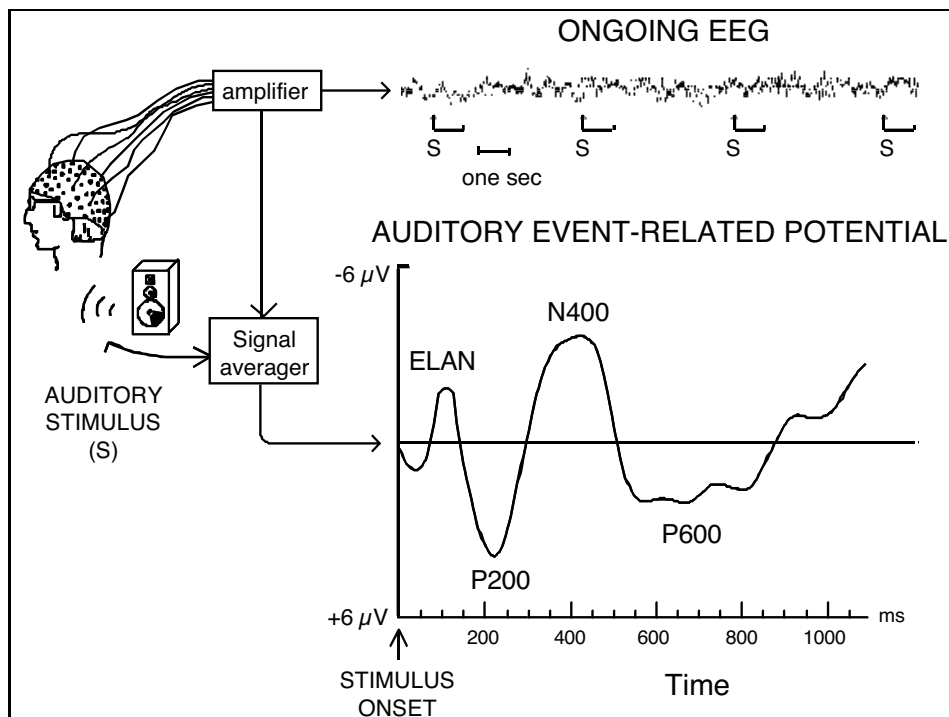


Illustration of the steps involved in computing ERPs from a continuous EEG. Adapted from Coles and Rugg (1995).

a particular variable of interest. In order to achieve this the electroencephalogram is acquired while participants are confronted with a sufficient number² of experimental stimuli of different categories. Once the recording is complete, the EEG responses to stimuli of the same type are averaged for each participant, starting with a pre-defined point in time (for example, the onset or offset of stimulation). Two assumptions are crucial here: the electrophysiological brain response to comparable stimuli is taken to remain constant, and the noise in the data is taken to vary unsystematically.³ Thus, while the effects of the ex-

perimental manipulation are assumed to add up over multiple measurements, negative and positive signal deflections that are due to noise are taken to cancel each other out.

Finally, the mean ERPs for each category are averaged across participants. The resulting data set can then be used for visualization and statistical analysis, resulting in the possibility to test hypotheses regarding the differences between stimulus categories. Significant voltage differences in the ERPs recorded for different experimental conditions are commonly designated by combining their polarity (P for positive, N for negative) and their latency (e.g. “N400” denotes a negativity occurring after 400 milliseconds). Further properties of the measured signal (i.e. amplitude and topography) may be taken into account in order to differentiate components that are similar with regard to the first two criteria - for example, a negativity occurring 300-500 ms post-stimulus onset with a focus on left-frontal electrodes is known as a “left anterior negativity” (LAN) in electrophysiological language research (also see Section 2.3.2; for comprehensive reviews, the reader is referred to Friederici et al., 2002a and Friederici and Weissenborn, 2007). While this brain reaction is often seen in response to morphosyntactic mismatches, a negativity occurring in the same time range, but having a centro-parietal distribution (the N400) is generally interpreted as a marker of semantic integration difficulties.

While ERPs supply information about ongoing cognitive operations with a temporal resolution on the millisecond scale, the neuroanatomical correlates of the corresponding processes are more suitably investigated with imaging methods that allow for a more accurate spatial localization of the observed effects. In the experiments described in Chapters 6 and 7, fMRI was used for this purpose. The developmental history and the basic principles of this technique are described in the following sections.

1.3 Functional Magnetic Resonance Imaging

1.3.1 Introduction

Magnetic resonance as a phenomenon was discovered independently by Felix Bloch (Bloch, 1946; Bloch et al., 1946) and Edward Purcell (Purcell et al., 1946) in 1946. Their discovery (for which they received the Nobel Prize in Physics in 1952) led to the development of Nuclear Magnetic Resonance (NMR) Spectroscopy, a technique that allowed the analysis of the chemical composition of a wide variety of substances. However, NMR Spectroscopy

²The number of stimuli per category that is needed to extract a measurable signal is determined by a number of factors, most prominently the anticipated strength of the electrophysiological response. In language research, 20-30 items are generally regarded as a minimum (Hahne, 1998).

³This is a crucial assumption. Non-random noise (i.e. due to regular eye blinks) has to be tackled by more intricate mathematical methods and may have a detrimental effect on the results if it goes undetected.

only yielded one-dimensional information about the properties of a sample as a whole and was mainly used in physics and chemistry until the 1970s.

In 1971, Raymond Damadian made the groundbreaking discovery that different types of biological tissue gave off different NMR signals (Damadian, 1971). Two years later, in 1973, Peter Lauterbur demonstrated the use of magnetic field gradients to extract two-dimensional information from a given sample (Lauterbur, 1973). This method allowed the reconstruction of tomographic images from NMR data, essentially setting off the development of anatomical NMR imaging. Other researchers like Richard Ernst (most widely known for his contribution to the publication by Kumar et al., 1975) and Peter Mansfield (Mansfield, 1977) further refined the technique, and by the beginning of the 1980s the first commercial magnetic resonance imaging (MRI) scanners intended for medical research were built.

The relationship between cortical blood flow and the strength of the MRI signal that forms the basis of functional magnetic resonance imaging was discovered by Seiji Ogawa in 1990 (Ogawa et al., 1990). In the years following this discovery, both fMRI acquisition methods as well as the procedures for data analysis have been improved considerably, and functional MR imaging is now widely regarded as an indispensable tool for neurocognitive research.

1.3.2 MRI Physics

Magnetic resonance is a behavior exhibited by particles and atoms with non-zero spin.⁴ While "spin" is a quantum mechanical concept, a useful (though strictly speaking inaccurate) analogy from classical physics is angular momentum: in a way, particles can be thought of as constantly rotating around their own center of mass. Importantly, having angular momentum as well as an electrical charge results in having a magnetic moment since rotating electrical charges generate magnetic fields - so effectively, charged particles behave like tiny magnets. For MR imaging, the most important particle is the positively charged proton since it is abundant in living tissue in the form of hydrogen.

As long as there is no strong external magnetic field, the north and south poles of the protons in a tissue sample are oriented randomly and do not produce a measurable net magnetization. When a static magnetic field (called B_0 in an MRI context) is present, however, the protons align with it, resulting in a net magnetization that is called "longitudinal". Because of their intrinsic rotational movement in combination with the directional force exerted by B_0 , this alignment is not static: the particles exhibit a behavior known as "precession". Thus, the north and south poles of each proton rotate around an imaginary axis between the north and south poles of the external magnetic field. The frequency of this

⁴The following descriptions are based on Buxton (2002) and Papanicolaou (1998).

precession, called the Larmor frequency (ω), is dependent on the gyromagnetic ratio of the protons (γ) and the strength of B_0 , as expressed in the Larmor equation:

$$\omega = \gamma B_0$$

Protons have a gyromagnetic ratio of 42.58 megahertz (MHz) per Tesla, resulting in a Larmor frequency of 127.74 Mhz at 3 Tesla, which is a common field strength in fMRI. If a second magnetic field (called B_1) oscillating at the Larmor frequency of the protons is applied at a 90° angle to B_0 , they will start to precess around the axis of B_1 as well. To an external observer this combined precession results in the net magnetization spiraling down from the z-axis into the x-y plane (and beyond, if B_1 is applied for a sufficient time). This effectively turns the longitudinal magnetization into what is called "transversal" magnetization. Importantly, the precession is phase coherent during the application of B_1 - otherwise, the magnetization vectors of protons pointing in different directions would cancel each other out.

Once B_1 is turned off the protons align with B_0 again. This return of the longitudinal magnetization along the z-axis is called T1 relaxation. At the same time, their precession in the x-y plane starts to dephase, resulting in a loss of transversal magnetization that is called T2 relaxation. The speed of T1 relaxation is dependent on the type of tissue that is imaged, so by measuring the T1 relaxation times at a sufficient number of coordinates in a sample (for example, a human brain), it is possible to compute an image with different brightness values representing different tissue types. This is the basis of anatomical MR imaging.

T2 relaxation speed per se is similarly dependent on tissue types, but is additionally influenced by small magnetic field inhomogeneities that are caused (among other factors) by the presence of deoxygenated hemoglobin. Because of this, the transversal magnetization in brain tissue decays with a speed called T2* relaxation time (which is always faster than T2 alone). Because T2* is dependent on the amount of deoxygenated hemoglobin that is present in the brain region that is imaged, measuring T2* times allows inferences about the intensity of the oxygen metabolism in that area. Since an increase in oxygen consumption is an indication of an increase in neural activity, this is the basis of functional MR imaging.

1.3.3 Hemodynamic Imaging

As mentioned above, the presence of deoxygenated hemoglobin reduces the strength of the MR signal. Consequently, brain areas in which the regional cerebral metabolic rate of oxygen (rCMO₂) increases become less visible in T2*-weighted images - but not for very long. In response to the increase in oxygen uptake a disproportionately large increase in

Figure 1.3: BOLD-Response

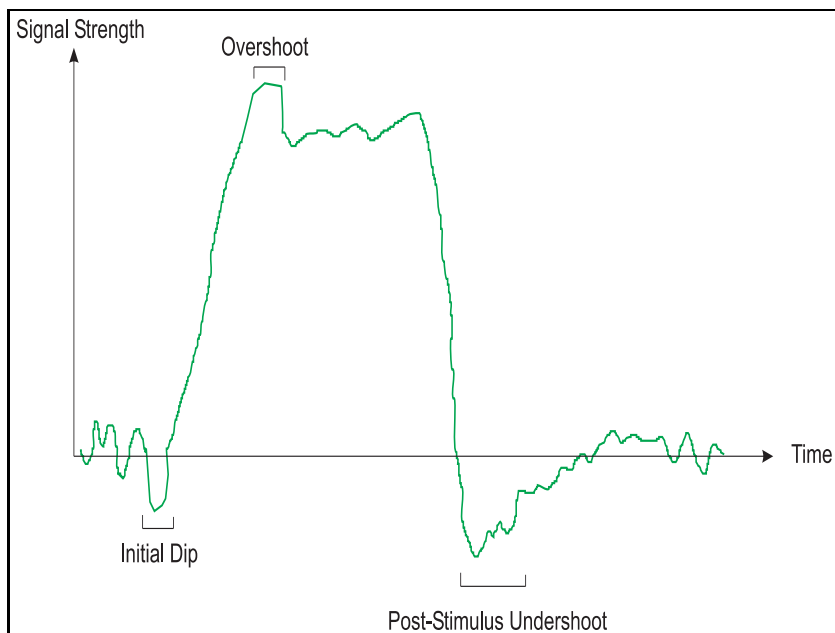


Illustration of the BOLD response. Three typical features (initial dip, overshoot and undershoot) are marked.

regional cerebral blood flow (rCBF) occurs, followed by an increase in regional cerebral blood volume (rCBV).

In effect, deoxygenated blood is quickly washed out and replaced by its oxygen-rich counterpart, leading to a decrease in the concentration of deoxyhemoglobin and a corresponding increase in MR signal strength - this is called the "blood oxygen level dependent" or "BOLD" response (see Figure 1.3). While the initial reduction of the T2* contrast, also called the "initial dip", already occurs 1 to 2 seconds post-stimulus, only lasts about a second and is spatially confined down to the level of individual cortical columns, the following increase in signal strength has a time-to-peak of about 5 seconds post-stimulus, a full-width at half-maximum of about 4 seconds and a spatial distribution of 3-5 mm (Norris, 2006). It is important to keep in mind that this imposes physiological restrictions on both the spatial and the temporal resolution of functional MR imaging, although these limitations can partly be overcome by clever methods of experimental design and statistical analysis (i.e. jittering; see Dale, 1999).

While the general mechanisms depicted in the last paragraph are well established, the exact nature of the coupling between neural activity, hemodynamics and the MR signal is complex and still not understood completely. It is assumed that the vascular response is primarily caused by local synaptic activity, not by neuronal spiking - that is, it is dependent on the amount of input to a particular brain region as well as intra-regional neuromodulation and not on the amount of output that is generated (Logothetis, 2008; Norris, 2006).⁵ With regard to the relation between increases in T2* contrast and specific neuronal events like inhibition or excitation, it has been proposed that the former may be energetically less demanding than the latter (Waldvogel et al., 2000) so that the BOLD response would be primarily driven by excitatory synaptic activity. However, this is a matter of ongoing debate and further research is clearly needed in order to clarify the exact relation between hemodynamic activity and neuronal activity.

The remaining questions discussed above notwithstanding, fMRI has been established as a highly useful tool for the investigation of human brain function. However, the observation of isolated "hot spots" of hemodynamic activity is certainly not sufficient for the full-fledged appreciation of the neural networks subserving cognition: information about the communicative infrastructure of the brain is essential in this regard. The following section describes an MRI-based data acquisition technique that is suited to investigate this latter aspect of neuroanatomy by tracking white matter fiber pathways in vivo.

1.4 Diffusion Tensor Imaging

1.4.1 Introduction

Diffusion Tensor Imaging is an MRI-based data acquisition technique offering the possibility to estimate the amount and direction of the movement (i.e. "diffusion") of water molecules in brain tissue. At normal temperatures, particles and molecules move about randomly due to Brownian Motion. However, this movement is only truly random if it occurs in an isotropic medium, that is, a medium that is uniform in all directions. In an anisotropic medium like the human brain the thermal motion of the particles is determined by the structure of the surrounding tissue. In gray matter (which is not truly isotropic, but also not systematically anisotropic), diffusion is not focused in any particular direction. In white matter, however, diffusion mainly occurs along myelinated fiber bundles since they are not easily permeable. Information about the main direction of diffusion in the voxels of a brain scan (as gathered during diffusion-weighted imaging) can thus be used to infer the position and orientation of white matter tracts.

⁵Nevertheless, an increased hemodynamic response often at least partly reflects an increase in neuronal spiking because of a basic proportionality between input and output.

While methods for measuring diffusion with MRI have been under development since the 1950s (Hahn, 1950), Basser et al. (1994) were the first to introduce the concept of the "diffusion tensor" in 1994. Since then, DTI has become an increasingly used tool in anatomical neuroimaging, especially since the development of analytic techniques like white matter tractography and tractography-based cortical parcellation. Both methods will be briefly introduced in Section 1.4.3, following a more general discussion of diffusion-weighted imaging.

1.4.2 Measuring Diffusion

A DTI scanning sequence consists of two magnetic field gradients that are applied in succession. Each of these gradients can be described as a magnetic field whose strength decreases linearly in a particular direction. Since protons in a magnetic field precess with a speed that is proportional to the strength of the field, an inhomogeneous field will cause differing precession speeds and thus a loss of phase coherence. The effects of such a gradient field can be reversed by the application of a second magnetic gradient in the opposite direction - however, this only works for protons that do not move⁶ while the field gradients are switched on. Otherwise, the second gradient will not perfectly reverse the effects of the first, and some phase incoherence will remain.

Brain regions in which protons have a lower phase coherence produce a weaker MRI signal - so effectively, the higher the amount of diffusion in the direction of the field gradient, the lower the strength of the MRI signal that will be picked up. As a result, the main direction of diffusion in a particular brain region (for example, a voxel) can be estimated by conducting multiple diffusion-weighted MRI measurements with magnetic field gradients along different directions.

1.4.3 Tractography and Cortical Parcellation

Starting at an arbitrary voxel, the likely paths that fiber bundles passing through the corresponding patch of neural tissue take can be computed with a random walk algorithm (Behrens et al., 2003; Koch et al., 2002). The basic idea here is to simulate the movement of an imaginary particle, originating at a pre-defined point in space (the "seed voxel") and then moving to an adjacent voxel, the probability of movement in a particular direction being dependent on the main direction of diffusion in the seed voxel and the potential target voxels. Once a target voxel has been selected, the whole procedure is repeated with the target voxel as the new point of origin. The algorithm stops when it encounters gray matter or leaves the brain. If this method is applied several thousand times, the paths that were taken

⁶Note that only movement along the direction of the gradients will have an effect.

Figure 1.4: Parcellation Procedure

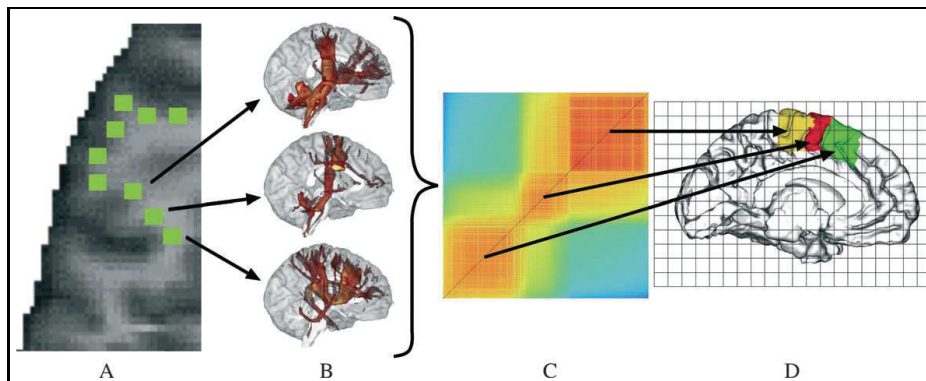


Illustration of the parcellation procedure, adopted from Anwander et al. (2007). A: a region of interest consisting of voxels at the gray matter - white matter interface is defined manually. B: a tractogram is computed for each voxel. C: the similarity between all tractograms is computed and plotted in matrix form. D: a clustering algorithm is used to delineate sets of voxels that share similar tractograms.

most often during the random walk represent the most probable paths that fiber bundles take from the seed voxel.

The tractogram associated with a voxel can be thought of as a fingerprint: voxels in the same brain region will have similar tractograms while voxels in different brain regions will not. Thus, by categorizing voxels into groups based on the similarity of their tractograms it is possible to automatically parcellate a cortical area into patches of brain tissue that exhibit similar anatomical connectivity patterns (for example via a k-means clustering algorithm; see Figure 1.4 and Anwander et al., 2007). Having comparable connections to other brain regions can be understood as an indication for sharing one or more common functions, making DTI based cortical parcellation a useful tool when searching for the neural correlates of cognitive processes.

1.5 Summary and Discussion

As has been discussed above, the methods described here have their drawbacks and advantages. While it has to be kept in mind that they rely on the measurement of very different phenomena (fast-paced post-synaptic potentials, slow-paced hemodynamics and basic thermal diffusion), they can be regarded as complementary: if the same cognitive process is investigated both with ERPs and fMRI, inferences about both its timecourse and its func-

CHAPTER 1. TOOLS OF THE TRADE

tional localization are possible.⁷ Information about the anatomical connectivity of the relevant brain regions that is gained via DTI adds a further level of depth to the analysis and - hopefully - the understanding of the neurobiological processes subserving cognition. In this dissertation, all three techniques will be utilized to this end (see Chapters 5, 6 and 7). In the following chapter, I will discuss both classical and current models of the brain basis of language processing.

⁷This does, of course, not imply a one-to-one mapping between ERP components and fMRI results.

Chapter 2

Past and Present Models of Language Processing

2.1 Introduction

The following sections comprise a brief overview of key ideas about the biological foundations of language that have been formulated from ancient times until today. Three relatively recent models will be discussed in detail: the classical account by Broca, Wernicke, Lichtheim and Geschwind (see Section 2.2.2) is based on aphasiological observations and can be seen as the first serious scientific treatise on the brain basis of language processing. The Neurocognitive Model by Angela D. Friederici (see Section 2.3.2) and the Dual-Stream Model by Gregory Hickok and David Poeppel (see Section 2.3.3) are both based on aphasiology as well as neuroimaging and represent the current state of affairs in the neuroscientific investigation of this topic.

2.2 Historical Accounts

2.2.1 Introduction

While the study of aphasic syndromes can be traced back to antiquity and beyond, some of the older beliefs about the physiological correlates of mental capabilities appear quite strange from a modern perspective. The greek philosopher Aristotle (384 BC - 322 BC) was of the opinion that the heart and not the brain was the seat of the mind. Galen (AD 129 - ca. 216), a greek physician, correctly assumed that the brain was somehow involved in cognitive processing, but wrongly regarded the ventricles as the critical sites. In western medicine, this view was not questioned until 1543, when Andreas Vesalius opposed the

ancient ventricular theory, based on the observation that the organization of the ventricles was similar in humans and animals without animals having comparable mental abilities.

However, the idea that the brain itself was the locus of cognition and that different cognitive functions could be attributed to different regions of the cortex did not gain prominence until the 18th and 19th century. Franz Gall (1758- 1828) is generally credited as being the first to advocate such a theory of brain function, although his school of thought (called "Phrenology") was controversial during his lifetime and several of his key assumptions have been refuted by modern neuroscience. Nevertheless, his hypotheses spawned a number of neuroanatomical experiments and investigations that effectively led to the formation of brain science as we know it today - among them the works of Broca, Wernicke and others that will be discussed in the following section.

2.2.2 The Broca-Wernicke-Lichtheim-Geschwind Model

In 1874, Carl Wernicke proposed a neuroanatomic model of language processing (Wernicke, 1874) that still remains influential today and is widely regarded as a milestone in the history of aphasiology and neurolinguistics. Wernicke had incorporated ideas by Pierre-Paul Broca and Theodor Hermann Meynert into his work, and his writings were in turn elaborated upon by Ludwig Lichtheim (Lichtheim, 1885) and Norman Geschwind (Geschwind, 1965). In his seminal 1874 monograph, Wernicke had postulated that there were two major language centers in the brain, one in the left inferior frontal lobe and one in the left superior temporal lobe, both connected to each other via a white matter tract and additionally connected to distributed cortical representations of non-verbal "concepts".

The left frontal region in Wernicke's model had first been described as relevant for motor aspects of language processing by Pierre-Paul Broca in 1861 and 1865 (Broca, 1861, 1865), and is now commonly known as "Broca's Area". Broca's initial discovery was based on the post-mortem examination of the brain of one of his patients¹, Monsieur Leborgne, who was able to comprehend speech normally and communicate via gestures but could only utter the single syllable "tan" (Broca, 1861). After Leborgne's death, Broca conducted an autopsy and found that his patient had suffered from a superficial lesion of the posterior left inferior frontal gyrus. In the following years, Broca collected a number of additional cases, all involving a loss of productive language capacity and lesions to the same general cortical area that he had found damaged in Leborgne's brain, concluding that articulatory functions of language could be localized to this region (Broca, 1865).

Carl Wernicke himself discovered evidence for a brain region that seemed to be essential for speech comprehension - this area is now known as "Wernicke's Area". In post-mortem

¹Broca was a surgeon at the Hôpital Bicêtre in Paris at the time.

examinations, Wernicke observed that a number of his patients² who had exhibited severe language deficits during their lifetimes showed no signs of lesions to Broca's area, but had suffered damage to a brain region situated in the posterior left superior temporal gyrus (Wernicke, 1874). In addition, the aphasic symptoms that they had shown were not related to speech production and articulation, but to speech perception and the understanding of word and sentence meaning. Wernicke concluded that he had discovered a second language center that subserved distinct functions from the frontal brain region described by Broca.

Based on ideas by Theodor Hermann Meynert, he additionally postulated that both language areas were connected by a large fiber bundle - Meynert had made groundbreaking discoveries with regard to the anatomy and function of white matter tracts, and had been among the first to recognize the importance of connections between different cortical regions of a single hemisphere (Meynert, 1865, 1867, 1868). Wernicke originally believed that the fiber bundle that facilitated communication between the productive and the receptive language center was traversing the insula, but later renounced this view and proposed that the arcuate fasciculus was the relevant neural pathway. In addition to this major route, Wernicke thought that both language areas were connected to widely distributed cortical representations of general non-verbal concepts.

Wernicke used this neuroanatomical model to develop a typology of language disorders which was later refined and extended by Ludwig Lichtheim and became known as the Wernicke-Lichtheim-Model (Lichtheim, 1885). While initially being largely accepted by the scientific community, Wernicke's and Lichtheim's ideas were heavily criticized at the end of the 19th and the beginning of the 20th century, most prominently by Sigmund Freud (Freud, 1891) and Henry Head (Head, 1926). The Wernicke-Lichtheim Model fell into disregard for almost 70 years, but was revived again by Norman Geschwind in 1965 (Geschwind, 1965).

Today, most researchers would probably agree that Broca's area and Wernicke's area are relevant for language processing. However, they are neither functionally nor anatomically homogeneous, and there is a large number of additional brain regions that are involved in the production and perception of speech (see, for example, Hickok and Poeppel, 2000). So while the classical Broca-Wernicke-Lichtheim-Geschwind Model remains a groundbreaking achievement of early cognitive neuroscience, most of its tenets can not be upheld in the light of current research. Two modern views on the neuroanatomical correlates of language processing will be discussed in the following chapter.

²Wernicke was an assistant doctor at the Allerheiligenhospital in Breslau during this time.

2.3 Modern Concepts

2.3.1 Introduction

While Broca, Wernicke and their contemporaries had to rely solely on aphasiology and post-mortem examinations in the construction and refinement of their models, current researchers in the fields of neuro- and psycholinguistics have a wealth of methods at their disposal. Three of these (ERPs, fMRI and DTI) have already been introduced in Chapter 1. Additional techniques include positron emission tomography (PET), magnetoencephalography (MEG) and transcranial magnetic stimulation (TMS; the reader is referred to Kimberley and Lewis (2007) and Shibasaki (2008) for comprehensive introductions into these methods). At the same time, aphasiology is, of course, still a valuable source of information.

As the number of empirical techniques used to investigate language processing has increased, the amount of research in the field has grown accordingly. The state of the art is reviewed and recapitulated regularly, with attempts to integrate and interpret recent results from different sources resulting in data-driven models about the neural basis of language processing. Prominent accounts of this type include the Neurocognitive Model (Friederici, 1995, 2002; Friederici and Kotz, 2003) and the Dual-Stream Model (Hickok and Poeppel, 2004, 2007); both will be discussed in detail in the following two sections.

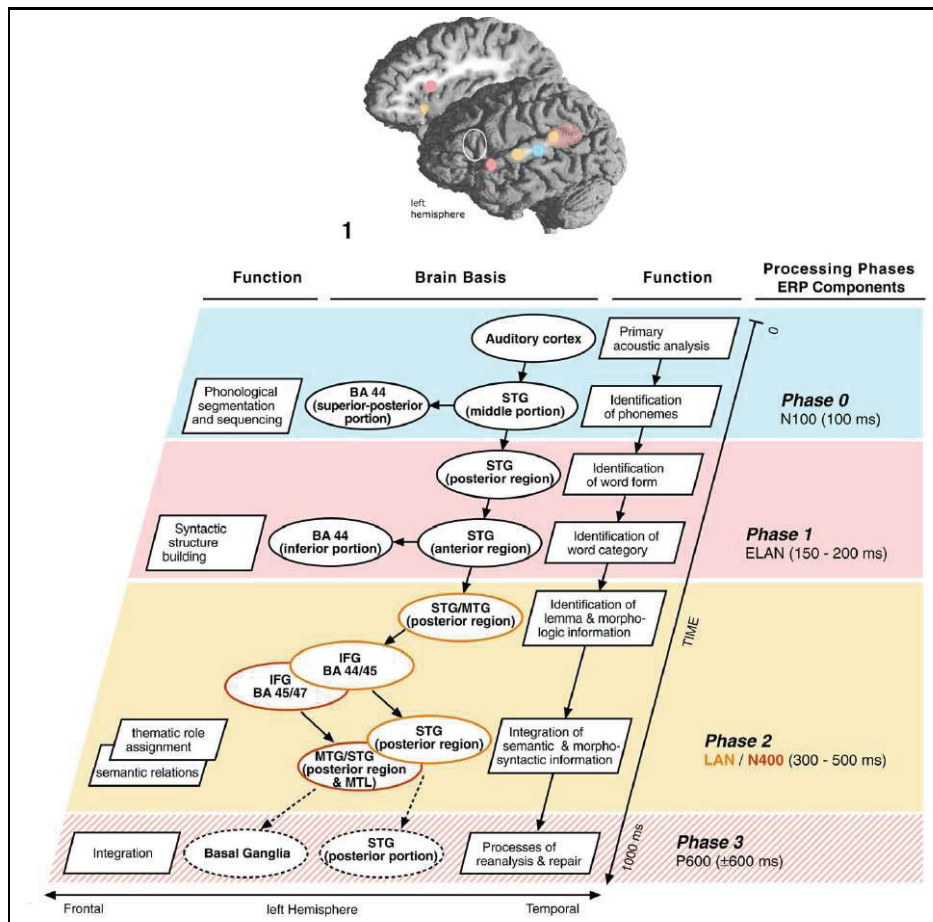
2.3.2 The Neurocognitive Model

The model of language comprehension that will be discussed in this section has been proposed by Angela Friederici in 2002 and 2003 (Friederici, 2002; Friederici and Kotz, 2003), extending an earlier account already formulated in 1995 (Friederici, 1995) and incorporating both information about the timecourse and the neuroanatomical correlates of language processing (see Figure 2.1). New empirical evidence has been discussed in relation to the original model in a number of recent publications (for reviews, see Grodzinsky and Friederici, 2006 and Friederici and Weissenborn, 2007) and is included in the text below.

Based on ERP and MEG data, Friederici identifies four critical phases in the temporal progression of speech comprehension: during phase 0, primary acoustic processing and phoneme identification occur (0-100ms). In phase 1 (100-300ms), word-category information is retrieved and used to build up the basic syntactic structure of a sentence. In phase two (300-500ms), access to lexical-semantic information occurs, morphosyntactic information (e.g. case marking) is processed and thematic roles are assigned. Finally, sentence-level integration of different information types (i.e. syntax and semantics) takes place in phase three (500-1000ms). If necessary, revision and repair also occur in this time window.

Crucially, Friederici argues that phase one solely reflects processes of word-category identification and phrase structure building with no semantic processing occurring in paral-

Figure 2.1: Illustration of the Neurocognitive Model



Adopted from Friederici and Kotz (2003). Original legend reads: *Displayed are the syntax- and semantic-related brain regions. The blue circle marks the region supporting acoustic processes. The other colored circles and ellipses represent the maxima of the fMRI activation for syntactic in the IFG (41, 2, 13) and the anterior STG (53, 1, 0) indicated by red-filled circles, in addition, and in the posterior STG (61, 40, 20) indicated by the red-striped ellipsis in the STG. This area is striped as it was found to be active during syntactic and semantic processes in a recent fMRI experiment (Friederici et al., 2003c). Activations indicated by the red-filled circles mark regions involved in early syntactic processes as patients with lesions in these regions do not demonstrate an ELAN, an ERP component correlated with early local structure building processes. The red-striped ellipsis marks a region assumed to be involved in late syntactic processes as patients with lesions in this region do not display a P600, an ERP component correlated with late syntactic integration processes. The open white circle marks the area known to support the processing of syntactically complex, noncanonical sentences (for a review see Friederici, 2002). Semantic processes are subserved by those regions indicated by orange circles in the IFG and the STG.*

lel. Semantic information is first utilized in phase two, and only words that can be successfully incorporated into the existing phrase structure during phase one are integrated semantically at all (Friederici, 2002; Friederici and Kotz, 2003; Friederici and Weissenborn, 2007). Disruptions of phase one are reflected as an early left-anterior negativity (ELAN) in ERP measurements, followed by a late positivity during phase three (see below). Friederici notes that the ELAN is early with respect to the word category decision point, not with respect to word onset, thus explaining some of the variance that has been reported with regard to the latency of this ERP component (Friederici and Kotz, 2003; Friederici and Weissenborn, 2007).

Friederici assumes that during phase two, lexical-semantic and morphosyntactic information is processed in parallel, but non-interactively (Friederici, 2002; Friederici and Kotz, 2003), although she cautions that there may be interactivity between morphosyntactic and lexical-semantic processes that pertain to elements within the same phrase (see Friederici and Weissenborn, 2007, for a discussion of the evidence). While morphosyntactic violations elicit a left-anterior negativity after 300-500ms followed by a late positivity (see below), semantic anomalies elicit a negativity with a central distribution after 400ms (N400). In Friederici's model, syntactic and semantic information only interact during phase three. In this phase, processes of revision and repair take place, resulting in a central positivity after 600ms (P600; Friederici, 2002; Friederici and Kotz, 2003; Friederici and Weissenborn, 2007).

With regard to the neuroanatomical correlates of language processing, Friederici assumes that the left anterior superior temporal gyrus (aSTG) is involved in syntactic processing (Friederici, 2002; Friederici et al., 2003) and plays an important role in the construction of local phrase structure. In this respect, the aSTG appears to form a network with inferior frontal areas, especially the deep frontal operculum (fOp) and possibly the ventral premotor cortex (vPMC; for anatomical evidence for a structural connection between these regions via the uncinate fasciculus, see Friederici et al., 2006a). fOp and vPMC are implicated in the construction of local phrase structure (Friederici, 2002; Friederici et al., 2006a; Friederici and Kotz, 2003) and in the detection of mismatches between the expected input and the input that is actually encountered (Friederici et al., 2006a,b). The aSTG, on the other hand, is assumed to be involved in word-category identification (Friederici, 2002; Friederici et al., 2006a; Friederici and Kotz, 2003). Predictions about the elements that are most likely to be encountered next may be based on local transition probabilities alone (computed in fOp and vPMC themselves according to simple phrase structure rules) as well as on more complex representations of hierarchical dependencies that are computed in Brodman Area (BA) 44/45 (Friederici et al., 2006a).

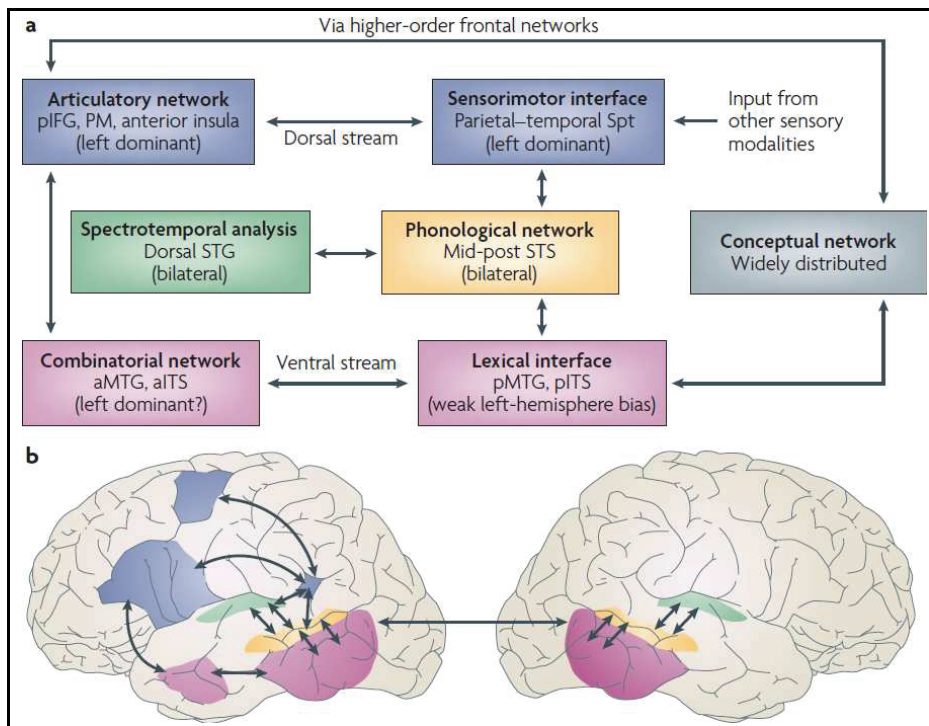
As already mentioned briefly above, BA 44/45 are taken to be involved in the reconstruction of underlying hierarchical structures from sequential input (Friederici, 2004, 2006; Friederici et al., 2006b). BA 45 may have a stronger relevance for lexically-based processes whereas BA 44 is especially implicated in processes that are related to syntactic movement (Friederici et al., 2006b). Friederici notes that activation in BA 44/45 may also partly be driven by increases in working memory load (Friederici, 2002; Friederici et al., 2006b, 2003), although she stresses that this can not explain the entire pattern of brain responses that is observed for this region (Friederici et al., 2006b). BA 44/45 are taken to be connected to the posterior STG via the superior longitudinal fasciculus (Friederici et al., 2006a). The latter brain region is claimed to contain the neural correlates of processing mechanisms that map syntactic, semantic and pragmatic information onto each other in order to arrive at a coherent interpretation at the sentence level (Friederici et al., 2006a; Friederici and Kotz, 2003; Friederici et al., 2003). The left middle temporal gyrus (MTG) is identified as the locus of semantic processes on the word level (Friederici, 2002). Suprasegmental information and especially prosody is taken to be processed in right superior temporal and frontal regions (Friederici, 2002; Friederici and Alter, 2004).

2.3.3 The Dual-Stream Model

The neuroanatomical model proposed by Gregory Hickok and David Poeppel in 2004 is based on the assumption that there are two "streams" of processing in language comprehension, analogous to the dorsal "where" and the ventral "what" paths in visual perception (see Rauschecker (1998); Rauschecker and Tian (2000) for earlier formulations of similar ideas, with a focus on basic auditory processing in non-human primates). The text below is based on the most recent formulation of this framework (see Figure 2.2 and Hickok and Poeppel, 2007), but takes older (and more detailed) instantiations into account where appropriate (Hickok and Poeppel, 2004). In contrast to the Friederici Model discussed above, Hickok and Poeppel's account does not include a detailed ERP-based description of the timecourse of language comprehension and has a slightly different empirical focus, relying on deficit-lesion data to a larger degree.

Hickok and Poeppel assume that a considerable amount of auditory and phonological processing takes place before the postulated dorsal and ventral streams diverge. Heschl's gyrus and the surrounding dorsal STG in both hemispheres are assumed to be involved in primary auditory processing, amounting to a first spectro-temporal analysis of the incoming acoustic signal. Information on the phoneme and syllable level is taken to be processed in the middle and posterior STS (Hickok and Poeppel, 2004). The authors propose that during this sublexical processing stage, computations on a comparatively slow timescale (150-300 ms, corresponding to the syllable level) are lateralized to the right hemisphere

Figure 2.2: Illustration of the Dual-Stream Model



Adopted from Hickok and Poeppel (2007). Original legend reads: *Schematic diagram of the dual-stream model. The earliest stage of cortical speech processing involves some form of spectrotemporal analysis, which is carried out in auditory cortices bilaterally in the supratemporal plane. These spectrotemporal computations appear to differ between the two hemispheres. Phonological-level processing and representation involves the middle to posterior portions of the superior temporal sulcus (STS) bilaterally, although there may be a weak left-hemisphere bias at this level of processing. Subsequently, the system diverges into two broad streams, a dorsal pathway (blue) that maps sensory or phonological representations onto articulatory motor representations, and a ventral pathway (pink) that maps sensory or phonological representations onto lexical conceptual representations. b – Approximate anatomical locations of the dual-stream model components, specified as precisely as available evidence allows. Regions shaded green depict areas on the dorsal surface of the superior temporal gyrus (STG) that are proposed to be involved in spectrotemporal analysis. Regions shaded yellow in the posterior half of the STS are implicated in phonological-level processes. Regions shaded pink represent the ventral stream, which is bilaterally organized with a weak left-hemisphere bias. The more posterior regions of the ventral stream, posterior middle and inferior portions of the temporal lobes correspond to the lexical interface, which links phonological and semantic information, whereas the more anterior locations correspond to the proposed combinatorial network. Regions shaded blue represent the dorsal stream, which is strongly left dominant. The posterior region of the dorsal stream corresponds to an area in the Sylvian fissure at the parietotemporal boundary (area Spt), which is proposed to be a sensorimotor interface, whereas the more anterior locations in the frontal lobe, probably involving Broca’s region and a more dorsal premotor site, correspond to portions of the articulatory network. aITS, anterior inferior temporal sulcus; aMTG, anterior middle temporal gyrus; pIFG, posterior inferior frontal gyrus; PM, premotor cortex.*

while computations on faster timescales (20-50 ms, corresponding to the phoneme level) occur bilaterally (Boemio et al., 2005; Hickok and Poeppel, 2007; Poeppel et al., 2008). This latter view is in contrast to other accounts (Schönwiesner et al., 2005; Zatorre et al., 2002) holding that fast temporal processing is left-lateralized, possibly at the expense of spectro-temporal resolution. However, it is suggested that the left hemisphere may be more adept at representing auditory information in terms of phonemic categories than the right hemisphere (Hickok and Poeppel, 2007; also see Liebenthal et al., 2005). Despite this suggested division of labor, both hemispheres are assumed to be able to mediate between auditory/phonetic and conceptual systems. This contention is based on neuropsychological evidence indicating that unilateral superior temporal lobe lesions do not generally result in functional deafness for speech, but bilateral lesions do (Hickok and Poeppel, 2004).

Starting in the sublexical processing regions described above, the proposed ventral stream first projects to posterior and middle areas of the middle and inferior temporal lobe where lexical semantic access is assumed to occur (Hickok and Poeppel (2000, 2004); the authors cite evidence from semantic dementia and transcortical sensory aphasia in support of this claim). The stream continues into the anterior temporal lobe - Hickok and Poeppel suggest that here, syntax and combinatorial semantics may be processed, but caution that the existing empirical evidence is not conclusive yet. Finally, a connection from the anterior temporal lobe to inferior frontal regions is indicated³, but not discussed in depth.

The dorsal stream is taken to have origins in both sublexical processing areas as well as in primary and secondary auditory cortex with a strong lateralization to the left hemisphere (this latter claim is based on evidence from conduction aphasia, a syndrome in which unilateral damage to the left posterior dorsal temporal lobe results in frequent phonemic errors during speech production; see Hickok and Poeppel, 2007). In contrast to earlier proposals by different authors (Rauschecker, 1998), Hickok and Poeppel suggest that the primary function of this pathway is sensori-motor integration, not spatial hearing (Hickok and Poeppel, 2000, 2004). This implicates that the dorsal stream fulfills crucial functions in the acquisition of new vocabulary, phonological short-term memory, monitoring and repetition. The starting regions described above first project to a site at the boundary of the temporal and parietal lobes (called "area Spt"). Here, the authors claim, sensory representations are recoded as motor representations. Area Spt is said to respond both during speech production and the reproduction of non-linguistic tonal sequences (i.e. humming), but is apparently tuned to a particular motor effector system (the vocal tract) as it does not respond well if tone sequences are to be reproduced using a keyboard. The stream continues by projecting into premotor regions and the inferior frontal cortex, which are taken to subservise articulatory functions.

³See Figure 1 in Hickok and Poeppel (2007).

Hickok and Poeppel explicitly address the implications of their model for the understanding of a variety of aphasic syndromes (Hickok and Poeppel, 2004). As has already been indicated above, word deafness is taken to result from bilateral damage to superior temporal systems involved in acoustic-phonetic processing. Conduction aphasia (characterized by impaired production, but relatively spared comprehension) is assumed to result from unilateral cortical lesions (the classical account of conduction aphasia as a disconnection syndrome is rejected) of area Spt, resulting in the disruption of sensori-motor integration processes. Transcortical sensory aphasia is viewed as a "complementary" syndrome to conduction aphasia: here, damage to inferior temporal lobe regions results in problems that are related to the mediation between sound and meaning while sparing the auditory-motor interface. Finally, Wernicke's aphasia is described as a "composite disorder" involving lesions of both sensori-motor and auditory-conceptual integration systems.

2.4 Summary and Discussion

The systematic investigation of the neural correlates of language processing began with Broca and Wernicke in the 19th century. While they correctly assumed central roles for the left inferior frontal and superior temporal lobes, they failed to appreciate the contributions of other brain regions (e.g. inferior temporal and parietal areas and right-hemispheric sites). Contemporary models generally incorporate a much larger set of cortical structures and stress the importance of the anatomical and functional connectivity between brain regions.

Broadly summarizing the current state of psycho- and neurolinguistic research, one can describe an auditory language network that is organized around bilateral auditory processing regions extending ventro-laterally from Heschl's gyrus. This central area is hierarchically organized, starting with cortex subserving basic acoustic analysis and moving on to regions involved in progressively more complex auditory computations, finally reaching a speech-specific phonological stage in the lateral middle STG and STS. Two distinct dorsal and ventral pathways diverge from this shared starting point, forming a ventral processing route that is primarily concerned with the extraction of meaning (including the necessary syntactic analyses) and a dorsal route that is mainly involved in the mediation between auditory representations and motor codes. The ventral stream connects lexical-syntactic processing areas in the left posterior lateral STG to lexical-semantic regions in the left middle temporal gyrus and inferior temporal lobe, continuing into areas subserving syntactic analysis in the anterior STG and terminating in grammatical processing regions in the inferior frontal lobe (including BA 44 and 45 and possibly the deep frontal operculum). The dorsal stream connects a sensori-motor integration region on the left planum temporale (area Spt) to areas involved in motor planning and articulatory functions in the frontal lobe. While the ven-

tral stream is bilaterally organized, the dorsal stream is left-lateralized. Areas subserving prosodic processing are located in the right temporal and frontal lobes. In general, auditory processing in the right hemisphere appears to occur in wider integration windows than in the left hemisphere.

The models described in Sections 2.3.2 and 2.3.3 are in good agreement with regard to this general architecture. In fact, they can be seen as complementary since the Neurocognitive Model has a focus on sentence-level grammatical processing in superior temporal and inferior frontal brain regions while the Dual-Stream Model is mainly concerned with word-level auditory-conceptual and auditory-motor processing in inferior temporal and inferior parietal areas.

Although the fine-grained organization of the language network remains far from being understood completely and certain aspects of the description given above are discussed controversially (e.g. the role of the anterior temporal lobe in syntactic processing), the models described in this chapter constitute comprehensive accounts of the current state-of-the-art in the investigation of the neurocognition of language. With regard to the issues investigated in this dissertation, the role of the STG in auditory language comprehension is of particular relevance and will be discussed in detail in Chapter 3.

Chapter 3

The Left Superior Temporal Gyrus

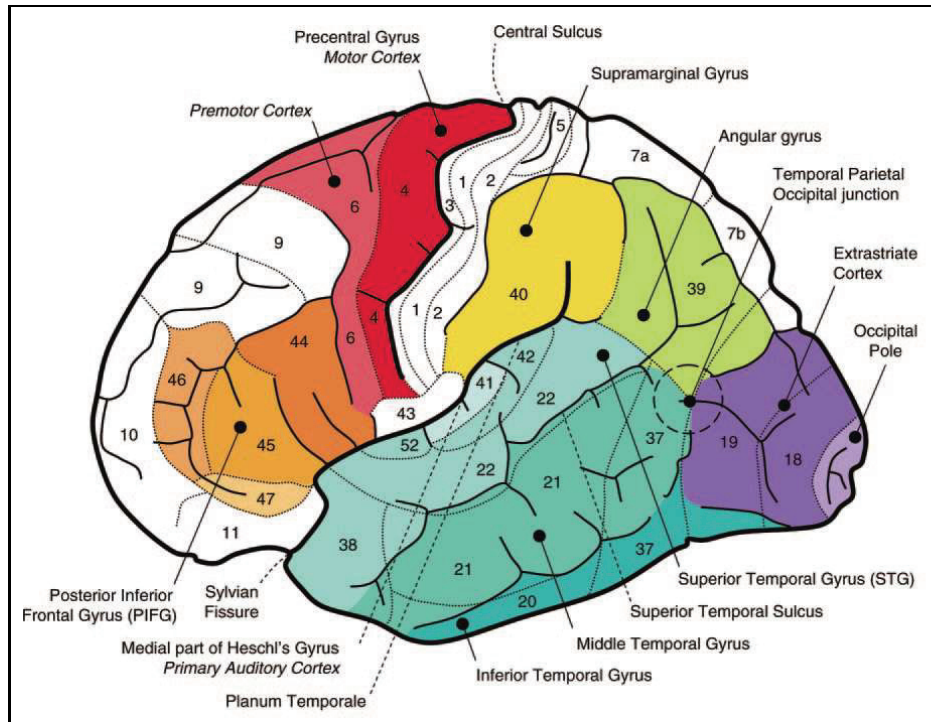
3.1 Introduction

As has already been alluded to in the previous chapter, the superior temporal lobe of the human brain plays a prominent role in language comprehension. The STG is the seat of primary and secondary auditory cortex, and can thus be regarded as the central cortical "hub" for auditory speech processing. In addition, superior temporal areas are involved in higher-level aspects of language comprehension like syntax and semantics. However, before attempting to elucidate the functional relevance of this (or any) brain region, it is imperative to understand its macro- and microanatomical structure as well as the organization of its "hard-wired" connections to other areas of the brain. The following sections provide a review of the current state of research in these respects.

3.2 Anatomical Delineation

The superior temporal gyrus borders on the Sylvian fissure dorsally and the superior temporal sulcus ventrally. While the former is an easily identifiable anatomical landmark, the patterning of the latter is quite variable across individuals (Ono et al., 1990), making the definition of a clear-cut lower boundary of the STG somewhat difficult (especially in cases where the STS is interrupted at one or more points, leading to continuous transitions from the superior to the middle temporal gyrus). Finding the anterior and posterior "ends" of the STG is still more difficult: there is no visible anatomical border between the superior temporal gyrus and the temporal pole (anteriorly) or the angular and supramarginal gyri (posteriorly). There are, however, histological differences (see, for example, Brodmann (1909) which is still widely used as a reference; also see Figure 3.1): while anterior and posterior STG correspond to BA 22, the temporal pole corresponds to BA 38, the angular

Figure 3.1: Brain Regions Involved in Language Processing



Adopted from Démonet et al. (2005). The illustration shows a lateral view of the left hemisphere of the brain. Anatomical landmarks of particular interest are labeled and colored. Brodmann areas are indicated by numbers.

gyrus corresponds to BA 39 and the supramarginal gyrus corresponds to BA 40. Medially, the superior temporal gyrus borders on the insula anteriorly and on the transverse temporal gyri (TTG; also called Heschl's gyri, HG) posteriorly. The dorsal surface of the STG extending posteriorly from the transverse temporal gyri is called the planum temporale (PT) while the cortical region extending anteriorly to the temporal pole is called the planum polare. The dorsal surface of the superior temporal gyrus as a whole is often referred to as the supratemporal plane.

3.3 Anatomical Structure and Subregions

The superior temporal gyrus can be divided into subregions based on a number of cytoarchitectonic and histochemical criteria. While classification schemes based on human post-mortem brains do exist (like the seminal work of Brodmann (1909) that has already been mentioned), studies directly relating anatomical microstructure to brain function have almost exclusively been conducted with non-human primates and other animals for ethical reasons. In spite of the inherent difficulty of neurobiological cross-species comparisons, research on monkeys (especially macaques) has become a useful source of information for modeling the neuroanatomy of auditory processing in humans (Hackett et al., 2001; Hall et al., 2003). In particular, primary and non-primary auditory cortex (both situated on the STG) can reliably be identified cytoarchitectonically in both human and non-human primates.

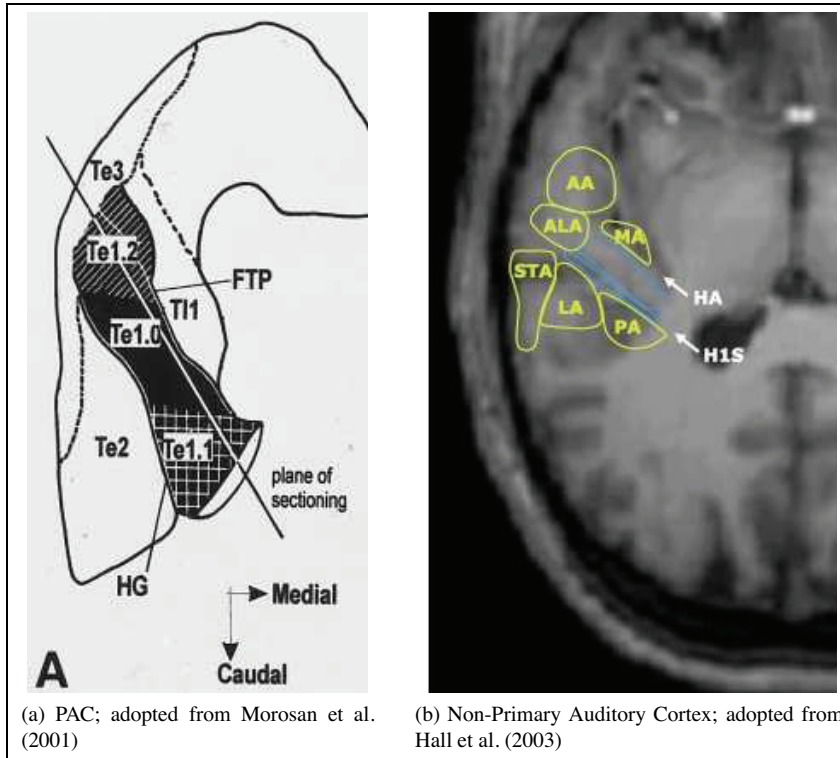
3.3.1 Primary Auditory Cortex

Like all primary sensory areas, the primary auditory cortex (PAC) contains an extraordinarily well-developed layer IV which consists of small, densely packed granule cells. Cytoarchitectonically, PAC is thus classified as "granular cortex" or "koniocortex" (Sanides, 1972). Because of this particular cellular structure and its dense myelination, it is comparatively easy to localize PAC with staining techniques (however, this is not possible *in vivo*): if there is only a single transverse temporal gyrus, primary auditory cortex roughly occupies the postero-medial two thirds; if there are two or more transverse temporal gyri, it is most often (but not always) restricted to the most anterior one (Rademacher et al., 2001). Importantly, primary auditory cortex can not be accurately localized by referring to macroanatomical landmarks (*ibid*).

In the macaque monkey, PAC has been shown to contain at least two subregions based on microelectrode recordings (Merzenich and Brugge, 1973; Morel et al., 1993; Pfingst and O'Connor, 1981): a relatively large caudal area (A1) and an adjacent, more rostral region of similar size (R), both exhibiting strong tonotopic gradients (see Section 3.5.2). A considerably smaller, still more rostral area (RT) is generally assumed to represent a third subregion of primary auditory cortex, but has to be considered a less certain member than A1 and R because its primary-like cytoarchitectonic features (*i.e.* its granularity) are less pronounced (Kaas and Hackett, 1998; Morel et al., 1993).

In humans, the picture is more blurry. Microelectrode recordings are only rarely available here (Howard et al., 1996), and while PAC is not strictly homogeneous with regard to cytoarchitecture, differences within the region are very subtle and consistent classifications are hard to obtain. Several different histological classification schemes for primary

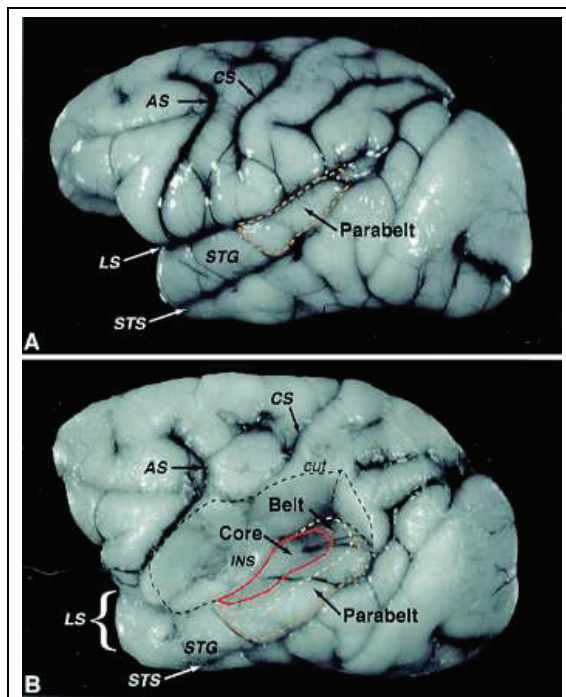
Figure 3.2: Primary and Non-Primary Auditory Cortex



auditory cortex in humans have been proposed: while Brodmann (1909) only identified a single cytoarchitecturally homogeneous region containing PAC (BA 41), Galaburda and Sanides (1980) report a medial and a lateral koniocortical subregion and Morosan et al. (2001) even describe a third antero-lateral area¹ (see Figure 3.2a). Various other classification schemes exist, with the number of observed PAC subregions going up to over 20 (Beck, 1928). However, since only Morosan et al. (2001) employed an observer-independent, statistically based classification method, their results will be regarded as the most reliable ones for the rest of this dissertation. Thus, primary auditory cortex will be assumed to contain three subareas: a highly granular central region (Te 1.0), a slightly less granular, but still clearly koniocortical postero-medial area (Te 1.1) and an antero-lateral transition zone (Te 1.2) bordering on non-primary regions.

¹However, the authors acknowledge that this could be a transitional zone between primary and secondary auditory processing regions.

Figure 3.3: Auditory Cortex in Macaques



Adopted from Kaas and Hackett (2000). The Figure shows a lateral view of the macaque cerebral cortex. Core, belt and parabelt are labeled and marked.

3.3.2 Non-Primary Auditory Cortex

In non-human primates (see Figure 3.3), PAC is often referred to as the "core" while the cortex immediately surrounding it is called the "belt", which in turn borders on the "parabelt" (Hackett et al., 2001; Hall et al., 2003; Kaas and Hackett, 1998, 2000; Pandya and Sanides, 1973). While both belt and parabelt are distinctly different from the core with regard to cytoarchitecture, myelination and histochemistry, the evidence for their involvement in auditory processing as well as the delineation of belt and parabelt subregions is mainly based on short-range connection patterns (Kaas and Hackett, 2000): core areas project to adjacent belt areas, which in turn project to adjacent parabelt areas. Interestingly, there are no direct connections from core to parabelt - the belt is a necessary intermediate processing step.

In humans, the distinction between core, belt and parabelt is usually replaced by a more general differentiation of primary and non-primary auditory cortex (Hall et al., 2003). Non-primary auditory cortex covers significant parts of the supratemporal plane surrounding PAC, but mostly does not extend onto the lateral surface of the STG (with the exception of area STA; see below). While the definition of anatomical subregions of non-primary auditory cortex based on cyto- and myeloarchitecture is possible, the results of such attempts vary to a certain degree: while Brodmann only distinguished three areas (Brodmann, 1909), other researchers differentiate up to eight subregions (Galaburda and Sanides, 1980). Several recent studies employing a wider range of histochemical markers (Rivier and Clarke, 1997; Wallace et al., 2002) broadly agree on a classification along the following lines (see Figure 3.2b): on Heschl's gyrus, PAC occupies the postero-medial two-thirds and borders onto a distinct antero-lateral region (called ALA). On the planum polare, two further areas can be distinguished, an antero-lateral one (called AA) and a more medial region (called MA). In addition, PAC borders onto two regions on the planum temporale, one lateral (called LA) and one medial to that (called PA). Finally, LA borders onto an area that extends onto the lateral convexity of the STG (called STA). Since this latter region exhibits a very different cytoarchitectonic profile than the other areas, it may be regarded as higher-level association cortex (Rivier and Clarke (1997); also see Section 3.3.3).

3.3.3 Beyond Auditory Cortex

While the supratemporal plane is largely occupied by primary and secondary auditory processing regions, the lateral convexity of the STG is generally regarded as higher-level association cortex. Because many of the cognitive operations assumed to be subserved by this area are exclusive to humans (e.g. language comprehension), studies on monkey neuroanatomy are considerably less informative here than with regard to primary sensory regions. However, a number of cytoarchitectonically based classification schemes for humans exist. In fact, most authors assume that the lateral STG corresponds to one single microanatomically defined area (Brodmann, 1909; Morosan et al., 2005; Rivier and Clarke, 1997; Wallace et al., 2002).² In contrast, von Economo and Koskinas (1925) reported a subdivision into a caudal and a rostral region (called TA1 and TA2). Galaburda and Sanides (1980) distinguish a strictly lateral STG area (PaAe) and a region mostly situated on the supratemporal plane, but partly extending onto the STG (PaAi). Since Morosan et al. (2005) both implemented an observer-independent classification technique as well as corroborating their cytoarchitectonic results with receptorarchitectonic investigations, their assumption of

²It should be noted that area STA as defined by Wallace et al. (2002) and Rivier and Clarke (1997) only comprises the posterior lateral STG.

a microanatomically uniform lateral STG area (called Te3) will be adopted for the remainder of this manuscript.

3.3.4 Summary

Based on microanatomical criteria, primary and non-primary auditory processing regions of the superior temporal lobe can be distinguished in humans as well as in non-human primates. In the human brain, PAC can be localized to the postero-medial part of Heschl's gyrus and can be further parcellated into three subregions. It is surrounded by eight non-primary processing areas that can be distinguished using histochemical techniques. In contrast to the supratemporal plane, the lateral convexity of the STG can not be readily subdivided based on cyto- or receptorarchitectonic criteria.

3.4 Anatomical Connectivity

Post-mortem examinations of fiber tracts in the human brain exist since the 16th century, when Andreas Vesalius first described the corpus callosum in man. However, detailed accounts of the organization and structure of white matter pathways were dependent on technical advances in microscopy and brain fixation which did not occur until the early 19th century. The seminal work of Karl Friedrich Burdach (Burdach, 1819) is generally regarded as the first serious attempt to systematically distinguish and categorize different fiber bundles based on gross dissection (Schmahmann and Pandya, 2007). Probably the most influential classical work on white matter anatomy that is still cited today was published by Joseph Jules Dejerine in 1895 (Dejerine, 1895).

During the past decade, Diffusion Tensor Imaging-based techniques have allowed researchers to investigate the organization of fiber tracts in the human brain in vivo (also see Chapter 1.4). Several large-scale studies have recently been published (Catani et al., 2002; Mori et al., 2002; Wakana et al., 2004), complementing and extending the existing knowledge from post-mortem examinations. Classical studies and modern accounts generally agree that there are several major fiber bundles that pass through the STG or its vicinity. Most prominently, the superior longitudinal fasciculus (SLF) connects the posterior superior temporal gyrus to caudal superior parietal and superior frontal areas. Both the inferior fronto-occipital fasciculus (IFO) and the inferior longitudinal fasciculus (ILF) pass from caudal to rostral beneath the STS. While the former connects occipital areas to inferior frontal and orbital regions, the latter facilitates communication between occipital and anterior temporal and temporo-polar parts of the cortex. Finally, the uncinate fasciculus (UF) connects orbito-temporal areas to fronto-orbital regions.

3.5 Functional Relevance

3.5.1 Introduction

Existing theories on the cognitive relevance of separate sections of the superior temporal gyrus are largely based on hemodynamic imaging (PET and fMRI) and patient studies. Such sources indicate that there is a broad distinction to be made between the anterior, middle and posterior STG, with all three regions being involved in different aspects of linguistic processing. In addition, a hierarchical organization in the dorsal-to-ventral direction is particularly apparent with regard to auditory and phonological processing regions in the middle STG and STS. A review of relevant studies dealing with the functional localization of language processes in the superior temporal lobe is given in the sections below.

3.5.2 The Basics

Primary Auditory Processing

Every auditory speech stream is a highly complex signal, not only with regard to abstract concepts like syntax and semantics, but already at the level of phonology and even acoustics. The processing of pure tones and other comparatively simple stimuli can be investigated both in humans and monkeys, with models derived from studies on the latter often informing research on the former.

In non-human primates, areas A1 and R of the primary auditory cortex exhibit mirror-image tonotopic gradients; that is, while the most caudal neurons of A1 respond best to high frequencies and the most rostral neurons respond best to low frequencies, this spatial pattern is reversed in R which thus shares a low-frequency border with A1 (Kosaki et al., 1997; Merzenich and Brugge, 1973; Morel et al., 1993). RT is sometimes assumed to have a tonotopic structure that is analogous to that of A1 (which would mean that it shares a high frequency border with R), but this is a matter of debate (Hall et al., 2003; Kaas and Hackett, 2000). Belt regions also exhibit tonotopic gradients, albeit to a lesser degree than core areas (Kosaki et al., 1997; Merzenich and Brugge, 1973). In addition, neurons in the belt respond less well to pure tones and better to spectrally more complex stimuli such as conspecific vocalizations (Rauschecker and Tian, 2000; Rauschecker et al., 1995; Tian et al., 2001). The functional relevance of the parabelt is not well studied, but it is assumed to represent a further level of complex auditory processing (Hall et al., 2003; Kaas and Hackett, 1998, 2000).

Tonotopic gradients have also been found in human auditory cortex. The most direct evidence comes from studies using intracerebral microelectrode recordings in pre-operative neurosurgical patients: Howard et al. (1996) and Liégeois-Chauvel et al. (2001) report

location-dependent frequency tuning of neurons in Heschl's gyrus, with higher frequencies being represented postero-medially and lower frequencies being represented antero-laterally. Tonotopy in humans has also been studied using PET and fMRI. However, while all authors report indications for some form of tonotopic organization (Bilecen et al., 1998; Engeliën et al., 2002; Formisano et al., 2003; Langers et al., 2007; Lauter et al., 1985; Le et al., 2001; Lockwood et al., 1999; Scarff et al., 2004; Schönwiesner et al., 2002; Talavage et al., 2000, 2004; Upadhyay et al., 2007; Wessinger et al., 1997; Yetkin et al., 2004), results are quite variable with regard to the number of frequency-specific areas that are reported, their detailed topography and their interpretation as being representative of frequency gradients (or the end-points of such gradients) or discrete processing regions. As of yet, there is no consensus with regard to these unresolved discrepancies. Since the fine-grained tonotopic organization of primary auditory processing areas is not of direct relevance to the empirical questions discussed in this dissertation, no particular frequency mapping of PAC will be assumed here.

Non-primary Auditory Processing

Areas on the supratemporal plane surrounding primary auditory cortex are involved in the processing of acoustic stimuli with more complex properties than single pure tones. These regions include the posterior part of the planum polare, the anterior part of the planum temporale and the dorso-lateral STG (see Section 3.3.2). As has been shown both in monkeys (Rauschecker and Tian, 2000) and in humans (Hall et al., 2002; Hart et al., 2004; Wessinger et al., 2001), neurons in these auditory "belt" areas respond much more vigorously to band-passed noise bursts and frequency-modulated tones than to pure tones. Moreover, particular neuronal populations are fine-tuned to certain bandwidths, certain center frequencies and certain rates of modulation (Rauschecker and Tian, 2000; Wessinger et al., 2001). As has been reported by Zatorre and Belin (2001) and Jamison et al. (2006) in PET and fMRI studies with human participants, cortical regions surrounding PAC not only respond strongly to single spectrally or temporally complex sounds, but show a comparable reaction to sequences of individually simple tones if these sequences are complex due to variable spectral content and variable temporal patterning. Thus, there is strong evidence indicating an intricate cortical processing system for the integration of spectral and temporal auditory information in non-primary auditory areas adjacent to PAC.

In addition, a more posterior region of the planum temporale beyond the immediate vicinity of PAC has been implicated in the detection of sound source location (Barrett and Hall, 2006) and the combination of spatial and non-spatial information during the identification and tracking of auditory objects (Griffiths and Warren, 2002; Hall et al., 2005; Hart et al., 2004), which fits with the idea of a dorsal "where"-pathway in auditory per-

ception (Rauschecker and Tian, 2000). Some recent models have additionally discussed the PT in the context of sensori-motor integration (Hickok and Poeppel (2007); also see Section 2.3.3). The idea here is that one of the functions that the PT performs is to map auditory-perceptual representations onto motor representations, which would make it a crucial structure for language acquisition, overt repetition and silent rehearsal.

Speech-specific Auditory Processing

As described above, the neural correlates of the processing of basic acoustic information have been studied extensively. Speech, however, is an auditory signal that contains a much greater amount of spectro-temporal variability than band-passed noise bursts or frequency modulated tones. As has been shown by Binder et al. (2000), a dorsal-to-ventral progression from simple, non-linguistic auditory processing to complex, speech-specific auditory processing can be described in the STG: while white noise, sequences of spectrally variable pure tones and stimuli with phonetic content (words as well as pseudo-words) all activate Heschl's gyrus, only tone sequences and phonetic stimuli activate the dorso-lateral middle STG (words and pseudo-words more strongly than tones), and finally, only words and pseudo-words activate the ventro-lateral middle STG, extending into the STS.

Further evidence for the involvement of areas centered around the middle STG and STS in phonological processing comes from studies utilizing sub-lexical stimuli. Rimol et al. (2005) report activations of the middle and posterior ventral STG and STS for single consonants and consonant-vowel syllables when compared to matched noise. Obleser et al. (2007) report similar results, albeit with a more anterior activation focus, for the processing of isolated stop consonants. Finally, Liebenthal et al. (2005) describe anterior and middle STG and STS activations in response to the discrimination of different phonemes as opposed to the discrimination of non-phonemic sounds, similar to results reported by Jacquemot et al. (2003) for phonemic versus non-phonemic contrasts in pseudo-word stimuli.

Summary

In sum, auditory processing in humans is apparently organized in a hierarchical manner, comparable to other primate species. Primary auditory cortex in Heschl's gyrus responds to all types of acoustic stimuli and contains neuronal populations that are fine-tuned to particular frequencies. Areas on the surrounding supratemporal plane, extending onto the dorso-lateral convexity of the STG, are tuned to broader bandwidths and are capable of detecting temporal variation. Finally, regions in the ventral middle STG and STS, often extending into more anterior areas, are able to extract speech-specific phonetic information which is the basis of lexical, semantic and syntactic processing that occurs further "downstream".

3.5.3 Syntax and Semantics

Anterior and posterior regions of the lateral STG are generally taken to contain the neural correlates of higher-level linguistic processing. As has been discussed in the previous section, dorsal parts of the posterior STG subserve auditory processing functions that are relevant, but not exclusive to language comprehension. The ventro-lateral posterior STG (extending into the STS), on the other hand, has been implicated in a number of highly language-specific processes mainly related to the integration of syntactic and lexical-semantic information (Bornkessel et al., 2005; Friederici et al., 2003; Grewe et al., 2007). In particular, this brain region is apparently involved in the "linking" of semantic and syntactic arguments. The underlying theoretical idea here is that the lexical entry of a verb carries information about the number and type of arguments that it may be used with - semantically speaking, this relates to the potential participants of the event that is described. The verb "to hit", for example, has two obligatory arguments, an "agent" (who is performing the hitting) and a "patient" (who is hit). During language comprehension, this lexical-semantic information pertaining to the verb has to be mapped onto sentential elements (that is, each noun phrase in a sentence has to receive a "thematic role"). Thematic role assignment or "argument linking" is performed on the basis of a range of language specific sources of information, among them morphological case, position in the syntactic structure and semantic properties like animacy. Crucially, this entails that this process is reliant on the integration of morphosyntactic and lexical-semantic features.

Evidence for an involvement of the posterior superior temporal sulcus in argument linking comes from a study by Bornkessel et al. (2005). The authors found the left posterior STS to be active for the processing of sentences in which the argument bearing the "undergoer" role preceded the argument bearing the "actor" role. This effect was independent of purely syntactic aspects of sentence configuration (subject-before-object or object-before-subject word order), suggesting that it is due to the violation of a semantics-to-syntax mapping principle stating that semantically prominent arguments (i.e. actors) should also be syntactically prominent (i.e. linearly precede other types of arguments). Grewe et al. (2007) found the same cortical area to show an increased hemodynamic response to sentences containing an animate agent as well as an animate patient, a construction that the authors describe as a deviation from "unmarked transitivity" (a principle basically stating that in a transitive sentence, the actor should be animate and the undergoer should be inanimate). As in Bornkessel et al. (2005), the effect was independent of the order of subject and object, indicating that it is caused by an increased difficulty in thematic role assignment. Friederici et al. (2003) report a slightly more lateral and dorsal region in the posterior STG to respond to both sentences with an anomalous phrase structure and sentences containing selection restriction violations. While this result is not directly related to processes of argument linking and

thematic role assignment as discussed above, it suggests a general involvement of the posterior superior temporal lobe in the integration of different types of linguistic information (i.e. syntactic and lexical-semantic).

Thus, the existing empirical evidence indicates that ventral aspects of the posterior STG, extending into the STS, subserves the integration of syntactic and lexical-semantic information. However, matters are less clear with regard to the anterior STG and STS. While it is uncontroversial that this brain region plays an important role during sentence comprehension, its particular involvement in syntactic and semantic processing is still debated. To some degree, this is owed to the fact that anterior STG and STS are often found to be active when stimulation with intelligible sentences is compared to stimulation with unintelligible sentences or word lists (Crinion et al., 2003; Narain et al., 2003; Scott et al., 2000, 2006; Stowe et al., 1998): intelligible sentences are more complex than the latter types of stimuli both with regard to syntax and combinatorial semantics, making a differentiation of these two aspects of language processing impossible.

Several authors have developed paradigms aimed at a remediation of this state of affairs. Humphries et al. (2006), extending a design by Vandenberghe et al. (2002), investigated auditory stimuli carrying different amounts of syntactic and semantic information in an fMRI study. Two factors were tested in a fully crossed design: "syntactic structure" (word lists vs sentences) and "semantic congruence" (congruent content words vs random content words vs pseudo-words). The main effect of syntactic structure revealed a region of the left anterior STS (aSTS) in which the BOLD response was significantly enhanced for sentences compared to word lists, regardless of semantic congruence. Conversely, a large network of more posterior temporal lobe areas (including MTG, inferior temporal gyrus (ITG) and more caudal parts of the anterior STS) as well as frontal regions was found to respond more strongly to congruent than to random or pseudo-word stimuli, regardless of syntactic structure. Finally, a region of the aSTS posterior to the area responding exclusively to syntactic structure was found to be involved in both syntactic and semantic processing. Compatible results are reported by Friederici et al. (2003), who investigated the processing of auditorily presented sentences containing syntactic or semantic anomalies. Ungrammatical stimuli with local phrase-structure violations elicited an increase in brain activity in the left anterior superior temporal gyrus, the left frontal operculum and the left putamen that was not seen for semantically anomalous stimuli.

While no definitive conclusions can be drawn from the existing evidence, the studies discussed in the last paragraph suggest that the anterior STG and STS is more involved in syntactic than in semantic aspects of sentence processing. This is in line with recent proposals implicating the anterior temporal lobe together with the frontal operculum and ventral premotor cortex in the processing of local phrase structure (Grodzinsky and Friederici,

2006). However, the specific contribution of the anterior STG and its particular relevance in this network remain to be investigated.

3.5.4 Summary

Starting in the postero-medial transverse temporal gyrus and extending up to mid-lateral parts of the superior temporal gyrus, a hierarchy of primary and secondary auditory processing regions has been described (Binder et al., 2000; Rauschecker and Tian, 2000). The section of the supratemporal plane lying caudal to Heschl's gyrus (the planum temporale) has been implicated in auditory-motor integration (Hickok and Poeppel, 2007) and may be a crucial part of the "phonological loop" (Baddeley and Hitch, 1974). The ventral middle STG is involved in phonological processing (Binder et al., 2000). Ventral parts of the posterior STG and STS contain the neural correlates of argument linking and multi-modal syntactic-semantic integration (Bornkessel et al., 2005; Friederici et al., 2003). The functional relevance of the rostral part of the superior temporal gyrus is still debated; however, there are indications that this region is involved in syntactic operations on a local level (Grodzinsky and Friederici, 2006; Humphries et al., 2006).

Together with the more general account of existing models of language processing that was given in Chapter 2, the overview of STG anatomy, connectivity and function that has been provided in the previous sections forms the conceptual and empirical basis for the studies described in Chapters 5, 6 and 7. In the following final chapter of part 1 of this dissertation, I will briefly discuss several critical methodological aspects of the use of pseudo-word stimuli in neuroimaging studies that will be picked up again in Chapter 6.

Chapter 4

On Different Types of Pseudo-words

Since the experiments reported in this dissertation critically rely on word-like, but presumably meaningless stimuli (e.g., pseudo-words or non-words), it is imperative to take a closer look at the brain mechanisms underlying pseudo-word processing. In addition to this methodological point, the observation of differences in the neural response to pseudo-words and real words can yield valuable insights with regard to the role of the STG in phonological, lexical and semantic processing.

Pseudo-word stimuli have been used extensively in psycholinguistic neuroimaging research in order to determine the network underlying lexical-semantic processing, and despite the particular methodologies and thematic foci of experiments dealing with pseudo-words being manifold, almost all studies include a direct comparison of changes in brain activity induced by real words compared to those induced by semantically "empty" stimuli. This contrast is most often taken to reveal parts of a functional network for lexical and semantic processing, with the underlying rationale that pseudo-word stimuli are not processed semantically at all as they are meaningless. However, they may impose enhanced demands on brain regions subserving lexical access as the search for a fitting lexical entry never succeeds. Surprisingly, the results of this comparison vary considerably among experiments (Mechelli et al., 2003), exceeding the level of variation that could readily be attributed to differences in task demands or experimental design.

In terms of the results that are reported in the literature, the most basic distinction to be made with regard to the functional differences between real words and pseudo-words is that between studies that simply fail to find any difference at all (Binder et al., 2000; Prabhakaran et al., 2006; Valdois et al., 2006) and studies that find differences (Baciu et al., 2002; Bellgowan et al., 2003; Fiebach et al., 2002; Hagoort et al., 1999; Henson et al., 2002; Kotz et al., 2002; Majerus et al., 2002; Newman et al., 2001; Orfanidou et al., 2006; Price et al., 1996; Rissman et al., 2003; Vigneau et al., 2005; Xiao et al., 2005). Within the

latter group, a further differentiation can be made between studies exclusively reporting an increase in activation for words (Fiebach et al., 2002; Orfanidou et al., 2006; Rissman et al., 2003), exclusively reporting an increase in activation for pseudo-words (Baciu et al., 2002; Newman et al., 2001) or reporting increases in activation for both words and pseudo-words, but in dissociating brain regions (Bellgowan et al., 2003; Hagoort et al., 1999; Henson et al., 2002; Kotz et al., 2002; Majerus et al., 2002; Price et al., 1996; Vigneau et al., 2005; Xiao et al., 2005). Although these differences are quite striking, an interesting commonality emerges when considering the particular brain regions that are reported to show an increase in activity for real words: here, activations in left or bilateral inferior and middle temporal areas (Fiebach et al., 2002; Hagoort et al., 1999; Kotz et al., 2002; Majerus et al., 2002; Orfanidou et al., 2006; Rissman et al., 2003; Vigneau et al., 2005; Xiao et al., 2005) as well as activations in left or bilateral inferior parietal areas around the temporo-parietal junction point (Bellgowan et al., 2003; Henson et al., 2002; Kotz et al., 2002; Orfanidou et al., 2006; Rissman et al., 2003; Vigneau et al., 2005; Xiao et al., 2005) are consistently observed. Interestingly, no similarly consistent pattern of activations is found for the reverse contrast of pseudo-words minus real words, although the bilateral STG is often involved (Hagoort et al., 1999; Kotz et al., 2002; Majerus et al., 2002; Newman et al., 2001).

How can these varying results be accommodated? In addition to presentation modality, experimental task, and imaging equipment used, three major factors may determine the differentiability of real words and pseudo-words. The first is lexical transparency: the closer a pseudo-word is to a real word in terms of its constituent phonemes as well as its metric and its syllabic structure, the more likely it is to engage lexical processes thus minimizing or eliminating any detectable processing differences when compared to real word stimuli. Pseudo-words derived from real words by changing one phoneme are lexically transparent in this sense, whereas pseudo-words generated by randomly combining syllables into phonotactically legal units are not and can be called "lexically opaque". The second factor is deviation point. This factor only applies to lexically transparent pseudo-words created in the manner described above: the larger the initial part of a pseudo-word that still constitutes the possible beginning of a real word, the more likely this pseudo-word is to engage lexical processes. That is, the further to the end of a real word a modification is made in order to turn it into a pseudo-word, the more difficult it will be to differentiate the two types of stimuli. The third and final factor is phonotactic legality: since non-words contain outright violations of the rules that govern the formation of multi-phoneme structures in a given language, they may be processed very differently from both legal pseudo-words and real words. Thus, what was previously treated as a homogeneous set of stimuli ("pseudo-words") may in fact be an amalgam of at least two major subcategories of items (see Bedny et al., 2007, for a similar argument regarding the generalizability of particular item sets to

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stimulus categories), namely lexically transparent and lexically opaque pseudo-words. The experiment reported in Chapter 6 sets out to investigate the empirical validity of this claim.

Part II

Empirical Data

Chapter 5

DTI Data Analysis

5.1 Introduction

As has been discussed in Chapter 3, the superior temporal gyrus plays a crucial role in auditory language processing. Functionally, it is apparent that at least three STG subregions can be distinguished (see Section 3.5): an anterior area that is primarily involved in syntactic processing, a middle area that is involved in basic auditory and phonological processing and a posterior area that is involved in lexical-syntactic integration. However, language-related functional activations often extend from the ventral STG into dorsal parts of the superior temporal sulcus and are sometimes even restricted to the STS, making the definition of a ventral "border" between STG and STS difficult. Thus, two questions arise: firstly, is the functional differentiation of the STG somehow reflected in its anatomical organization? Secondly, can STG and STS regions be differentiated with regard to their anatomical structure?

In this chapter, these issues will be investigated by taking a close look at the cortico-cortical connectivity of STG and STS with the help of DTI-based white matter tractography and tractography-based parcellation techniques. As has been elaborated in Section 1.4, the basic reasoning here is that regions of the brain that exhibit a homogeneous pattern of connections to other brain areas are also likely to be homogeneous with regard to other anatomical features and perform cognitive functions that are reliant on similar communicative networks. In contrast to traditional anatomical parcellation techniques, the DTI-based method has the crucial advantage of being applicable *in vivo* - thus, it is possible to directly relate functional results on the differentiation of STG and STS subregions to corresponding connectivity-pattern based results within the same participants.

Based on the evidence discussed in Chapter 3, it is plausible to hypothesize that there are three subregions of the STG that can be differentiated with regard to their long-range

cortico-cortical connectivity. The anteriormost of these areas will be connected to the frontal lobe via the uncinate fasciculus or the IFO and extend from the caudal end of the temporal pole to the rostro-lateral end of Heschl's Gyrus while the posteriormost region will extend from the caudo-lateral end of Heschl's Gyrus to the rostral end of the angular gyrus and will be connected to the frontal lobe via the SLF. A comparatively small area situated between these two latter regions (and containing primary and secondary auditory cortex) will exhibit both ventro-rostral and dorso-caudal connections to frontal areas. It is open whether it will be possible to differentiate STG and STS regions based on their connectivity patterns.

5.2 Methods

In this dissertation, a parcellation procedure that classifies cortical regions based on the long-range connectivity of the adjacent white matter and has been described in detail by Anwander et al. (2007) was implemented. This method is based on data acquired with diffusion-weighted magnetic resonance imaging (see Section 1.4) and works as follows: probabilistic tractography profiles (or "connectivity profiles") are computed for all voxels at the gray matter - white matter interface in a given region of interest (ROI). Technically, such connectivity profiles can be described as ordered lists of values, with each value representing the likelihood of a connection from the profiled voxel to a particular target voxel and the number of target voxels being equal to the total number of voxels in the measured volume. The degree to which the probability of being connected to each target voxel covaries between two connectivity profiles can be expressed as a correlation coefficient. This coefficient can then be used as a measure of similarity between these profiles. Once the amount of correlation between the connectivity profiles of all seed voxels in a given ROI is known, voxels with similar connectivity patterns can be grouped together.

In the study described here, this step was carried out by using a k-means clustering algorithm. This procedure assumes a pre-defined number of subgroups and tries to assign each voxel to one of these sets in a way that maximizes the similarity between the voxel-wise connectivity profiles within each group. This is implemented in the following way: first, a random voxel is assigned to each group and defined as the initial "prototypical member" (also called the "centroid"). Next, all remaining voxels are assigned to the group with the centroid that is most similar to them. Following this step, a new centroid is computed for each group by averaging across all group members. Finally, all voxels are again assigned to the group with the centroid that is most similar to them, and the whole procedure is repeated until group membership does not change anymore. While this algorithm produces robust categorizations, it is agnostic with regard to the optimal number of subgroups for a given data set (as mentioned above, this has to be defined manually).

Determining the optimal number of categories amounts to finding a clustering model that is as simple as possible while at the same time adequately describing the structure of the data: the simplest model (with only one category for all voxels) will miss relevant distinctions in many cases while the most complex model (with one separate category for each voxel) will not capture relevant similarity patterns. Based on the anatomical and functional evidence discussed in previous chapters, it was assumed that a categorization into three subregions would be the best choice. In order to test this hypothesis, parcellations into 2 to 10 categories were computed for each participant. These were then compared with regard to two criteria: individual clusters should be continuous and the relative size and spatial location of all clusters should be comparable across subjects. If no other categorization was superior in this sense, the parcellation into three subregions was assumed to be the most plausible one (as per the initial hypothesis).

The procedure described above was applied to data from 10 healthy participants. Two separate regions of interest were defined for each individual along the left superior temporal gyrus and the left superior temporal sulcus. In addition, the same classification procedure was applied to an averaged DTI image of all 10 subjects.

"Connectivity fingerprints" were calculated for all subregions that were identified by applying the clustering algorithm to this average image - that is, the average strength of the connectivity from all voxels in each subregion to all voxels in a number of manually defined target regions was determined. After careful visual inspection of the tractographic results associated with each STG/STS subregion, the following target areas were selected for the fingerprint analysis: the left anterior inferior frontal gyrus (BA 45/46), left BA 47, left BA 44, the left ventral premotor cortex (BA 6) and the left inferior parietal lobe.¹

Diffusion-weighted data and high-resolution T1-weighted images were acquired on a whole-body 3 Tesla Magnetom Trio scanner (Siemens, Erlangen) equipped with an 8-channel head array coil. Written informed consent was obtained from all subjects in accordance with the ethical approval from the University of Leipzig. Diffusion-weighted images were acquired with twice-refocused spin echo echo-planar-imaging sequence (Reese et al., 2003), TE = 100 ms, TR = 12 s, 128 x 128 image matrix, FOV = 220 x 220 mm², providing 60 diffusion-encoding gradient directions with a b-value of 1000 s/mm² (gradient duration: delta1=12.03 ms, delta2=19.88 ms, delta3=21.76 ms, delta4=10.15 ms). Seven images without any diffusion weighting were obtained at the beginning of the scanning sequence and after each block of 10 diffusion-weighted images as anatomical reference for offline motion correction. The interleaved measurement of 72 axial slices with 1 mm thick-

¹It should be noted that the fingerprint analysis does not yield an exhaustive description of the connectivity of each STG/STS subregion, but is intended as an analytical tool facilitating the detection of differences and commonalities between brain regions with regard to a subset of cortical destinations that are particularly relevant for the investigation at hand.

ness (no gap) covered the entire brain. Random noise in the data was reduced by averaging 3 acquisitions, resulting in an acquisition time of approximately 45 minutes. Cardiac gating was not employed in order to limit the acquisition time. Additionally, fat saturation was employed together with 6/8 partial Fourier imaging, Hanning window filtering and parallel acquisition (generalized auto-calibrating partially parallel acquisitions, GRAPPA reduction factor = 2).

The T1-weighted structural scans were used for skull-stripping and the brain images were then co-registered into Talairach space (Talairach and Tournoux, 1988). The 21 images without diffusion weighting distributed in the whole sequence were used to estimate motion correction parameters using rigid-body transformations (Jenkinson et al., 2002), implemented in FSL (Smith et al., 2004). Motion correction for the 180 diffusion-weighted images was combined with a global registration to the T1 anatomy computed with the same method. The gradient direction for each volume was corrected using the rotation parameters. The registered images were interpolated to the new reference frame with an isotropic voxel resolution of 1.72 mm and the three corresponding acquisitions and gradient directions were averaged. Finally, for each voxel, a diffusion tensor was fitted to the data.

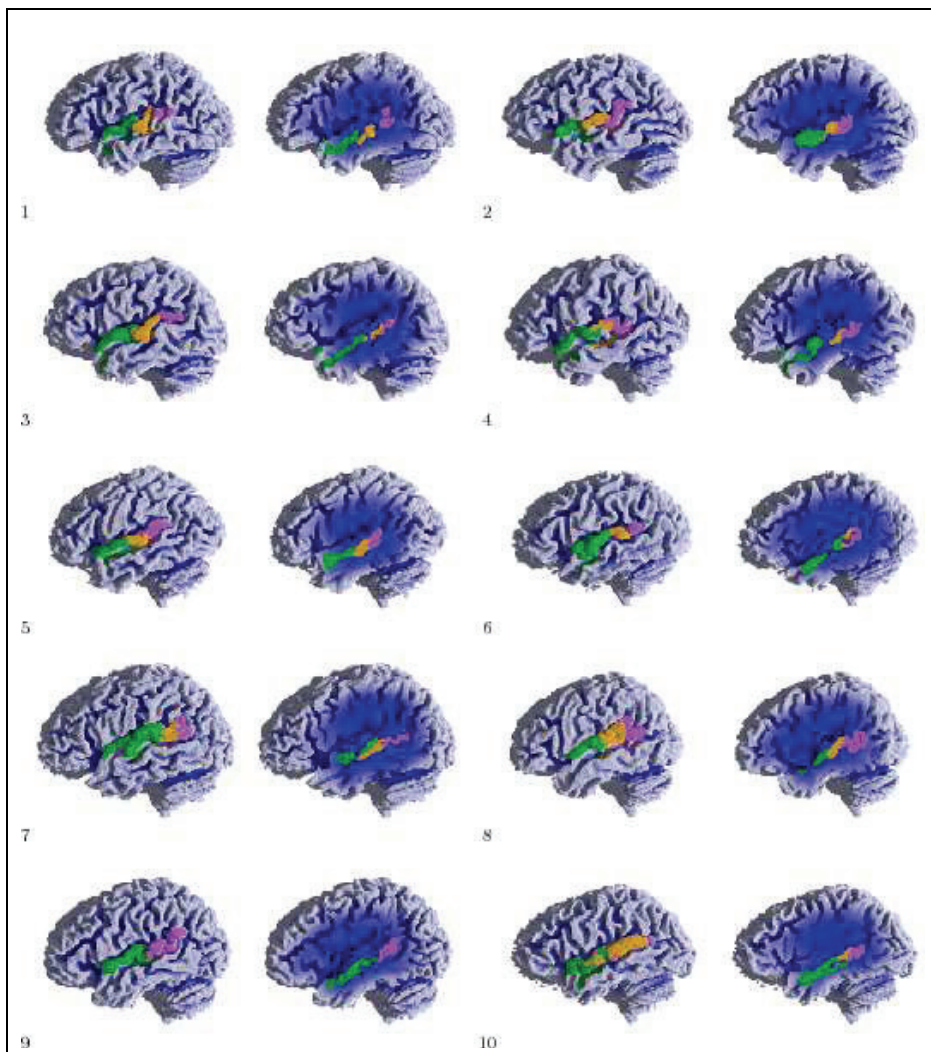
5.3 Results

The parcellation algorithm revealed a consistent clustering into three STG and three STS subregions for 8 out of 10 participants (see Figure 5.1, 1-8). For one participant, only two clusters per ROI could be reliably distinguished (see Figure 5.1, 9). A second participant did not show any parcellation that conformed to the criterion of resulting in continuous subregions (see Figure 5.1, 10). Parcellations into more than three clusters were not consistent across participants.

The plausibility of the clustering results was further examined by measuring the comparability of the voxel-wise connectivity profiles within and between clusters and ROIs for each participant. The two participants showing deviant results during clustering were excluded from this analysis. In order to determine the overall amount of similarity between any two clusters, the correlation coefficients representing the degree of similarity between the connectivity profiles of each single voxel in cluster one and the connectivity profiles of each single voxel in cluster two were transformed into Fisher's z values and then averaged. To compute the similarity within a single cluster, cluster one and cluster two were defined as being one and the same while discarding autocorrelations and repeated comparisons.

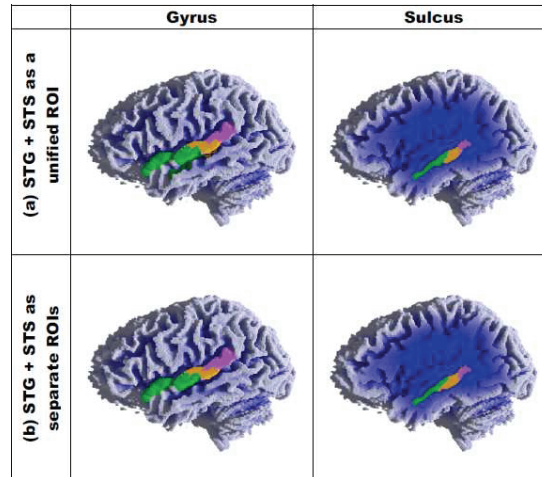
For five participants, this analysis confirmed the categorization into three subregions and indicated a high degree of similarity between the connectivity profiles of STG and STS areas, with both the similarity within each cluster and the similarity between homologous

Figure 5.1: White Matter Projections: Individual Subjects



Parcellations are shown for STG and STS as a unified ROI for 10 individuals.

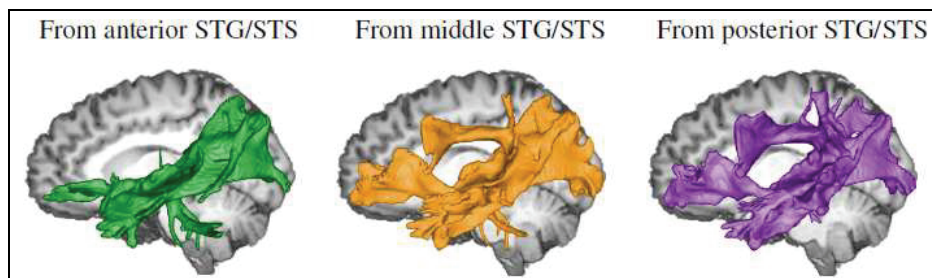
Figure 5.2: White Matter Projections: Average



Parcellations are shown for STG and STS, averaged across all 10 participants.

STG and STS clusters being higher than the similarity between different clusters (see Figure 5.5a for the mean correlation coefficients in this subgroup and Table 5.1 and Table 5.2, rows 1-5 for the individual values). Three participants exhibited a distribution of cluster similarity values that differed slightly from this pattern (see Table 5.1 and Table 5.2, rows 6-8): for one participant, the similarity between anterior and middle clusters on both the STG and STS was comparatively high (Fisher's $z = 0.57$ and 0.538 , respectively) and while still being substantially lower than the similarity within each cluster (range: Fisher's $z = 0.79$ to Fisher's $z = 1.13$), both values were higher than the similarity between the anterior STG and STS clusters (Fisher's $z = 0.471$) and about equal to the similarity between the posterior STG and STS clusters (Fisher's $z = 0.551$). A second participant showed a comparatively high degree of similarity between the anterior and middle STG clusters (Fisher's $z = 0.714$) as well as between the middle and posterior STG clusters (Fisher's $z = 0.58$) and the middle and posterior STS clusters (Fisher's $z = 0.583$). While all three values are considerably lower than the similarity within clusters (range: Fisher's $z = 0.946$ to Fisher's $z = 1.45$) and the similarity between homologous anterior and posterior STG and STS clusters (Fisher's $z = 0.874$ and Fisher's $z = 0.731$, respectively), they are higher than the similarity between the middle STG and STS clusters (Fisher's $z = 0.578$). Finally, a third participant exhibited a very high degree of similarity between the middle and posterior STG (Fisher's $z = 0.75$),

Figure 5.3: Mean Tractograms



Tractograms are shown for the anterior (left), middle (middle) and posterior (right) subregions as uncovered by computing the parcellation of STG and STS as a uniform ROI for the averaged DTI data.

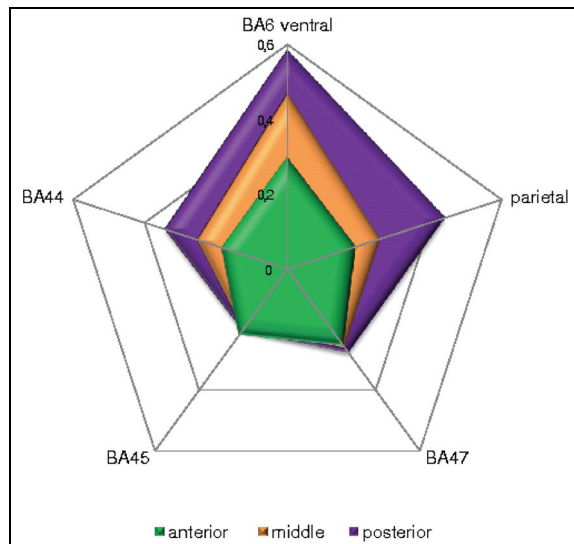
which was higher than the similarity between anterior STG and STS (Fisher's $z = 0.637$), middle STG and STS (Fisher's $z = 0.696$) and posterior STG and STS (Fisher's $z = 0.559$) and nearly as high as similarity within the posterior STS cluster (Fisher's $z = 0.791$).

The differences discussed above notwithstanding, including these three participants when computing group averages did not substantially change the general pattern of results (see Figure 5.5b). Additionally taking into account that the aforementioned deviations were generally not strong enough to render the individual parcellations into three subregions implausible, they were regarded as a reflection of expectable inter-subject variability, not precluding a further group analysis.

Next, the parcellation of a DTI image that was averaged across all participants was computed. This analysis yielded a consistent clustering into three STG and three STS subregions (see Figure 5.2b). Applying the clustering algorithm to a combined STG and STS ROI did not result in a differentiation of separate STG and STS clusters but instead yielded subregions spanning across STG and STS (see Figure 5.2a). This further indicates that connectivity profiles are more similar in the dorsal-to-ventral direction than in the anterior-to-posterior direction and corroborates the participant-wise analysis of the similarity between homologous STG and STS clusters.

As can be seen from the mean tractograms computed for the average DTI data with STG and STS as a unified ROI (see Figure 5.3) as well as from the corresponding connectivity fingerprints (see Figure 5.4), the three subregions of the STG and STS as determined by the parcellation procedure differ in their tractographic profiles. All three areas have potential connections to superior occipital, temporo-polar and inferior frontal destinations via the inferior fronto-occipital fasciculus and the inferior longitudinal fasciculus. Since both

Figure 5.4: Connectivity Fingerprints



Connectivity Fingerprints: Amount of connectivity from the STG/STS in 6 cortical target regions. Numbers (from 0.0 - 1.0) indicate the proportion of fibers reaching each area.

uncinate and IFO traverse through the external and extreme capsule, it is not possible to clearly differentiate the two from this point onwards with current DTI-based tractographic techniques. Within the frontal lobe, BA 45 is the primary language-relevant destination of connectivity through the IFO / uncinate for all three STG/STS subregions, although this structural link is comparatively weak.

Only the middle and posterior STG/STS compartments exhibit strong connectivity to ventral premotor areas (BA 6) via the SLF. Moreover, this pathway is more articulated for the posterior STG/STS. A slightly weaker structural link to ventral BA 44 via the SLF is also evident, with a similar patterning among the STG/STS subareas. All three regions are connected to inferior parietal areas via the caudal section of the SLF; however, this link is again strongest for the posteriormost region.

5.4 Discussion

In the sections above, it was shown that the superior temporal gyrus and sulcus can be reliably parcellated into three subregions based on DTI white matter tractography. As far as

can be determined with current imaging techniques, STG and STS do not differ substantially with regard to their cortico-cortical long-range connectivity.

5.4.1 Connectivity Patterns

Although it has to be kept in mind that DTI tractography is only an indirect measure of anatomical connectivity, the differences between STG/STS subregions that were found with regard to their apparent links to other brain areas merit discussion. The most striking distinction certainly concerns the SLF: middle and posterior STG/STS have much stronger connections through this pathway than anterior areas of the STG/STS, both in terms of destinations in the frontal lobe as well as in terms of destinations in the parietal lobe (see Figures 5.4, 5.5). Posterior and middle STG/STS can be further differentiated, with posterior regions having stronger SLF connectivity with frontal and parietal areas than middle regions.

A possible explanation for this pattern of results is that the middle STG has no strong direct connection to the frontal lobe, but is instead mainly linked to the posterior superior temporal gyrus via a short-range projection system (Upadhyay et al., 2008). Functionally, this would suggest that raw auditory information that is processed with regard to basic acoustic properties in cortex surrounding Heschl's gyrus is relayed to the posterior STG, where it is processed with regard to more complex spectro-temporal features (Griffiths and Warren, 2002) and possibly integrated with sensory-motor representations (Hickok and Poeppel, 2007). The results of these operations may then be transmitted to BA 44 and BA 6 (and possibly additional frontal destinations) via the SLF, either through an intermediate stop in the parietal lobe (Catani et al., 2005) or directly (Rilling et al., 2008).

Table 5.1: Within-cluster Similarity

	STG			STS			STG vs STS		
	ant	mid	pos	ant	mid	pos	ant	mid	pos
1	1.071	0.920	0.965	1.103	1.012	0.896	0.803	0.623	0.776
2	1.147	1.117	0.905	1.167	0.920	0.947	0.881	0.661	0.704
3	0.965	1.060	1.103	0.809	0.853	0.900	0.689	0.677	0.707
4	1.055	0.986	1.171	0.966	0.795	0.720	0.709	0.600	0.529
5	0.777	1.049	0.767	0.753	0.760	0.741	0.461	0.662	0.484
6	1.087	1.122	1.245	1.449	0.946	0.952	0.874	0.578	0.731
7	1.131	0.837	0.929	0.790	0.922	0.880	0.471	0.703	0.551
8	0.807	1.009	1.086	0.928	0.936	0.791	0.637	0.696	0.559

Mean correlation coefficients within clusters (Fisher's z values) for eight participants.

Other authors have reported SLF trajectories that are generally compatible with this hypothesis, both with respect to humans (Catani et al., 2005; Glasser and Rilling, 2008; Makris et al., 2005; Nucifora et al., 2005) and non-human primates (Rilling et al., 2008; Schmahmann et al., 2007). However, it should be noted that there is an ongoing debate concerning possible subdivisions of this fiber bundle. While Glasser and Rilling (2008) assume two pathways constituting the SLF, one connecting the posterior STG to BA 44 and 6 and one connecting the MTG to BA 44, 6, 9 and 45, Catani et al. (2005) propose an SLF subdivision into a direct temporo-frontal link and an additional indirect link via the parietal lobe. The data from the fingerprint analysis that were presented above are consistent with both views since they point to the existence of a connection from the superior temporal to the inferior parietal lobe as reported in Catani et al. (2005) in addition to supplying evidence for a strong link from the posterior STG to BA 6 and BA 44. The connection to BA 45 is weak, which could be explained by the finding of a dominant connection from BA 45 to the MTG (not the STG) as expressed in Glasser and Rilling (2008). Speculatively, this may be taken as an indication for both separate STG and MTG pathways to the frontal lobe in addition to a further subdivision of the STG pathway into a direct link and an indirect link (via the parietal lobe). A third classification scheme (see Makris et al. (2005) for data on the human brain and Schmahmann et al. (2007) for data on non-human primates) distinguishes three SLF subbundles in the parietal and frontal lobes (SLFI - SLFIII) as well as two arcuate bundles (AFh and AFv), analogous to results from tracer studies in monkeys; however, the results presented here do neither support nor contradict this view.

All three STG/STS subregions exhibit connectivity to the frontal lobe via the inferior fronto-occipital fasciculus, with no clear differentiation among subregions (see Figures 5.4, 5.5). There is some connectivity from the anterior STG/STS to rostral language-relevant areas (BA 45 and 47) via the IFO, possibly through the extreme capsule (also see Section 8.1). More caudal regions (BA 44 and 6) are primarily connected to the posterior STG/STS through the SLF, which is in line with previous results on the parcellation of Broca's area (Anwander et al., 2007). When deriving tractograms from seed points directly planted in BA 45 and BA 47 (Anwander et al., 2007), the connectivity to temporal areas through the inferior fronto-occipital fasciculus is much more articulated than when using seed points in the temporal lobe (as in the current study); this is a result of the tractographic procedure, which can only model the actual white matter anatomy imperfectly and does not necessarily work equally well in all cases when tracking the same fiber bundle in different directions. It is therefore possible that the connectivity of superior temporal areas to BA 45 and 47 via the IFO may be underestimated in the data discussed here.

Table 5.2: Between-cluster Similarity

	STG			STS		
	Ant+mid	Mid+pos	Ant+pos	Ant+mid	Mid+pos	Ant+pos
1	0.422	0.255	0.091	0.502	0.316	0.131
2	0.417	0.408	0.122	0.445	0.473	0.160
3	0.478	0.564	0.121	0.315	0.392	0.065
4	0.504	0.489	0.147	0.431	0.284	0.061
5	0.293	0.343	0.011	0.313	0.365	0.055
6	0.714	0.580	0.203	0.475	0.583	0.150
7	0.570	0.218	0.059	0.538	0.401	0.222
8	0.314	0.750	0.097	0.454	0.352	0.084

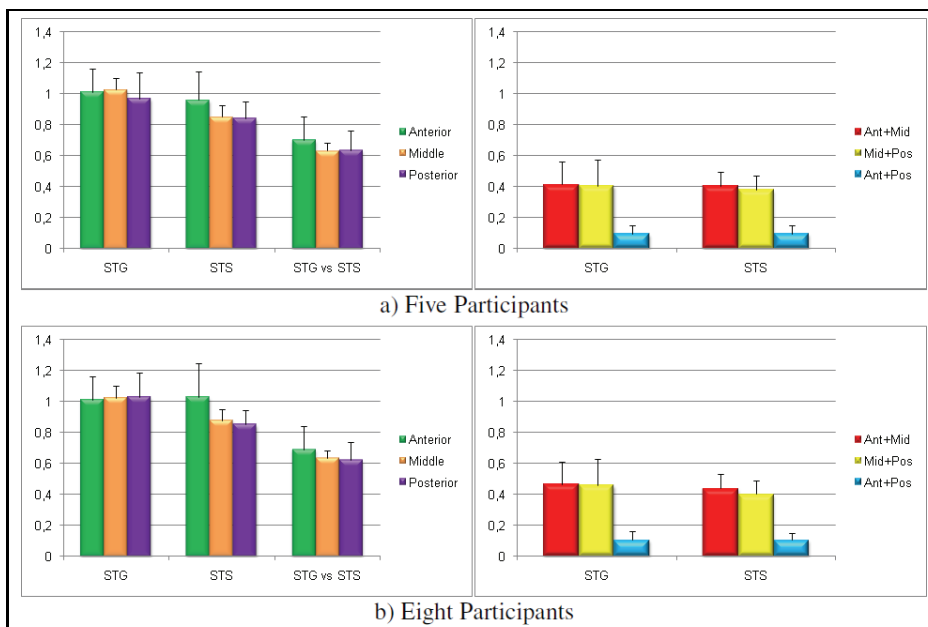
Mean correlation coefficients between clusters (Fisher's z values) for eight participants.

5.4.2 Clustering Results

The connectivity profiles of the middle STG/STS cluster did exhibit a comparatively high degree of similarity to the profiles of the anterior and posterior clusters for a number of participants (see the "Results" section and Table 5.2, rows 3 and 6-8). While to a certain extent, this is certainly due to the close proximity of voxels at the border of adjacent clusters, the existence of such a region with convergent or mixed connectivity profiles is also compatible with recent proposals of dorsal and ventral processing streams originating in primary and secondary auditory areas (Hickok and Poeppel, 2004, 2007; Rauschecker and Tian, 2000; Upadhyay et al., 2008). Because both streams share a common starting region, a certain amount of overlap between the individual fibers that constitute the two pathways may be expected in this area. Since DTI-based tractography can only determine average connectivity profiles for comparatively large volumes of tissue, such a crossover would result in "mixed" connectivity profiles on the voxel level as seen in the current study. However, the data do not allow for any definitive conclusions in this regard and further investigations are certainly necessary.

Homologous clusters on the STG and STS generally exhibited a substantial degree of similarity (see Figure 5.5). In particular, the similarity between corresponding STG and STS clusters was generally higher than the similarity between neighboring clusters on either the STG or the STS on their own. Thus, while STG and STS are not completely identical with regard to their long-range cortico-cortical connectivity, they are comparable to a large extent as far as can be measured with current imaging techniques. First and foremost, this is an anatomical observation. Nevertheless, a broad implication for functional models is that ho-

Figure 5.5: Mean correlation coefficients (Fisher's z values)



Mean correlation coefficients are shown for comparisons between and within clusters and ROIs. Abbreviations: ant=anterior, mid=middle, pos=posterior.

mologous STG and STS regions are part of the same general processing network since they target similar brain regions. By the same logic, adjacent STG and STS areas are anatomically well suited to be the neural correlates of either similar or complementary cognitive processes, producing outputs that are relevant to similar target systems. However, formulating more precise hypotheses is difficult: DTI tractography only has limited accuracy, so while STG and STS subregions certainly connect to similar cortical destinations on the macroscale, relevant differences on the meso- or even microscale may still go undetected. Combined studies of anatomical connectivity, effective connectivity and stimulus-related hemodynamic activity could shed more light on this issue, but ultimately, more precise imaging methods are needed in order to allow for more fine-grained differentiations.

The three-region parcellation as determined by the clustering algorithm that was implemented here can not be directly mapped onto any of the major histological classification schemes currently available (Brodmann, 1909; Galaburda and Sanides, 1980; Morosan et al., 2005; von Economo and Koskinas, 1925). There are some broad correspondences - for example, the anterior, middle and posterior STG/STS regions as defined in the current study appear to be comparable to areas TA2, TA1 and ventral PFcm (von Economo and Koskinas, 1925), respectively. However, as DTI radically differs from cyto-, myelo- and receptorarchitectonic techniques both with respect to the scale of the measured data as well as with respect to the neuroanatomical variables that are investigated, parcellations based on connectivity patterns and parcellations based on histological patterns do not necessarily need to yield similar results. Both approaches should be seen as complementary - that is, both cytoarchitectonically based subdivisions as well as connectivity based subdivisions need to be taken into account in order to appreciate the full range of anatomical and functional differentiation in the human brain.

5.4.3 Conclusions

Both the general delineation of three distinct superior temporal subareas as well as the connectivity profiles associated with each of these regions are in accordance with the neurophysiological literature and anatomical post-mortem examinations and can be mapped onto language functions. Thus, this study further stresses the usefulness and importance of diffusion-based clustering procedures as an analytical tool at the interface between anatomical and functional brain mapping. Furthermore, it complements existing DTI data on the frontal lobe (Anwander et al., 2007) - taken together, the investigation described in the current chapter and the study by Anwander et al. (2007) constitute a comprehensive analysis of the connectivity patterns of the two major sites of language processing in the human brain. With regard to the functional imaging experiments reported in Chapters 6 and 7 of this dis-

CHAPTER 5. DTI DATA ANALYSIS

sertation, it will be interesting to see if the anatomical parcellation of the STG as reported above is reflected in a corresponding neurocognitive differentiation.

Chapter 6

Experiment One (fMRI): Words and Pseudo-words

6.1 Introduction

As described in Chapter 4, the existing evidence on pseudo-word processing is heterogeneous. In the same chapter, it was suggested that the inconsistent pattern of results may be due to three factors pertaining to the nature of the stimuli: lexical transparency, deviation point and phonotactic legality.

To test this hypothesis, the processing of different types of pseudo-words compared to real words was investigated in the fMRI experiment presented in the current section, with pseudo-words being matched as closely as possible to the real words with regard to syllable frequency, syllabic structure and metric structure. Pseudo-words were systematically varied in terms of their lexical transparency: two sets of stimuli were created by only exchanging the nucleus vowel of either the second or the third syllable of a real word, resulting in pseudo-words still being very close to real words with regard to their acoustic form (example: "elephint" derived from "elephant"), while a third set of stimuli was created by rearranging the constituent syllables of different real words, resulting in perfectly pronounceable pseudo-words that could not be related to any real word template at all (example: "thratofant"; cf. Valdois et al. (2006)). A fourth set of stimuli was created by making opaque pseudo-words phonotactically illegal by turning the initial two sounds into a consonant sequence that is impossible in German (example: "tkratofant").

Based on the previous literature, a marked difference in brain activation is predicted for the contrast of real words versus all types of pseudo-words (factor: LEXICALITY), with activation foci for real words in the bilateral temporo-parietal junction area (including the angular gyrus) and bilateral middle to inferior temporal areas, as well as activation increases

Table 6.1: Conditions

Code	Condition	Items	Example	Translation
cra	real words, concrete animate	30	Elefant	Elephant
cri	real words, concrete inanimate	30	Anorak	Jacket
abs	real words, abstract inanimate	60	Adjektiv	Adjective
3rd	pseudo-words, transp., 3rd syl.	30	Elefunt	Elephant
2nd	pseudo-words, transp., 2nd syl.	30	Elufant	Eluphant
pnd	pseudo-words, opaque	30	Dradofent	Thratofant
pil	non-words, phon. illegal	30	Dkdofent	Tkratofant
-	null events	30	-	-

Abbreviations: syl=syllable, phon=phonotactically, tranp=transparent; cra = concrete, animate; cri = concrete, inanimate; abs = abstract; 3rd = third-syllable; 2nd = second-syllable; pnd = opaque; pil = phonotactically illegal.

for pseudo-words in middle parts of the bilateral superior temporal gyri. The difference between transparent pseudo-words and opaque pseudo-words is expected to resemble the contrast between real words and pseudo-words in general (factor: TRANSPARENCY) as the former encourage lexical processing while the latter cannot be processed lexically at all. This effect could possibly be graded further by the position of the syllable that is modified to generate the transparent pseudo-word stimuli (factor: DEVIATION POINT), with pseudo-words created by modifying the third syllable of a real word being processed more word-like than pseudo-words created by modifying the second syllable. The phonotactically illegal stimuli used in this study were always lexically opaque - thus, it is expected that they will elicit a pattern of brain activations similar to that observed for phonotactically legal opaque pseudo-words (factor: PHONOTACTIC LEGALITY), possibly with additional activation increases in regions involved in phonological and phonotactic analysis (e.g., the bilateral middle superior temporal gyri or even the superior temporal sulcus; cf., Démonet et al. (2005)).

The results of the current experiment will be critical in order to determine the type of pseudo-word that is to be used in experiment two: only pseudo-words that do not induce any lexical-semantic processing at all are suitable for the investigation of syntactic processes in the absence of semantics. In addition, selective activation of STG areas for either pseudo-words or real words can yield important insights with regard to the involvement of this brain region in word-level phonological processes as well as lexical access.

6.2 Materials and Methods

6.2.1 Participants

After giving informed consent, 16 native speakers of German (8 male; mean age 26 years; age range 21-34 years) participated in the study. No participant had any history of neurological or psychiatric disorders. All participants had normal hearing and were right-handed (laterality quotients of 90-100 according to the Edinburgh handedness scale (Oldfield, 1971)).

6.2.2 Stimuli and task

120 three-syllable real words were chosen for presentation during the experiment, 60 concrete and 60 abstract. Abstract words were only included as fillers in order to have an equal number of real words and pseudo-words for the lexical decision task; they were not included in the statistical analysis of the functional data. All real words were matched for frequency of occurrence according to the "Wortschatzprojekt"-Corpus (Biemann et al., 2004). In order to construct the pseudo-word conditions (with 30 items each) and in order to have a set of real words of equal size for later statistical comparisons, a set of 30 concrete real words (abbreviation: "rea") was carefully selected so that it constituted a representative sample of the superset with respect to syllable structure frequency (e.g., if the 60-word superset contained 30 words with consonant (C) vowel (V)-CV-CV syllable structure, the 30-word subset contained 15 words with CV-CV-CV syllable structure) and stress pattern frequency (e.g., if the superset contained 30 words with first-syllable stress, the subset contained 15 words with first-syllable stress). All pseudo-word conditions except the phonotactically illegal one exactly matched the syllable structure- and stress pattern frequencies of these 30 real words.

Four pseudo-word conditions were constructed from the selected real words: transparent pseudo-words recognizable as such on the second syllable ("2nd"), transparent pseudo-words recognizable as such on the third syllable ("3rd"), opaque pseudo-words ("pnd") and phonotactically illegal pseudo-words ("pil"). Transparent pseudo-words were created by exchanging the nucleus of one syllable of each real word, controlling for exchange probability (that is, an "a" was equally often replaced by an "i" as by every other vowel). Opaque pseudo-words were created by intermixing the syllables of the real words amongst each other while sticking to their relative positions within the word (that is, if "ba" only occurred as a first syllable in the real word condition it also only occurs as a first syllable in the pseudo-word condition), thereby matching syllable frequencies per position across pseudo-words and real words (Valdois et al., 2006). The resulting pseudo-words were phonotactically legal and sounded natural, but did not resemble any existing real words. Phonotactically illegal pseudo-words were created by making the first syllable of all opaque pseudo-

words an illegal consonant-consonant cluster (e.g. "dk").¹ See Table 6.1 for a complete list of all conditions with example stimuli.

All stimuli were spoken by a trained female native speaker of German, recorded digitally and subsequently normalized to 75 dB using the PRAAT software package (Boersma, 2001). During auditory word presentation, volume was controlled by the software gain controls and the manual configuration of the sound card. Mean stimulus intensity and mean stimulus duration did not differ significantly across conditions. There was a significant main effect of mean fundamental frequency, but F0 differences between conditions were very small (below 8 Hz) in absolute terms, making it highly unlikely that they had any influence on the functional results.

Participants were briefed on the task (lexical decision) outside of the scanner and performed a short training exercise. An experimental session consisted of 270 trials lasting 6 seconds each, resulting in 27 minutes duration per session. Within each 6 second trial (except for null events), a single item was presented (either real word or pseudo-word). During each trial, 3 functional volumes were acquired. Stimulus onset was jittered randomly (equally distributed across conditions) relative to the beginning of the first of these volumes by either 0, 500, 1000, or 1500 milliseconds to allow for measurements to be taken at numerous time points along the BOLD signal curve, thus providing a higher resolution of the BOLD response (Miezin et al., 2000). Trials were presented in a pseudo-randomized fashion. In order to prevent priming effects between transparent pseudo-words and the corresponding real words, stimuli were arranged in such a way that in 50% of all cases, both transparent pseudo-word variants preceded the real word while for the remaining 50% the real word preceded both transparent pseudo-word variants. 2nd-syllable transparent pseudo-words preceded their 3rd-syllable counterparts equally often as vice versa.²

Participants lay supine inside the scanner and wore earphones, making their responses with a button box. All auditory stimulation was delivered binaurally. To reduce scanner noise, external ear defenders and perforated ear plugs that conducted the sound directly into the auditory passage were applied.

¹Phonotactically illegal pseudo-words were pronounced by a trained speaker who was specifically instructed to avoid the insertion of a schwa-like vowel. This method was chosen over a synthetic one like splicing or filtering in order to ensure that the stimuli sounded as natural as possible.

²In order to rule out priming as a source of effects in the analysis of the functional data, the direct contrast of (2nd+3rd primed)-(2nd+3rd not primed) was also computed. There were no statistically significant differences between both sets of items, not even at a threshold of $p < 0.001$ uncorrected per voxel and no minimum cluster size. This allows for the conclusion that transparent pseudo-words were not processed more word-like when preceded by their real word counterparts - that is, differences between transparent pseudo-words and opaque pseudo-words cannot be due to priming of the transparent pseudo-words.

6.2.3 fMRI Data Acquisition

The experiment was carried out on a 3T scanner (Siemens TRIO, Erlangen). For functional imaging, 18 axial slices parallel to the AC-PC plane and covering almost the whole brain were acquired using a gradient-echo echo-planar imaging (EPI) sequence with a time-to-echo (TE) of 30ms, a flip angle of 90 degrees, a time-to-repetition (TR) of 2 seconds, and an acquisition bandwidth of 116 kHz. The matrix acquired was 64x64 with a field of view (FOV) of 19.2cm, resulting in an in-plane resolution of 3x3 mm. The slice thickness was 4 mm with an interslice gap of 1 mm. Prior to the functional runs, 18 T1-weighted MDEFT (Ugurbil et al., 1993) images (data matrix 256x256, TR 1.3 s, TE 7.4 ms) were obtained with a non slice-selective inversion pulse followed by a single excitation of each slice (Norris, 2000). Additionally, a set of 18 T1-weighted spin-echo EPI images (TE 14 ms, TR 3000 ms) was taken with the same geometrical parameters and the same bandwidth as used for the fMRI data for registration purposes.

6.2.4 fMRI Data Analysis

Data processing was performed with the software package LIPSIA (Lohmann et al., 2001). This software package contains tools for pre-processing, co-registration, statistical evaluation, and visualization of fMRI data. Functional data were motion-corrected offline with the Siemens motion correction protocol. Five images at the start of each session were discarded to allow the EPI signal to reach equilibrium. To correct for the temporal offset between the slices acquired in one scan, a cubic-spline-interpolation was applied. A temporal highpass filter with a cut-off frequency of 1/72 Hz was used for baseline correction of the signal and a spatial Gaussian filter with 5.65 mm full-width at half-maximum (FWHM) was applied.

To align the functional data slices with a 3D stereotactic coordinate reference system, a rigid linear registration with six degrees of freedom (3 rotational, 3 translational) was performed. The rotational and translational parameters were acquired on the basis of the MDEFT (Norris, 2000; Ugurbil et al., 1993) and EPI-T1 slices to achieve an optimal match between these slices and the individual 3D reference data set. This 3D reference data set was acquired for each participant during a previous scanning session. The MDEFT volume data set with 160 slices and 1mm slice thickness was standardized to the Talairach stereotactic space (Talairach and Tournoux, 1988). The rotational and translational parameters were subsequently transformed by linear scaling to a standard size. The resulting parameters were then used to transform the functional slices using trilinear interpolation, so that the resulting functional slices were aligned with the stereotactic coordinate system. This linear normalization process was improved by a subsequent processing step that performed an additional nonlinear normalization (Thirion, 1998).

The statistical evaluation was based on a least-squares estimation using the general linear model for serially autocorrelated observations (Friston, 1994, 1995; Friston et al., 1995; Worsley and Friston, 1995). The design matrix was generated with a synthetic hemodynamic response function (Friston et al., 1998; Josephs et al., 1997) and its first derivative.

The model equation, including the observation data, the design matrix and the error term, was convolved with a Gaussian kernel of dispersion of 4 s FWHM to deal with the temporal autocorrelation (Worsley and Friston, 1995). In the following, contrast-images, i.e. estimates of the raw-score differences between specified conditions, were generated for each participant. As noted before, each individual functional dataset was aligned with the standard stereotactic reference space so that a group analysis based on the contrast-images could be performed. The single-participant contrast-images were then entered into a second-level random effects analysis for each of the contrasts. The group analysis consisted of a one-sample t-test across the contrast images of all participants that indicated whether observed differences between conditions were significantly distinct from zero (Holmes and Friston, 1998). Subsequently, t-values were transformed into Z-scores. Only correctly answered trials were included in the analysis.

To protect against false positive activations, a Monte Carlo randomization procedure was used to identify the probability of obtaining erroneous activation clusters. This procedure generates voxels at a rate equal to the significance criterion specified, proportional to the total number of voxels in the dataset, and calculates a cluster size that corresponds to the true false-positive rate for these conditions. Using 1,000 iterations, a false positive cluster probability of $p < 0.05$ was achieved with a minimum cluster size of 405 mm^3 at a threshold of $p < 0.001$ (uncorrected) for individual voxels. This synthetically determined statistical threshold was then applied to all voxels in the real data (that is, only clusters of at least 405 mm^3 at $p < 0.001$ per voxel are reported, resulting in $p < 0.05$ at the cluster level). The advantages of combining a voxel-based threshold with a minimum cluster size have been described elsewhere (Forman et al., 1995).

In addition to generating contrast images, the mean percent signal change per condition was calculated in a 3-8 second time window for all voxels of each cluster of activation that reached supra-threshold level. These results are reported relative to null events as a baseline (that is, the amount of percent signal change induced by null events was subtracted from the amount of percent signal change induced by each experimental condition).

In addition, a conjunction analysis for two of the relevant contrasts is reported. Here, voxels in which activation differences reached supra-threshold significance in both individual contrast images are plotted.

Table 6.2: Behavioral Results

Condition	% Accuracy (SD)
real words	89 (6)
second-syllable pseudo-words	88 (10)
third-syllable pseudo-words	88 (6)
opaque pseudo-words	94 (4)
phonotactically illegal pseudo-words	97 (5)
all words	90 (6)

Values are means for all participants. SD=standard deviation.

6.3 Results

6.3.1 Behavioral Results

An analysis of variance (ANOVA) with the factor WORD TYPE (real words, second-syllable pseudo-words, third-syllable pseudo-words, opaque pseudo-words, phonotactically illegal pseudo-words) was conducted in order to assess differences in terms of accuracy³ (also see Table 6.2). The corresponding main effect was highly significant ($F_{4,60} = 9.05$, $p < 0.0001$) and was further evaluated by computing contrasts between single conditions. Response accuracy was significantly different between real words and phonotactically illegal pseudo-words ($F_{1,15} = 19.64$, $p = 0.0005$) as well as between real words and opaque pseudo-words ($F_{1,15} = 9.36$, $p = 0.0079$), but not between real words and either second- or third-syllable transparent pseudo-words. Phonotactically illegal pseudo-words were responded to more accurately than all other types of pseudo-words (second-syllable: $F_{1,15} = 28.28$, $p < 0.0001$; third-syllable: $F_{1,15} = 15.0$, $p = 0.0015$; opaque: $F_{1,15} = 8.45$, $p = 0.0108$). Similarly, the response to opaque pseudo-words was more accurate than the response to either second- ($F_{1,15} = 11.19$, $p = 0.0044$) or third-syllable pseudo-words ($F_{1,15} = 7.42$, $p = 0.0157$). No significant difference emerged between second- and third-syllable pseudo-words.

6.3.2 fMRI Results

In order to test the hypotheses, direct contrasts were computed between single experimental conditions as well as between sets of conditions. The results of these comparisons will be presented below (also see Table 6.3). All abbreviations are as introduced in Section 6.2.2. Only the subset of real words matched to the pseudo-word stimuli in terms of sample size,

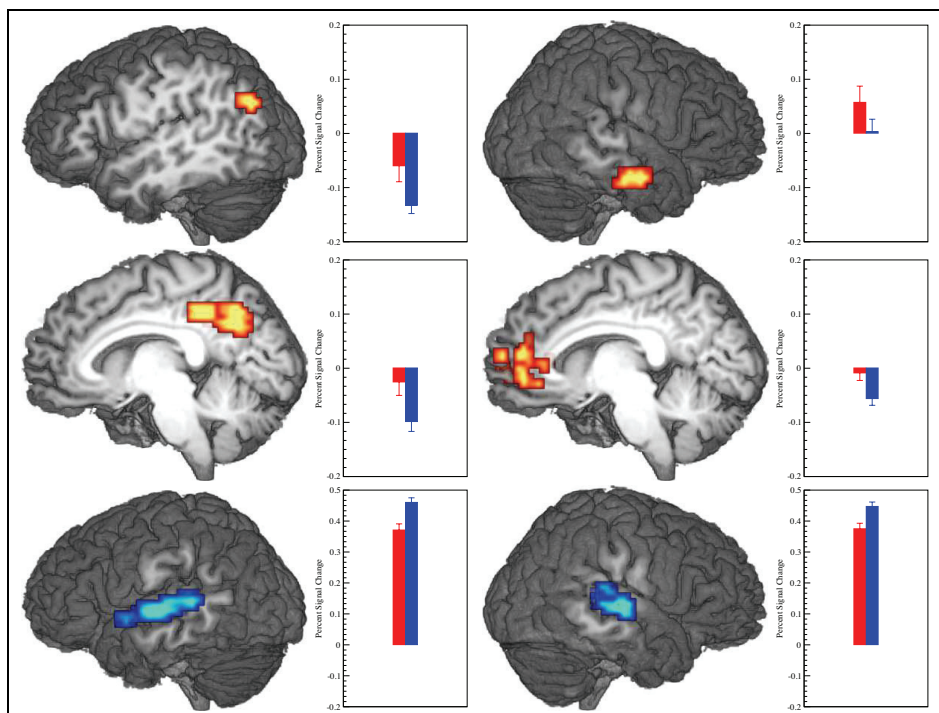
³Note that reaction times were measured from stimulus onset to prevent false time outs due to participants responding too early and are thus not sufficiently accurate to merit a detailed analysis.

Table 6.3: Functional Results: Peak Voxel Coordinates

Contrast	x	y	z	z Value	Volume	Region
rea > 2nd+3rd+pnd+pil	-5	-67	30	3.62	6345	Left Precuneus
	-47	-70	27	3.56	729	Left MTG
	-8	38	0	3.39	3699	Left aCC
	61	-13	-15	3.48	891	Right ITG
2nd+3rd+pnd+pil > rea	58	-25	6	-3.72	1431	Right STG
	-62	-34	9	-3.57	3375	Left STG
2nd+3rd+pnd > pil	No activation found					
pil > 2nd+3rd+pnd	No activation found					
2nd+3rd > pnd	-44	-67	45	3.29	648	IPL
pnd > 2nd+3rd	No activation found					
2nd > 3rd	40	-64	30	3.45	702	Right AG
	1	56	18	3.35	810	Right MFG
	25	44	18	3.30	891	Right SFG
	7	41	-9	3.40	1512	Right MFG
	-29	-34	-9	3.36	513	Left PhG
3rd > 2nd	No activation found					

Volumes are given in mm³, z values are mean values for each cluster. aCC = anterior cingulate cortex, AG = angular gyrus, MFG = medial frontal gyrus, PhG = parahippocampal gyrus, IPL = inferior parietal lobule, STG = superior temporal gyrus, ITG = inferior temporal gyrus, MTG = middle temporal gyrus. Abbreviations for experimental conditions are as introduced in Section 6.2.2.

Figure 6.1: Lexicality effect : rea - (2nd+3rd+pnd+pil)



Red color scale ($Z=+3.09$ to $Z=+4.72$): real words > pseudo-words. Blue color scale ($Z=-3.09$ to $Z=-5.23$): pseudo-words > real words. Mean percent signal change is shown for a 3-8 second time window, averaged across all voxels of each cluster and plotted relative to null events as a baseline (red=real words, blue=pseudo-words).

syllable structure and metric structure was used for comparisons (abbreviation: "rea"). All of the differences in percent signal change that are reported were significant at a level of $p < 0.05$.

Lexicality: rea - (2nd + 3rd + pnd + pil)

Confirming the predictions, a number of pronounced differences between real words and pseudo-words was found (across all four types; see Figure 6.1): real words elicited a stronger hemodynamic brain response in the left posterior middle temporal and angular gyri, the caudal part of the bilateral cingulate gyri, the medial parts of the bilateral pre-cuneus, the bilateral anterior cingulate gyri and the right inferior temporal gyrus. As can be seen from the analysis of percent signal change (PSC), the statistical differences between

conditions observed in all regions except the right ITG are due to pseudo-words producing a stronger deactivation than real words.

Pseudo-words induced stronger activations than real words along the entire length of the superior temporal gyrus bilaterally, favoring the left hemisphere in terms of activation extent (3375 mm³ vs 1431 mm³). Judging from the PSC analysis, this is due to pseudo-words eliciting considerably more activation than real words (however, there is no deactivation for real words).

Phonotactic Legality: (2nd + 3rd + pnd) - pil

Phonotactically illegal pseudo-words did neither elicit more brain activity than phonotactically legal ones nor vice versa.

Transparency: (2nd + 3rd) - pnd

When compared to opaquely derived pseudo-words transparently derived pseudo-words elicited an increased hemodynamic brain response in the left inferior parietal lobule (see Figure 6.3). The analysis of PSC suggests that this is due to transparent pseudo-words eliciting a weaker deactivation than opaque pseudo-words.

Deviation point: 2nd - 3rd

Transparently derived pseudo-words modified on the second syllable elicited a stronger hemodynamic brain response than their third-syllable modification counterparts in a number of widely distributed brain regions (see Figure 6.2). In the right hemisphere, the superior frontal gyrus, the medial frontal gyrus and the angular gyrus were activated significantly. The parahippocampal gyrus was activated in the left hemisphere.

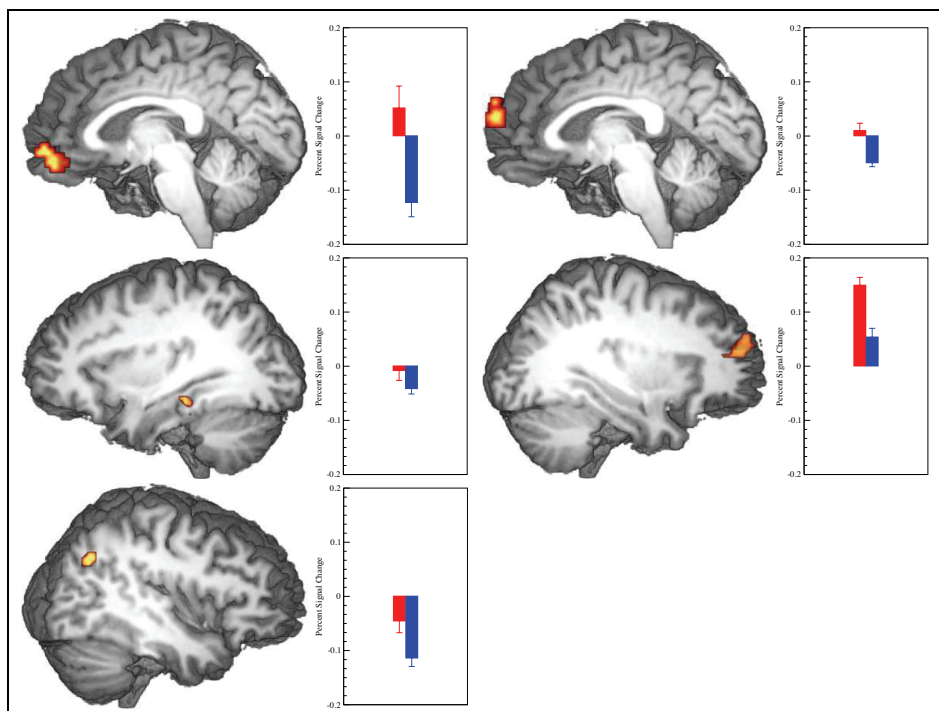
Third-syllable deviation pseudo-words did not elicit a significantly stronger hemodynamic brain response than second-syllable deviation pseudo-words anywhere in the brain.

Looking at the analysis of percent signal change, the differences between conditions in the parahippocampal gyrus and the right angular gyrus seem to be mostly due to stronger deactivations for 3rd-syllable pseudo-words than for 2nd-syllable pseudo-words. In all frontal regions, however, differences appear to be due to increases in activation for 2nd-syllable pseudo-words.

Summary

The behavioral results indicate that participants listened to the auditory stimuli attentively and were able to solve the task easily. Participants responded more accurately to pseudo-words than to real words. Within the set of pseudo-word conditions, responses to phonotac-

Figure 6.2: Deviation point effect : 2nd-3rd

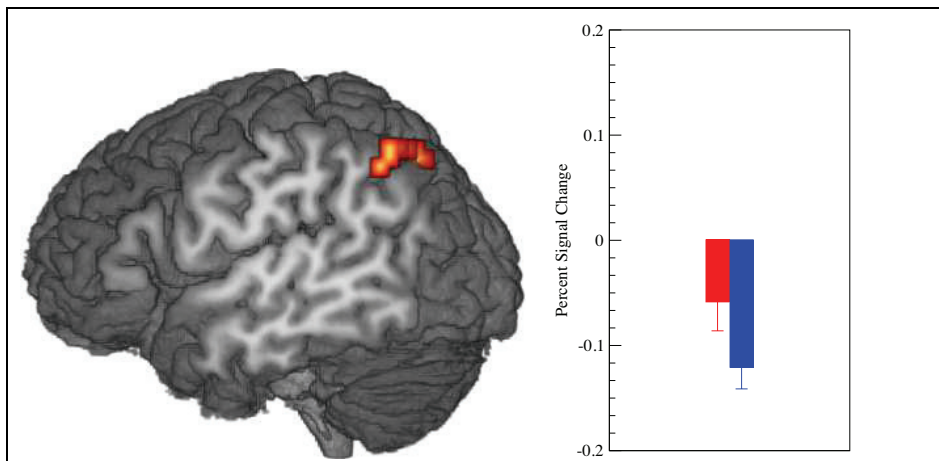


Red color scale ($Z=+3.09$ to $Z=+4.39$): 2nd-syllable pseudo-words > 3rd-syllable pseudo-words. Mean percent signal change is shown for a 3-8 second time window, averaged across all voxels of each cluster and plotted relative to null events as a baseline (red=2nd-syllable pseudo-words, blue=3rd-syllable pseudo-words).

tically illegal and opaquely derived stimuli were more accurate than responses to transparently derived stimuli. I will refrain from interpreting the reaction time data for the technical reasons outlined in Section 6.3.1.

Brain activations were larger for real words than for pseudo-words in medial frontal and parietal as well as in lateral posterior temporo-parietal and inferior temporal regions bilaterally. Derivational transparency as well as deviation point proved to be differentiating factors among pseudo-word types, with transparently derived pseudo-words eliciting more brain activity than opaque pseudo-words and transparent pseudo-words modified on the second syllable eliciting stronger brain responses than pseudo-words transparently derived by changing the third syllable. Phonotactic legality as implemented in the current study did not make a significant difference in terms of activation patterns. All types of pseudo-words

Figure 6.3: Transparency effect : (2nd+3rd)-pnd



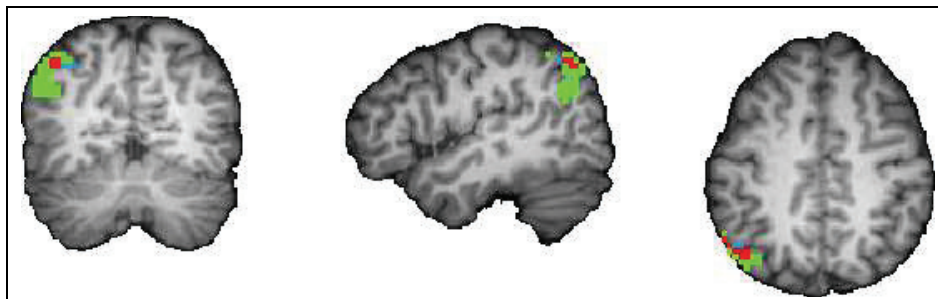
Red color scale ($Z=+3.09$ to $Z=+3.7$): transparent pseudo-words > opaque pseudo-words. Mean percent signal change is shown for a 3-8 second time window, averaged across all voxels of each cluster and plotted relative to null events as a baseline (red=transparent pseudo-words, blue=opaque pseudo-words).

elicited a markedly stronger brain response than real words in the bilateral superior temporal gyri.

6.4 Summary and Discussion

Generally speaking, the results reported above fit quite well with data from previous research: bilateral activations around the temporo-parietal junction point and angular gyrus as well as bilateral activations in middle and inferior temporal regions have consistently been reported for real words when compared to pseudo-words (Fiebach et al., 2002; Hagoort et al., 1999; Henson et al., 2002; Kotz et al., 2002; Majerus et al., 2002; Orfanidou et al., 2006; Rissman et al., 2003; Vigneau et al., 2005; Xiao et al., 2005), and are most often taken to reflect efforts in word-level semantic processing. Activations for pseudo-words in the bilateral superior temporal gyrus are not as common, but have also been observed (Hagoort et al., 1999; Kotz et al., 2002; Newman et al., 2001); they are commonly interpreted as reflecting attempts at pseudo-word interpretation due to a perceived similarity to real words (Kotz et al., 2002) or an increase in phonological and lexical processing cost due to low word frequency (Newman et al., 2001).

Figure 6.4: Conjunction analysis: real words and transparent pseudo-words compared to opaque pseudo-words



Green: activation increase for real words when compared to opaque pseudo-words (sre-pnd). Blue: activation increase for transparent pseudo-words when compared to opaque pseudo-words (2nd-3rd). Red: activation increase for both real words and transparent pseudo-words when compared to opaque pseudo-words ((sre-pnd)+(2nd+3rd)-pnd) .

Real-word related increases of brain activity in the anterior and caudal cingulate cortex as well as in the precuneus are more difficult to reconcile. Activations in similar regions have been reported in a number of previous studies on single word processing (Henson et al., 2002; Orfanidou et al., 2006; Rissman et al., 2003), but are generally not taken to subservise any language-specific functions. The caudal cingulate as well as the precuneus have both been implicated in more general aspects of cognition, especially episodic memory retrieval (Cavanna and Trimble, 2006; Lundstrom et al., 2005; Maddock and Buonocore, 1997; Maddock et al., 2001; Vogt et al., 1992) and mental imagery (Cavanna and Trimble, 2006; Fletcher et al., 1995). The anterior cingulate cortex is commonly associated with emotional processing (Bush et al., 2000; Devinsky et al., 1995), performance monitoring (Carter et al., 1998) and executive control (Devinsky et al., 1995).

Relating these findings to the current study, a plausible suggestion is that the activation of the anterior cingulate that was observed for real words is due to response competition: when there is no easily detectable "error" or modification in a stimulus (which is the case for real words, but not for pseudo-words), it may be more difficult to come up with a decision about the lexical status of the item under consideration.

No significant difference between phonotactically illegal and phonotactically legal stimuli was found in the current study. While it might be the case that this type of non-word is just not processed differently from legal pseudo-words, it cannot be ruled out that the phonotactic violation that was implemented here was either not strong enough to yield a statistically significant effect or was not recognized as a violation at all - for example, par-

ticipants may have perceived illusory ephentetic vowels within the consonant-consonant clusters. Dupoux et al. (1999) report a phenomenon like this for native speakers of Japanese when confronted with phonotactically illegal syllable structures. Although this point has no direct bearing on the main line of argumentation, it does imply that when investigating the impact of phonotactic violations on speech processing, the application of some synthetic procedure (like splicing or filtering) to the stimuli is advisable in order to produce unambiguous results.

Regarding the general interpretation of the results, substantial evidence is reported in support of the claim that the degree to which pseudo-words engage lexical processes (i.e. are treated similarly to real words) during processing is largely dependent on two factors. The first is lexical transparency: transparent pseudo-words elicit comparable brain responses to real words (when contrasted to opaque pseudo-words) in a left temporo-parietal region (see Figure 6.3). The second is the deviation point: transparent pseudo-words modified on the second syllable elicit an increased hemodynamic response in a number of medial frontal as well as temporal regions when compared to transparent pseudo-words modified on the third syllable.

Basically this evidence shows that only opaque pseudo-words reliably prevent successful lexical access and consequently inhibit subsequent semantic processing since they cannot be related to any existing entry in the mental lexicon. With transparent pseudo-words, much depends on the particular way in which they are constructed. Apparently, processing pseudo-words that already deviate from the expected phonological form of their real word template on the second syllable requires more cognitive resources than processing pseudo-words that do so on the third and final syllable. What I would like to propose here is that this effect is due to the way in which the brain handles lexical access: all of the real word stimuli that were used in the current study had their uniqueness point after the second syllable - that is, after having heard the first two syllables of one of these real words, there was only one candidate word left for lexical selection. The same was true for the 3rd-syllable deviation pseudo-words, but obviously not for the 2nd-syllable deviation stimuli. My suggestion is that the lack of an uniquely determined target real word makes it harder to detect the erroneous nature of the latter type of stimulus: after having heard the first two syllables of a 3rd-syllable deviation pseudo-word like "Granati", participants have accumulated enough information to conclude that the non-modified word form has to be "Granate" and can easily compare this to the final syllable that they actually encounter. After having heard the first two syllables of a 2nd-syllable deviation pseudo-word like "Granute", however, no such straightforward comparison is possible since "Granu" is not the beginning of an actual word. This does imply that a lexical non-match (i.e., hearing a stimulus that does not allow an easy selection of a particular entry in the mental lexicon) is harder to detect than an lexi-

cal mismatch (i.e., hearing a stimulus that has a clear target entry in the mental lexicon, but deviates from that entry), explaining the pattern of results that were obtained here.

These results can at least partly explain the inhomogeneity of the differences between real words and pseudo-words that are reported in previous neuroimaging studies. However, applying the categories that were established here (lexically transparent and lexically opaque) to the existing literature is a delicate task for two reasons: firstly, it is not always possible to determine which types of pseudo-word stimuli (transparent or opaque) were actually used since this is not often explicitly stated and cannot always be inferred from the description of the stimuli provided in "methods" sections. Secondly, the effects of numerous other factors that have a considerable impact on inter-study variability (in particular, stimulus length in terms of the number of syllables, auditory versus visual modality and fMRI versus PET scanning) cannot easily be disentangled from the effect of lexical transparency. For example, Kotz et al. (2002) used pseudo-words that would have to be called lexically transparent when strictly applying the definition presented in this paper, but nevertheless report results that are quite comparable to the ones presented here. This effect is probably mainly due to the length of their pseudo-word stimuli, which were relatively short two-syllable items: the shorter the stimulus, the harder it is to reconstruct the original real word template because less information is available to do so. This effectively reduces the lexical transparency of such items even if they only differ from a particular real word by one phoneme. Newman et al. (2001), on the other hand, report a very different set of results while using very short one-syllable pseudo-words. In this case, the apparent discrepancy to Kotz et al. (2002) and the current study is likely due to differences in the mode of stimulus presentation and the task that was used: Newman et al. (2001) used a blocked design and a phoneme monitoring task, while in the study by Kotz et al. (2002) and the the current study, an event-related design and a lexical decision task were implemented (for a similar argument, also see Rissman et al. (2003)).

In conclusion, the data discussed in this chapter demonstrate that lexical processing due to word form reconstruction is a factor to be reckoned with when utilizing pseudo-words transparently derived from real words. Opaque pseudo-words are to be preferred in most contexts since only they reliably induce a reduced amount of semantic processing. Regarding functional localization, further evidence was provided for the claim that the middle temporal and angular gyrus are critically involved in lexical-semantic processing. In addition, it was shown that medial parietal structures including the anterior and posterior cingulate gyrus and the precuneus play a role as well, albeit probably not due to linguistic processing, but rather due to a number of more general cognitive processes that are only induced by meaningful stimuli. With regard to the experiments described in Chapter 7, the results of

CHAPTER 6. EXPERIMENT ONE (FMRI): WORDS AND PSEUDO-WORDS

the current study strongly support the use of lexically opaque pseudo-word stimuli in order to ensure a successful suppression of lexical-semantic processing.

Chapter 7

Experiment Two (fMRI and ERPs): The Influence of Local Predictability and Lexicality on Syntactic Processing

7.1 Introduction

Syntactic well-formedness is dependent on both local and non-local structural configurations within a sentence: while morphosyntactic relations such as agreement often apply to words that are separated by a considerable number of intervening phrases (see Example 7.1), the legality of a sentence's phrase structure is solely dependent on rules concerning immediately adjacent elements (see Example 7.2).¹

(7.1) **Die Händler, die gestern Fisch*
The.D.PL.NOM trader.N.PL.NOM who.D.PL yesterday.ADV fish.N.SG.ACC
verkauften, wird heute verhaftet.
sell.V.3PL.PAST be.AUX.3SG.PRES today.ADV arrest.V.PTCP
*The traders who sold fish yesterday is arrested today.

(7.2) **Die Gans wurde im*
The.D.SG.NOM goose.N.SG.NOM is.AUX.3SG.PAST in_the.P.SG.DAT
gefüttert.
feed.V.PTCP
*The goose was in the fed.

¹Note that Example 7.1 is ungrammatical because the initial subject noun phrase (NP) "Die Verkäufer" does not agree with the final auxiliary "wurde" in number whereas Example 7.2 is ungrammatical because in German, the head of a prepositional phrase must be followed by a noun or an adjective.

In terms of on-line sentence comprehension, this leads to an important difference in terms of the predictive value of morphosyntactic and phrase structure information: while the latter can be used to restrict the set of words that can legally follow a particular lexical item (i.e. as illustrated in the example above, a preposition can not be followed by a verb), the former only allows for long-term predictions of a more general nature (i.e. encountering an NP that bears nominative case and is marked as singular permits the inference that a verb with a singular inflection will be encountered at *some* later point, but this verb need not be the next word). Crucially, the distinction described above has to be considered when investigating the brain response to morphosyntactic and phrase structure violations: any difference that is observed between these two types of grammatical anomalies may as well be due to the strength and the locality of the linguistic predictions that are refuted by the violation as it may be due to differences in the processing of morphosyntactic and phrase structure information per se (see Hasting and Kotz, 2008; Lau et al., 2006, for similar lines of argumentation).

Thus, the experiments described in this chapter were designed to control for this potential confound by employing sentences containing phrase structure and morphosyntactic violations that were both limited to a strictly local level, thereby making the two manipulation conditions as similar as possible in this respect. To this end, the experimental material was constructed in a way that yielded verbal stimuli in which both morphosyntactic and phrase structure violations depended on two immediately adjacent words occurring at precisely the same point in the sentence - in fact, grammatical anomalies even occurred at precisely the same point in the critical word (namely the inflectional suffix). Both types of violations also always concerned lexically identical word stems (see Section 7.2 for details).

The use of such a highly controlled sentence context that is as similar as possible across experimental conditions allows for a maximum amount of comparability between different grammatical manipulations. If differential responses are obtained in both conditions, it is highly likely that they are caused by genuine differences in the processing of morphosyntactic and phrase structure information and are not simply due to differences in local predictability. If, on the other hand, similar brain responses are observed for the processing of phrase structure and morphosyntactic violations, it is likely that this convergence is due to the use of overlapping mechanisms for the detection of local prediction mismatches.

While the procedure described above should minimize any confounding effects of locality and prediction strength across both syntactic violation conditions, a more general problem for studies utilizing ungrammatical stimuli arises from the fact that syntactic violations always have implications for semantic interpretation. Simply put, understanding the intended meaning of a sentence is more difficult if it contains ungrammaticalities, and it is quite plausible that world knowledge and general semantic resources are drawn upon

in order to either repair an illegal syntactic structure or to at least extract as much information from it as possible. With fMRI, it is not feasible to separate early automatic detection processes from late attempts at repair; therefore, activation increases observed for ungrammatical sentences might as well be induced by syntactic as by semantic processing. In order to be able to assess the severity of this potential confounding factor, all sentences were tested both in real word and pseudo-word form. The inclusion of pseudo-word stimuli allows for the direct comparison of the effects of grammatical anomalies in meaningful and meaningless sentential contexts. Brain activations that are observed in both real word and pseudo-word sentences can not be caused by late semantic processes and have to be due to genuine syntactic processing.

The same sentence material was tested both in an fMRI and an ERP study, thus yielding the opportunity to assess both hemodynamic and electrophysiological differences between morphosyntactic and phrase structure processing. Preceding the fMRI and ERP experiments, a behavioral pre-test was conducted (see Section 7.3) in order to test whether participants would be able to accurately judge the grammaticality of pseudo-word sentences at all.

7.2 Stimuli

Real word and pseudo-word sentences that were either grammatically correct or contained one of two violation types (phrase structure or morphosyntax) were constructed for the experiments described below, resulting in a 2x2x2 design with the factors LEXICALITY (real words or pseudo-words), TYPE (phrase structure or morphosyntax) and GRAMMATICALITY (correct or incorrect). The whole stimulus set consisted of 200 sentences that were equally distributed across all factors (see Table 7.1), resulting in 25 items per experimental condition.

All sentences had the same basic structure (see Examples 7.3 and 7.4 and Table 7.1), consisting of a third person singular female pronoun ("Sie" / "she") followed by an inflected verb ("sieht" / "sees" for the real word sentences and the pseudo-verb "rehmt" for the pseudo-word sentences) and a sentence complement.

(7.3) *Sie* *sieht,* *dass* *ein* *Segel*
 She.PRON.3SG.NOM see.V.3SG.PRES that.C a.D.SG.NOM sail.N.SG.NOM
und *alle* *Masten* *intakt* *sind.*
 and.CONJ all.Q.PL.NOM mast.N.PL.NOM intact.ADJ be.AUX.3PL.PRES
 She sees that a sail and all masts are intact.

Figure 7.1: Stimulus Material: Example Sentences

Code	Example	Items
mlr	Sie sieht, dass er segelt und alle Masten intakt sind.	13
	Sie sieht, dass du bügelst und alle Hemden neu sind.	12
mlf	*Sie sieht, dass er segelst und alle Masten intakt sind.	13
	*Sie sieht, dass du bügelst und alle Hemden neu sind.	12
plr	Sie sieht, dass ein Segel und alle Masten intakt sind.	13
	Sie sieht, dass ein Bügel und alle Hemden neu sind.	12
plf	*Sie sieht, dass ein segelt und alle Masten intakt sind.	13
	*Sie sieht, dass ein bügelst und alle Hemden neu sind.	12
mdr	Sie remt, dass er mäschelt und alle tsümrel osteft sind.	13
	Sie remt, dass du defelst und alle tschoper älmadink sind.	12
mdf	*Sie remt, dass er mäschelst und alle tsümrel osteft sind.	13
	*Sie remt, dass du defelt und alle tschoper älmadink sind.	12
pdr	Sie remt, dass ein mäschel und alle tsümrel osteft sind.	13
	Sie remt, dass ein defel und alle tschoper älmadink sind.	12
pdf	*Sie remt, dass ein mäschelt und alle tsümrel osteft sind.	13
	*Sie remt, dass ein defelst und alle tschoper älmadink sind.	12

Abbreviations: m=morphosyntax, p=phrase structure, l=lexical, d=non-lexical, r=correct, f=incorrect

(7.4) *Sie* *sieht,* *dass er*
She.PRON.3SG.NOM see.V.3SG.PRES that.C he.PRON.3SG.NOM
segelt und alle Masten intakt
sail.V.3SG.PRES and.CONJ all.Q.PL.NOM mast.N.PL.NOM intact.ADJ
sind.
be.AUX.3PL.PRES
She sees that he sails and (that) all masts are intact.

This object sentence was introduced by the complementizer "dass" / "that", followed by either a pronoun (in the morphosyntactic condition) or an indefinite article (in the phrase structure condition). The experimental manipulation always concerned the relation between pronoun or article and the following verb or noun: in grammatical sentences in the morphosyntactic condition, a third person singular or a second person singular pronoun was followed by a verb with the correct agreement features (e.g. third person singular pronoun and third person singular verb) while in ungrammatical sentences in the morphosyntactic condition, the pronoun was followed by a verb with incorrect agreement features (e.g. third

person singular pronoun and second person singular verb). Second person and third person matches and mismatches were balanced across the stimulus set (see Table 7.1.²)

In grammatical sentences in the phrase structure condition, a singular article was followed by a singular noun while in ungrammatical sentences in the phrase structure condition, the article was followed by an inflected verb (again, third person and second person inflection was balanced as good as possible; see Table 7.1). Only words with stem forms from which both verbal and nominal derivations with masculine gender exist (e.g. "Taucher" / "diver" [noun], "tauch-en" / "to dive" [verb]) were used as critical items. This was necessary in order to be able to have the same overall structure for both the morphosyntactic and the phrase structure violation. For similar reasons, the critical verb or noun was followed by a conjoined clause containing a quantifier ("alle" / "all") and a plural noun followed by an adjective and an inflected plural auxiliary ("sind" / "are") in all sentences. In addition, this served to prevent sentence wrap-up effects in the ERP study.

As a further constraint on the choice of suitable critical words, the verb form of the stimuli had to have distinct second person and third person inflections (e.g. a word like "Haus" was unfit for use in the morphosyntactic manipulation; see Examples 7.5 to 7.7).

(7.5) *Ein Haus*
A.D.SG house.N.SG

(7.6) *Er haus - t*
He.PRON.3SG dwell - s.V.3SG.PRES

(7.7) *Du haus - t*
You.PRON.2SG dwell - Ø.V.2SG.PRES

In addition, the critical word had to be usable without a direct object in its verbal form (e.g. the verb "meistern" / "to master" could not be used because a sentence like "Sie sieht, dass er meistert." / "She sees that he masters." has a very low acceptability). Furthermore, it had to be possible to come up with a plausible conjunctive phrase following the critical word. While initially only noun-verb combinations where the stem corresponds to the nominal form and the verb form is derived by adding an overt suffix (see Examples 7.8 to 7.9) were to be included as critical items, the narrow restrictions described above made it necessary to broaden the set of candidate words by allowing items where both the verbal and the nominal form are derived by overt suffigation (see Examples 7.10 to 7.11).

(7.8) *Ein Ruder - Ø*
An.D.SG oar - Ø.N.SG

²It has to be noted that since there were 25 items per experimental condition, a minor imbalance (a difference of one item) was inevitable.

CHAPTER 7. EXPERIMENT TWO (FMRI AND ERPS): LOCAL PREDICTABILITY

(7.9) *Er ruder - t*
He.PRON.3SG row - s.V.3SG.PRES

(7.10) *Ein Tauch - er*
A.D.SG dive - r.N.SG

(7.11) *Er tauch - t*
He.PRON.3SG dive - s.V.3SG.PRES

Pseudo-word sentences were constructed by replacing all content words of the real word sentences with opaque pseudo-words that had exactly the same syllable structure and metric structure as the lexical stimuli, leaving function words (complementizers, articles, conjunctions, pronouns, auxiliary verbs) and grammatical inflections intact. This procedure resulted in each real word sentence having a perfectly matched pseudo-word counterpart. While all pseudo-words were designed to be lexically opaque as defined in Section 6.1, the particular procedure for the generation of the pseudo-word stimuli had to be slightly modified: the original process of "recombining" the syllables of different real words while keeping their relative positions within a word (see Section 6.2.2 for details) turned out to yield unsatisfactory results because all critical words only had two syllables, with the final syllable being highly similar across items (i.e. ending in "-el" or "-er" for the nouns). Thus, single pseudo-word items were not constructed by syllable recombination, but by randomly combining phonemes into phonotactically legal, pronounceable stimuli that could carry the same suffixes as the real words that we used (e.g. 25 of the pseudo-word stimuli ended in "-er" or "-el", 25 ended in an adjective plural "-en" suffix, etc). To ensure that the pseudo-words were not lexicalizable, they were first checked automatically by a custom-made computer program that compared them to the CELEX database and rejected all stimuli that could be turned into a real word by changing a single phoneme; the remaining pseudo-words were then carefully checked by hand and all stimuli that still even remotely resembled a real word were removed. The pseudo-word sentences that were constructed by combining these items (each pseudo-word only being used in one set of conditions) were perfectly legal in terms of syllable structure, metric structure and phonological rules, but did not bear any semantic content at all.

Grammatical versions of all sentences were spoken by a trained female speaker and recorded digitally via microphone. However, these recordings were not directly used as stimuli: the experimental material was created by implementing an auditory splicing procedure. An initial stimulus fragment that included the indefinite article or pronoun following the complementizer (see Examples 7.12 and 7.13) was combined with a second sentence fragment that included the verb or the noun (see Examples 7.14 and 7.15). This procedure was implemented in order to prevent participants from using subtle acoustic cues to determine the correctness of a sentence before the critical word was encountered (such cues may

inadvertently be introduced into the experimental material when a speaker is asked to articulate grammatically anomalous sentences). Ungrammatical stimuli were created by either adding a verb fragment to an initial fragment that ended in a determiner (i.e. Example 7.12 plus Example 7.15) or by combining fragments with mismatching agreement features between pronoun and verb (i.e. Example 7.13 plus Example 7.16). Analogously, grammatical sentences were created by combining fitting sentence fragments (i.e. Example 7.12 plus Example 7.14 or Example 7.13 plus Example 7.15) from different recordings of the same stimulus. Thus, correct and incorrect sentences did not differ in terms of the procedure that was used to generate them.

(7.12) *Sie sieht, dass ein ...*
She sees that a ...

(7.13) *Sie sieht, dass er ...*
She sees that he ...

(7.14) ... *Segel und alle Masten intakt sind.*
... sail and all masts intact are.

(7.15) ... *segelt und alle Masten intakt sind.*
... sails and all masts intact are.

(7.16) ... *segelst und alle Masten intakt sind.*
... sails and all masts intact are.

All stimuli were normalized to 75 dB using the PRAAT software package (Boersma, 2001). During auditory word presentation, the volume was controlled by the software gain controls and the manual configuration of the sound card. Mean sentence duration was 3.06 seconds, with a minimum duration of 2.56 seconds and a maximum duration of 3.73 seconds.³

7.3 Pre-Test (Behavioral)

7.3.1 Introduction

As indicated in Section 7.1, a behavioral pre-test was conducted with the same experimental material (see Section 7.2) that was to be used in the fMRI and ERP experiments. The purpose of this test was to assess and evaluate if participants were able to accurately judge the grammaticality of the pseudo-word sentences without any prior training and - if not - to determine a suitable training procedure.

³Duration differences between correct and incorrect versions of a sentence were negligible because the only difference was the suffix ("t", "st", "er" or none).

CHAPTER 7. EXPERIMENT TWO (FMRI AND ERPS): LOCAL PREDICTABILITY

Three groups of participants (with 5 participants each) were tested. Group 1 did not receive an explicit training and performed the pre-test without any feedback regarding the accuracy of their responses. Group 2 performed the same experiment as group 1, but here, feedback was provided after each trial, thus allowing for a certain degree of implicit learning. Group 3 was tested with the same experimental setup as group 1 (no feedback), but received a short training exercise on the day prior to the pre-test. During this training, participants were familiarized with the critical pseudo-word items and their morphological properties. The familiarization procedure consisted of two short exercises (each lasting about 15 minutes) that were performed while sitting in front of a computer screen: first, infinitival forms of the pseudo-word verbs were presented visually and participants were instructed to read these verbs (self-paced). During this first training phase, each verb was presented 9 times, although the same verb never occurred two times in succession as the item set was pseudo-randomized. A third of all trials contained an additional task: participants saw two short phrases containing a pronoun or an article and a verbal or a nominal derivation of the most recent infinitive. In each trial, one of the phrases was correct (see Examples 7.17, 7.19) and one was incorrect (see Examples 7.18, 7.20). Participants were instructed to choose the correct form via button press and received visual feedback about their accuracy.

(7.17) *Er* *ginel* - *t*
He.PRON.3SG STEM - V.3SG.PRES
(Pseudo-words)

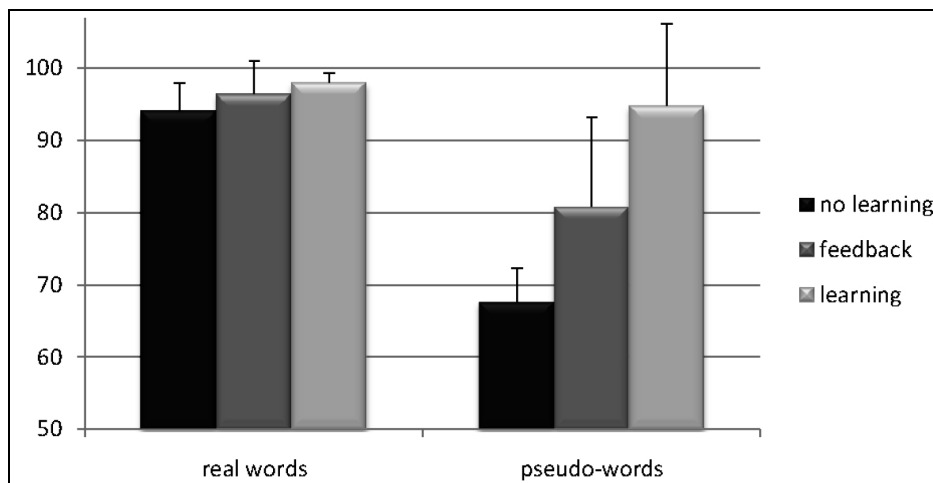
(7.18) **Er* *ginel* - *st*
He.PRON.3SG STEM - V.2SG.PRES
(Pseudo-words)

(7.19) *Ein* *ginel* - \emptyset
A.D.SG STEM - \emptyset .N.SG
(Pseudo-words)

(7.20) **Ein* *ginel* - *st*
A.D.SG STEM - V.2SG.PRES
(Pseudo-words)

Following this exercise, phase 2 of the training commenced. Here, participants performed a short test in which they were presented with two-word phrases (see Examples 7.17 to 7.20) containing verbal and nominal forms of the pseudo-words they had just learned. In contrast to phase 1, the infinitival forms were not presented again and had to be recalled from memory. Participants were instructed to judge the correctness of the stimuli that they saw.

Figure 7.2: Accuracy Rates, Pre-Test



7.3.2 Results

An analysis of variance (ANOVA) with the within-subject factors TYPE (morphosyntax, phrase structure) and LEXICALITY (real words, pseudo-words) and the between-subject factor VARIANT (no learning, feedback, learning) was conducted on the mean accuracy rates per participant. Since the goal of the pre-test was to identify differences between the three experimental variants that were tested, only main effects and interactions including the factor VARIANT will be reported below.

The main effect of VARIANT ($F_{2,12} = 49.87$, $p < 0.0001$) was highly significant, but was also further qualified by the interaction of LEXICALITY x VARIANT. The step-down analysis revealed that the factor VARIANT had a significant influence on accuracy rates in the pseudo-word condition ($F_{2,12} = 84.87$, $p < 0.0001$), but not in the real word condition ($F_{2,12} = 3.62$, $p > 0.05$), as was to be expected - participants should not need any special training in order to be able to judge the grammaticality of simple two-word utterances in their native language. Single contrasts between the levels of the factor VARIANT in the pseudo-word condition showed that each experimental variant differed significantly from both other variants ($p < 0.0001$ in all cases). As can be seen from Figure 7.2, this was due to accuracy rates being very high in the “learning” variant (94.8%), considerably lower in the “feedback” variant (80.8%) and very low in the “no learning” variant (67.6%). The interactions TYPE x VARIANT ($F_{2,12} = 2.97$, $p = 0.09$) and TYPE x LEXICALITY x VARIANT ($F_{2,12} = 0.99$, $p = 0.4$) were not statistically significant.

Only the group that was trained with the critical pseudo-word items on the day prior to testing achieved equivalent accuracy rates with both real word and pseudo-word sentences. The same training procedure was therefore adopted for the ERP and fMRI experiments.

7.4 Experiment 2a (fMRI)

7.4.1 Participants

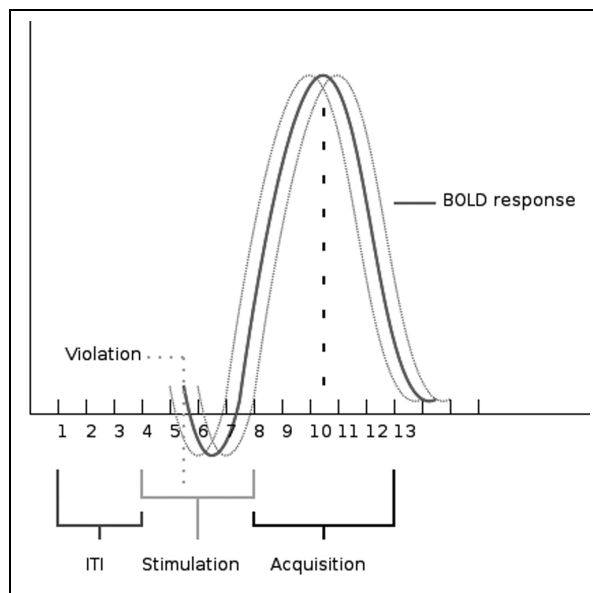
After giving informed consent, 20 native speakers of German participated in the study. No participant had any history of neurological or psychiatric disorders. All participants had normal hearing and were right-handed (laterality quotients of 90-100 according to the Edinburgh handedness scale (Oldfield, 1971)). Five participants were excluded from all further processing steps because of excessive error rates or due to technical problems, resulting in a final group of 15 participants (7 male; mean age 27 years; age range 23-36 years) entering the analysis of the behavioral and functional data.

7.4.2 Experimental Procedure

All subjects participated in a 30 minutes training session on the day prior to fMRI scanning. This exercise was identical to the one used during the pre-test and described in Section 7.3. On the day of the fMRI scan, participants were briefed on the task (a grammaticality judgment) and performed a short practice run with 20 sentences that were not used during the actual experiment. The following test session in the scanner consisted of 225 trials lasting 12 seconds each (200 experimental trials and 25 null events), resulting in 45 minutes duration per session (see Section 7.2 for a detailed description of the stimulus material). Each 12 second trial (except for null events) contained a single sentence. Trials were presented in a pseudo-randomized fashion. The following randomization constraints were implemented:

- Trials with the same LEXICALITY or TYPE or GRAMMATICALITY were not allowed to occur more than three times in a row.
- Trials with the same LEXICALITY and TYPE and GRAMMATICALITY were not allowed to occur more than two times in a row.
- Trials that were constructed from the same set of words or pseudo-words were separated by at least ten intervening trials.
- The occurrence of each level of the factors LEXICALITY, TYPE and GRAMMATICALITY was evenly distributed across 25-trial blocks.

Figure 7.3: ISSS Acquisition Sequence: Schematic Plot



BOLD response is plotted relative to violation onset. Dotted lines represent approximate variation of this onset in the auditory stimuli.

Functional data were acquired with an Interleaved Silent Steady State (ISSS) sequence (Schwarzbauer et al., 2006). This acquisition protocol was derived from the classical sparse sampling paradigm: each trial consisted of a silent period during which experimental stimuli were presented, followed by a noisy period of fMRI scanning. In contrast to the regular sparse sampling procedure, the ISSS sequence included a number of relatively silent "dummy" scans that were used to keep the magnetization level constant during the stimulation phase (note that no actual BOLD signal can be extracted from these scans). Following this, normal "noisy" functional scans were acquired.

In the current experiment, each trial started with a 3 second period of silence (3 dummy scans) as an inter-trial interval (see Figure 7.3). Following this, auditory stimulation started and lasted between 2.55 and 3.75 seconds (4 dummy scans), resulting in a subsequent silent period between 1.45 and 0.25 seconds until scanner noise set in (5 functional scans). Irrespective of total sentence length, the violation (or non-violation) always occurred approximately 1.5 seconds after sentence onset as the first part of all sentences always consisted of a pronoun, a verb and a complementizer followed by the critical verb or noun. Assuming a

5-second lag of the BOLD response, the peak of the activation that was induced by grammatical violations thus occurred around 9.5 seconds into the trial. This is exactly the middle of the functional scanning period following the stimulation period.

Participants lay supine inside the scanner and wore earphones, making their responses with a button box. All auditory stimulation was delivered binaurally. To reduce scanner noise, external ear defenders and perforated ear plugs that conducted the sound directly into the auditory passage were applied.

7.4.3 fMRI Data Acquisition

The experiment was carried out on a 3T scanner (Medspec 30/100, Bruker, Ettlingen). For functional imaging, 15 axial slices parallel to the AC-PC plane and covering almost the whole brain were acquired using a gradient-echo EPI sequence with a TE of 28ms, a flip angle of 62.4 degrees, a TR of 1 second, and an acquisition bandwidth of 100 kHz. The matrix acquired was 64x64 with a FOV of 19.2cm, resulting in an in-plane resolution of 3x3 mm. The slice thickness was 4 mm with an interslice gap of 1 mm. Prior to the functional runs, 15 T1-weighted MDEFT (Ugurbil et al., 1993) images (data matrix 256x256, TR 1.3 s, TE 10.3 ms) were obtained with a non slice-selective inversion pulse followed by a single excitation of each slice (Norris, 2000).

7.4.4 fMRI Data Analysis

Data processing was performed with the software package LIPSIA (Lohmann et al., 2001). This software package contains tools for pre-processing, co-registration, statistical evaluation, and visualization of fMRI data. Five images at the start of each session were discarded to allow the EPI signal to reach equilibrium. To correct for the temporal offset between the slices acquired in one scan, a cubic-spline-interpolation was applied. A temporal highpass filter with a cut-off frequency of 1/72 Hz was used for baseline correction of the signal and a spatial Gaussian filter with 5.65 mm FWHM was applied.

To align the functional data slices with a 3D stereotactic coordinate reference system, a rigid linear registration with six degrees of freedom (3 rotational, 3 translational) was performed. The rotational and translational parameters were acquired on the basis of the MDEFT (Norris, 2000; Ugurbil et al., 1993) and EPI-T1 slices to achieve an optimal match between these slices and the individual 3D reference data set. This 3D reference data set was acquired for each participant during a previous scanning session. The MDEFT volume data set with 160 slices and 1mm slice thickness was standardized to the Talairach stereotactic space (Talairach and Tournoux, 1988). The rotational and translational parameters were subsequently transformed by linear scaling to a standard size. The resulting parameters

were then used to transform the functional slices using trilinear interpolation, so that the resulting functional slices were aligned with the stereotactic coordinate system. This linear normalization process was improved by a subsequent processing step that performed an additional nonlinear normalization (Thirion, 1998).

The statistical evaluation was based on a least-squares estimation using the general linear model for serially autocorrelated observations (Friston, 1994, 1995; Friston et al., 1995; Worsley and Friston, 1995). The design matrix was generated with a synthetic hemodynamic response function (Friston et al., 1998; Josephs et al., 1997) and its first derivative.

The model equation, including the observation data, the design matrix and the error term, was convolved with a Gaussian kernel of dispersion of 4 s FWHM to deal with the temporal autocorrelation (Worsley and Friston, 1995). In the following, contrast-images, i.e. estimates of the raw-score differences between specified conditions, were generated for each participant. As noted before, each individual functional dataset was aligned with the standard stereotactic reference space so that a group analysis based on the contrast-images could be performed. The single-participant contrast-images were then entered into a second-level random effects analysis for each of the contrasts. The group analysis consisted of a one-sample t-test across the contrast images of all participants that indicated whether observed differences between conditions were significantly distinct from zero (Holmes and Friston, 1998). Subsequently, t-values were transformed into Z-scores. Only correctly answered trials were included in the analysis.

To protect against false positive activations, a Monte Carlo randomization procedure was used to identify the probability of obtaining erroneous activation clusters. This procedure generates voxels at a rate equal to the significance criterion specified, proportional to the total number of voxels in the dataset, and calculates a cluster size that corresponds to the true false-positive rate for these conditions. Using 1,000 iterations, a false positive cluster probability of $p < 0.05$ was achieved with a minimum cluster size of 405 mm^3 at a threshold of $p < 0.001$ (uncorrected) for individual voxels. This synthetically determined statistical threshold was then applied to all voxels in the real data (that is, we only report clusters of at least 405 mm^3 at $p < 0.001$ per voxel, resulting in $p < 0.05$ at the cluster level). The advantages of combining a voxel-based threshold with a minimum cluster size have been described elsewhere (Forman et al., 1995).

No timecourse analysis could be computed because of the non-constant TR of the ISSS acquisition sequence.

Table 7.1: Behavioral Results

Condition	% Accuracy (SD)
phrase structure, real words, correct	99 (1)
phrase structure, real words, incorrect	98 (3)
morphosyntax, real words, correct	98 (3)
morphosyntax, real words, incorrect	94 (4)
phrase structure, pseudo-words, correct	92 (7)
phrase structure, pseudo-words, incorrect	88 (8)
morphosyntax, pseudo-words, correct	93 (8)
morphosyntax, pseudo-words, incorrect	96 (5)

Values are means for all participants. SD=standard deviation.

7.4.5 Results

Behavioral Results

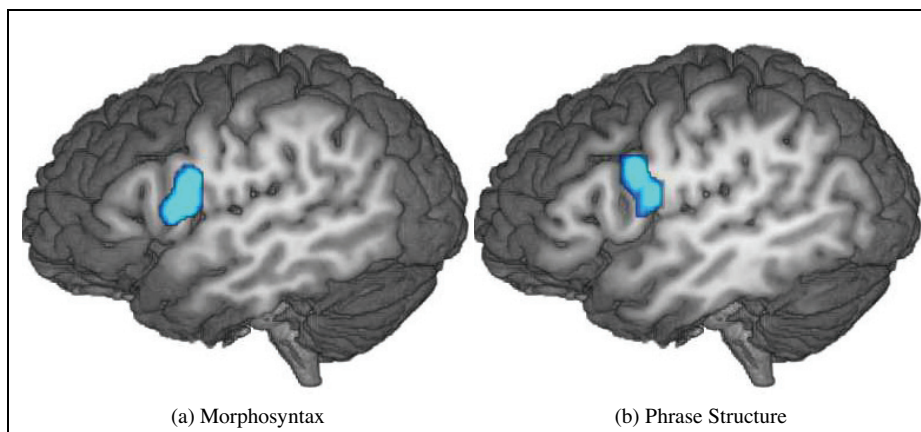
An analysis of variance with the factors LEXICALITY (real words, pseudo-words), TYPE (morphosyntax, phrase structure) and GRAMMATICALITY (correct, incorrect) was conducted in order to assess differences in terms of accuracy⁴ between the experimental conditions (also see Table 7.1). Only the main effect of LEXICALITY was statistically significant ($F_{1,14} = 23.78$, $p = 0.0002$) and was further qualified by an interaction of TYPE x LEXICALITY ($F_{1,14} = 26.52$, $p = 0.0001$) and GRAMMATICALITY x TYPE x LEXICALITY ($F_{1,14} = 10.27$, $p = 0.0064$). The step-down analysis revealed that the interaction of TYPE x LEXICALITY only reached significance for ungrammatical sentences ($F_{1,14} = 26.62$, $p = 0.0001$). A further resolution by the factor TYPE showed that for grammatically anomalous stimuli, the factor LEXICALITY had a significant effect in the phrase structure condition ($F_{1,14} = 29.07$, $p < 0.0001$), but not in the morphosyntactic condition. This effect shows that real word sentences containing a phrase structure violation were detected with higher accuracy than pseudo-word sentences containing an analogous anomaly. No further main effects or interactions reached statistical significance.

fMRI Results

The impact of the factor GRAMMATICALITY was evaluated by computing direct contrasts between correct and incorrect sentences. In order to assess the effect of different processing

⁴As in the experiment described in Chapter 6, reaction times were measured from stimulus onset to prevent false time outs due to participants responding too early and are thus not sufficiently accurate to merit a detailed analysis.

Figure 7.4: Incorrect > Correct, Real Words, Resolved by Type



Blue color scale ($Z=0$ to $Z=-4.32$): incorrect sentences > correct sentences in the real word condition. Only activations with p (corrected) < 0.05 at the cluster level are shown.

conditions as determined by *LEXICALITY* and *TYPE*, separate analyses were conducted on each level of both factors (see Table 7.2). Moreover, the effect of the factor *LEXICALITY* in the absence of grammatical violations was evaluated by computing the contrast between correct real word sentences and correct pseudo-word sentences (collapsed over *TYPE*; see Table 7.2).

As can be seen from Figure 7.4 and Table 7.2, both morphosyntactic as well as phrase structure violations occurring in real word sentences elicited an increased amount of brain activity in the left ventral premotor cortex when compared to sentences not containing any syntactic anomaly. On the other hand, correct real word sentences elicited a stronger brain response than incorrect real word sentences in the bilateral anterior middle temporal gyrus in the morphosyntactic manipulation condition (see Figure 7.6 and Table 7.2), but not in the phrase structure manipulation condition. The grammaticality effects observed for real word sentences vanished when analogous syntactic anomalies were presented in a pseudo-word context.

However, as can be seen from Figure 7.5, the hemodynamic response in the entire language processing network (including the left vPMC) was generally much stronger in pseudo-word sentences than in real word sentences (potentially making a further differentiation between grammatical and ungrammatical sentences difficult or even impossible; see Section 7.4.6 for an elaboration of this point). Real word sentences elicited an increase in

Table 7.2: Activated Brain Regions

x	y	z	Mean Z	Volume (mm ³)	Region
<i>phrase structure, real words, correct > phrase structure, real words, incorrect</i>					
no activation found					
<i>phrase structure, real words, correct < phrase structure, real words, incorrect</i>					
-44	-4	15	-3.52	1269	Left ventral premotor cortex
<i>phrase structure, pseudo-words, correct > phrase structure, pseudo-words, incorrect</i>					
no activation found					
<i>phrase structure, pseudo-words, correct < phrase structure, pseudo-words, incorrect</i>					
no activation found					
<i>morphosyntax, real words, correct > morphosyntax, real words, incorrect</i>					
49	-13	-12	3.67	3348	Right middle temporal gyrus
-56	-19	-9	3.42	1431	Left middle temporal gyrus
<i>morphosyntax, real words, correct < morphosyntax, real words, incorrect</i>					
-47	-1	18	-3.41	1134	Left ventral premotor cortex
<i>morphosyntax, pseudo-words, correct > morphosyntax, pseudo-words, incorrect</i>					
no activation found					
<i>morphosyntax, pseudo-words, correct < morphosyntax, pseudo-words, incorrect</i>					
no activation found					
<i>real words, correct > pseudo-words, correct</i>					
-57	-67	20	4.259	-	Left posterior MTG / Angular gyrus
<i>real words, correct < pseudo-words, correct</i>					
Bilateral Network ^a					
-65	-23	9	-4.83	-	Left superior temporal gyrus
-49	-64	-4	-4.51	-	Left inferior temporal gyrus
-46	-40	37	-4.53	-	Left parietal Lobe
-44	6	24	-5.09	-	Left inferior frontal and premotor cortex
-34	15	9	-4.67	-	Left anterior insula
49	-18	3	-3.99	-	Right superior temporal gyrus
45	6	20	-4.56	-	Right inferior frontal and premotor cortex

^aAt the given statistical threshold, activation in this condition was so widespread that separating different activation clusters became impossible. Therefore, peak z-values (with corresponding coordinates) within the single continuous "blob" that resulted from the group analysis are reported. Note that these peaks do not have an extent since they refer to individual voxels.

brain activity in the left posterior middle temporal and angular gyrus (this will be discussed in depth in Section 8.3, together with the very similar result described in Chapter 6).

As already mentioned in Section 7.4.4, it was not possible to compute a timecourse analysis because of the non-constant TR of the ISSS acquisition sequence.

7.4.6 Discussion

In the following sections, I will discuss the results described above. I will first elaborate upon the grammaticality effect that was observed in the vPMC for real word sentences and suggest an explanation for the absence of additional activations in the anterior STG. Following this, I will address the lack of a significant difference between correct and incorrect stimuli that was reported for pseudo-word sentences. Finally, I will briefly discuss the activations that were observed for correct sentences in the morphosyntactic condition.

Expect the Unexpected: Syntactically-based Sequential Predictions in the Ventral Premotor Cortex

In real word sentences, phrase structure violations as well as morphosyntactic violations elicited an increase in brain activity in the left ventral premotor cortex, a brain region that has classically been implicated in preparatory motor functions (Wise, 1985). However, recent evidence strongly points to an involvement of the vPMC in a number of more general cognitive operations.

With regard to non-linguistic functions, several empirical studies utilizing the "serial prediction task" (SPT) as developed by Schubotz (1999) report activations of the vPMC that are not directly related to motoric processes. In the SPT paradigm, participants are presented with progressions of sensory events that are grouped into short sequences - for example, each basic sequence may consist of three consecutive auditory tones. A "standard" sequence is established by presenting the same basic sequence several times in succession. The last basic sequence of such a hypersequence either conforms to the standard pattern or deviates from it with regard to a particular dimension (sticking to the example of tone sequences that was given above, the final tone could have a different frequency or it could occur sooner or later than expected). Participants are asked to detect hypersequences that contain pattern violations.

Schubotz et al. (2003) were able to show that performing a serial prediction task with auditory stimuli elicits a strong hemodynamic response in the ventro-lateral premotor cortex when compared to a non-predictive control task. Schubotz and von Cramon (2004) reported very similar results when using abstract visual sequences instead of auditory stimuli. Schubotz (2007) argues that these observations can be explained by assuming that the

vPMC houses the cortical architecture for the computation of "forward models" that are suited to generate predictions about the evolution of simple linear event sequences. Compatible views are expressed by Fiebach and Schubotz (2006) and Schubotz and von Cramon (2003). As will be elaborated upon in the following paragraphs, this concept of serial predictions - with the vPMC as the neuroanatomical locus of their generation - is also highly relevant for language processing. Consequently, a plausible explanation for the pattern of results that was observed in the current experiment can be given under the assumption that both types of grammatical anomalies as implemented here represent "special cases" of mismatches between linear sequences of events and rule-based expectations.

With regard to phrase structure, sequential predictions as described above can be straightforwardly derived from simple syntactic templates. Such templates have been assumed to be part of the grammatical knowledge that all native speakers of a particular language have (Bornkessel and Schlesewsky, 2006; Frazier, 1989); they can be conceived of as precompiled outputs of phrase structure rules in the form of very basic, linearly ordered "prototypes" for grammatically legal sequences of word categories that are used to rapidly generate "working hypotheses" about the syntactic structure of an incoming speech stream. During language comprehension, the selection of particular phrase structure templates is triggered by appropriate verbal input - i.e., hearing the determiner "the" activates a corresponding template (i.e., "Det N"). As stated above, templates allow for simple sequential predictions (i.e., "the next word will be a noun") as well as for the timely assignment of local structure. In addition, they offer a quick-and-dirty mechanism for error detection: whenever an incoming word does not match the predicted word category, there is a potential problem.⁵ Thus, it is conceivable that this matching metric serves as the basis for grammaticality judgments as required in the current study - after all, this would amount to simply "recycling" the output of a cognitive procedure (checking the validity of a local prediction) that is employed automatically in any case.

Morphosyntactic relations, on the other hand, can not generally be used to make local predictions as they do not necessarily concern adjacent elements of a sentence - thus, it is not feasible to assume the existence of global "morphosyntactic templates". In the current experiment, however, sentences were designed to allow for local predictions on the basis of morphosyntactic information in order to keep the effects of serial predictability constant across the experimental manipulation conditions (see Section 7.1). The main verb always immediately followed the subject pronoun - thus, just like in the phrase structure condition, the grammaticality of the sentences in the morphosyntactic condition was always dependent

⁵However, this does not necessarily have to be the case: local phrase structure is flexible within certain limitations. For example, the determiner "the" does not have to be immediately followed by a noun - an adjective may intervene. However, the mechanisms for the selection of an initial template among a set of possible alternatives as well as other processing issues related to local ambiguity are irrelevant here.

on the relation between the word following the complementizer (a determiner or a pronoun; "Sie sieht, dass *ein/er*") and the next word (a noun or a verb; "*Segel/segelt/segelst...*"). Apparently, participants made use of this particular regularity by establishing an ad hoc-mechanism for the generation of local morphosyntactic predictions that were checked in the vPMC, just like their template-based counterparts in the phrase structure condition. As described above, the outcome of such a comparison between expectations and actual input could then have served as the basis for the grammaticality judgment.

The establishment of such a generalized procedure for evaluating the grammaticality of each experimental sentence in terms of the fulfillment of local rule-based predictions would be highly economical because it can be applied to both phrase structure and morphosyntactic manipulations. While it has to be noted that the predictions are based on different types of syntactic information (depending on the experimental manipulation condition), the generation of the predictions themselves has to occur both in correct and in incorrect sentences and is therefore unlikely to generate a differential brain response with regard to the factor "grammaticality". The detection of a prediction mismatch, on the other hand, only occurs in anomalous sentences, thus rendering it potentially detectable in a contrast of correct and incorrect stimuli - however, as the results of the current experiment indicate, this mismatch detection in itself is not necessarily informative with regard to the different types of linguistic rules that were used to generate the predictions that it is based on.

Support for the view that the vPMC is crucial for the generation and checking of sequential predictions during language processing comes from a number of previous studies on artificial grammar processing. Opitz and Friederici (2004) observed activations of the vPMC when participants had to learn a novel rule for the establishment of legal stimulus sequences in an artificial language ("BROCANTO"). Crucially, this new rule allowed for sequences that were not encountered during the initial training phase and that were thus unexpected. In a similar vein, Opitz and Friederici (2007) report increased activity in the vPMC for the processing of local sequential violations in sentences from the same artificial grammar. In natural languages, violations of phrase structure constraints (Brauer and Friederici, 2007; Friederici et al., 2003) and violations of local expectancies in general (Fiebach et al., 2004; Friederici et al., 2006b)⁶ have also been shown to elicit hemodynamic responses in the vPMC and the medially adjacent posterior deep frontal operculum (also

⁶In both studies, the experimental material consisted of three conditions containing sentences of increasing complexity and one condition containing ungrammatical sentences. The ungrammatical condition differed from all other conditions in that the first NP was followed by a verb (e.g. "Heute hat der Opa geschenkt dem Jungen den Lutscher." / "Today has the grandpa given the boy the lollipop."), not another NP (e.g. "Heute hat der Opa dem Jungen den Lutscher geschenkt." / "Today has the grandpa the boy the lollipop given."). Thus, it is plausible to assume that participants developed a sequential expectation for a second NP following the first NP as this was the most common pattern in the stimulus sentences (actually, this aspect of the paradigm is comparable to the serial prediction task). As this expectation was not borne out in ungrammatical sentences, the activation of the vPMC can be explained straightforwardly.

see the reviews by Fiebach and Schubotz, 2006; Friederici, 2004, 2006; Grodzinsky and Friederici, 2006).

In sum, the existing evidence is convergent in that the vPMC appears to have a critical role in the generation of sequential predictions and in the detection of mismatches between serial expectations and actual sequences of events. While this function certainly is of critical importance for motor planning and action understanding, it is equally useful in other domains - one of them being language comprehension, as has been shown in the current experiment.

A Null Result: What About the STG ?

It has been previously proposed that the anterior STG may play a critical role in processes of early phrase structure building (Brauer and Friederici, 2007; Friederici et al., 2003; Rueschemeyer et al., 2005). However, no corresponding brain activity was observed for sentences containing phrase structure violations in the current study. How can this heterogeneous pattern of results be explained ?

To begin with, there are a number of structural differences concerning the experimental materials that were used here and in previous studies. Friederici et al. (2003) as well as Rueschemeyer et al. (2005) implemented sentences of the form depicted in Examples 7.21 and 7.22 while Brauer and Friederici (2007) utilized stimuli of the form depicted in Examples 7.23 and 7.24 (recall that in the current study, sentences were of the form depicted in Examples 7.25 and 7.26).

(7.21) **Die Gans wurde im gefüttert.*
 The.D.SG.NOM goose.N.SG.NOM is.V.3SG.PAST in_the.P feed.V.PTCP
 *The goose was in the fed.

(7.22) *Die Gans wurde gefüttert.*
 The.D.SG.NOM goose.N.SG.NOM is.V.3SG.PAST feed.V.PTCP
 The goose was fed.

(7.23) **Das Eis am schmeckt.*
 The.D.SG.NOM icecream.N.SG.NOM on_a.P taste_good.V.3SG.PRES
 *The icecream on a tastes good.

(7.24) *Das Eis schmeckt.*
 The.D.SG.NOM icecream.N.SG.NOM taste_good.V.3SG.PRES
 The icecream tastes good.

(7.25) *Sie* *sieht,* *dass ein* *Segel*
 She.PRON.3SG.NOM see.V.3SG.PRES that.C a.D.SG.NOM sail.N.SG.NOM
und *alle* *Masten* *intakt* *sind.*
 and.CONJ all.Q.PL.NOM mast.N.PL.NOM intact.ADJ be.AUX.3PL.PRES
 She sees that a sail and all masts are intact.

(7.26) *Sie* *sieht,* *dass ein* *segelt*
 She.PRON.3SG.NOM see.V.3SG.PRES that.C a.D.SG.NOM sails.V.3SG.PRES
und *alle* *Masten* *intakt* *sind.*
 and.CONJ all.Q.PL.NOM mast.N.PL.NOM intact.ADJ be.AUX.3PL.PRES
 *She sees that a sails and all masts are intact.

It is apparent that the general sentence structure differs considerably between experiments, ranging from simple active sentences in the present tense (Brauer and Friederici, 2007) via passive sentences in the past tense (Friederici et al., 2003; Rueschemeyer et al., 2005) to a more complex matrix clause / subordinate clause - construction in the present study. Most importantly, Friederici et al. (2003), Rueschemeyer et al. (2005) and Brauer and Friederici (2007) all implemented sentences in which the phrase structure violation occurred in an optional prepositional phrase (PP) adjunct while in the current study, the grammatical anomaly concerned an obligatory determiner phrase (DP) argument. Thus, it is conceivable that the anterior STG activations observed in these previous studies are tied to the presence of an optional constituent.

Pursuing this argument further, the absence of anterior STG activations for grammatical anomalies in argument XPs could be due to the fact that obligatory phrases are always expected whereas optional adjunct XPs require a certain amount of syntactic reorganization in order to be accommodated. Crucially, the sentences containing phrase structure violations in the studies by Friederici et al. (2003), Rueschemeyer et al. (2005) and Brauer and Friederici (2007) always contained the head of an optional PP while correct sentences only contained argument XPs.⁷ The activation of the anterior STG that was observed for incorrect sentences in these studies could at least partly be due to this general structural difference, or it may be the case that grammatical anomalies are processed differently depending on their occurrence in an adjunct phrase or an argument XP (for a general discussion of the relevance of the distinction between arguments and adjuncts during language comprehension, see Tutunjian and Boland, 2008). However, a definitive resolution of this issue clearly requires further research.

A further difference between the studies cited above and the current experiment relates to the linguistic manipulations that were implemented: Friederici et al. (2003), Rueschemeyer

⁷As Rueschemeyer et al. (2005) note, this also entails a potential confound with regard to the number of words in each sentence. However, as the authors further point out, this should mainly affect brain activation patterns in basic auditory processing regions, i.e. the middle STG.

et al. (2005) and Brauer and Friederici (2007) tested sentences that were either correct or contained two very different types of violations, a syntactic one (see Example 7.27) and a semantic one (see Example 7.28), while the current study only contained syntactic violations.

(7.27) **Das Eis am schmeckt.*
The.D.SG.NOM icecream.N.SG.NOM on_a.P taste_good.V.3SG.PRES
*The icecream on a tastes good.

(7.28) **Der Stein blutet.*
The.D.SG.NOM stone.N.SG.NOM bleed.V.3SG.PRES
The stone bleeds.

The inclusion of a semantic anomaly in a general "acceptability judgment"-task may have led participants to focus their attention on the conceptual coherence of the sentences, which is disturbed by both the semantic and the syntactic manipulation. This stands in contrast to the current experiment in which the meaning of the experimental sentences was not only irrelevant, but non-existent in half of the stimuli (the pseudo-word sentences). Consequently, the anterior STG activation that was observed in the studies cited above could be due to the combinatorial-semantic anomaly that was caused by the phrase structure violation⁸ while the syntactic anomaly per se is reflected in the heightened hemodynamic response in the left frontal operculum that was reported by Friederici et al. (2003) and Brauer and Friederici (2007). The lexical-semantic problem in the selection restriction violation condition is apparently subserved by different brain regions (i.e. the left posterior STG; see Brauer and Friederici, 2007; Friederici et al., 2003).

Furthermore, the anterior STG activation that has been previously observed in response to sentences containing phrase structure violations may be related to processing difficulties that arise when an item with an unexpected word category has to be identified. According to this account, hearing a preposition (i.e. "im" / "in the") would syntactically prime nouns and potentially adjectives (see Nicol, 1996, for a general discussion of syntactic priming effects). When the next word that is actually encountered has the anticipated category, its identification is facilitated. When the lexical search space has to be extended in order to include unexpected word categories, the resulting processing costs manifest themselves as an increase in brain activity in the anterior STG. In the current study, this effect may have been attenuated because the word stem of incorrect and correct words was identical

⁸Note that there is a missing argument following the head of the prepositional phrase - thus, the preposition can not assign its thematic role (Caplan, 2007). Also note that the processing of prepositional arguments (i.e. the complement NP of a preposition) may be different from the processing of verbal arguments (i.e. the complement NP of a verb) - the latter has been associated with the posterior STG/STS and inferior frontal regions (Bornkessel et al., 2005; Grewe et al., 2007).

- thus, while the syntactic prime (the determiner) was misleading with regard to the word category of the following word, the target was closely related to the expected item with regard to both its phonological word form and its semantics. Crucially, this was not the case in the studies by Friederici et al. (2003), Rueschemeyer et al. (2005) and Brauer and Friederici (2007). The anterior STG activation observed in the corresponding experiments could thus be due to difficulties in word-category identification resulting from a syntactic prime (a preposition) that is followed by a word that bears neither syntactic nor phonological nor semantic resemblance to the target while in the current study, such phonological and semantic similarities reduced the effects of "incorrect" syntactic priming.

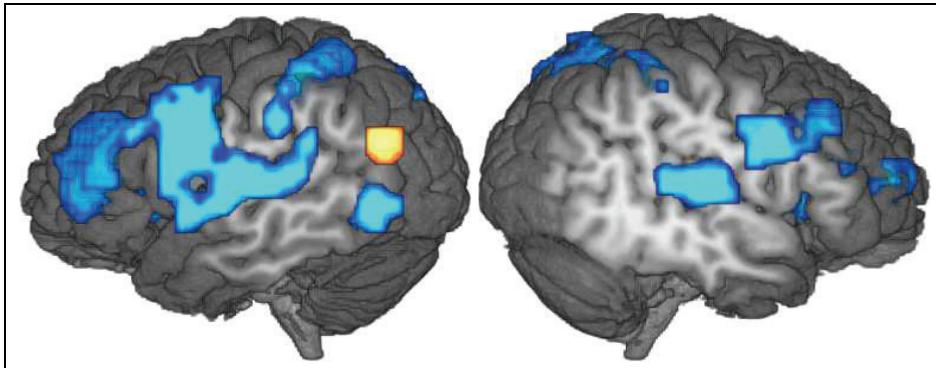
In sum, the fact that no activation of the anterior STG was observed in the current experiment may be due to a number of factors including the syntactic status of the XP containing the grammatical anomalies (argument vs adjunct), residual syntactic priming (made possible by similar word stems for different word categories) and an attenuation of combinatorial-semantic effects that could be caused by the presence of pseudo-word sentences or by the absence of a semantic acceptability judgment. Future research will have to clarify the exact role of the anterior STG in language comprehension, i.e. by implementing a paradigm that allows for the direct comparison of argument and adjunct processing in correct sentences.

"Making Sense" of Pseudo-Word Sentences

In the pseudo-word condition, correct and incorrect sentences could not be differentiated with regard to the brain activation patterns that they elicited, regardless of the type of grammatical manipulation that was employed. Crucially, this result is not due to a general lack of hemodynamic activity in response to pseudo-word sentences - on the contrary, both correct and incorrect sentences in the pseudo-word condition produced large-scale brain activations in a number of broadly distributed areas, including the entire language processing network (the bilateral STG, the left IFG, the left MTG; see Figure 7.5).

Comparable increases in brain activity in response to the processing of grammatically correct pseudo-word sentences have been reported in a number of previous studies. Friederici et al. (2000) presented auditory real word sentences, pseudo-word sentences, real word lists and pseudo-word lists in an fMRI study, observing a stronger hemodynamic brain response to pseudo-word sentences than to any other type of stimulus in the bilateral frontal operculum and the bilateral superior temporal gyrus. Meyer et al. (2003) report comparable results for the processing of pseudo-word sentences (compared to the processing of real word sentences) when participants were asked to perform a lexicality judgment. In a second experiment with an extended set of stimuli and a different task, the authors observed that in response to sentences that were made unintelligible by an acoustic filtering procedure, brain activity in the bilateral frontal operculum was even stronger than for pseudo-word

Figure 7.5: Pseudo-Words > Real Words (Correct Sentences Only)



Blue color scale ($Z=0$ to $Z=-5.52$): pseudo-word sentences > real word sentences; red color scale ($Z=0$ to $Z=4.25$): real word sentences > pseudo-word sentences. The contrast shows grammatically correct sentences collapsed over manipulation type. Only activations with p (corrected) < 0.05 at the cluster level are shown.

sentences. Crucially, participants were asked to perform a "forced choice" task in which they had to decide if the stimuli that they heard were active or passive sentences - thus, participants had to try to extract syntactic information from the filtered stimuli although this was actually impossible. In consequence, it is plausible to assume that the strong hemodynamic response in the frontal operculum that was observed for the filtered sentences reflects an increase in processing effort that was caused by attempts to perform syntactic analyses on stimuli that only vaguely resembled everyday language. Thus, the results reported by Friederici et al. (2000) and Meyer et al. (2003) indicate that there is a strong brain response to "unusual" linguistic stimuli even in the absence of outright grammatical violations.

Nevertheless, the fact that in the current experiment syntactically anomalous pseudo-word sentences elicited a hemodynamic response that was indistinguishable from the brain reaction to grammatically correct pseudo-word sentences remains puzzling. Even if pseudo-word sentences are generally harder to process than real word sentences, syntactic anomalies in meaningless stimuli may still be expected to entail an additional increase in processing costs. However, it is conceivable that the ensuing heightened metabolic demands were satisfied without a further increase in cortical blood flow. Such an explanation can be construed along the following lines: the similarity of the brain response to correct and incorrect pseudo-word sentences is at least partly caused by a "preparatory" supply of oxygenated blood to cortical regions that are expected to experience a heightened processing load once a particular type of stimulus (i.e., a pseudo-word sentence) has been detected (cf. the dis-

cussion of the results reported by Meyer et al., 2003, above). The oversupply of oxygenated blood that is triggered by the processing of pseudo-word sentences regardless of their grammaticality is sufficient to compensate for the slight increase in oxygen consumption that is caused by the presence of a syntactic anomaly - thus, there is no further measurable hemodynamic response to ungrammatical pseudo-word sentences because of a hemodynamic saturation effect (see Indefrey et al., 2001b, for a similar line of argumentation).

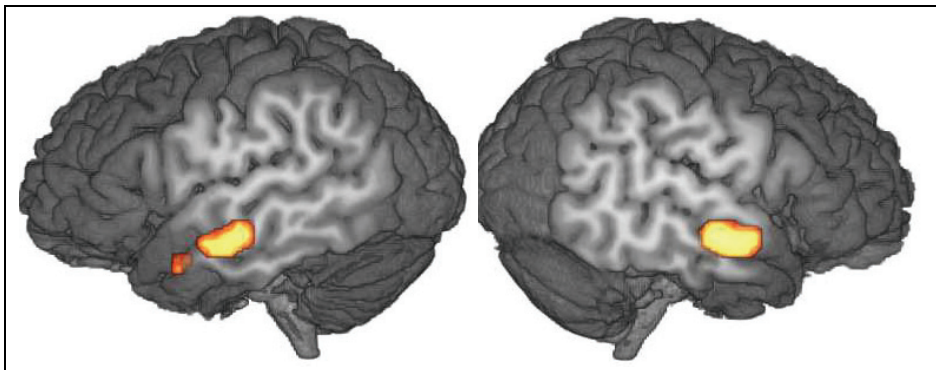
While the pattern of brain activations observed in the current study can be accounted for in this way, it has to be noted that a number of previous studies report different patterns of brain activations for different types of pseudo-word sentences (Moro et al., 2001; Röder et al., 2002) - however, this apparent contradiction to the results discussed above can be explained by the dissimilar experimental paradigms that were utilized.

Moro et al. (2001) tested pseudo-word sentences containing different types of linguistic anomalies in a PET study, but did not report contrasts between correct and incorrect sentences. Instead, they compared different experimental tasks: blocks in which stimuli had to be judged with regard to their syntactic well-formedness were compared to blocks in which stimuli had to be judged with regard to their phonotactic legality. The authors report a number of activation differences between these two experimental conditions. However, since morphosyntactic and phonotactic blocks varied along a number of linguistic and cognitive dimensions (among them the syntactic complexity of the sentences that were used, attentional focus on grammaticality or orthographic deviations, the difficulty of detecting the respective anomaly and potential repair processes on different levels of processing), it is far from obvious which one of these is causing the observed patterns of brain activity, thus making the results of this study hard to interpret.

Röder et al. (2002) tested real word and pseudo-word sentences in an fMRI study focusing on varying degrees of sentence complexity. While the authors report effects for complex vs simple sentences that are stronger in the real word condition, they implemented a blocked design - that is, real word and pseudo-word sentences were presented separately. It is conceivable that the "preparatory" hemodynamic response to pseudo-word sentences that was observed in the current study is diminished when several "unusual" stimuli of the same type have to be processed in succession.

Put differently, the brain response to pseudo-word sentences may be particularly strong - encouraging unwanted hemodynamic saturation effects - when such lexically "anomalous" stimuli are presented together with "normal", real word speech. While event-related designs as implemented in the current study are generally preferable because they provide more statistical power and are less prone to habituation effects, the results discussed here lead to an important conclusion: in order to investigate grammatical processing within pseudo-

Figure 7.6: Correct > Incorrect, Real Words, Morphosyntax



Red color scale ($Z=0$ to $Z=5.13$): correct sentences > incorrect sentences in the real word condition (morphosyntax only). Only activations with p (corrected) < 0.05 at the cluster level are shown.

word sentences, blocked designs may be the better choice since they allow participants to get used to the general "oddness" of the stimuli.

Beyond Grammatical Anomalies: Activations for Correct Sentences

In the morphosyntactic manipulation condition of the experiment under discussion, correct real word sentences elicited a stronger hemodynamic brain response than incorrect sentences in the bilateral anterior superior temporal sulcus and middle temporal gyrus. While this pattern of results was unexpected, it can be explained as resulting from sentence-level semantic and interpretive processes that are blocked by the presence of a grammatical anomaly (and accordingly elicit an increase in signal strength for correct sentences). Crucially, syntactic violations have been shown to impede semantic processing in a number of previous studies using a "double violation" paradigm in which the critical word of a sentence constitutes both a semantic and a syntactic anomaly (see, for example, Friederici et al., 2004).

This is, of course, a post-hoc interpretation - however, there is some independent empirical support for its potential validity. The anterior STS has been implicated in sentence- and discourse-level processing in a number of studies comparing intelligible and unintelligible stimuli (Crinion et al., 2003; Narain et al., 2003; Scott et al., 2000). While syntactic and semantic processes could not be separated in the corresponding experiments, it is plausible to assume that at least some of the brain activity that was reported for the pro-

cessing of intelligible sentences may be due to combinatorial-semantic operations or other interpretation-related cognitive processes.

With regard to the current study, the establishment of pronominal reference and the extraction of propositional content may be of particular relevance here. Sentences in the morphosyntactic condition were more complex than sentences in the phrase structure condition with regard to both processes: only sentences in the morphosyntactic condition contained pronouns at all, and while sentences in the phrase structure condition contained a complex subject consisting of two conjoined NPs (see Example 7.29), sentences in the morphosyntactic condition contained two conjoined VPs with independent subjects (see Example 7.30). As a result of this structural difference, the latter type of sentence is more complex in terms of its propositional content: the sentence given in Example 7.31 contains at least three different propositions (somebody is sailing; all masts are intact; both facts are observed by someone). The sentence given in Example 7.32, on the other hand, contains only two propositions (a sail and all masts are intact; this is seen by someone).⁹

(7.31) Sie sieht, dass er segelt und alle Masten intakt sind.

She sees that he sails and (that) all masts are intact.

(7.32) Sie sieht, dass ein Segel und alle Masten intakt sind.

She sees that a sail and all masts are intact.

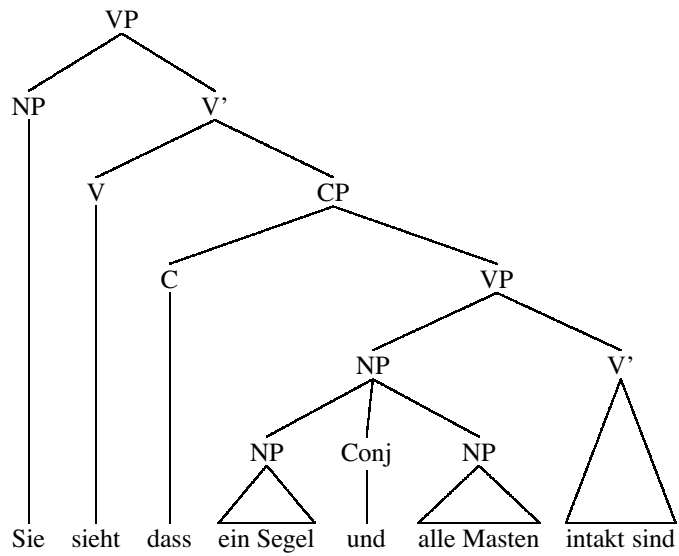
It is conceivable that the reconstruction of pronominal reference and the interpretation of the propositional content of the experimental stimuli was blocked or at least attenuated when a grammatical anomaly was present, which would in turn lead to activation increases in response to correct sentences. The fact that correct sentences in the phrase structure condition did not elicit a similar amount of hemodynamic activity could be due to the differences in terms of referential and propositional complexity that were described above. However, this interpretation is admittedly speculative and needs to be corroborated by future research.

7.4.7 Summary

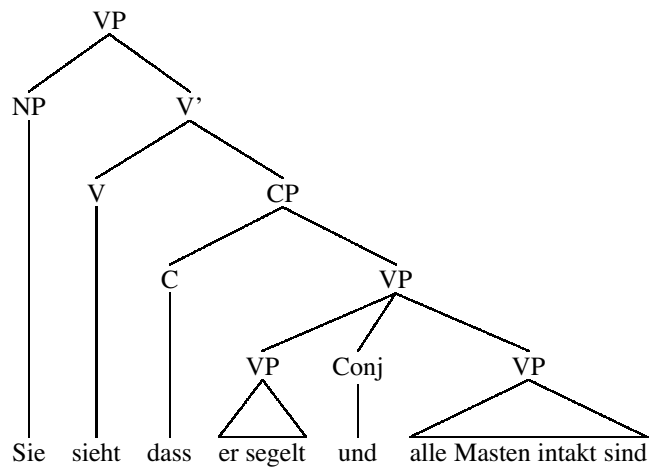
The results of the fMRI study indicate that both phrase structure and morphosyntactic anomalies in real word sentences were processed as violations of syntactically based sequential predictions (with the left ventral premotor cortex as the neuroanatomical correlate). With regard to pseudo-word sentences, a strong hemodynamic brain response to correct

⁹Alternatively, the sentence could be analyzed as containing three propositions, two of which are conceptually similar and based on the same predicate (a sail is intact; all masts are intact. The third proposition is that this is observed by someone).

(7.29)



(7.30)



stimuli that encompassed the entire language processing network precluded the detection of an analogous effect of ungrammaticality. The electrophysiological experiment that is reported in the following section, however, provides more conclusive results with regard to this latter issue as the ERP method has a more fine-grained temporal resolution and depends on a physiological variable that is not prone to saturation effects.

7.5 Experiment 2b (ERPs)

7.5.1 Participants

After giving informed consent, 24 native speakers of German participated in the study. No participant had any history of neurological or psychiatric disorders. All participants had normal hearing and were right-handed (laterality quotients of 90-100 according to the Edinburgh handedness scale (Oldfield, 1971)). Seven participants were excluded from all further processing steps because of excessive error rates or due to technical problems, resulting in a final group of 17 participants (10 male; mean age 26 years; age range 22-33 years) entering the analysis of the behavioral and functional data.

7.5.2 Stimuli and Task

The same stimulus material, task, and experimental setup as in the fMRI experiment (see Section 7.2) was used for the ERP study. This includes the randomization of the stimuli as well as the inter-stimulus interval (ISI) of 12 seconds. While this entails a relatively long pause between sentences, it ensures an optimal amount of comparability between the fMRI and the ERP experiment in terms of the experimental procedure.

7.5.3 Data Acquisition and Analysis

EEGs were recorded from 59 Ag/AgCl electrodes fixed to an elastic cap (Electro Cap International) and placed according to the extended 10-20 system (Jasper (1958); also see Figure 7.7). Online recordings were referenced to the left mastoid. The EEG from the right mastoid was also recorded in order to allow later rereferencing. Participants were grounded via an electrode placed at the sternum. In order to allow for the detection of eye movement artifacts, electrooculograms (EOGs) were recorded from additional electrodes placed at the outer canthus of each eye (horizontal EOG) and above and below the right eye (vertical EOG). Electrode impedances were kept below 5 k Ω . EEG recording occurred at a sampling rate of 500 Hz.

A finite impulse response (FIR) filter (0.3 - 20Hz) was applied to the raw EEG data in order to remove slow drifts. Trials containing eye movement artifacts were excluded from

Figure 7.7: The International 10-20 System

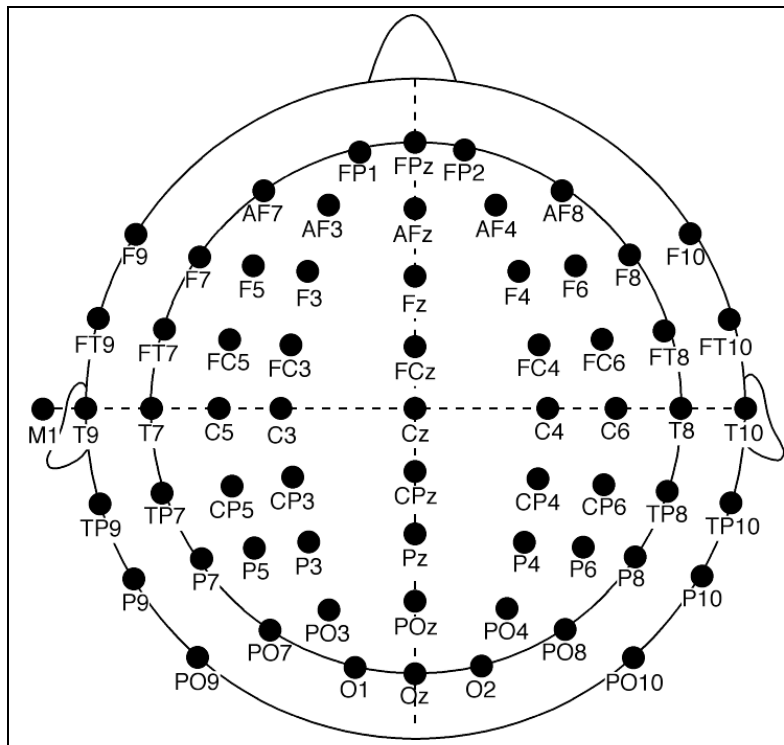


Table 7.3: Behavioral Results

Condition	% Accuracy (SD)
phrase structure, real words, correct	99 (2)
phrase structure, real words, incorrect	99 (2)
morphosyntax, real words, correct	99 (3)
morphosyntax, real words, incorrect	97 (7)
phrase structure, pseudo-words, correct	97 (3)
phrase structure, pseudo-words, incorrect	95 (5)
morphosyntax, pseudo-words, correct	97 (4)
morphosyntax, pseudo-words, incorrect	98 (3)

Values are means for all participants. SD=standard deviation.

the analysis. Artifact identification was conducted by first applying an automatic detection algorithm to the raw data and then checking and refining the results of this procedure by visual inspection.

Artifact-free trials were averaged per condition per participant, time-locked to the onset of the critical word in each sentence. The single averages were then used as data points in a repeated measures analysis of variance with the factors GRAMMATICALITY (correct/incorrect), LEXICALITY (real words/pseudo-words), TYPE (morphosyntax/phrase structure) and ROI (see below). ROIs were defined as follows: Left anterior (LA) = AF7 AF3 F9 F7 F5 F3; middle anterior (MA) = AFZ FZ; right anterior (RA) = AF4 AF8 F4 F6 F8 F10; left central (LC) = FT7 FC5 T7 C5 TP7 CP5; middle central (MC) = FCZ CZ CPZ; right central (RC) = FT8 FC6 T8 C6 TP8 CP6; left posterior (LP) = P9 P7 P5 P3 PO7 PO3; middle posterior (MP) = PZ POZ; right posterior (RP) = P10 P8 P6 P4 PO8 PO4. Based on a visual inspection of the group data, two time windows were determined for the statistical analysis (200ms-800ms, 800ms-1300ms). Only main effects and interactions containing the relevant factor GRAMMATICALITY are reported. Significant interactions ($p < 0.05$) were resolved hierarchically, starting with the factor ROI (if applicable) and continuing with the factors LEXICALITY and TYPE (in that order) provided that the effects on the previous level were significant (i.e., an interaction between GRAMMATICALITY x LEXICALITY x ROI would first be resolved by ROI. In all ROIs in which the interaction between GRAMMATICALITY x LEXICALITY reached significance, a further resolution by LEXICALITY would then be computed).

7.5.4 Results

Behavioral Results

An analysis of variance with the factors LEXICALITY (real words, pseudo-words), TYPE (morphosyntax, phrase structure) and GRAMMATICALITY (correct, incorrect) was conducted in order to assess differences in terms of accuracy between the experimental conditions¹⁰ (also see Table 7.3). The main effects of LEXICALITY ($F_{1,16} = 6.84, p < 0.05$) and GRAMMATICALITY ($F_{1,16} = 7.10, p < 0.05$) were significant and were further qualified by the interactions of LEXICALITY x TYPE ($F_{1,16} = 5.89, p < 0.05$) and LEXICALITY x TYPE x GRAMMATICALITY ($F_{1,16} = 6.91, p < 0.05$). Resolving the interaction of LEXICALITY x TYPE by TYPE revealed that the factor LEXICALITY was only significant in the phrase structure condition ($F_{1,16} = 14.38, p = 0.0016$). A resolution of the three-way interaction of LEXICALITY x TYPE x GRAMMATICALITY by TYPE indicated that the interaction of LEXICALITY x GRAMMATICALITY was not significant in the phrase structure condition ($F_{1,16} = 1.66, p > 0.2$), but approached significance in the morphosyntactic condition ($F_{1,16} = 3.11, p = 0.0967$). However, because of the weakness of this effect, no further step-down analyses were conducted.

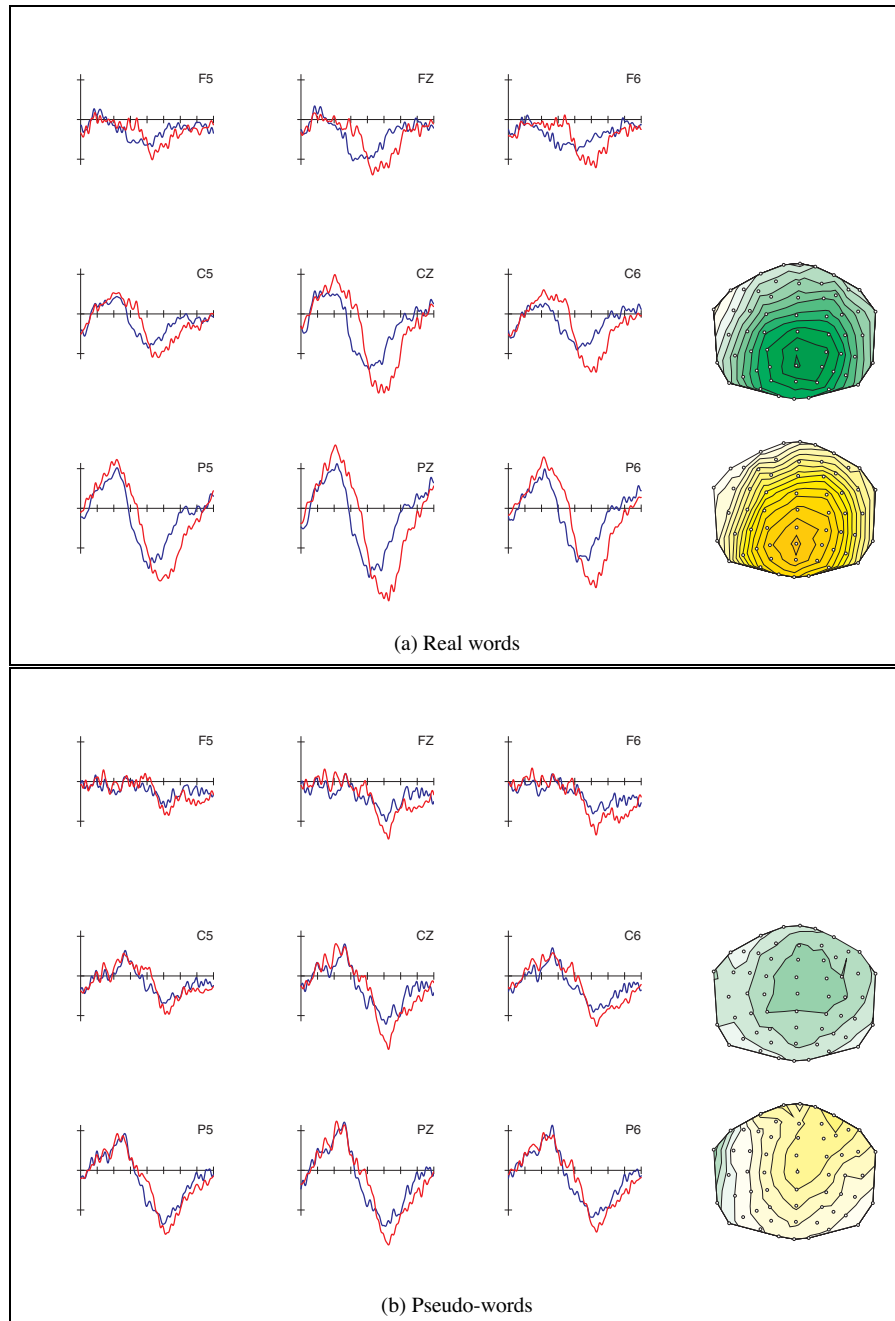
Electrophysiological Results

As can be seen in the ERP plots (see Figures 7.8 and 7.9), incorrect sentences elicited a biphasic response, consisting of a negativity between 200ms and 800ms post-stimulus onset and a positivity between 800ms and 1300ms post-stimulus onset.

The statistical analysis in the first time window (200ms-800ms) revealed a significant main effect of GRAMMATICALITY ($F_{1,16} = 20.92, p = 0.0003$) that was further qualified by interactions between GRAMMATICALITY x LEXICALITY ($F_{1,16} = 4.72, p < 0.05$), GRAMMATICALITY x ROI ($F_{8,128} = 6.34, p = 0.0048$) and GRAMMATICALITY x LEXICALITY x ROI ($F_{8,128} = 8.65, p = 0.0004$). Resolving the three-way interaction by the factor ROI revealed significant interactions between GRAMMATICALITY x LEXICALITY in middle to posterior ROIs (MC: $F_{1,16} = 6.99, p < 0.05$; LP: $F_{1,16} = 13.30, p = 0.0022$; MP: $F_{1,16} = 21.12, p = 0.0003$; RP: $F_{1,16} = 17.54, p = 0.0007$) that were strongest over centro-parietal electrodes (ROI MP). Within these ROIs, a further resolution by the factor LEXICALITY revealed that the effect of GRAMMATICALITY was more pronounced in real word sentences (MC: $F_{1,16} = 34.05, p < 0.0001$; LP: $F_{1,16} = 32.04, p < 0.0001$; MP: $F_{1,16} = 37.26, p <$

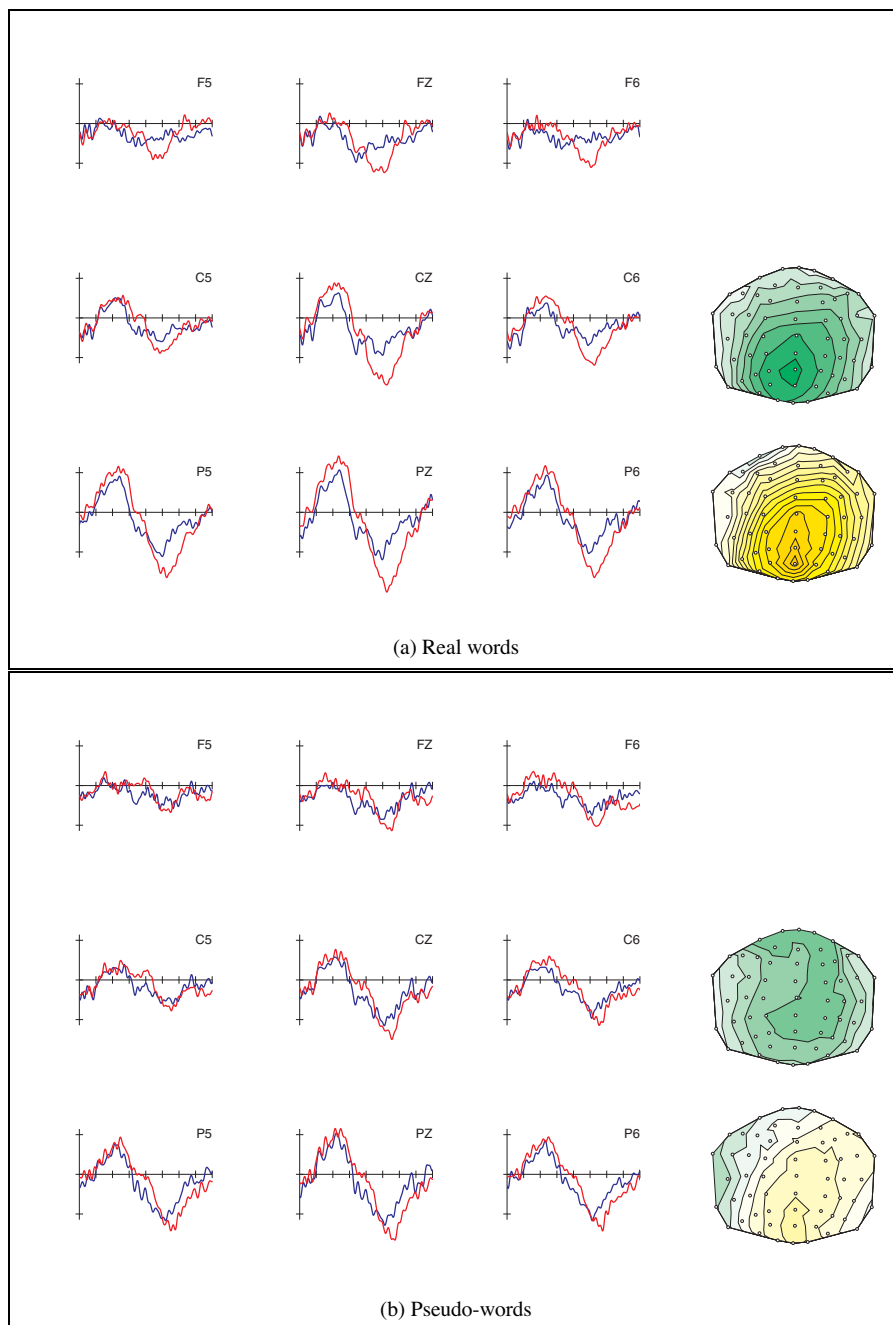
¹⁰As described in Section 7.4.5 and Chapter 6, reaction times were measured from stimulus onset to prevent false time outs due to participants responding too early and are thus not accurate enough to merit a detailed analysis.

Figure 7.8: Correct vs Incorrect, Morphosyntax



Red: incorrect sentences. Blue: correct sentences. Negativity is plotted upwards, the x-axis depicts time in 200ms increments (post stimulus onset). Maps are shown for time windows between 200-800ms (top) and 800-1300ms (bottom). Green=Negative, Yellow=Positive.

Figure 7.9: Correct vs Incorrect, Phrase Structure



Red: incorrect sentences. Blue: correct sentences. Negativity is plotted upwards, the x-axis depicts time in 200ms increments (post stimulus onset). Maps are shown for time windows between 200-800ms (top) and 800-1300ms (bottom). Green=Negative, Yellow=Positive.

0.0001; RP: $F_{1,16} = 44.10$, $p < 0.0001$) than in pseudo-word sentences (MC: $F_{1,16} = 5.82$, $p < 0.05$; LP: $F_{1,16} = 2.45$, $p > 0.1$; MP: $F_{1,16} = 4.99$, $p < 0.05$; RP: $F_{1,16} = 4.78$, $p < 0.05$).

In the second time window (800ms-1300ms), a similar pattern of results was observed. In addition to a main effect of GRAMMATICALITY ($F_{1,16} = 18.31$, $p = 0.0006$), interactions between GRAMMATICALITY x LEXICALITY ($F_{1,16} = 12.93$, $p = 0.0024$), GRAMMATICALITY x ROI ($F_{8,128} = 8.01$, $p = 0.0017$) and GRAMMATICALITY x LEXICALITY x ROI ($F_{8,128} = 4.97$, $p < 0.05$) were observed. A resolution of the three-way interaction by the factor ROI revealed a significant interaction between GRAMMATICALITY x LEXICALITY over middle and posterior electrodes (ROIs LC: $F_{1,16} = 13.12$, $p = 0.0023$; LP: $F_{1,16} = 38.46$, $p < 0.0001$; MC: $F_{1,16} = 22.69$, $p = 0.0002$; MP: $F_{1,16} = 47.28$, $p < 0.0001$; RC: $F_{1,16} = 19.52$, $p = 0.0004$; RP: $F_{1,16} = 40.43$, $p < 0.0001$) that was again strongest in the centro-parietal ROI (MP). In all ROIs in which the GRAMMATICALITY x LEXICALITY interaction reached significance, the effect of GRAMMATICALITY was more pronounced in real word sentences (LC: $F_{1,16} = 19.0$, $p = 0.0005$; LP: $F_{1,16} = 25.35$, $p = 0.0001$; MC: $F_{1,16} = 32.12$, $p < 0.0001$; MP: $F_{1,16} = 38.51$, $p < .0001$; RC: $F_{1,16} = 34.08$, $p < 0.0001$; RP: $F_{1,16} = 32.67$, $p < 0.0001$;) than in pseudo-word sentences (LC: $F_{1,16} = 0.05$, $p > 0.8$; LP: $F_{1,16} = 0.62$, $p > 0.4$; MC: $F_{1,16} = 5.89$, $p < 0.05$; MP: $F_{1,16} = 3.37$, $p = 0.0853$; RC: $F_{1,16} = 4.8$, $p < 0.05$; RP: $F_{1,16} = 1.18$, $p > 0.2$).

7.5.5 Discussion

Incorrect sentences elicited a biphasic ERP response that was not influenced by violation type, but modulated by lexicality: both the early negativity and the late positivity were significantly more articulated in the real word condition, and the positivity was virtually absent in pseudo-word sentences. Both ERP components exhibited centro-parietal maxima. In the following two sections, I will first discuss the effects in real word sentences before taking a closer look at the ERP responses in pseudo-word sentences.

Sequential Predictions Revisited: The Early Negativity

The similarity of the ERP components that were observed for both violation types in the current study can be explained analogously to the overlapping fMRI activation clusters discussed in Section 7.4.6. It appears that the defining characteristic of both types of grammatical violations as implemented in the current study is their locality, resulting in the possibility to process them via a general mechanism for the generation and checking of sequential predictions. An explanation along these lines entails that while such predictions may be based on a number of different sets of rules (i.e., regarding morphosyntactic agreement and phrase structure legality), mismatches between the corresponding expectations and the actual input

are detected by similar or even identical brain systems - at least as long as the detection itself is based on a homogeneous source of information (i.e. morpho-phonology as in the current study).

Supporting evidence for this interpretation comes from a recent study on local morphosyntactic and phrase-structure violations in two-word utterances (Hasting and Kotz, 2008). The authors report ERP results that are very similar to the ones observed in the current experiment: both types of grammatical anomalies elicited an early negativity that was taken to reflect the refutation of a rule-based sequential prediction. Crucially, the experimental material that was utilized consisted of combinations of a pronoun or a determiner and an inflected verb or a noun (see Examples 7.33 to 7.34), allowing the build-up of morpho-phonological expectations that are very similar to the predictions that have been assumed in Section 7.4.6 and in the last paragraph.

(7.33) *Er segel - t.*
 He.PRON.3SG.NOM sail - s.V.3SG.PRES
 He sails.

(7.34) **Er segel - st.*
 He.PRON.3SG.NOM sail - Ø.V.2SG.PRES
 *He sail.

(7.35) **Er Segel - Ø*
 He.PRON.3SG.NOM sail - Ø.N.SG
 * He sail

(7.36) *Ein Segel - Ø*
 A.D.SG sail - Ø.N.SG
 A sail

(7.37) **Ein segel - t.*
 A.D.SG sail - Ø.V.3SG.PRES
 * A sails.

(7.38) **Ein segel - st.*
 A.D.SG sail - Ø.V.2SG.PRES
 *A sail

Bahlmann et al. (2006) observed a comparable negativity for violations of serial predictions in syllable sequences that were organized according to an artificial "Finite State Grammar" - a type of rule system that relies exclusively on local dependencies between immediately adjacent elements. Violations in sequences that were based on a non-local "Phrase Structure Grammar" did not elicit a similar negativity, indicating the involvement

of different cognitive mechanisms for the resolution of long-distance dependencies. Further evidence comes from an earlier study using a full-fledged artificial "mini language" (named "BROCANTO"): Friederici et al. (2002b) report two relatively early negativities in response to local structural violations that may have been detected via the disconfirmation of rule-based serial phonological predictions. The second negativity is discussed as a possible instantiation of the "Phonological Mismatch Negativity" (PMN) as described by Connolly and Phillips (1994). This ERP component has been found in response to the presence of unexpected word-initial phonemes (Connolly and Phillips, 1994; Newman et al., 2003). As has already been discussed in the paragraphs above, the Negativity observed in the current study may similarly be a reflection of cognitive processes that rely on serial morpho-phonological predictions in order to detect grammatical anomalies.

It is critical to note that the negative ERP deflection discussed above appears to be elicited by a general expectancy-mismatch detection mechanism, not by grammatical processing per se. While the linguistic rules that are used to generate the necessary predictions have to differ between phrase structure and morphosyntactic violations, the subsequent "checking" procedure seems to be largely invariable - at least when the context in which the grammatical anomalies occur is highly controlled, violations only concern adjacent elements and morpho-phonological information plays a critical role, as was the case in the current study. The early left anterior negativity (ELAN) and the (later) left anterior negativity (LAN) that have been previously observed in response to phrase structure and morphosyntactic violations, respectively (for reviews, see Friederici, 2002; Friederici and Weissenborn, 2007) may reflect more specific processes that are utilized when anomalies can not be uniformly detected with the help of syntactically-based phonological expectations. In turn, the fact that the negativity that was observed in the current study has a different topography and a different timecourse than the "classical" syntactic ERP components (i.e. the ELAN and the LAN) and more closely resembles the PMN supports the claim that it reflects a general prediction-mismatch detection mechanism (possibly based on morpho-phonology) and is not directly related to syntactic processing.

Integration and Repair: The Late Positivity

Late positivities similar to that observed in the current study - commonly referred to as SPS, "syntactic positive shift" (Hagoort et al., 1993), or P600 (Osterhout and Holcomb, 1992) - have been discussed as the electrophysiological reflection of a number of different language-related processes. Classically, the P600 is taken to be elicited by the attempted repair of ungrammatical sentences and by the reanalysis of ambiguous sentences that are disambiguated towards a non-preferred reading (Friederici, 2002). It has been proposed that the "repair"-P600 has a centro-parietal topography while the "reanalysis"-P600 has a fronto-central dis-

tribution (Friederici et al., 2002a), although the latter component has also been implicated as a general marker of sentence complexity (Kaan and Swaab, 2003). In recent years, the P600 has increasingly been discussed as a reflection of processes that relate to the integration of semantic and syntactic representations (for reviews, see Bornkessel-Schlesewsky and Schlesewsky, 2008; Kuperberg, 2007). In contrast to very early ERP components like the ELAN, the P600 is modulated by the experimental task (Hahne and Friederici, 2002) and the proportion of anomalous stimuli in the experimental material (Hahne and Friederici, 1999), but is relatively impervious to manipulations of low-level perceptive stimulus properties like visual contrast (Gunter et al., 1999).

Since sentences in the current study were not structurally ambiguous, it is unlikely that the P600 observed here is related to processes of reanalysis. The centro-parietal distribution of the component as well as its elicitation by ungrammatical stimuli are more compatible with an interpretation of the late positivity as a reflection of attempts at repairing the anomalous sentences. Comparable ERP responses have been consistently reported for both phrase structure violations (Friederici et al., 2004, 1996; Gunter et al., 1999; Hahne and Jescheniak, 2001; Hasting and Kotz, 2008; Yamada and Neville, 2007) as well as morphosyntactic violations (Ericsson et al., 2008; Gunter et al., 2000, 1997; Hasting and Kotz, 2008; Münte et al., 1997) in real word sentences. With pseudo-word stimuli, however, the picture is more complicated. This will be discussed in detail in the following section.

The Jabberwocky Factor: Why Lexicality Matters

Previous findings on the processing of grammatical violations in pseudo-word sentences are heterogeneous. In studies utilizing non-lexical stimuli, the P600 is sometimes reported to be completely absent (Ericsson et al., 2008; Münte et al., 1997) while other authors only find it to be attenuated (Yamada and Neville, 2007) or even not significantly different from the corresponding positivity in real word sentences at all (Hahne and Jescheniak, 2001). With regard to earlier negativities, some authors report equally strong effects for real word and pseudo-word sentences (Hahne and Jescheniak, 2001; Yamada and Neville, 2007) while others do not find any negativity (Ericsson et al., 2008) or even report a negativity that is only observed for pseudo-word sentences, but not for real word stimuli (Münte et al., 1997). In order to shed some light on this apparently contradictory pattern of results, each of the studies mentioned above will be discussed in more detail in the paragraphs below.

Münte et al. (1997) conducted two experiments with visually presented pseudo-word sentences that were either grammatically correct or contained a morphosyntactic violation (see Examples 7.39 to 7.42). In the first experiment, only pseudo-word sentences were utilized and participants had to perform a memory task (every five sentences, a probe sentence was displayed and participants had to judge if they had been exposed to this particular stim-

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ulus before). The authors report a sustained negativity starting at 280ms post-onset of the critical word for incorrect sentences, but no late positivity. In the second experiment, both pseudo-word and real word sentences (see Examples 7.43 to 7.46) were presented and participants were asked to judge the grammaticality of each stimulus. Again, morphosyntactic violations in pseudo-word sentences elicited a negativity starting at 280ms post-onset of the critical verb but no late positivity. The authors report no negativity for incorrect real word sentences; instead, a centro-parietal positivity starting at 400ms post-onset of the critical word is found.

While these results appear quite striking at first, a closer look at the experimental materials that were implemented in this study reveals several potential pitfalls that make an interpretation of the ERP effects very difficult and suggest that in fact, most of the electrophysiological modulations that are reported may be due to critical confounding factors.

(7.39) *Der Krucke plötzt den Schruck.*
 The.D.NOM.SG N.NOM.SG V.3SG.PRES the.D.ACC.SG N.ACC.SG
 (Pseudo-words)

(7.40) **Das Klenck frunen den Wech.*
 The.D.NOM.SG N.NOM.SG V.3PL.PRES the.D.ACC.SG N.ACC.SG
 (Pseudo-words)

(7.41) *Viele Wenken donzen den Tend.*
 Many.Q.NOM.PL N.NOM.PL V.3PL.PRES the.D.ACC.SG N.ACC.SG
 (Pseudo-words)

(7.42) **Manche Verzinker trögelt den Blotz.*
 Some.Q.NOM.PL N.NOM.PL V.3SG.PRES the.D.ACC.SG N.ACC.SG
 (Pseudo-words)

(7.43) *Der Junge schlägt den Hund.*
 The.D.NOM.SG boy.N.NOM.SG hit.V.3SG.PRES the.D.ACC.SG dog.N.ACC.SG
 The boy hits the dog.

(7.44) **Der Mann trinken das Bier.*
 The.D.NOM.SG man.N.NOM.SG drink.V.3PL.PRES the.D.ACC.SG
 beer.N.ACC.SG
 *The man drink the beer.

(7.45) *Viele Passagiere zahlen die Fahrkarten.*
 Many.Q.NOM.PL passenger.N.NOM.PL pay.V.3PL.PRES the.D.ACC.PL
 ticket.N.ACC.PL
 Many passengers pay the tickets.

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(7.46) **Manche* *Lehrer* *bestraft* *die*
Some.Q.NOM.PL teacher.N.NOM.PL punish.V.3SG.PRES the.D.ACC.PL
Schüler.
pupil.N.ACC.PL
Some teachers punishes the pupils.

Crucially, sentences that have the syntactic structure depicted in Examples 7.40, 7.42, 7.44 and 7.46 are not necessarily incorrect at the position that the authors deemed to be critical (the verb) - depending on the gender of the first NP as well as the semantics of the predicate and the animacy of its arguments, the sentence fragments up to and including the verb *do* have grammatical continuations. For example, sentences 7.47 and 7.48 would be perfectly acceptable in grammatical terms¹¹ - however, they involve a non-standard word order (object before subject) which has consequences on both a syntactic level (regarding movement) and a semantic level (regarding thematic role assignment).

(7.47) *Manche* *Verzinker* *trögelt* *der* *Blotz.*
Some.Q.ACC.PL N.ACC.PL V.3SG.PRES the.D.NOM.SG N.NOM.SG
(Pseudo-words)

(7.48) *Manche* *Lehrer* *bestraft* *der*
Some.Q.ACC.PL teacher.N.ACC.PL punish.V.3SG.PRES the.D.NOM.SG
Schüler.
pupil.N.NOM.SG
The pupil punishes some teachers.

Since it remains entirely unclear how many of the purportedly incorrect experimental sentences were susceptible to such an analysis and, more importantly, it is beyond doubt that this confound affected pseudo-word and real word sentences differently (note that the object-before-subject reading may be blocked by the semantics of the verb and the animacy of the arguments in real word sentences, but not in pseudo-word sentences), the results reported by Münte et al. (1997) can not be readily interpreted.

Hahne and Jescheniak (2001) investigated the processing of phrase structure violations (see Example 7.49 and 7.50) in auditorily presented real word and pseudo-word sentences.

(7.49) **Die* *Birne* *wurde* *im* *gepflückt.*
The.D.NOM.SG pear.N.NOM.SG is.AUX.3SG.PAST in_the.P pluck.V.PTCP
*The pear was in the plucked.

¹¹At the position of the verb, the real word sentence would also be semantically acceptable as there are plausible continuations: consider a sentence like "Manche Lehrer bestraft der Direktor." / "The headmaster punishes some (of the) teachers." which has the same structure as the sentence in Example 7.46 by Münte et al. (1997), but is just fine in grammatical as well as in conceptual terms.

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(7.50) *Die Glabbe wurde im gerottert.
The.D.NOM.SG N.NOM.SG is.AUX.3SG.PAST in.the.P V.PTCP
(Pseudo-words)

Lexical and non-lexical stimuli were tested in different sessions, but with the same participants. The task to be performed was a grammaticality judgment. For incorrect sentences in both pseudo-word and real word sentences, the authors report an early anterior negativity (distributed bilaterally and extending up to central electrodes) between 100ms-250ms post-onset of the critical word followed by a centro-parietal positivity between 500ms-1000ms.

The fact that Hahne and Jescheniak (2001) found both the early negativity and the late positivity to be equally strong in real word and pseudo-word sentences (in contrast to the findings reported in Section 7.5.4 of the current study) can be explained by the different positions of the relevant grammatical affixes. In the current study, the grammaticality of the sentences depended on the suffix of the critical word while in the experiment conducted by Hahne and Jescheniak (2001), this information was encoded in the prefix. In the latter case, detecting a mismatch between the expected word category and the actual word category amounts to detecting a particular word-initial syllable (in the Hahne and Jescheniak (2001) study, this was always "ge-" in incorrect sentences) that also constituted a violation of the expected stress pattern: the "ge-" prefix of the participle that followed the preposition in incorrect sentences was unstressed whereas a member of the expected word category (a noun) would have had a stressed first syllable in most cases.

Importantly, detecting the prefix and the associated word-category mismatch precedes the processing of the word stem and the corresponding lexical information. Hahne and Jescheniak (2001) argue that this fact can explain the presence of the P600 following grammatical violations in pseudo-word sentences in their experiment: according to what they term the "timing hypothesis", the P600 will only be attenuated (or absent) if information about the lexical status of the critical word is processed *before* the word-category violation is encountered. This was the case in the current study, but not in the study by Hahne and Jescheniak (2001). The similarity of the early negativity in real word and pseudo-word sentences that is reported by Hahne and Jescheniak (2001) can be explained along the same lines: in their experiment, the detection of the prefix and the corresponding word-category violation preceded the processing of the word stem and was thus independent of the lexicality of the critical word. In the current study, however, the word stem was processed before the anomalous suffix could be detected. Crucially, knowing the word stem can aid in the morpho-phonological separation and detection of the suffix in real word sentences, but not in pseudo-word sentences since pseudo-word stems are not represented in the mental lexicon, resulting in a violation that is less clear and may thus elicit a less articulated electrophysiological response.

Yamada and Neville (2007) conducted an experiment with visually presented real word and pseudo-word sentences. Half of the critical experimental stimuli contained phrase-structure violations (see Example 7.51).

(7.51) *Mommy can cut the meat with her that knife.

In addition, a small number of irrelevant filler sentences was included. Lexical and non-lexical stimuli were presented intermixed, and participants were asked to perform a grammaticality judgment after every trial (an additional probe question had to be answered following the presentation of 10% of all sentences). The authors report an early negativity (180ms-250ms) followed by a later positivity (500ms-900ms) for both real word and pseudo-word sentences; however, there were significant quantitative differences regarding amplitude strength and topography. While the early negativity was not modulated by the lexicality of the sentences over temporal electrodes, it was stronger for real word stimuli over anterior sites with a right-hemispheric bias. The positivity had a centro-parietal maximum for both sentence types, but was stronger for real word sentences over the left hemisphere.

In principle, the results reported by Yamada and Neville (2007) are comparable to the observations made by Hahne and Jescheniak (2001): both an early negativity as well as a later positivity are clearly present in real word and pseudo-word sentences. The minor variations in the topography of the negativity found by Yamada and Neville (2007) may be due to the fact that the grammatical violations that they implemented included both a mismatch between the expected and the actual word category (noun vs determiner/complementizer) and a mismatch between an expected open-class word (a noun) and an actual closed-class word (a determiner or complementizer) - the latter anomaly may well have a more pronounced effect in real word sentences in which the open-class words actually carry semantic meaning. An analogous point can be made with regard to the late positivity.

Ericsson et al. (2008) tested visually presented sentences of three different types: semantically coherent real word sentences (see Example 7.52), semantically incoherent real word sentences (see Example 7.53) and pseudo-word sentences (see Example 7.54). Half of the sentences in each condition were correct while the other half contained a violation of article-noun agreement (see Example 7.55). Article and noun were always separated by an uninflected adjective. Participants had to perform an acceptability judgment task. The authors report a late centro-parietal positivity (500ms-1000ms) for incorrect sentences when compared to correct sentences in the semantically coherent condition and in the semantically incoherent condition, but not in the pseudo-word condition. This ERP component was significantly stronger for semantically coherent sentences than for semantically incoherent sentences.

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(7.52) *Vandraren såg det svaga skenet från
Hiker.N.SG see.V.3SG.PAST the.D.NEUTR faint.ADJ light.N.NEUTR from.P
brasan.
fire.N.SG*
The hiker saw the faint light from the fire.

(7.53) *Borsten flyttade det vita priset
Brush.N.SG move.V.3SG.PAST the.D.NEUTR white.ADJ prize.N.NEUTR
från ådern.
from.P vein.N.SG*
The brush moved the white prize from the vein.

(7.54) *Bolpen präkade det krässiga prulet från gollen.
N.SG V.3SG.PAST the.D.NEUTR ADJ N.NEUTR from.P N.SG*
(Pseudo-words)

(7.55) **Vandraren såg den svaga skenet från
Hiker.N.SG see.V.3SG.PAST the.D.COMM faint.ADJ light.N.NEUTR from.P
brasan.
fire.N.SG*
*The hiker saw the faint light from the fire.

The fact that Ericsson et al. (2008) did not observe an early negativity in response to grammatical anomalies in any of their experimental conditions can be easily explained by the non-locality of the syntactic violations that they implemented: the determiner allowing for a local grammatical prediction regarding gender was always followed by an uninflected adjective that preceded the critical noun. If - as has been argued so far - locality in the sense of strict adjacency is a critical factor with regard to the brain response that is observed for the processing of syntactic anomalies, the absence of an early negativity on the noun is actually expected. The missing P600 can be accounted for straightforwardly with the "timing hypothesis" by Hahne and Jescheniak (2001): since the information determining the grammaticality of the sentences in the study by Ericsson et al. (2008) was coded in the suffix, it is plausible that information about the lexical status of the words was processed before the syntactic anomaly was detected, thus resulting in processing problems on two levels (syntax and lexical semantics) and a blocking of the processes underlying the P600.

In sum, the heterogeneous pattern of results that has been reported for the processing of grammatical violations in real word and pseudo-word sentences can be reconciled when the locality of the syntactic anomalies and the temporal availability of lexical information is taken into account. Local ungrammaticalities elicit an early negativity that appears to be more pronounced when the relevant stimulus features are readily discernible (i.e., when the identification of the relevant affix is facilitated by information about the phonological

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form of the word stem¹²). A later positivity occurs in response to both local and non-local violations, but is markedly attenuated or even completely absent when information about the lexical status of the critical word is available before the syntactic anomaly is encountered (which is the case when the violation is encoded in a suffix, but not when it is encoded in a prefix).

Thus, the available ERP evidence indicates that both the lexical status of the stimuli and the locality of the violations that are implemented have a profound effect on the processing of ungrammatical sentences. In the following final chapter of this dissertation, the electrophysiological results that were just discussed will be integrated with the corresponding observations from the fMRI studies that have been reported in Chapter 6 and Section 7.4. The DTI data discussed in Chapter 5 will also be taken into account.

¹²See Dikker et al. (2009); Gunter et al. (1999) for compatible lines of argumentation regarding the recognizability of the critical features of the stimuli

Part III

General Discussion

Chapter 8

Summary and Conclusions

In this dissertation, a variety of different methodologies and data acquisition techniques was utilized in order to shed light on both the neuroanatomical architecture and the electrophysiological timecourse of language processing. In the following sections, I will summarize the main results of the studies described in Chapters 5 to 7 and discuss the broader implications of the observed data patterns. A number of critical conclusions can only be reached by integrating observations and interpretations across different studies: both experiment one and experiment two allow for a comparison of real word and pseudo-word processing on different levels (single words and sentences). In experiment 2a and experiment 2b, the same sentence material was investigated with two complementary data acquisition methods, resulting in the opportunity to make inferences about both the neuroanatomical substrates (as measured with fMRI) and the time course (as measured with ERPs) of the processing of local syntactic anomalies. Finally, the anatomical parcellation and connectivity information that was derived from the DTI data can aid in the interpretation of the fMRI experiments. In addition, both the tractography data and the parcellation data are intrinsically valuable because they add a number of novel insights to a growing body of evidence dealing with the white matter pathways that connect distant nodes of the language processing network.

8.1 A Look at the Brain's Communicative Infrastructure

Using diffusion tensor imaging, the left superior temporal gyrus and sulcus were shown to house three distinct anatomical subregions that could be differentiated with regard to their long-range cortico-cortical connectivity (see Chapter 5): while the posterior STG/STS proved to be strongly connected to caudal aspects of the frontal lobe (i.e. the ventral premotor cortex and BA 44) via a dorsal pathway (possibly corresponding to the superior longitudinal fasciculus or the arcuate fasciculus; see below), the anterior STG/STS lacked SLF/AF

connectivity and turned out to be mainly linked to rostral frontal areas (i.e. BA 45) via a ventral pathway (this latter pathway was about equally strong for all three STG/STS areas and may correspond to the extreme capsule or the uncinate fasciculus; see below). The middle STG/STS region was demonstrated to have an indirect connection to the frontal lobe via an intermediate "stop" in the posterior STG/STS (also see Upadhyay et al., 2008). The connectivity profiles of homologue STG and STS areas were shown to be more similar than horizontally adjacent regions within gyrus or sulcus alone. The data also indicated the existence of two separate SLF pathways from posterior temporal to frontal areas (a direct link and an indirect link via the parietal lobe) in addition to a potential third pathway from the anterior frontal lobe (BA 45) to the middle temporal gyrus.

In classical neuroanatomical models of the language processing network (Geschwind, 1965, 1970; Lichtheim, 1885; Wernicke, 1874), the dorsal pathway connecting the posterior STG/STS to the caudal frontal lobe would have been identified as the arcuate fasciculus, first described by Burdach and Dejerine (Burdach, 1819; Dejerine, 1895). However, recent evidence points to a more complex picture involving a number of distinct fiber bundles in the temporal, parietal and frontal lobes. Glasser and Rilling (2008) provided evidence for two separate dorsal pathways connecting the rostral frontal lobe (BA 45) to the posterior MTG (also see Rilling et al., 2008) and the caudal frontal lobe (BA 44 and 6) to the posterior STG. Furthermore, Makris et al. (2005) were able to differentiate five different components of the dorsal pathway in a DTI study with human participants, supplying evidence for a vertical (AfV) and a horizontal (AfH) part of the arcuate fasciculus as well as three separate SLF bundles (SLF I - III) connecting the parietal and frontal lobes. In the account by Makris et al. (2005), AfH and SLF II form a compact bundle that courses rostrally above and along the Sylvian fissure. Using autoradiographic tract tracing and Diffusion Spectrum Imaging (DSI), Schmahmann et al. (2007) uncovered a homologue system of fiber bundles in macaque monkeys. Moreover, Catani et al. (2005) differentiated a "long segment" of the arcuate fasciculus (roughly corresponding to its classical definition) that directly connects the posterior STG and the frontal lobe from two shorter segments that connect the posterior STG to the parietal lobe and the parietal lobe to the frontal lobe. However, taking the data by Makris et al. (2005) and Schmahmann et al. (2007) into account, it is conceivable that the different arcuate pathways that were described by Catani et al. (2005) are actually artifacts that are due to the inherent spatial imprecision of DTI-based virtual tractography: while the "long" segment of the AF may correspond to a combination of AfV, AfH and SLF II, the "short" segments connecting temporal and parietal and parietal and frontal regions may be conglomerates of AfV, SLF I and SLF III fibers (for a similar line of argument, see Frey et al., 2008). Nevertheless, the available evidence clearly points to the existence of more than one fiber bundle connecting temporal, parietal and frontal areas.

It is likely that the dorsal pathway that was identified by DTI tractography in the study described in Chapter 5 represents a collection of fibers from the AFv and AFh as well as fibers from the SLF II as defined by Makris et al. (2005). The existence of extensive connections to the parietal lobe is in line with the account by Catani et al. (2005) (suggesting that fibers of the indirect temporo-frontal pathway may also be included), but can also be explained by parietal connectivity through SLF I-III (Makris et al., 2005; Schmahmann et al., 2007). The relatively weak connectivity to BA 45 (compared to rather strong connections to BA 44) is completely compatible with the description of the STG pathway by Glasser and Rilling (2008), although it has to be noted that the data under discussion here are agnostic with regard to the MTG pathway suggested by the same authors and Rilling et al. (2008).

The ventral pathway connecting temporal and inferior frontal regions is likely to consist of fibers from the extreme capsule (EmC) and the uncinate fasciculus. While the latter tract has long been known to connect the anterior superior temporal lobe (as well as subcortical structures such as the amygdala) to the prefrontal cortex (Burdach, 1819; Dejerine, 1895), the role of the extreme capsule as a fronto-temporal projection system has only recently become the focus of scientific scrutiny. Makris and Pandya (2009) argue that the EmC (and not the arcuate fasciculus) may, in fact, be the most relevant fiber bundle connecting anterior and middle temporal regions to the frontal lobe (and BA 45 in particular). The existence of the EmC pathway has been confirmed in a number of studies (Anwander et al., 2007; Frey et al., 2008; Saur et al., 2008), although there is currently no agreement with regard to the relative importance of the EmC and the AF in the language processing network (cf. Friederici, 2009). The tractographic results described in Chapter 5 suggest that while the anterior STG/STS is mainly connected to the frontal lobe via the uncinate fasciculus, middle and posterior STG/STS are connected to frontal regions via both the extreme capsule (to BA 45) and the AF/SLF projection system (to BA 44 and 6).

In sum, the tractographic results of the DTI study that was conducted as part of this dissertation lend additional neuroanatomical support to functionally-based models of the language processing network (also see Chapter 2) that assume distinct dorsal and ventral routes for different aspects of auditory language processing. In particular, they are highly compatible with the account by Friederici (2002) (also see Friederici, 2009): here, it is assumed that the anterior STG and the frontal operculum (primarily connected via the uncinate fasciculus) form a network for non-hierarchical syntactic processing while the posterior STG and BA 44 / 45 (primarily connected via the extreme capsule and the AF/SLF system) form a network for complex (hierarchical) syntactic and semantic processing and integration. The connectivity data are also broadly in line with the model by Hickok and Poeppel (2007), although this account is very much focused on computational "processing streams" without

explicitly discussing their potential white matter correlates (however, see Saur et al. (2008) and Glasser and Rilling (2008) for recent attempts at a neuroanatomical specification).

Furthermore, the parcellation of the STG and STS into three distinct subregions is compatible with functional data implicating these areas in dissociating cognitive operations like basic auditory and phonological processing (middle region), basic syntactic processing (anterior region) and syntactic-semantic integration (posterior region; also see Section 3.5). While the similarity between homologue STG and STS regions is surprising from a functional perspective (see, for example, Binder et al., 2000), it has recently gained anatomical plausibility since the extreme capsule as well as the middle longitudinal fasciculus (MdLF) appear to be connected to both superior temporal gyrus and sulcus (Makris and Pandya, 2009), thus rendering a connectivity-based differentiation difficult. This discrepancy between functionally and anatomically based distinctions leads to an important methodological conclusion: a classification of brain areas that is based on their long-range cortico-cortical connectivity can only capture a subset of the relevant neurocognitive distinctions. However, similar shortcomings apply to all parcellation techniques - for example, the lateral convexity of the STG has been classified as a homogeneous single area with regard to its cytoarchitecture (see Brodmann, 1909). Thus, a combination of different (and complementary) measures like connectivity, receptorarchitecture, cytoarchitecture and functional relevance remains the only way to arrive at an exhaustive description of the neurofunctional differentiation of this (or any) brain region.

8.2 A New Approach to the Generation of Pseudo-Words

The processing of different types of pseudo-words was investigated in an fMRI experiment (see Chapter 6). Real words were shown to elicit an increase in hemodynamic activity in a number of brain regions, most notably the left posterior MTG / angular gyrus and the right anterior STS and MTG. Pseudo-word processing led to heightened brain activity in the bilateral superior temporal gyrus, regardless of pseudo-word type. Lexically opaque pseudo-words (i.e. phonotactically legal pseudo-words that were not derived from existing real words) were shown to be the most effective in blocking lexical and semantic processing.

Crucially, this study revealed that lexically transparent pseudo-words (i.e. pseudo-words that are derived from existing real words by a minor change of one phoneme) and lexically opaque pseudo-words are processed differently, with only transparent pseudo-words still allowing for lexical access and a limited amount of semantic processing. Consequently, opaque pseudo-words should be preferred in experimental contexts that require truly meaningless verbal stimuli. For transparent pseudo-words, the "deviation point" (i.e. the word-internal location at which the "pseudo-word" status of an item became apparent) also turned

out to make a difference: pseudo-words in which the first two syllables remained unchanged with regard to the corresponding real word were processed more easily than pseudo-words in which the second syllable was altered (recall that in the study under discussion, all words had three syllables, with the uniqueness point of the real words occurring between the second and the third syllable). This was interpreted as indicating that lexical mismatches and lexical non-matches are processed differently, with the term "lexical mismatch" referring to situations in which there is a unique real word target (following two intact syllables of a pseudo-word that has its deviation point on the third syllable) and the term "lexical non-match" referring to situations in which there is no unique real word target (since the intact portion of a pseudo-word that deviates from its real "base word" on the second syllable is not sufficient to allow for lexical access).

8.3 Lexicality Effects at the Word- and Sentence Level

Both fMRI studies yielded consistent results with regard to the processing of real word and pseudo-word stimuli. The bilateral middle superior temporal gyrus was shown to be particularly important for the processing of pseudo-words on both the single word and the sentence level. This replicates findings from previous studies (Davis et al., 2008; Kotz et al., 2002; Meyer et al., 2003, 2000; Newman et al., 2001) and can be explained by increased cognitive demands related to the nature of the stimuli: pseudo-words are language-like, but lack a representation in the mental lexicon. As a result, there is no top-down information that can aid the identification of phonemes in cases of acoustic ambiguity (Davis and Johnsrude, 2007; Ganong, 1980; Myers and Blumstein, 2008; van Linden et al., 2007). Furthermore, when pseudo-words are combined into sentences, additional processing costs may arise because the identification of word boundaries is more difficult in the absence of lexical information (Davis and Johnsrude, 2007; Mattys et al., 2005). Finally, the auditory sensory percept - also called the "echoic memory" trace (Buchsbaum et al., 2005; Cowan, 1984) - of each individual pseudo-word has to be kept active for a longer time since lexical access never occurs. In contrast, the basic acoustic representation of a real word can be discarded once its lexical entry has been retrieved (Davis and Johnsrude, 2007).

The left posterior MTG / angular gyrus, on the other hand, was shown to be critically involved in the processing of meaningful stimuli, with very similar patterns of activation being elicited by entire sentences and single words. This finding replicates results from the existing literature and has been previously interpreted as indicating that the brain region under discussion is involved in lexical-semantic processing and phonological word form identification (Fiebach et al., 2002; Hagoort et al., 1999; Henson et al., 2002; Kotz et al., 2002; Rissman et al., 2003). While this explanation is completely compatible with the data

reported in Chapters 6 and 7 of this dissertation, it is still somewhat vague as it implies that either the absence of post-lexical semantic processing, the absence of lexical access, or both may be responsible for the decrease in hemodynamic activity that was observed in response to pseudo-word stimuli (cf. Lau et al., 2008). However, since the existing empirical evidence (including the data presented here) is inconclusive in this regard, determining which of the three options just discussed represents the most accurate account has to remain an issue of further investigation.

A number of additional brain regions were only active for the processing of pseudo-word sentences, but not for the processing of single pseudo-words (the left inferior and superior parietal lobe, the left superior and middle frontal gyrus, the left inferior frontal gyrus and ventral premotor cortex, the left inferior temporal gyrus). Interestingly, these areas correspond strikingly well to the network of cortical destinations that has been shown to be connected to the left STG with the help of DTI fiber tracking (see Chapter 5). This anatomical observation lends additional support to the claim that the detection of lexically anomalous stimuli like pseudo-word sentences leads to a cascade of increases in cortical blood supply in the entire language processing network that can be seen as a preparatory response intended to boost task performance (see Section 7.4.6). The fact that single pseudo-words did not elicit a similarly widespread hemodynamic response may be due to the different tasks that were used in the respective experiments: performing a lexical decision on individual items as in the study described in Chapter 6 does not require any linguistic processing beyond the single-word level; thus, once the lexical status of a stimulus has been determined, there is no need for further cognitive effort. This stands in contrast to the grammaticality judgment that participants were asked to perform in the experiment described in Section 7.4: here, the identification of a pseudo-word stimulus did not constitute the successful accomplishment of the task, but merely indicated that the subsequent syntactic analysis would be considerably more difficult.

8.4 The Brain Response to Local Grammatical Anomalies

Lexically opaque pseudo-words were used to create the sentence material for two further experiments that were conducted in order to investigate the interactions of local predictability, lexicality and syntactic processing (see Chapter 7). Utilizing an fMRI acquisition sequence that was particularly designed to allow for auditory stimulation in the absence of scanner noise (see Section 7.4.2), local morphosyntactic and phrase-structure violations in real word sentences were shown to elicit an increased hemodynamic response in the left ventral premotor cortex, a brain region that has been implicated in the detection of mismatches between serial predictions and actual sequences of events.

Crucially, activations for morphosyntactic and phrase structure violations were almost identical. While it is theoretically possible that this is due to a very close spatial proximity of functionally distinct brain systems subserving both aspects of linguistic processing, it is much more likely that the observed data pattern is due to a shared anomaly detection mechanism and not due to grammatical processing per se (note that as stated above, the ventral premotor cortex has previously been implicated in the detection of sequential prediction mismatches, but not in morphosyntactic processing). This account is further supported by studies on artificial grammar learning (Opitz and Friederici, 2004, 2007) which indicate that the vPMC may have a particular role in the establishment (and application) of transient rules dealing with local transition probabilities (possibly based on statistical learning procedures; cf. Schubotz, 2007; Schubotz and von Cramon, 2004).

While this result is surprising, it has an important implication: apparently, the locality of a grammatical anomaly critically determines the way in which it is processed. Thus, experiments comparing local and non-local violations need to account for both working memory confounds (cf. Fiebach et al., 2005) and sequential predictability if they are to yield meaningful results. In studies investigating morphosyntactic processing in sentence contexts that do not allow for the build-up of strong local expectations (see, for example, Raettig et al., 2009), the left posterior STG has been implicated; thus, this brain region may be involved in processes of "genuine" lexical-syntactic integration in the absence of sequential predictions. Similarly, activations in the left anterior STG have been observed in studies on phrase structure violations (see Friederici et al., 2003), generally co-occurring with a strong hemodynamic response in the vicinity of the vPMC or the adjacent deep frontal operculum. Therefore, it is conceivable that the anterior STG is involved in linguistically more specific cognitive operations (regarding the construction of local phrase structure or - possibly - other aspects of sentence structure, i.e. related to the presence of an additional adjunct PP; see Section 7.4.6) while the vPMC / frontal operculum has the aforementioned role in the detection of sequential prediction mismatches.

This account is completely compatible with the idea of a posterior-to-anterior "complexity gradient" regarding the cognitive processes that are subserved by inferior frontal lobe regions (Fiebach and Schubotz, 2006; Friederici, 2004, 2006; Friederici et al., 2006a; Koechlin and Jubault, 2006): while the most posterior areas of the IFL (i.e. the vPMC and the deep frontal operculum) deal with comparatively simple sequential events, anterior regions (i.e. BA 44 and BA 45) are involved in progressively more complex computations relying on the extraction of hierarchical structures. The functional differentiation described above is further supported by histological evidence (Amunts et al., 1999; Friederici, 2004, 2006): while vPMC has an agranular cell structure (and is thus phylogenetically older), BA 44 is dysgranular and BA 45 is granular (and is thus phylogenetically younger).

In contrast to the processing of real word sentences, the processing of pseudo-word sentences was associated with widespread increases in brain activity regardless of grammatical correctness, an effect that was attributed to a hemodynamic "saturation" effect (see Indefrey et al., 2001a, for a similar line of argument) caused by a preparatory supply of oxygenated blood to language-related processing regions that occurred when highly unusual stimuli (i.e. pseudo-word sentences) were encountered (also see Friederici et al., 2000). Note that it can still be assumed that grammatical anomalies in pseudo-word sentences are processed similarly to corresponding anomalies in real word sentences: the behavioral results indicate that participants were able to reliably identify syntactic violations even in the absence of lexical content; in addition, the ERP study (see Chapter 7) revealed that there is a significant electrophysiological brain response to such grammatical anomalies in pseudo-word sentences (although this effect was weaker than in the real word condition). However, it was not possible to register analogous results with fMRI because of the nature of the hemodynamic brain response to pseudo-word sentences as discussed above and in Section 7.4.6. Crucially, this is an important result in itself that has critical implications for the design of future imaging experiments utilizing pseudo-word sentences in violation paradigms (see Chapter 9).

An ERP experiment with the same sentence material revealed an early centro-parietal negativity followed by a late centro-parietal positivity in response to both morphosyntactic and phrase structure violations. This biphasic pattern was evident for both real word and pseudo-word sentences, but was significantly weaker for the latter. While the relatively late onset of the effect can partly be explained by the fact that the relevant morphosyntactic and word-category information was only available once the suffix was encountered, its distribution remains distinct from "classical" syntactic effects (i.e., the ELAN and LAN; see Friederici and Weissenborn, 2007). Thus, the negativity under discussion probably does not reflect grammatical processing per se, but the detection of the sequential prediction mismatch that was present in both real word and pseudo-word sentences and in both the morphosyntactic and the phrase-structure manipulation condition. As this mismatch detection was dependent on the identification of a morphophonological feature (i.e. the suffix of the critical word), the observed effect may be an instantiation of the phonological mismatch negativity (cf. Connolly and Phillips, 1994; Hasting and Kotz, 2008; Newman et al., 2003). The late positivity, on the other hand, has a latency and a topography linking it to the P600 component, indicating processes of repair. If the prediction mismatch detection mechanism that is indexed by the early negativity also serves as a heuristic for error detection as proposed in Section 7.4.6, it is plausible to assume that it can trigger more language-specific cognitive operations that are executed in order to reconcile the corresponding anomaly (and that are reflected in the late positivity).

The results from both the fMRI and the ERP studies presented in Chapter 7 are quite striking in that they suggest that the processing of local syntactic anomalies is based on the establishment of sequential morpho-phonological expectations when the circumstances are suitable (for compatible lines of argument, see Bahlmann et al., 2006; Dikker et al., 2009; Hasting and Kotz, 2008; Lau et al., 2006). Although the underlying predictions have to be based on grammatical knowledge, the expectancy-check mechanism itself seems to be instantiated by a rather simple "template matching" process (cf. Bornkessel and Schlesewsky, 2006; Fiebach and Schubotz, 2006; Friederici, 2006) that is tied to superficial stimulus properties (i.e. the presence or absence of a particular suffix; see Dikker et al., 2009). Crucially, non-generalizable templates (e.g. regarding local morphosyntactic relations) appear to be generated "ad hoc" if the stimulus material is regular enough (see Section 7.4.6).

While it is likely that the establishment of a simplified procedure for the detection of grammatical violations as described above is dependent on verbal input that is structurally invariable to a degree that is only encountered in laboratory settings, the results discussed here still add to a growing body of evidence suggesting that "forward models" (Schubotz, 2007) play a critical role during language comprehension. Consequently, the language processing system may be even more flexible than has been previously assumed, relying both on a "persistent" set of grammatical rules that are established during language acquisition and a highly variable set of "volatile", regularity-based "rules of thumb" that are utilized in order to predict and evaluate verbal input and that are generated spontaneously if and when the circumstances allow. This high degree of adaptability is also evident in studies on semantic and syntactic priming (Baumgärtner et al., 2002; Kutas and Federmeier, 2000; Lau et al., 2008; Pulvermüller and Shtyrov, 2003; Wright and Garrett, 1984) and is thus not restricted to the processing of grammatical anomalies.

Evidently, these results and the data discussed in previous chapters have a number of important implications for psycho- and neurolinguistic research to come. This will be reviewed in the final chapter of this dissertation.

Chapter 9

Future Directions

With regard to the use of pseudo-word sentences in imaging experiments, the experiment described in Section 7.4 has shown that the brain response to such stimuli is so strong (even in the absence of grammatical anomalies) that it is difficult to detect more subtle changes related to particular aspects of linguistic processing. As has already been suggested in Section 7.4.6, a potential solution for this problem may be the use of blocked rather than event-related designs since paradigms of the former type allow participants to get used to the "oddness" of the pseudo-word stimuli. Thus, it may be interesting to conduct a new fMRI experiment based on the setup described in Section 7.4, but presenting real word and pseudo-word sentences in separate blocks or sessions.

A different approach would be to familiarize participants more extensively with the individual pseudo-words used to build the sentences, possibly resulting in actual lexical entries (without semantic content) for the novel words (cf. Davis et al., 2008). In a similar vein, including the non-critical items in the familiarization procedure may further serve to reduce the non-specific, oddity-related brain response to pseudo-word sentences (note that in the experiments described in Chapter 7, only the critical verbs and nouns were learned on the day prior to testing; see Section 7.3).

In the experiment described in Section 7.4, phrase structure violations did not elicit an increase in brain activity in the anterior STG. Since this stands in contrast to the results reported in several previous studies (Brauer and Friederici, 2007; Friederici et al., 2003; Rueschemeyer et al., 2005), it would be interesting to determine the reasons for this discrepancy. As discussed in Section 7.4.6, it is conceivable that the anterior STG is particularly involved in the processing of adjunct XPs; further possibilities include a specific role in the computation of propositional content or pronominal reference. Teasing these possibilities apart would be a valuable contribution to our understanding of the functional role of this brain region. Experimental designs geared towards this end (especially the latter

two points) would not have to be violation-based, but could instead compare sentences of variable propositional complexity, containing either nominal or pronominal references.

Furthermore, the role of the ventral premotor cortex in language processing should be investigated in more detail. While it is apparent that the cognitive mechanisms involved in the detection of sequential prediction mismatches that are subserved by this brain region are not necessarily speech specific, it is still conceivable that particular subareas of the vPMC are implicated in linguistic operations (i.e. the retrieval, selection or application of phrase structure templates). In addition, it would be critical to address the relation between the ventral premotor cortex and the adjacent deep frontal operculum: as of yet, it is not clear if these two regions can be functionally separated (also see Grodzinsky and Friederici, 2006). One possibility would be that while the frontal operculum mainly deals with "persistent" sets of rules or templates, the ventral premotor cortex specializes in the generation of "volatile" ad hoc templates.

The DTI data presented in Chapter 5 point to the existence of two different temporo-frontal pathways, the "classical" system consisting of fibers from the arcuate and superior longitudinal fasciculus and an additional connection via the extreme capsule that has only recently been discussed in the scientific community (see Makris and Pandya, 2009). However, the relevance of both routes for language processing remains to be determined (cf. Friederici, 2009). In addition, both direct and indirect arcuate connections from the STG to the frontal lobe (Catani et al., 2005) as well as separate MTG and STG pathways (Glasser and Rilling, 2008) have been suggested - future studies utilizing advanced imaging techniques (like DSI) may be able to resolve the remaining issues regarding the correspondence of "virtual" fiber bundles as determined by tractographic techniques to actual white matter pathways.

The DTI data discussed here could be further refined by determining the functional connectivity of the cortical subregions that were determined anatomically - that is, it would be interesting to find out under which circumstances the "hard-wired" connections to different brain regions (as revealed by DTI fiber tracking) are actually utilized. Furthermore, it should be possible to design experiments that selectively activate the different STG and STS subregions that were identified by the parcellation procedure. While the experiment described in Chapter 7 was originally anticipated to result in a data pattern along these lines (with phrase structure and morphosyntactic processing selectively triggering a stronger hemodynamic response in anterior and posterior STG subareas, respectively), it turned out that the shared local predictability of the grammatical anomalies that were tested led to a very homogeneous brain reaction to both violation types (see Chapter 7 and Section 8.4).

Regarding this apparent use of a morpho-phonologically based prediction-mismatch check in order to detect ungrammatical sentences (see Sections 7.4.6 and 7.5.5), includ-

ing filler sentences with a more variable structure into the experimental material might force participants to rely on more language-specific mechanisms instead. A further option for the investigation of morphosyntactic and phrase structure processing without the prediction-mismatch detection confound would be the implementation of a paradigm that does not rely on grammatical anomalies. However, coming up with a suitable experimental procedure may prove to be tricky: syntactic priming would not be an optimal choice since it relies on the predictability of certain stimulus features. Similarly, complexity-based paradigms have to cope with confounds such as working memory load and processing difficulty. Sticking to the violation paradigm, an alternative possibility (in order to prevent the prediction-mismatch check from being applied) would be the inclusion of an intervening word (i.e. an adverb or adjective) between the items constituting the grammatical anomaly. This relatively simple approach could prove to be sufficient because the applicability of the sequential prediction mechanism seems to be highly dependent on the immediate adjacency of the critical words (cf. Ericsson et al., 2008).

In sum, the results that were discussed above pose a number of important questions for future research. While only constituting a small contribution in the grand scheme of things, the data that were gathered and discussed in this dissertation will hopefully be seen as a valuable extension of our current knowledge about the neural correlates of language processing.

Part IV

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Appendix A

List of Stimuli

Table A.1: Experiment 1 - Real Word Stimuli

Concrete, Animate	Concrete, Inanimate	Abstract	
Ameise	Annanas	Allegro	Kalauer
Apostel	Anorak	Allergie	Kollektiv
Adjutant	Atrappe	Anarchie	Konjunktiv
Advokat	Antenne	Apathie	Litanei
Bariton	Banane	Appetit	Maxime
Elefant	Baracke	Adjektiv	Metapher
Experte	Batterie	Akustik	Minimum
Forelle	Etikett	Alphabet	Monarchie
Genosse	Fregatte	Amnestie	Monopol
Geselle	Getreide	Antike	Nostalgie
Hebamme	Granate	Askese	Parabel
Kabeljau	Herberge	Attribut	Parodie
Kamerad	Hospital	Blamage	Parole
Kavalier	Kalender	Blasphemie	Privileg
Kardinal	Kassette	Botanik	Prozedur
Kollege	Kartoffel	Charisma	Prädikat
Komplize	Kommode	Debakel	Pseudonym
Kontrahent	Laterne	Dezibel	Quantität
Krokodil	Matratze	Didaktik	Resistenz
Magister	Melone	Diskrepanz	Sakrileg
Matrose	Orange	Domäne	Satire
Märtyrer	Palette	Elektrik	Schlamassel
Offizier	Paprika	Epilog	Semantik
Papagei	Patrone	Exotik	Stakkato
Pelikan	Perücke	Folklore	Symmetrie
Rabbiner	Plakette	Hierarchie	Synonym
Samurai	Posaune	Hyterie	Terminus
Sekretär	Rakete	Idiom	Trilogie
Veteran	Salami	Intellekt	Unikum
Walküre	Schatulle	Intrige	Zölibat

Table A.2: Experiment 1 - Pseudo-Word Stimuli

2nd-Syllable	3rd-Syllable	Opaque	Illegal
Fre'gutte	Fre'gattu	Free'wodda	P'tralle
Gra'neete	Gra'naatii	Gra'badde	T'pricke
'Paprakaa	'Paprikoo	E'tralle	Tpa'ter
Ge'traude	Ge'treidii	A'prikke	Bf'krelle
Ma'tretse	Ma'tratso	Ba'krelle	Bg'treime
Ma'truise	Ma'troosu	Ba'traime	Vs'trooge
Sekra'tär	Sekre'teu	We'trooge	'Gtrügei
'Heebomme	'Heebammo	'Gerügai	'Lpfijau
Offa'tsier	Offi'tseu	'Lafijau	'Sfreakaa
Batto'rii	Batta'roo	'Serekaa	Fb'dinne
Fo'ralle	Fo'rella	Opa'ter	Kbrii'tsier
Ge'sille	Ge'sello	Fo'dinne	Kpnaa're
Ka'sutte	Ka'setta	Karii'tsier	Mb'loote
Ko'looge	Ko'leegi	Kaanaa're	Mfkü'rii
Ko'mmiide	Ko'mmoodi	Ma'loote	Pg'saute
La'teune	La'terna	Maküü'rii	Pk'moone
Me'liine	Me'loona	Pe'leede	Pk'tertse
Pe'racke	Pe'rücko	Pa'moone	Pt'leede
Pappu'gai	Papa'gau	Pa'saute	'Hgnoket
Po'seine	Po'sauno	Po'terze	Gfta'rak
'Anirack	'Anorick	'Heenoket	Kpti'kaat
'Baruutoon	'Baritaan	Geta'rak	Ktse'raan
Ettu'kett	Eti'katt	Koti'kaat	Mfta'naal
Veti'raan	Veta'reen	Mata'naal	Kp'giste
'Kaaboljau	'Kabeljai'	Ka'giste	Kt'beltse
Ka'lunnda	Ka'lendu	Ko'beltse	Mp'lenta
Ma'gesta	Ma'giste	Me'lenta	Frt'wodda
Wal'keere	Wal'küüru	Kar'ganne	Grk'badde
Atwe'kaat	Atwo'keet	'Walzeton	Kfr'ganne
Kardu'naal	Kardi'nool	Aze'raan	'Wflsetoon

Primary stress is indicated by an apostrophe. Pseudo-word orthography is intended to reflect the actual pronunciation.

APPENDIX A. LIST OF STIMULI

Table A.3: Experiments 2a and 2b - Real Word Sentences

<p>Sie sieht, dass er segelt und alle Masten intakt sind. Sie sieht, dass er *segelst und alle Masten intakt sind. Sie sieht, dass ein Segel und alle Masten intakt sind. Sie sieht, dass ein *segelt und alle Masten intakt sind.</p>
<p>Sie sieht, dass du bügelst und alle Hemden weiß sind. Sie sieht, dass du *bügelt und alle Hemden weiß sind. Sie sieht, dass ein Bügel und alle Hemden weiß sind. Sie sieht, dass ein *bügelst und alle Hemden weiß sind.</p>
<p>Sie sieht, dass er bechert und alle Flaschen leer sind. Sie sieht, dass er *becherst und alle Flaschen leer sind. Sie sieht, dass ein Becher und alle Flaschen leer sind. Sie sieht, dass ein *bechert und alle Flaschen leer sind.</p>
<p>Sie sieht, dass du hobelst und alle Bretter abgenutzt sind. Sie sieht, dass du *hobelt und alle Bretter abgenutzt sind. Sie sieht, dass ein Hobel und alle Bretter abgenutzt sind. Sie sieht, dass ein *hobelst und alle Bretter abgenutzt sind.</p>
<p>Sie sieht, dass er kellnert und alle Gäste unzufrieden sind. Sie sieht, dass er *kellnerst und alle Gäste unzufrieden sind. Sie sieht, dass ein Kellner und alle Gäste unzufrieden sind. Sie sieht, dass ein *kellnert und alle Gäste unzufrieden sind.</p>
<p>Sie sieht, dass du paddelst und alle Boote verschmutzt sind. Sie sieht, dass du *paddelt und alle Boote verschmutzt sind. Sie sieht, dass ein Paddel und alle Boote verschmutzt sind. Sie sieht, dass ein *paddelst und alle Boote verschmutzt sind.</p>
<p>Sie sieht, dass er rätselt und alle Hinweise verwirrend sind. Sie sieht, dass er *rätselst und alle Hinweise verwirrend sind. Sie sieht, dass ein Rätsel und alle Hinweise verwirrend sind. Sie sieht, dass ein *rätselt und alle Hinweise verwirrend sind.</p>
<p>Sie sieht, dass du ruderst und alle Schiffe hölzern sind. Sie sieht, dass du *rudert und alle Schiffe hölzern sind. Sie sieht, dass ein Ruder und alle Schiffe hölzern sind. Sie sieht, dass ein *ruderst und alle Schiffe hölzern sind.</p>

APPENDIX A. LIST OF STIMULI

Table A.3: Experiments 2a and 2b - Real Word Sentences

<p>Sie sieht, dass er stempelt und alle Aufdrucke verschmiert sind. Sie sieht, dass er *stempelst und alle Aufdrucke verschmiert sind. Sie sieht, dass ein Stempel und alle Aufdrucke verschmiert sind. Sie sieht, dass ein *stempelt und alle Aufdrucke verschmiert sind.</p>
<p>Sie sieht, dass du würfelst und alle Spielfiguren rot sind. Sie sieht, dass du *würfelt und alle Spielfiguren rot sind. Sie sieht, dass ein Würfel und alle Spielfiguren rot sind. Sie sieht, dass ein *würfelst und alle Spielfiguren rot sind.</p>
<p>Sie sieht, dass er hämmert und alle Nägel hochwertig sind. Sie sieht, dass er *hämmerst und alle Nägel hochwertig sind. Sie sieht, dass ein Hammer und alle Nägel hochwertig sind. Sie sieht, dass ein *hämmert und alle Nägel hochwertig sind.</p>
<p>Sie sieht, dass du bohrst und alle Dübel verbogen sind. Sie sieht, dass du *bohrt und alle Dübel verbogen sind. Sie sieht, dass ein Bohrer und alle Dübel verbogen sind. Sie sieht, dass ein *bohrt und alle Dübel verbogen sind.</p>
<p>Sie sieht, dass er bastelt und alle Tüftler neugierig sind. Sie sieht, dass er *bastelst und alle Tüftler neugierig sind. Sie sieht, dass ein Bastler und alle Tüftler neugierig sind. Sie sieht, dass ein *bastelt und alle Tüftler neugierig sind.</p>
<p>Sie sieht, dass du fährst und alle Passagiere müde sind. Sie sieht, dass du *fährt und alle Passagiere müde sind. Sie sieht, dass ein Fahrer und alle Passagiere müde sind. Sie sieht, dass ein *fährt und alle Passagiere müde sind.</p>
<p>Sie sieht, dass er raucht und alle Trinker kurzatmig sind. Sie sieht, dass er *rauchst und alle Trinker kurzatmig sind. Sie sieht, dass ein Raucher und alle Trinker kurzatmig sind. Sie sieht, dass ein *raucht und alle Trinker kurzatmig sind.</p>
<p>Sie sieht, dass du spendest und alle Sponsoren großzügig sind. Sie sieht, dass du *spendet und alle Sponsoren großzügig sind. Sie sieht, dass ein Spender und alle Sponsoren großzügig sind. Sie sieht, dass ein *spendest und alle Sponsoren großzügig sind.</p>

APPENDIX A. LIST OF STIMULI

Table A.3: Experiments 2a and 2b - Real Word Sentences

<p>Sie sieht, dass er bettelt und alle Passanten unfreundlich sind. Sie sieht, dass er *bettelst und alle Passanten unfreundlich sind. Sie sieht, dass ein Bettler und alle Passanten unfreundlich sind. Sie sieht, dass ein *bettelt und alle Passanten unfreundlich sind.</p>
<p>Sie sieht, dass du joggst und alle Wanderer langsam sind. Sie sieht, dass du *joggt und alle Wanderer langsam sind. Sie sieht, dass ein Jogger und alle Wanderer langsam sind. Sie sieht, dass ein *joggst und alle Wanderer langsam sind.</p>
<p>Sie sieht, dass er hilft und alle Sanitäter erschöpft sind. Sie sieht, dass er *hilfst und alle Sanitäter erschöpft sind. Sie sieht, dass ein Helfer und alle Sanitäter erschöpft sind. Sie sieht, dass ein *hilft und alle Sanitäter erschöpft sind.</p>
<p>Sie sieht, dass du forschst und alle Laboranten tüchtig sind. Sie sieht, dass du *forschst und alle Laboranten tüchtig sind. Sie sieht, dass ein Forscher und alle Laboranten tüchtig sind. Sie sieht, dass ein *forschst und alle Laboranten tüchtig sind.</p>
<p>Sie sieht, dass er malt und alle Lehrlinge gestresst sind. Sie sieht, dass er *malst und alle Lehrlinge gestresst sind. Sie sieht, dass ein Maler und alle Lehrlinge gestresst sind. Sie sieht, dass ein *malt und alle Lehrlinge gestresst sind.</p>
<p>Sie sieht, dass du redest und alle Journalisten hektisch sind. Sie sieht, dass du *redet und alle Journalisten hektisch sind. Sie sieht, dass ein Redner und alle Journalisten hektisch sind. Sie sieht, dass ein *redest und alle Journalisten hektisch sind.</p>
<p>Sie sieht, dass er reitet und alle Pferde aufgereggt sind. Sie sieht, dass er *reitest und alle Pferde aufgereggt sind. Sie sieht, dass ein Reiter und alle Pferde aufgereggt sind. Sie sieht, dass ein *reitet und alle Pferde aufgereggt sind.</p>
<p>Sie sieht, dass du schwimmst und alle Taucher leichtsinnig sind. Sie sieht, dass du *schwimmt und alle Taucher leichtsinnig sind. Sie sieht, dass ein Schwimmer und alle Taucher leichtsinnig sind. Sie sieht, dass ein *schwimmst und alle Taucher leichtsinnig sind.</p>

APPENDIX A. LIST OF STIMULI

Table A.3: Experiments 2a and 2b - Real Word Sentences

<p>Sie sieht, dass er dichtet und alle Kritiker erfreut sind. Sie sieht, dass er *dichtest und alle Kritiker erfreut sind. Sie sieht, dass ein Dichter und alle Kritiker erfreut sind. Sie sieht, dass ein *dichtet und alle Kritiker erfreut sind.</p>
<p>Sie sieht, dass du spielst und alle Schiedsrichter unfähig sind. Sie sieht, dass du *spielt und alle Schiedsrichter unfähig sind. Sie sieht, dass ein Spieler und alle Schiedsrichter unfähig sind. Sie sieht, dass ein *spielst und alle Schiedsrichter unfähig sind.</p>
<p>Sie sieht, dass er handelt und alle Geschäfte profitabel sind. Sie sieht, dass er *handelst und alle Geschäfte profitabel sind. Sie sieht, dass ein Handel und alle Geschäfte profitabel sind. Sie sieht, dass ein *handelt und alle Geschäfte profitabel sind.</p>
<p>Sie sieht, dass du pinselst und alle Farben teuer sind. Sie sieht, dass du *pinselt und alle Farben teuer sind. Sie sieht, dass ein Pinsel und alle Farben teuer sind. Sie sieht, dass ein *pinselst und alle Farben teuer sind.</p>
<p>Sie sieht, dass er schwindelt und alle Täuschungen verwerflich sind. Sie sieht, dass er *schwindelst und alle Täuschungen verwerflich sind. Sie sieht, dass ein Schwindel und alle Täuschungen verwerflich sind. Sie sieht, dass ein *schwindelt und alle Täuschungen verwerflich sind.</p>
<p>Sie sieht, dass du singst und alle Chorknaben leise sind. Sie sieht, dass du *singt und alle Chorknaben leise sind. Sie sieht, dass ein Sänger und alle Chorknaben leise sind. Sie sieht, dass ein *singst und alle Chorknaben leise sind.</p>

APPENDIX A. LIST OF STIMULI

Table A.4: Experiments 2a and 2b - Pseudo-Word Sentences

<p>Sie 'reemt, dass er 'määschelt und alle 'tsümrel os'teft sind. Sie 'reemt, dass er *'määschelst und alle 'tsümrel os'teft sind. Sie 'reemt, dass ein 'määschel und alle 'tsümrel os'teft sind. Sie 'reemt, dass ein *'määschelt und alle 'tsümrel os'teft sind.</p>
<p>Sie 'reemt, dass du 'koonelst und alle 'momfel 'düp sind. Sie 'reemt, dass du *'koonelt und alle 'momfel 'düp sind. Sie 'reemt, dass ein 'koonel und alle 'momfel 'düp sind. Sie 'reemt, dass ein *'koonelst und alle 'momfel 'düp sind.</p>
<p>Sie 'reemt, dass er 'beepat und alle 'schroomel 'kui sind. Sie 'reemt, dass er *'beepast und alle 'schroomel 'kui sind. Sie 'reemt, dass ein 'beepa und alle 'schroomel 'kui sind. Sie 'reemt, dass ein *'beepat und alle 'schroomel 'kui sind.</p>
<p>Sie 'reemt, dass du 'deefelst und alle 'tschooper 'äälmadink sind. Sie 'reemt, dass du *'deefelt und alle 'tschooper 'äälmadink sind. Sie 'reemt, dass ein 'deefel und alle 'tschooper 'äälmadink sind. Sie 'reemt, dass ein *'deefelst und alle 'tschooper 'äälmadink sind.</p>
<p>Sie 'reemt, dass er 'dääsgat und alle 'rööbtser 'ilnofroonich sind. Sie 'reemt, dass er *'dääsgast und alle 'rööbtser 'ilnofroonich sind. Sie 'reemt, dass ein 'dääsga und alle 'rööbtser 'ilnofroonich sind. Sie 'reemt, dass ein *'dääsgat und alle 'rööbtser 'ilnofroonich sind.</p>
<p>Sie 'reemt, dass du 'giinelst und alle 'päämer tso'snirl sind. Sie 'reemt, dass du *'giinelt und alle 'päämer tso'snirl sind. Sie 'reemt, dass ein 'giinel und alle 'päämer tso'snirl sind. Sie 'reemt, dass ein *'giinelst und alle 'päämer tso'snirl sind.</p>
<p>Sie 'reemt, dass er 'doischelt und alle 'fesjuuwe mi'faakebt sind. Sie 'reemt, dass er *'doischelst und alle 'fesjuuwe mi'faakebt sind. Sie 'reemt, dass ein 'doischel und alle 'fesjuuwe mi'faakebt sind. Sie 'reemt, dass ein *'doischelt und alle 'fesjuuwe mi'faakebt sind.</p>
<p>Sie 'reemt, dass du 'düümast und alle 'güüper 'posgich sind. Sie 'reemt, dass du *'düümat und alle 'güüper 'posgich sind. Sie 'reemt, dass ein 'düüma und alle 'güüper 'posgich sind. Sie 'reemt, dass ein *'düümast und alle 'güüper 'posgich sind.</p>

Primary stress is indicated by an apostrophe. Pseudo-word orthography is intended to reflect the actual pronunciation.

APPENDIX A. LIST OF STIMULI

Table A.4: Experiments 2a and 2b - Pseudo-Word Sentences

<p>Sie 'reemt, dass er 'grööbschelt und alle 'otschvaawer tsa'smoik sind. Sie 'reemt, dass er *'grööbschelst und alle 'otschvaawer tsa'smoik sind. Sie 'reemt, dass ein 'grööbschel und alle 'otschvaawer tsa'smoik sind. Sie 'reemt, dass ein *'grööbschelt und alle 'otschvaawer tsa'smoik sind.</p>
<p>Sie 'reemt, dass du 'jäänelst und alle 'schmiilforaadel 'nüp sind. Sie 'reemt, dass du *'jäänelt und alle 'schmiilforaadel 'nüp sind. Sie 'reemt, dass ein 'jäänel und alle 'schmiilforaadel 'nüp sind. Sie 'reemt, dass ein *'jäänelst und alle 'schmiilforaadel 'nüp sind.</p>
<p>Sie 'reemt, dass er 'dööschat und alle 'schüüjel 'laisfapem sind. Sie 'reemt, dass er *'dööschast und alle 'schüüjel 'laisfapem sind. Sie 'reemt, dass ein 'dööscha und alle 'schüüjel 'laisfapem sind. Sie 'reemt, dass ein *'dööschat und alle 'schüüjel 'laisfapem sind.</p>
<p>Sie 'reemt, dass du 'foomast und alle 'kiinel bi'toopüts sind. Sie 'reemt, dass du *'foomat und alle 'kiinel bi'toopüts sind. Sie 'reemt, dass ein 'fooma und alle 'kiinel bi'toopüts sind. Sie 'reemt, dass ein *'foomast und alle 'kiinel bi'toopüts sind.</p>
<p>Sie 'reemt, dass er 'ronskat und alle 'scheftmer 'baagewich sind. Sie 'reemt, dass er *'ronskast und alle 'scheftmer 'baagewich sind. Sie 'reemt, dass ein 'ronska und alle 'scheftmer 'baagewich sind. Sie 'reemt, dass ein *'ronskat und alle 'scheftmer 'baagewich sind.</p>
<p>Sie 'reemt, dass du 'rööpast und alle dubu'looker 'gaini sind. Sie 'reemt, dass du *'rööpat und alle dubu'looker 'gaini sind. Sie 'reemt, dass ein 'rööpa und alle dubu'looker 'gaini sind. Sie 'reemt, dass ein *'rööpast und alle dubu'looker 'gaini sind.</p>
<p>Sie 'reemt, dass er 'keepat und alle 'kribfer 'ruuboobnich sind. Sie 'reemt, dass er *'keepast und alle 'kribfer 'ruuboobnich sind. Sie 'reemt, dass ein 'keepa und alle 'kribfer 'ruuboobnich sind. Sie 'reemt, dass ein *'keepat und alle 'kribfer 'ruuboobnich sind.</p>
<p>Sie 'reemt, dass du 'tschölpast und alle schron'tsaafen 'schloonbüütich sind. Sie 'reemt, dass du *'tschölpat und alle schron'tsaafen 'schloonbüütich sind. Sie 'reemt, dass ein 'tschölpa und alle schron'tsaafen 'schloonbüütich sind. Sie 'reemt, dass ein *'tschölpast und alle schron'tsaafen 'schloonbüütich sind.</p>

Primary stress is indicated by an apostrophe. Pseudo-word orthography is intended to reflect the actual pronunciation.

APPENDIX A. LIST OF STIMULI

Table A.4: Experiments 2a and 2b - Pseudo-Word Sentences

<p>Sie 'reemt, dass er 'rälfat und alle ta'pärkel 'ilfromplich sind. Sie 'reemt, dass er *'rälfast und alle ta'pärkel 'ilfromplich sind. Sie 'reemt, dass ein 'rälfa und alle ta'pärkel 'ilfromplich sind. Sie 'reemt, dass ein *'rälfat und alle ta'pärkel 'ilfromplich sind.</p>
<p>Sie 'reemt, dass du 'gnaapast und alle 'dagzaake 'wülsat sind. Sie 'reemt, dass du *'gnaapat und alle 'dagzaake 'wülsat sind. Sie 'reemt, dass ein 'gnaapa und alle 'dagzaake 'wülsat sind. Sie 'reemt, dass ein *'gnaapast und alle 'dagzaake 'wülsat sind.</p>
<p>Sie 'reemt, dass er 'jölmat und alle näre'meeger o'nirft sind. Sie 'reemt, dass er *'jölmat und alle näre'meeger o'nirft sind. Sie 'reemt, dass ein 'jölma und alle näre'meeger o'nirft sind. Sie 'reemt, dass ein *'jölmat und alle näre'meeger o'nirft sind.</p>
<p>Sie 'reemt, dass du 'kuugast und alle 'rööfer 'aaplepenk sind. Sie 'reemt, dass du *'kuugat und alle 'rööfer 'aaplepenk sind. Sie 'reemt, dass ein 'kuuga und alle 'rööfer 'aaplepenk sind. Sie 'reemt, dass ein *'kuugast und alle 'rööfer 'aaplepenk sind.</p>
<p>Sie 'reemt, dass er 'düpfat und alle 'vaiminge go'schtrek sind. Sie 'reemt, dass er *'düpfat und alle 'vaiminge go'schtrek sind. Sie 'reemt, dass ein 'düpfa und alle 'vaiminge go'schtrek sind. Sie 'reemt, dass ein *'düpfat und alle 'vaiminge go'schtrek sind.</p>
<p>Sie 'reemt, dass du 'miftast und alle schnilgo'schusgen 'gaschtapf sind. Sie 'reemt, dass du *'miftat und alle schnilgo'schusgen 'gaschtapf sind. Sie 'reemt, dass ein 'mifta und alle schnilgo'schusgen 'gaschtapf sind. Sie 'reemt, dass ein *'miftast und alle schnilgo'schusgen 'gaschtapf sind.</p>
<p>Sie 'reemt, dass er 'jüüpat und alle telu'talchel 'gookpasch sind. Sie 'reemt, dass er *'jüüpast und alle telu'talchel 'gookpasch sind. Sie 'reemt, dass ein 'jüüpa und alle telu'talchel 'gookpasch sind. Sie 'reemt, dass ein *'jüüpat und alle telu'talchel 'gookpasch sind.</p>
<p>Sie 'reemt, dass du 'plemast und alle 'büümer 'memslinich sind. Sie 'reemt, dass du *'plemat und alle 'büümer 'memslinich sind. Sie 'reemt, dass ein 'plema und alle 'büümer 'memslinich sind. Sie 'reemt, dass ein *'plemast und alle 'büümer 'memslinich sind.</p>

Primary stress is indicated by an apostrophe. Pseudo-word orthography is intended to reflect the actual pronunciation.

APPENDIX A. LIST OF STIMULI

Table A.4: Experiments 2a and 2b - Pseudo-Word Sentences

<p>Sie 'reemt, dass er 'pelfat und alle 'schpooniker a'brom sind. Sie 'reemt, dass er *'pelfast und alle 'schpooniker a'brom sind. Sie 'reemt, dass ein 'pelfa und alle 'schpooniker a'brom sind. Sie 'reemt, dass ein *'pelfat und alle 'schpooniker a'brom sind.</p>
<p>Sie 'reemt, dass du 'schtäätsast und alle 'käältspichter 'iisdoias sind. Sie 'reemt, dass du *'schtäätsat und alle 'käältspichter 'iisdoias sind. Sie 'reemt, dass ein 'schtäätsa und alle 'käältspichter 'iisdoias sind. Sie 'reemt, dass ein *'schtäätsast und alle 'käältspichter 'iisdoias sind.</p>
<p>Sie 'reemt, dass er 'schoofrelt und alle ti'kismer schlööfe'däätosch sind. Sie 'reemt, dass er *'schoofrelst und alle ti'kismer schlööfe'däätosch sind. Sie 'reemt, dass ein 'schoofrel und alle ti'kismer schlööfe'däätosch sind. Sie 'reemt, dass ein *'schoofrelt und alle ti'kismer schlööfe'däätosch sind.</p>
<p>Sie 'reemt, dass du 'järgelst und alle 'fääschel 'kiiu sind. Sie 'reemt, dass du *'järgelt und alle 'fääschel 'kiiu sind. Sie 'reemt, dass ein 'järgel und alle 'fääschel 'kiiu sind. Sie 'reemt, dass ein *'järgelst und alle 'fääschel 'kiiu sind.</p>
<p>Sie 'reemt, dass er 'trosmelt und alle 'paischingen toi'rönkuf sind. Sie 'reemt, dass er *'trosmelst und alle 'paischingen toi'rönkuf sind. Sie 'reemt, dass ein 'trosmel und alle 'paischingen toi'rönkuf sind. Sie 'reemt, dass ein *'trosmelt und alle 'paischingen toi'rönkuf sind.</p>
<p>Sie 'reemt, dass du 'lomast und alle 'waiknoofen 'juuschu sind. Sie 'reemt, dass du *'lomat und alle 'waiknoofen 'juuschu sind. Sie 'reemt, dass ein 'loma und alle 'waiknoofen 'juuschu sind. Sie 'reemt, dass ein *'lomast und alle 'waiknoofen 'juuschu sind.</p>

Primary stress is indicated by an apostrophe. Pseudo-word orthography is intended to reflect the actual pronunciation.

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List of Abbreviations

aCC	Anterior Cingulate Cortex
AfH	Horizontal Segment of the Arcuate Fasciculus
AfV	Vertical Segment of the Arcuate Fasciculus
AG	Angular Gyrus
ANOVA	Analysis of Variance
aSTG	Anterior Superior Temporal Gyrus
aSTS	Anterior Superior Temporal Sulcus
BA	Brodman Area
BOLD (response)	Blood Oxygen Level Dependent (response)
DP	Determiner Phrase
DSI	Diffusion Spectrum Imaging
DTI	Diffusion Tensor Imaging
EEG	Electroencephalogram
ELAN	Early Left Anterior Negativity
EmC	Extreme Capsule
EOG	Electrooculogram
EPI	Echo-planar Imaging
ERP	Event-related Potential
FIR	Finite Impulse Response

LIST OF ABBREVIATIONS

fMRI	Functional Magnetic Resonance Imaging
fOp	Frontral Operculum
FOV	Field of View
FWHM	Full-width at Half-maximum
HG	Heschl's Gyrus
IFO	Inferior Fronto-Occipital Fasciculus
ILF	Inferior Longitudinal Fasciculus
IPL	Inferior Parietal Lobule
ISI	Inter-stimulus Interval
ISSS	Interleaved Silent Steady State
ITG	Inferior Temporal Gyrus
LAN	Left Anterior Negativity
MdLF	Middle Longitudinal Fasciculus
MEG	Magnetoencephalography
MFG	Medial Frontal Gyrus
MHz	Megahertz
MRI	Magnetic Resonance Imaging
MTG	Middle Temporal Gyrus
NMR	Nuclear Magnetic Resonance
NP	Noun Phrase
PAC	Primary Auditory Cortex
PET	Positron Emission Tomography
PhG	Parahippocampal Gyrus
PMN	Phonological Mismatch Negativity
PP	Prepositional Phrase

LIST OF ABBREVIATIONS

PSC	Percent Signal Change
PT	Planum Temporale
rCBF	Regional Cerebral Blood Flow
rCBV	Regional Cerebral Blood Volume
rCMO ₂	Regional Cerebral Metabolic Rate of Oxygen
ROI	Region of Interest
SLF	Superior Longitudinal Fasciculus
SNR	Signal-to-Noise Ratio
SPS	Syntactic Positive Shift
SPT	Serial Prediction Task
STG	Superior Temporal Gyrus
STS	Superior Temporal Sulcus
TE	Time-to-echo
TMS	Transcranial Magnetic Stimulation
TR	Time-to-repetition
TTG	Transverse Temporal Gyrus
UF	Uncinate Fasciculus
vPMC	Ventral Premotor Cortex

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