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When the hedgehog kisses the frog

A functional and structural investigation of syntactic processing in the developing brain

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WHEN THE HEDGEHOG KISSES THE FROG

A FUNCTIONAL AND STRUCTURAL INVESTIGATION OF SYNTACTIC PROCESSING IN THE DEVELOPING BRAIN

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Prof. Dr. Angela D. Friederici
Prof. Dr. Sonja A. Kotz

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PREFACE

It is an astonishing process children undergo when learning their first language. Within a short time, children successfully acquire distinctive characteristics of their native tongue in order to unveil the meaning of a word in the context of other words. Children are challenged to detect reliable linguistic regularities (Bates et al., 1988; Jackendoff, 2002), so-called language cues, which help to identify in a sentence "who is involved in an activity with whom". Previous studies have focused on the chronological acquisition of these distinct cues (e.g. word order, animacy, case-marking, noun-verb agreement markers, stress pattern) and tested children of various native languages to find the crucial factor why a distinct cue is acquired before another one (Slobin & Bever, 1982; Schaner-Wolles, 1989; Primus & Lindner, 1994; Lindner, 2003; Chan et al., 2009; Dittmar et al., 2008). The results indicate that important for cue detection and acquisition is the strength of this cue in the target language. The higher the frequency and the consistency of a cue, the faster a child acquires this specific cue. A strong cue to determine thematic relationships in sentences is word order. However, in contrast to languages such as English, German allows a relatively flexible word order and therefore, additional information is often needed to unambiguously identify the relation between sentential arguments. Thus, German children have to realize that, besides word order, other cues such as semantic features (e.g. animacy) and morphological markers (e.g. case-marking) convey crucial information.

The experiments presented in the current dissertation are based on the assumption that children at the age of five to six are sensitive to case-marking information (Schipke et al., 2012), but are not experienced enough to reliable use this information for sentence interpretation (Lindner, 2003; Dittmar et al., 2008). In German children the acquisition of the word order cue precedes the acquisition of the case-marking cue due to higher availability of the former one. This assumption is based on previous behavioural comprehension studies in German children that reported a relatively late acquisition of case-marking as a cue to identify thematic relationships in a sentence (Schaner-Wolles, 1989; Primus & Lindner, 1994; Lindner, 2003; Dittmar et al., 2008; Chan et al., 2009). According to these studies, children's awareness of which of the language cues will facilitate sentences comprehension develops with increasing age, and German children do not detect the strength of case-marking information, as a language cue, before the age of five to seven.

The present dissertation takes a closer look at which brain areas subserve acquisition of case-marking cues for role assignment in unambiguously case-marked object-initial sentences. It is currently unknown what underlying neural basis supports these processes in five to six-year-old children. The specific goal of the study was to examine the role of case-marking information when assigning thematic roles to the arguments in the sentence. So far, very few functional magnetic resonance imaging (fMRI) studies in children focus on the processing of specific language cues per se, and little is known about the neural networks that are involved in the processing of syntactically more complex sentences in children. However, studies focusing on sentence processing in children between the ages of 7 and 16 reported brain areas that were also found in fMRI studies investigating syntactic processing in adults. Interestingly, several studies found that activation in the left inferior frontal cortex correlated with individual language skills (Yeatman et al., 2010; Nuñez et al., 2011).

Based on prior findings from behavioural and functional imaging studies in children and adults, it was hypothesised that children at the age of five to six years old show a significant poorer behavioural performance in non canonical object-initial sentences compared to adults. Children at this age are expected to be already sensitive to case-marking information, but do not reliable use this information for sentence comprehension. This led us to the following central research questions:

- What are the neural underpinnings of processing syntactically more complex sentences in children at the age of five to six-years? Are similar brain areas involved as found in adults?
- How does the language proficiency influence the strategies used for thematic role assignment in object-initial sentences?
- Can individual differences in the functional data be explained by individual language proficiency?
- At this age, white matter structures in the developing brain are not completely myelinated. Do differences in fractional anisotrophy within language related brain areas correlate with language proficiency?

I addressed these questions in a series of experiments, utilizing behavioural, functional imaging (fMRI), and structural imaging (DWI/DTI) methods. The first part of this dissertation comprises theoretical, empirical and methodological background information. **Chapter 1** summarizes linguistic aspects important for the exposed studies. The chapter presents an overview of the functional neuroanatomy of language. It outlines two neurocognitive models of language comprehension and introduces syntactic processing in adults. Furthermore, the chapter gives an overview of the processes involved in language comprehension in children, and describes structural changes involved in the maturation of the developing brain. **Chapter 2** gives an overview of the techniques used for the investigations, such as fMRI, diffusion-weighted imaging (DWI) and diffusion tensor imaging (DTI). The subsequent experimental chapters[1] start with an outline of the research questions (**Chapter 3**) and

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[1] Results of experiments of chapter 4, 5, 6 and 7 have been partly published in (Knoll et al., 2012).

present the experiments aimed to answer them. In a behavioural session (**Chapter 4**), children were tested in order to assess the receptive grammatical development and to obtain behavioural correlates for the subsequent functional data analysis. **Chapter 5** describes a functional MRI experiment investigating the processing of case-marking information in syntactically complex sentences in adults. It also served as a control for the children study. The study in **Chapter 6** investigates the role of the IFG and other areas involved in the processing of case-marking information in children using fMRI. A follow-up investigation (**Chapter 7**) takes a closer look at the single subject-data and asks about individual differences in the group of previous tested children in order to provide additional information concerning the individual language development. The last study (**Chapter 8**) examines the structural precondition in the left IFG in order to explain children's language performance. Finally, **Chapter 9** presents a conclusion after reviewing the different experimental results and proposes a number of related research opportunities.

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Part I

THEORETICAL AND EMPIRICAL BACKGROUND

1

INTRODUCTION

The acquisition of language is one of the most impressive skills children have to accomplish in their very first years of life. But which steps do children have to complete before finally mapping a meaning to people's utterances? Before mastering sentence processing per se, one of the first major challenges for normal healthy infants in auditory language comprehension is the identification of phonemes. Starting from these smallest segmental units of sound, a gradual process starts that finally results in the comprehension of complex sentences based on meaning retrieval of each single word in that particular context.

In the very beginning of language acquisition, strategies have to be acquired to segment the speech stream and to associate a group of phonemes with a word form and a word meaning. Already right from birth, infants are sensitive to certain aspects of sound patterns (such as prosody) and show preference to listen to their native language over other languages (Dehaene-Lambertz & Houston, 1998; Mehler et al., 1988). Prosodic cues such as the alternation of strong and weak syllables have been shown to play a crucial role in very young infants' language learning (Jusczyk et al., 1999; Tincoff et al., 2005). Around the age of four to five months, they show the ability to distinguish their native language from a rhythmically similar language, and even between dialects of their native language (Bosch & Sebastian-Galles, 1997; Nazzi et al., 2000; Friederici et al., 2007).

Shortly after infants achieve proficiency at segmenting the phonemes of their native language, they are challenged by the next big step. They have to assign a meaning to the sound input. Infants are incredibly effective in accomplishing this goal. In general, they start to produce their first single word around the age of 12 months, produce the first multi word utterances around 18 months, and until school age they have a vocabulary of 8000 to 14000 words (Carey, 1978). However, the main underlying mechanisms that facilitate this learning process are still unclear and highly debated in the literature (e.g. Hollich et al., 2000; L. B. Smith, 2000; Tomasello, 2003). The association of a meaning to a specific phonological string that represents a lexical item, is not just a question of naming objects, such as "ball", or "apple"; the infant has to learn and remember the words from hearing other people using them in daily life situations, even in absence of the respective object. Besides, not only concrete words have to be learned, but also whole concepts have to be acquired. It is beyond question that this process is guided by innate (nature) and environmental (nurture) prerequisites (for reviews see Hauser & Bever, 2008; Sciullo et al., 2010; Gervain & Mehler, 2010). Children acquire their language too fast to be not provided by some innate mechanisms that guide them through the complex process of extracting all relevant information from another person's utterance. But they also need a stimulating social environment that initiates and supports this development. Children accomplish this form-to-meaning-mapping challenge in a very short period of time, and it is suggested that infants start learning their first words around six to eight months (for reviews see Swingley, 2009; Gervain & Mehler, 2010). Nevertheless it is an ongoing process that extends throughout childhood and adolescence, and even adults encounter situations in which they have to develop the meaning of an unfamiliar word. Nevertheless it is not enough to know the meaning of each single lexical item, comprehending a sentence requires more, bundles of words have to be interpreted in relation to each other.

Therefore, infants need to acquire the distinctive characteristics of their native language. They have to learn the way their native language is organized in terms of language domains, such as syntax (the structure of language), semantics (the meaning of language morphemes), phonology (the sound of language), and pragmatics (the mechanisms of language use and speech acts) in order to develop a strategy to unveil the meaning of a word in the context of other words. Thereby, another challenge in language acquisition is the detection of reliable linguistic regularities and cues (Bates et al., 1988; Jackendoff, 2002) in order to identify "who is doing what to whom" in a sentence. But which features are initially used as a cue (e.g. word order, animacy, noun-verb agreement markers, gender agreement, clitic pronouns, stress patterns) to determine this so-called thematic relationship in a sentence? A study by Slobin and Bever (1982) tested native-speaking English, Italian, Serbo-Croatian, and Turkish children, and concluded that the first cue used by children is their language's most valid one. These results are in line with the Competition Model postulated by Bates and MacWhinney (1987, 1989; Bates et al., 1984), which states that how fast a child acquires a specific cue for their target language depends on the strength of the given cue. This, in turn, depends on the consistency and frequency of this information, which is described in more detail in the following sections.

1.1 Linguistic framework

The main focus of this thesis is the acquisition and processing of specific language cues in German speaking children. The stimuli used in the experiments consisted of simple German transitive sentences. However, the following section illustrates distinctive linguistic features of the German language that are important for the experiments and their subsequent discussion.

1.1.1 Semantic, syntactic and morphological aspects of transitive German sentences

In the following, a brief overview of some important aspects of German verbs is provided. Traditionally German verbs can be categorized into three different groups (Handlungs-, Vorgangs- and Zustandsverben): verbs that designate an action, a process or a condition (Helbig & Buscha, 1993; Hentschel & Weydt, 1999). Action verbs such as “arbeiten” (work), “töten” (kill), and “essen” (eat) describe intentional and active actions of a subject and therefore an *agent* is always implicated. The second group of German verbs such as “frieren” (freeze), “ermüden” (fatigue), and “erwachen” (awake) describes a process the subject is exposed to. The third group of verbs describes a constant situation or circumstances, for instance such as “leben” (live), “liegen” (lie), and “umgeben” (surround). Additionally, a more specific categorisation going beyond the mentioned categories is controversial (see for instance Vendler, 1967). A detailed description will not be provided at this point, because all verbs used in the current study can be assigned to the first group: action verbs. A further and more elaborated discussion of this topic can be found in C. S. Smith (1997), Helbig and Buscha (1993), and Hentschel and Weydt (1999).

Another important aspect of verbs is the syntactic valency. More specifically, verbs can be classified according to their capability to bind nominal phrases and the particular morphological form they impose to these phrases. The valency of the verb determines how many of the nominal phrases can syntagmatically bind to the verb. Every verb offers a number of free positions for phrases; these can be mandatory or optional complements.

The studies described in the following chapters used a stimulus set with sentences exclusively containing transitive verbs. Transitive verbs offer only one complement position in the form of an accusative object. However, a classification as a transitive verb cannot be made in a single, concrete sentence, but on the basis of the verb’s actual binding. Hence, the verb “read” is transitive even if in the concrete sentence (1) no accusative object is necessary:

(1) Der Junge liest bis zum Morgengrauen.

[the boy]$_{nominative(NOM)}$ reads [_]$_{accusative(ACC)}$ until dawn

“The boy reads until dawn.”

Traditional grammar considers a transitive verb as transitive, if it takes an accusative direct object. However the Government and Binding Theory (Chomsky, 1982, 1988) for instance suggests another view: all verbs that govern a complement regardless of the case are considered transitive verbs. In the current study only transitive verbs that govern an accusative object were chosen for the experimental stimuli. Another criterion to classify transitive verbs concerns the transformation of an active voice into a passive voice construction. In transitive sentences the accusative object of the active voice sentence becomes the subject of the passive voice sentence.

One aspect that should also be briefly addressed is that verbs assign thematic roles to the arguments in a sentence (“Who is doing what to whom?”). Thematic roles, also known as semantic roles, can be distinguished by semantic aspects. For instance the thematic role *agent* (typically the animated actor of an ongoing action) carries a distinct number of characteristics (so-called agentivity properties) that are based on the type of verb. Here is an example:

(2a) Der Junge kauft das Buch.

[the boy]$_{NOM}$ buys [the book]$_{ACC}$

“The boy buys the book.”

(2b) Der Junge liebt das Buch.

[the boy]$_{NOM}$ loves [the book]$_{ACC}$

“The boy loves the book.”

In this case, the sentences (2a) and (2b) contain the same arguments: a nominative noun phrase referring to the subject (the boy) and an accusative noun phrase referring to the object of the sentence (the book). The verb (to buy and to love) in each sentence is different, and therefore specifies a different thematic role to the subject in the sentence. In the first example (2a) the subject is a person who performs an action and therefore conveys the role of an *agent*. In the second example (2b) the subject is realized as an *experiencer*, a role that is not actively doing anything, but undergoes a sensory, cognitive, or emotional experience (Agel et al., 2006: 464).

Most approaches that describe the properties of the thematic roles are based on Dowty 1991, who characterises two proto-roles: proto-*agent* and proto-*patient*. Based on the degree of agentivity it is possible to differentiate between the different thematic roles. A *patient* (animate or inanimate undergoer or affected object of an ongoing action) carries less agentivity properties than a *recipient* (generally animate, “endpoint” of an ongoing action), and a *recipient* accordingly less agentivity properties than an *agent*.

In the following study only transitive action verbs were used that - accordingly to their characteristics - open one syntactic position for an object in the sentence. All verbs demand an *agent* and a *patient*, and both thematic roles were unambiguously case-marked for nominative (agentive subject) and for accusative (patient object). However, it is important to point out that it would be misleading to draw conclusions about a clear-cut relationship between the thematic roles and the syntactic relations of arguments in a sentence. This so-called “linking” describes the question whether the same thematic role is realised in a specific syntactic position of the sentence (Fillmore, 1968; Jackendoff, 1983; Wunderlich, 1985). Even if there is not a distinct one-to-one mapping, relationships can be explained by hierarchies. An *agent* is the highest in the ranking of the thematic roles and correlates very often with the highest syntactic position, the subject of the sentence (*agent* = subject, *patient* = direct object, *recipient* = indirect object). Besides syntactic indicators also morpho-syntactic markers can be used to determine a thematic role. Also in this case, a hierarchical correlation has been described. Primus (1999) introduces this hierarchy and therefore the mapping of thematic roles onto cases in German as follows:

(3a) nominative $>$ accusative $>$ dative $>$ other oblique cases

(3b) *agent* $>$ *patient* $>$ *recipient* $>$ other roles

Once again, the case that is highest in the hierarchy correlates often with the highest thematic role. In turn, semantic information can be taken into account if the morpho-syntactic markers are ambiguous.

(4a) Den Käfer frisst die Katze.

[the bug]$_{ACC}$ eats [the cat]$_{NOM/ACC}$

"The cat eats the bug."

(4b) Die Fliege frisst die Katze.

[the fly]$_{NOM/ACC}$ eats [the cat]$_{NOM/ACC}$

"The cat eats the fly."

In the first sentence (4a) the definite article "den" indicates accusative and therefore the second article "die" clearly designates nominative, and consequently the subject (*agent*) of the sentence. This sentence is a prototypical example that the highest syntactic position marked with nominative correlates with the *agent* role. In the second sentence (4b), both definite articles "die" are ambiguously case-marked and only semantic or world knowledge information can be used to disentangle the correct meaning of the sentence. Finally it must be stated, that even if there is a relationship between thematic roles, syntactic function and morpho-syntactic information in German, these correlations are not always unambiguous and reliable. Hence, in German this information cannot be used for a one-to-one mapping, which brings us to the next key point that will be discussed in the following section. What information in a sentence can be used for its interpretation? Which cues do children need to acquire in order to determine the thematic relationships in a sentence for the correct interpretation of an utterance? In the following chapter a psycholinguistic model is presented that was developed to explain sentence processing and language acquisition by assuming that specific language cues interact with a form-function mapping (Bates et al., 1984, Bates & MacWhinney, 1989, 1987).

1.1.2 Cue strength and reliability

The theoretical framework of this thesis is based on the Competition Model by Bates and MacWhinney (Bates et al., 1984, Bates & MacWhinney, 1989, 1987). Supported by findings from cross-linguistic studies (Slobin, 1973; Slobin & Bever, 1982), Bates and MacWhinney (1984, 1989) specify pragmatic, syntactic, semantic, morphological and phonetic-phonological cues, which strongly control language comprehension (and production). These cues come into operation at the same time during language processing, support each other, but also compete with each other until finally one of the cues prevails due to its highest reliability and availability. Those cues that finally win the competition are not equally functional in all languages. However, these cues are the first ones that are acquired during first language learning (Bates et al., 1984, Bates & MacWhinney, 1989; Slobin & Bever, 1982).

As already pointed out before, there is no direct and reliable form-to-function mapping in German. The subject can be represented by the thematic role *agent*, and this thematic role can be identified due to the collation of the following cues: nominative case-marking, subject-verb agreement, animacy, and/or initial argument position in a sentence with canonical word order (Lindner, 2003). This formation of related forms and functions is suggested to happen because the number of formal categories is limited. However, the coalition of cues such as subject-verb agreement, animacy or initial argument position does not exclusively correlate with the subject (*agent*) of a sentence, these cues could also indicate another function.

Therefore, another important point of the model is illustrated in the following example (5). The name Competition Model derives from the fact that different cues seem to indicate the same function. If cues compete for a particular function e.g. the grammatical subject of the sentence, then the interpretation that has the strongest cue support will succeed.

(5) Den Großvater fragt der Enkel.

[the grandfather]$_{ACC}$ asks [the grandson]$_{NOM}$

“The grandson asks the grandfather.”

For example, only one noun phrase in the sentence (5) can be the subject and only one can be the object. The first noun phrase (den Großvater) stands in an initial sentence position, is animate and agrees with the verb, but is accusative case-marked. The second noun phrase (der Enkel) is also animate, agrees with the verb, and is nominative case-marked. The initial argument position typically points to the subject of the sentence (and therefore, due to the characteristics of the verb also to the *agent*), but the nominative case-marking of the second noun phrase is a stronger cue and wins the competition for the subject position and *agent* role, respectively.

The victory in a competition between the different cues depends on the strengthening of the connection between form and function in the specific language. For English speakers a valid and reliable cue to detect the subject of the sentence is word order, because a preverbal position is strongly associated with this syntactic function (Slobin & Bever, 1982; Haspelmath & Dryer, 2005). This is not the case in other languages such as Turkish. A preverbal position could point to the subject, but is generally beaten, in the competition, by the case-marking information because the inflection in Turkish is regular and explicit (Slobin & Bever, 1982). The strength of a cue depends on its *validity*, and cue *validity* is defined as the product of the *availability* of the cue and its *reliability* (Bates & MacWhinney, 1989). *Availability* is the frequency at which a cue is present in the input. If a cue is always available, such as word order, its *availability* is high. *Reliability* indicates how trustworthy the cue is. If a cue reliably leads to the correct interpretation of the function, such as case-marking in Russian (Kempe & MacWhinney, 1999), it has a high *reliability*. It could be concluded that the strength of a cue is objectively measurable by simply counting its presence in the input, but unfortunately, that would oversimplify the situation. Even if a cue has a high frequency, it can be hard to detect or costly to process. Bates and MacWhinney (1989) proposed the so-called *cue costs* as one reason why the acquisition of a specific cue is delayed even if it is highly reliable; examples are difficult to detect morphological markers that are phonological similar or markers of global agreement.

The Competition Model presumes that during language development the acquisition of the first cues is dependent on the *validity* of the cue, but with increasing age and experience cue *reliability* is a crucial factor to determine cue strength. And by adulthood, language use and processing is sophisticated enough to effectively use even the scarcest cue (cf. Sasaki & MacWhinney, 2006).

As already pointed out, word order is an important cue to identify thematic relationships in a sentence; it is a valid and reliable cue for English speakers (Slobin & Bever, 1982; Bates & MacWhinney, 1989). Studies that tested both production and comprehension in native English speaking children indicate that they are sensitive to word order from a very early age (Bloom, 1991; Braine, 1976; Akhtar, 1999). However, in contrast to English, German allows a relatively free word order, and therefore additional information is often needed to identify relational information between the arguments in a sentence. Thus, German children have to learn that, in addition to word order, other cues like phonetic-phonological, semantic features (e.g., animacy) and morphological case-markers convey decisive information. Crucial information indicated by the case-marking cue has been already described above. It is important to borne in mind that case-marking can be the only cue that provides information for correct sentence interpretation.

(6a) Der Großvater fragt den Enkel.

[the grandfather]$_{NOM}$ asks [the grandson]$_{ACC}$

“The grandfather asks the grandson.”

(6b) Den Enkel fragt der Großvater.

[the grandson]$_{ACC}$ asks [the grandfather]$_{NOM}$

“The grandfather asks the grandson.”

Whether the first noun phrase in the second transitive sentence (6b) functions as a subject or an object depends solely on morphological markings (case-markings). The accusative case “den” indicates “den Enkel” as the object and, crucially, as the undergoer (*patient*) in the sentence. The nominative case-marked finite article “der” points to the subject and actor (*agent*) of the scenario. Above all, and clearly indicated in this example, word order does not provide any reliable cue for the interpretation of (6a) and (6b). However, even if case-marking is a frequent cue in German its *reliability* is rather low due to syncretism and homonymy. In many cases, noun phrases are ambiguously case-marked, e. g. feminine and neuter singular nouns as well as plural noun phrases, as in the following example:

(7) Die Tochter fragt die Großmutter.

[the daughter]$_{NOM/ACC}$ asks [the grandmother]$_{NOM/ACC}$

“The daughter asks the grandmother.”

Assuming, that no additional information is provided, only the word order cue supports role assignment in ambiguous sentences, as in example (7).

Accordingly to the Competition Model and supported by empirical findings that will be outlined in the following sections, in German speaking children the acquisition of the word order cue precedes the acquisition of the case-marking cue due to higher *availability* of the former and, therefore, higher cue strength (Slobin and Bever, 1982; Bates et al. 1984; Bates and MacWhinney, 1987, 1989).

However, even though the major focus in this thesis was on syntactic processing in children, the following sections provide a review of auditory language processing in adults. Two speech processing models are presented and various aspect of auditory sentence processing in adults are discussed before going into detail on sentence processing in the developing brain.

1.2 Language processing in adults

Understanding language processing and the underlying anatomical structures and functions have been the focus of intense investigation for more than 130 years. The interest in the biological foundations of language can be tracked back to antiquity, it was Franz Gall (1758-1828) that created finally a map of multiple brain regions, which were thought to support a particular mental faculty. Initially, Gall's system of phrenology was a success, later it was controversially discussed and rejected (for a detailed overview see Price, 2012). In the middle of the 19th century, Paul Broca (1824-1880) studied a patient that was unable to speak meaningful words. After post-mortem examination of the patient's brain, Broca found lesions in the left inferior frontal gyrus (IFG) and concluded that this area supported speech production. This posterior region of the IFG (pars opercularis (Brodmann area (BA) 44) and the pars triangularis (BA 45)) has come to be known as Broca's area. In 1874, Carl Wernicke (1848-1905) presented his observations concerning language processing on the basis of a patient study (Wernicke, 1874). He claimed that damage to the posterior part of the superior temporal lobe, nowadays known as Wernicke's area, has severe consequences for speech perception. Adapting Wernicke's idea, Ludwig Lichtheim (1845-1928) incorporated additional interconnected areas and presented a model, which became known as the Wernicke-Lichtheim model (Lichtheim, 1885). In the 1960s, the model was extended by Norman Geschwind (1926-1984) to the Wernicke-Geschwind Model (Geschwind, 1965). The Model described language processing and production processes by a network involving Broca's area, Wernicke's area, the angular gyrus (AG), the arcuate fasiculus (AF), and other connecting pathways. Nowadays, further investigations on this field changed the view upon this model; the function of Broca's and Wernicke's areas is far more heterogeneous as previously postulated, and not only involved in speech processes. Nevertheless, the observations made by Broca, Wernicke, Lichtheim and Geschwind were an important landmark in early neuroscience.

1.2.1 Models of language processing

At the moment, different approaches exist that aim to describe the process of speech processing in a plausible model: e.g. *Asymmetric Sampling in Time* (Poeppel, 2003), *Neurocognitive Model of auditory speech processing* (Friederici, 2002, 2011, 2012a), *Dual-stream Model* (Hickok & Poeppel, 2000, 2004, 2007), *Integrative Speech Processing Framework* (Kotz & Schwartze, 2010, 2011). Due to the wide range of neuroimaging methods, current researchers do not have to rely solely on observation and post-mortem examinations. Rather, latest models aim at integrating recent findings, and are extended and refined on a regularly basis. In the following section, two prominent accounts the Dual-stream Model by Hickok and Poeppel (2000, 2004, 2007) and the Neurocognitive Model of auditory sentence comprehension by Friederici (2002, 2011, 2012a; Friederici & Kotz, 2003; Friederici & Alter, 2004) are described in more details.

The Dual-stream Model, mainly based on functional imaging and lesions data, focuses on the description of brain areas and pathways involved in speech processing. Hickok and Poeppel (2000, 2004, 2007, see Figure 1.1) assume that two distinct processing streams exist that mediate speech perception. A bilateral ventral pathway is responsible for speech comprehension, coordinates processes that analyse the acoustic input and combine later on phonological, lexical and conceptual information; that is, mapping sound onto meaning. Additional, the model suggests a left-lateralized

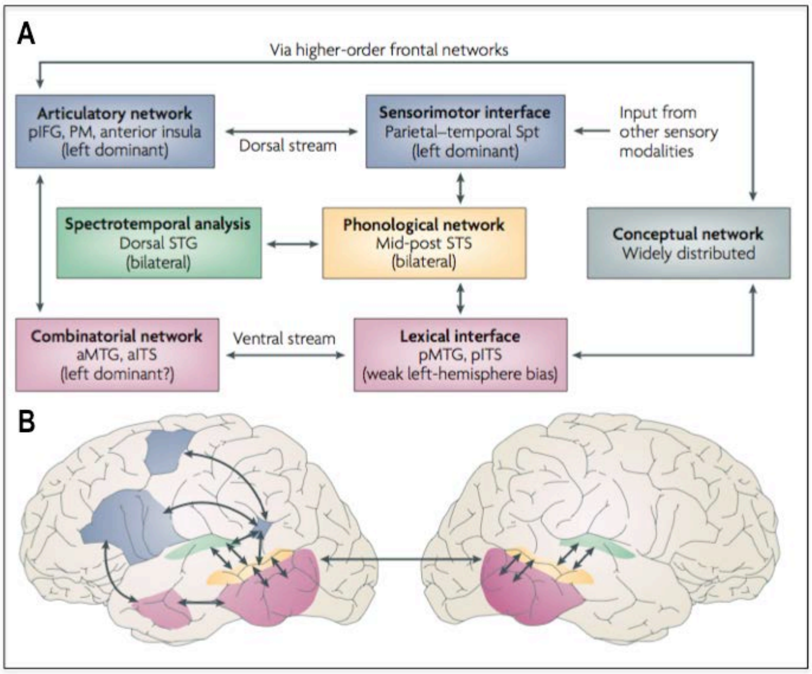

Figure 1.1: Illustration of the Dual-Stream Model. Adopted from Hickok and Poeppel (2007). (A) Schematic diagram of the dual-stream model. (B) Approximate anatomical locations of the dual-stream model components, specified as precisely as available evidence allows.

dorsal pathway supporting speech processing by integrating the input into sensory-motoric networks. Importantly, before the two streams start their particular analysis, the auditory cortices, bilaterally perform a spectrotemporal analysis of the incoming acoustic input. Subsequent analyses at the phonological level are supported by the middle to posterior superior temporal sulcus (STS) bilaterally, slightly left-lateralized (Hickok & Poeppel, 2004). Even though a bilaterally organized system is assumed, the systems are computationally different. In contrast to other models of speech recognition (Marslen-Wilson, 1987; McCLelland & Elman, 1986), the authors assume that different hemispheric streams support this process which differs in aspects of its sampling rate (gamma vs. theta range). This assumption is supported by neuropsychological evidences in unilateral superior temporal lobe lesions which do not necessarily limit spoken word recognition (Hickok & Poeppel, 2004, 2007). The left hemisphere is involved in temporal resolution and the right hemisphere in spectral resolution (Hickok, 2009; Zatorre et al., 2002). However, despite the asymmetry of function that indicates parallel pathways, the model states that both hemispheres mediate the processes of speech analysis. This assumption is supported by the fact that speech contains redundant cues to phonemic information that can be independently used by the bihemispheric system (Hickok, 2009).

After an initial auditory and phonological processing, in a next step, the proposed ventral stream attributes lexical, semantic and conceptual content to the phonological codes. The semantic interface where all information links into each other and sounds are mapped onto meaning seemed to be the posterior lateral, and inferior and medial temporal regions. In these regions conceptual-semantic information interacts with the analysed phonetic-level information coming from the STS (Hickok & Poeppel, 2004, 2007). The ventral pathway continues into anterior temporal regions where lexical-semantic and sentence-level processing is conducted (Rogalsky & Hickok, 2009; Maguire et al., 1999; C. Wong & Gallate, 2012), but Hickok and Poeppel note that further evidences are necessary to determine this hypothesis. Ultimately, the streams project into the IFG, a fact that is not discussed in detail by Hickok and Poeppel.

According to the model, the second stream, a left-lateralized dorsal fiber tract, mainly supports speech perception (Hickok & Poeppel, 2007). This pathway is considered to be involved in speech development, acquisition of new vocabulary, phonological short-term memory, monitoring and repetition. The dorsal stream projects to an area termed Spt, Sylvian parietal-temporal, located at the Sylvian fissure at the boundary between the parietal and temporal region (Hickok & Poeppel, 2007). This region responds both during speech perception and speech production even if production is covert (B. Buchsbaum et al., 2001, 2005; Hickok, 2009), and is responsible for translating sensory representation into motor representations (Hickok et al., 2003; Hickok & Poeppel, 2007). It was found to be highly correlated and probably also functional connected with BA 44 (B. Buchsbaum et al., 2001; Hickok, 2009), even though this activity is not assumed to be speech specific (Hickok et al., 2003). Finally, the stream ends in premotor regions and the IFG; areas that support articulatory functions.

The model does not comprise recent findings of studies using event-related brain potentials (ERP), and hence, neglects important information about the time-course of speech comprehension. It outlines the functional differences between the dual streams, but does not provide information where and when an interaction may occur (Cloutman, in press). Also subcortical structures are not introduced into the model. Nevertheless, the Dual-stream model can be considered an outstanding model concerning speech processing and comprehension at the word-level.

The Neurocognitive Model of auditory speech processing presented by Friederici (2002, 2011, 2012a; Friederici & Kotz, 2003; Friederici & Alter, 2004) incorporates functional neuroimaging data, time-course information[1] and white matter fiber tracking to sketch a clear picture of the functional neuroanatomy of language comprehension, including all the involved processes starting from auditory perception to sentence comprehension. Input-driven and top-down processes are supported via a cortical language circuit that controls language processing in temporo-frontal networks via a dorsal pathway assisting auditory-to-motor mapping, and a ventral pathway facilitating auditory-to-meaning mapping (Friederici, 2012a, see Figure 1.2).

Incoming acoustic input is acoustic-phonologically processed in the primary auditory cortex (PAC) and planum temporale (PT) in the first 100 ms after stimulation. Then, the information flow encompasses anterior and posterior parts of the superior temporal gyrus (STG) and STS, with evidences that the left anterior STS reacts generally as a function of intelligibility, is involved in syntactic phrase structure building (Brennan et al., 2012), and is suggested to be sensitive to semantic processes at the sentence level (Obleser, Zimmermann, et al., 2007; Price, 2012). The posterior STG

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[1] ERP components are not discussed in detail, but time-course information is incorporated in the presented overview.

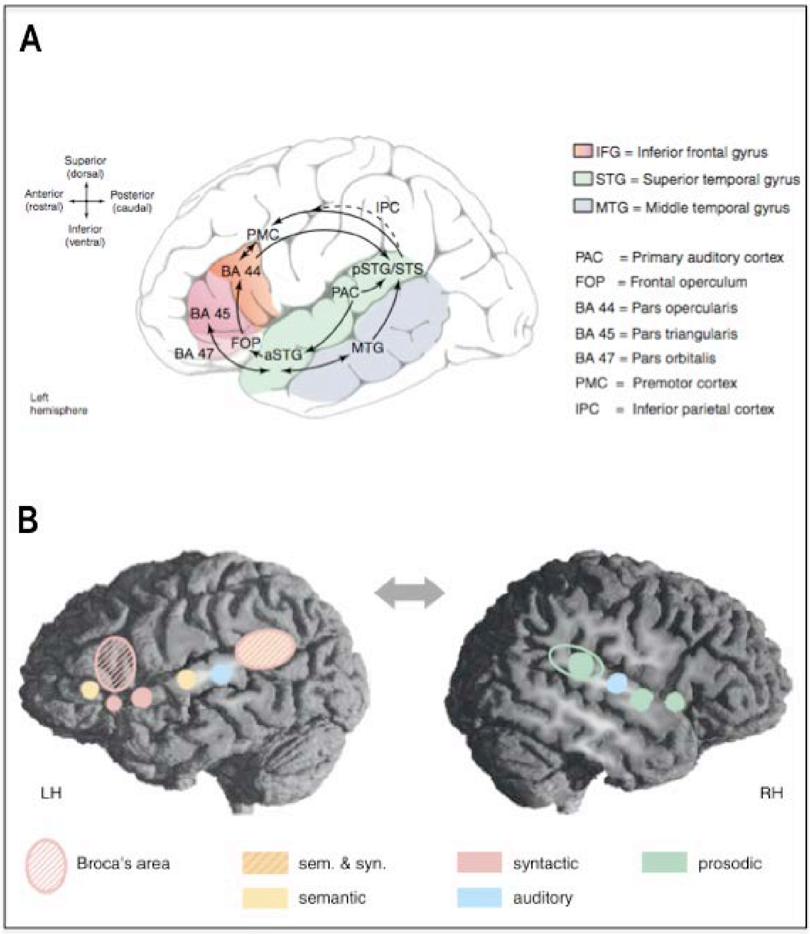

Figure 1.2: Illustration of the Neurocognition Model of auditory speech processing. Adopted from Friederici (2011, 2012). (A) The cortical language circuit. (B) The areas involved in auditory language comprehension.

and angular gyrus (AG) are found to assist predictions about upcoming sentence information (Obleser, Zimmermann, et al., 2007; Obleser & Kotz, 2010), but both areas are discussed as not being part of the same network (Friederici, 2012). Information flows also to the left IFG where higher-order syntactic and semantic processes take place (Bookheimer, 2002; Friederici, Fiebach, et al., 2006). Different pathways that directly connect different brain areas seem to facilitate information transmission. The model, which describes ventral and dorsal pathways that connect temporal and inferior frontal cortices, is in line with other neuroscientific models (Rauschecker & Scott, 2009; Hickok & Poeppel, 2004, 2007), but importantly, it assumes that two of each pathways exist. Owing to a ventral pathway (ventral pathway II) through the uncinate fasiculus (UF) connecting the anterior STG with the left frontal operculum (FO), a first syntactic processing step, namely the initial local structure building process, takes place within 120-200 ms after stimulus onset (Friederici et al., 1993; Isel et al., 2007; Herrmann et al., 2011). Because data indicated that semantic and syntactic information about relations in a sentence are processed between 300-500 ms (Kutas & Hillyard, 1984; Osterhout & Holcomb, 1992), parallel systems are assumed. The first can be described as a semantic left-lateralized temporo-frontal network that comprises the middle and posterior portions of the STG, the middle temporal gyrus (MTG) and IFG (BA 45/47) connected via a second ventral pathway (ventral pathway I) going through the extreme capsule fiber system (ECFS) (Saur et al., 2008). The second temporo-frontal network manages syntactic processes (Friederici, Balhmann, et al., 2006; Gow, 2012) and is connected via a dorsal pathway (dorsal pathway II) that links the posterior STG/STS with IFG (BA 44) via the arcuate fasciculus (AF) (Catani et al., 2005; Friederici, 2012b). Additionally, the model describes a second dorsal pathway (dorsal pathway I) connecting the temporal cortex and the premotor cortex (PMC) via the inferior parietal cortex (IFC) and parts of the superior longitudinal fasciculus (SLF). The dorsal pathway I is suggested to be involved in sensory-to-motor mapping (Hickok & Poeppel, 2004, 2007, Saur et al., 2008). Besides, Friederici (2011) suggested that the posterior STG/STS and the basal ganglia (BG) are involved in syntactic and semantic integration processes that start after 600 ms. A direct connection between the left and right temporal cortices through the Corpus Calosum (CC) is found to support inter alia the interaction of syntactic and suprasegemental prosodic information during language processing, which latter were found to take place in the right superior temporal and frontal regions (M. Meyer et al., 2002, 2004; Friederici & Alter, 2004). Having a closer look at Figure 1.2, it is obvious that the described information flow can be seen as a circuitry. Temporal regions are not only the origin of outgoing codes but also receive input from inferior frontal regions, AG and MTG (Friederici, 2012). Hence, Friederici (2012a) suggested a bidirectional orientation of the SLF supporting this top-down process.

In contrast to the Dual-steam Model by Hickok and Poeppel, the functional neuroanatomical processes subserved by the right hemisphere are assumed to be less dominant in sentence processing per se, and are mainly described as encoding of suprasegemental prosodic information. However, the contribution of subcortical structures to sentence processing should be elucidated and integrated into the model.

Finally, it must be stated that both presented models are able to explain many of the observations made in adults and patient studies. Although, further research is needed before the organization of the language network is fully understood. The following sections describe speech and sentence processing in adults, irrespective of a model, in more detail.

1.2.2 Speech processing in adults

Extensive data are available from neuroimaging studies investigating speech and auditory language perception in adults (for a review see Price, 2012; Grimaldi, 2012). Hierarchically structured subprocesses have been identified to organize the processing of the incoming speech signal to a final content analysis (Friederici, 2011). In an initial phase, the speech input has to be analysed on an acoustic-phonetic level, which is subserved by the middle STG (Giraud & Price, 2001; Liebenthal et al., 2005) and STS (Scott et al., 2000). Moreover, speech intelligibility effects have been reported in the anterior and posterior parts of bilateral STS; this area responded more strongly to more intelligible speech (Scott et al., 2000; Obleser, Wise, et al., 2007; Obleser & Kotz, 2010). In a next processing step, the incoming phonological information has to be analysed and mapped onto a phoneme level, and finally onto a word level. Recent studies indicated that STS bilaterally and adjacent areas play an important role in these processes (Friederici, 2002, 2010; Liebenthal et al., 2005; Obleser, Zimmermann, et al., 2007; Chang et al., 2010; Flinker et al., 2011). Once word forms are identified, words have to be processed in relation to each other in order to carve out all information contained in the sentence. This is done on the basis of word category information, which is used to organize the speech input by building a local phrase structure. In a subsequent phase, syntactic and semantic relations are computed, such as e.g. thematic role assignment. These syntactic processes are supported by a left-lateralized tempo-frontal network comprising the FO, IFG (BA 44 and BA 45), the anterior portion of the STG, the basal ganglia (BG), as well as the posterior portion of the STG (Friederici, 2002, 2003, 2011; Snijders et al., 2009; Brennan et al., 2012). While the temporal areas have been found to provide word category information, the IFG supports the local phrase structure building processes (for a review see Friederici, 2011). Furthermore, several studies have provided strong evidence for a neural network for semantic processes, which comprises the ventral portion of the left IFG (BA 45/47), the posterior portions of the MTG and STG, respectively and anterior STG (Friederici & Kotz, 2003; Musso et al., 2003; Hickok & Poeppel, 2007). In case the sentence processing is hindered due to ambiguous information e.g. thematic role assignment is not clearly indicated due to ambiguous cues (see chapter 1.1.2), additional information such as context or world knowledge can be enquired. Moreover, sentence-level prosody, an additional linguistic cue, interacts with all processing phases and modulates the syntactic and semantic processes by a temporo-frontal network primarily in the right hemisphere (M. Meyer et al., 2002, 2004, Friederici & Alter, 2004; for a review see Friederici, 2011).

1.2.3 Sentence processing in adults

Certainly, speech processing is a complex process and once, the auditory input is decoded as speech the next step is initiated. But also on this processing stage several subprocesses have to be accomplished before a global sentence interpretation is achieved. These subprocesses were outlined in the previous section. All these subsequent processes have to pass off as quickly as possible to guaranty an efficient communication. Language comprehension proceeds incrementally, i.e. incoming information is integrated and interpreted as soon as it is encountered and sometimes long before the whole sentence information is available (Marslen-Wilson, 1973; Crocker, 1994; Stabler, 1994; Tanenhaus et al., 1995; Altmann & Kamide, 1999). At what time the different information, such as word category information, thematic relations, etc. is processed is still up for debate. Modular models postulate an isolated and sequential processing of each specific aspect of language (Fodor, 1983) whereat divergent concepts exist concerning the chronological order of each processing step. Generally, these modular models are serial models, i.e. they assume that only one single aspect of sentence analysis is conducted at a time. It is assumed that the sentence parser processes syntactic before semantic information, so-called syntax-first, and a reanalyses due to previous ambiguous syntactic information can only be done if the initial analysis is incorrect or inconsistent with later sentence information (Frazier & Fodor, 1978; Ferreira & Clifton, 1986; Frazier, 1987). In contrast to these models, interactive models are characterized by taking immediately all possible syntactic and semantic information into account for sentence processing (Tyler & Marslen-Wilson, 1977; Marslen-Wilson & Tyler, 1980; MacDonald et al., 1994). Within the interactive models it exists at least two further concepts. A weak interactive model assumes that syntax information is still the first to be processed, but processing is influenced instantaneously by semantic aspects (Altmann & Kamide, 1999). In contrast to this, strong interactive models, also called constrained-based models, postulate that syntactic and semantic information are simultaneously processed and can interact at any time (Marslen-Wilson, 1975; MacDonald et al., 1994; Trueswell et al., 1994).

Evidence for a modular, syntax-first model comes from neuroimaging ERP-studies that provide a good temporal resolution in the range of milliseconds. This high temporal resolution is necessary to track syntactic processes relevant for the assignment of grammatical structures. A deeper understanding of the underlying cortical areas involved in these processes can be achieved by combining ERP with functional magnetic resonance imaging (fMRI). Because the empirical work of this dissertation investigated the processing of syntactic information such as word order and case-marking, the following section focuses on recent findings from fMRI studies investigating the processing of syntactically complex sentences in adults.

A wide range of neuroimaging approaches examined syntactic processing and most importantly, tried to disentangle different stages of this process. That has been accomplished by introducing various paradigms such as artificial grammar, violations on sentence-level, limitation or absence of syntactic information (e.g. word lists) or syntactic complexity variations of the sentence structure (e. g. manipulation of word order, syntactic ambiguities). A paradigm with sentence-level violations challenges the processing process e.g. in terms of working memory, higher processing demands and is a frequently used instrument for investigating sentence processing from various kinds of angles (Vandenberghe et al., 2002; Friederici et al., 2003; Suzuki & Sakai, 2003; Rogalsky & Hickok, 2009). A study by Friederici and colleagues (2003) found an increased activation of the STG when comparing sentences with a semantic or syntactic violation to correct sentences. Whereas semantically incorrect sentences recruited the mid-portion of the STG bilaterally and the insular cortex bilaterally, the syntactically incorrect sentences activated the anterior STG, the left posterior FO and the putamen in the left BG. The authors suggested that whereas the activation in the BG mirrors syntactic processing per se, the left FO and left anterior STG supports a local structure building process (Friederici et al., 2000, Friederici, Balhmann, et al., 2006). Concerning the anterior STG, data provided from several studies suggested that also this area is involved in syntactic structure processes (Vandenberghe et al., 2002; Rogalsky & Hickok, 2009), but is also considered as an area involved in semantic integration processes (Maguire et al., 1999; Humphries et al., 2001; C. Wong

& Gallate, 2012). Friederici and Kotz (2003) reported that distinct brain networks are responsible for early and late syntactic processes. Early processes i.e. local phrase structure building and semantic integration are supported by the IFG and anterior STG and later processes, i.e. syntactic revision and late integration, are subserved by the BG and posterior STG.

Several fMRI studies have focused on the processing of syntactic complexity in adults. A popular approach to investigate the underlying processes is to vary the argument hierarchies in sentences. As already pointed out in chapter 1.1, in German and in many other Indo-European languages, the unmarked and canonical sentence word order is a subject-initial structure. Sentences with a manipulation of their argument hierarchy are called non canonical sentences because one or more phrases of the sentence are displaced. Consider the following example:

(8a) Der Junge kauft dem Mädchen ein Eis.
[The boy]$_{NOM}$ buys [the girl]$_{Dative(DAT)}$ [an ice-cream] $_{NOM/ACC}$
"The boy buys an ice-cream for the girl."

(8b) Dem Mädchen kauft der Junge ein Eis.
[The girl]$_{DAT}$ buys [the boy]$_{NOM}$ [an ice-cream]$_{NOM/ACC}$
"The boy buys an ice-cream for the girl."

Neuroimaging studies have typically compared the brain responses for the processing of these two different sentences structures (sentence 8b compared to sentence 8a). The second sentence structure is considered syntactically more complex than the first one, which has a canonical structure. In general, activation attributed to syntactic complexity is mainly found in the posterior part of the superior temporal (Cooke et al., 2001; Röder et al., 2002; Ben-Shachar et al., 2004; Bornkessel et al., 2005; Kinno et al., 2008; Santi & Grodzinisky, 2010), and predominantly in the pars opercularis of the left IFG (Cooke et al., 2001; Röder et al., 2002; Ben-Shachar et al., 2004; Bornkessel et al., 2005; Fiebach et al., 2005; Grewe et al., 2005; Friederici, Fiebach, et al., 2006; Kinno et al., 2008; Santi & Grodzinisky, 2010; Obleser et al., 2011). Bornkessel and colleagues (2005) designed a stimuli set with German sentences containing three manipulated factors known to have an impact on the complexity of argument hierarchy construction, namely, order of the arguments, verb class and morphological ambiguity. Their results indicated an enhanced activation in a left lateralized network comprising the IFG, posterior STG, and premotor and parietal areas for sentences with increased syntactic complexity, whereat the three factors showed distinct influences in the temporo-frontal network. The authors suggested that activation in the left posterior STG indicated an enhanced process of mapping the morpho-syntactic argument hierarchy onto the semantic argument hierarchy of the verb. The left IFG (BA 44) responded to linearization of hierarchical linguistic dependencies solely and was suggested to play a crucial role in this process. Interestingly, imaging data by Friederici, Fiebach, et al. (2006) indicated that activation within the left BA 44 increases parametrically with syntactic complexity, as operationalized by the number of permutations of case-marked arguments in a sentence. However, Santi and Grodzinisky (2010) demonstrated in their fMRI study that not all factors of syntactic complexity are processed in the same manner in the cortex. The stimuli design focused on two dimensions of sentence complexity, one condition varied the embedding position (right-branched vs. center-embedding) while the other condition varied the movement type (subject vs. object). The results indicated that only syntactic movement engendered activation in BA 45 while BA 44 was sensitive to both dimensions: movement and embedding position.

Although Broca's area has been extensively studied, its role in sentence processing is still up for debate (Friederici et al., 2010; Just et al., 1996; Grodzinsky & Santi, 2008; Rogalsky & Hickok, 2011; Stromswold et al., 1996). The introduced studies generally state that this area is relevant for syntactic processes (Caplan et al., 2000, 2008; Makuuchi et al., 2009; Friederici et al., 2010; for an overview see Grodzinsky & Friederici, 2006), but others suggest it is partly associated with working memory mechanisms that are related to language processes (Fiebach et al., 2004, 2005) or simply rehearsal (Rogalsky et al., 2008; Rogalsky & Hickok, 2011). In addition, the different subregions of the IFG are associated with different aspects of sentence processing: whereas BA 44 is taken to be linked with syntactic structure building (Friederici, 2002), BA 44/45 is considered to be sensitive to thematic role assignment and also support the computation of syntactic movement (Osterhout & Nicol, 1999), and BA 45/47 is associated to semantic processes (Bookheimer, 2002; Friederici, 2002; Hagoort, 2005). More recently area 45 has been subdivided receptor-architectonically in an anterior portion (45a) and a posterior portion (45b) with the latter bordering area 44 (Amunts et al., 2010).

Down to the present day, a multitude of work has been accomplished to understand the underlying processes of syntactic processing in adults. Mainly left lateralized networks comprising the inferior frontal cortex and temporal cortex were shown to be engaged in these processes. Nevertheless, the particular function of the different IFG subregions is still up for discussion and further and more fine-grained work has to be done to decode and describe all aspects of this area.

1.3 Speech processing in the developing brain

Acquiring a language in just a couple of years is a tremendous achievement. In the beginning of this chapter a couple of milestones were already mentioned: speech segmentation, phoneme and word recognition as well as word learning are accomplished in the very first years of life. Besides behavioural research, many neuroscientific studies have explored the neural underlying architecture of speech processing and the differences to the adult maturated brain. Concerning the processing of speech, Dehaene-Lambertz and colleagues (2002, 2006) found remarkable similarities comparing the underlying structures of infants and adults. Comparing normal and reversed speech in sleeping 3-month-olds, Dehaene-Lambertz and colleagues

(2002) found activation in a left-lateralized network including STG and AG. But also the next processing steps, namely phonological, semantic and syntactic processes, demonstrated a pattern similar to adults (for a review see Kuhl, 2004, 2010; Friederici, 2005). For instance, most ERP studies in infants and children reported similar ERP components as found in adults but with a delayed onset, latency differences and longer duration (Hahne et al., 2004; Friedrich & Friederici, 2004, 2005; Oberecker et al., 2005). The next sections provide an overview of the recent findings in this field. Concerning the acquisition of case-marking information in particular, the review starts with mainly behavioural evidences and broadens the findings to functional studies of sentence processing in children, because so far, not many fMRI studies have dealt with syntactic processing and case-marking in particular.

1.3.1 Acquisition and processing of case-marking in children

The previous sections gave a summary about the latest findings, assumptions and models of speech and sentence processing in the maturated brain. Research in the developing brain has still a couple of gaps to fill concerning the development of brain functions. Nevertheless, there is a wide range of studies that has investigated the development of speech comprehension and production in children. Following, several studies are reviewed that focused mainly on the acquisition and processing of case-marking, as well as other language cues, in children (Schaner-Wolles, 1989; Lindner, 2003; Chan et al., 2009; Dittmar et al., 2011; Gertner & Fisher, 2012).

In a preferential-looking paradigm, Gertner and colleagues (2006) tested English-speaking children by showing them two scenarios that illustrated different novel causative actions with two characters. One character was the agent in one scenario and the patient in the other scenario and vice versa. Even 21-month-old children, who listened to a sentence describing a scenario, looked significantly longer than chance to the target scenario. Gertner and colleagues suggested that children at this age use word order information for transitive sentence comprehension, and interpreted the results as children's ability to correctly assign thematic roles to nouns preverbal and postverbal positions. A second study by Gertner and Fisher (2012) showed that 21-month-olds mistakenly used word order for interpretation of intransitive sentences (with a preverbal double noun conjoined-subject). In a similar vein, two studies with English-speaking children under the age of three-year-olds investigated transitive sentences with familiar and novel verbs in a pointing task (Dittmar et al., 2011; Noble et al., 2011). In both studies, children aged 2;03 (Nobel et al., 2011) and 2;01 (Dittmar et al., 2011) were able to make a thematic-role interpretation in transitive sentences with canonical word order.

In German, typically developing children usually produce the nominative case-marked definite article, indicating a subject role, before the accusative one. The accusative case-marked definite article, pointing to an object, is not used until the age of 3;0 (Szagun, 2006). Behavioural comprehension studies with German-speaking children that presented sentences with manipulated word order and additional information (e.g., case-marking and animacy), support this theory, and reported a relatively late acquisition of case-marking for argument interpretation (Primus & Lindner, 1994; Schaner-Wolles, 1989; Lindner, 2003; Dittmar et al., 2008; Chan et al., 2009). Chan and colleagues (2009) conducted an acting out task with Cantonese, German and English speaking children at the age of 2;6, 3;6, and 4;6. In their study, transitive sentences with two arguments were presented which were either cued redundantly by animacy and word order, by word order solely, or in a conflictive way, so that animacy clashed with word order. The results showed that if both cues pointed to the same interpretation even the youngest group was able to comprehend the tested sentences. Furthermore, the results indicated that with increasing age children rely on word order alone. However, Chan and colleagues pointed out that the strategy of which cue is used by the child depends on how informative the cue is in the child's native language. In a similar vein, Dittmar and colleagues (2008) tested German-speaking children at the age of 2;7, 4;10, and 7;3 in a pointing task. The results indicated that children are not able to reliably process solely morphological information before the age of seven years. Furthermore, while two-year-olds needed word order and case-marking information in combination to correctly identify the actor of an action presented in the test sentence, five-year-old children could use the word order cue alone, but not the information provided by case-marking alone (Dittmar et al., 2008). Other studies investigating the performance in sentences in which word order and case-marking conflict, reported contradictory findings in regard to at which exact age do children start to use case-marking information for sentence interpretation (Mills, 1977; Schaner-Wolles, 1989; Primus & Lindner, 1994). For example, Mills (1977) tested children at the age of five to eight using a paradigm with unambiguous and ambiguous case markers. She found that even younger children ignored the word order cue as long the argument in the initial position was unambiguously case-marked.

Nevertheless, a recent ERP-study by Schipke and colleagues (in press) investigated the neurophysiological underpinnings of the processing of case-marked topicalized object noun phrases in German-speaking children at the age of 3;0, 4;6 and 6;0, as well as in adults. The ERP results suggested that three-year-olds used word order for sentence interpretation, whereas children at the age of 4;6 were already sensitive to case-marking, although they did not use it for interpretation. Even though the ERP effects to object-initial noun phrases in the group of 6-year-olds were similar to adults, children still showed problems when it came to integrating the second noun phrase for interpretation. Another ERP-study that focused on the processing of case-marking violations in transitive sentences showed that already three-year-olds are sensitive to violations in subject-initial sentence structures (Schipke et al., 2011). Schipke and colleagues (2011) observed already in children at this young age the same ERP pattern for a double nominative sentence structure violation as in the adult control group. However, in sentences with a double accusative violation, an adult-like effect was not found even in their oldest group of children (six-year-olds).

The processing of object-initial structures in children was also tested in an ERP study by Mahlstedt (2008). She concluded that already three-year-old children are sensitive to case-marking information, but the findings should be judged cautiously because the processing of case-marking information was confounded with a semantic cue (animacy information).

In short, the studies reviewed indicate that children's awareness of which cues will help them to process even non prototypical sentences in their native language develops with increasing age. Moreover, children do not detect the strength of case-marking information, as a language cue in German, before the age of five to six years old.

Up to now, no functional MRI study has investigated the brain areas which subserve the acquisition of case-marking cues for argument interpretation in unambiguously case-marked object-initial sentences in young children. So far, very few fMRI studies in children focused on the processing of specific language cues per se, nonetheless many studies tried to shed light on the general question of language processing (Ahmad et al., 2003; Brauer & Friederici, 2007; Yeatman et al., 2010; Nuñez et al., 2011). Early neuroimaging studies in children have been primarily interested in language lateralization (Balsamo et al., 2002; Dehaene-Lambertz et al., 2002; Peña et al., 2003). These studies have shown a gradual process of functional lateralization in the perisylvian cortex for language processing. More specifically, the results indicated a very early left lateralization for human speech already in neonates and infants (Dehaene-Lambertz et al., 2002; Peña et al., 2003). Left hemispheric language dominance was also demonstrated in older children using fMRI. Balsamo and colleagues (2002) revealed highly lateralized activation in the left MTG and STG for an auditory responsive naming paradigm in children between the ages of 7;3 and 9;6 years. While findings from Ahmad et al. (2003) also indicated left hemisphere language dominance in temporal and frontal areas for listening to stories with a reverse speech control condition in children aged 5;6 to 7;9, other studies failed to find this lateralization effect (Ulualp et al., 1998; Booth et al., 2000). Nevertheless, the degree of lateralization seems to increase with age, but more importantly the results indicate that the effect is task and brain region dependent. Holland and colleagues (2007) reviewed several fMRI studies in children and adolescents of five to eighteen years old and concluded that tasks involving syntactic processing produce a more bilateral distribution of activation in both the anterior and posterior language areas than tasks involving semantic processing.

So far, little is known about the neural networks that are involved in the processing of syntactically more complex sentences in younger children. A neuroimaging study by Brauer and Friederici (2007) investigated the processing of sentences in a syntactic and semantic violation paradigm, including a judgment task. Sentences were presented auditorily to five to six-year-old German children and adults. Activation found in adults was distinct function-specific and was observed in the STG and FO for syntactic violations. The results in children revealed a significant overlap for syntactic and semantic processes in the left STG, and in the IFG bilaterally. They concluded that at this age the language networks for semantic and syntactic processes are not fully developed as they are in adults. Nuñez and colleagues (2011) tested English speaking children at the age of 7;2 to 15;8 years old. Functional MRI results showed a relation between syntactic proficiency and activation in the left IFG, superior frontal gyrus (SFG), and middle frontal gyrus (MFG) independent of age of the children. The amount and extent of activation within the right IFG during syntactic processing (contrasted with a resting condition) was negatively correlated with cortical thickness in this region. Nuñez interpreted the results as a shift of this process from the right to the left hemisphere at this age. Additionally, the group of older children (above the age of 10.7 years old) revealed an activation in BA 44 for syntactic processing versus semantic processing, which was not found in the group of younger children. Another fMRI study (Yeatman et al., 2010) tested English speaking children and adolescents at the age of 10 to 16 years old, and while they did not find IFG activation at the group level, a post hoc analysis demonstrated a higher involvement of the IFG in children with better receptive language skills, as tested outside the scanner.

Taken together, these findings suggest that sentence processing in children between the ages of 7 and 16 years involves the same brain areas (especially left IFG/MFG/STG) as found in fMRI studies investigating syntactic processing in adults. However, the studies in children often failed to find significant results at the group level, indicating a high variance in language proficiency that is not related to a specific age. Rather, several studies reported that activation in the left frontal cortex correlates with individual language skills (Yeatman et al., 2010; Nuñez et al., 2011).

1.3.2 Maturation of the developing brain

Besides functional MRI studies in children, a wide range of studies investigated the maturation of the developing brain to draw conclusions about possible correlations with children's cognitive, memory, motor, sensory, and executive performance (Barnea-Goraly et al., 2005; Beaulieu et al., 2005; Drobyshevsky et al., 2007; Tamnes, Ostby, Walhovd, et al., 2010; Cantlon et al., 2011). Maturation of the brain is a dynamic ongoing process during infancy, childhood and adolescence (Giedd et al., 1999; Paus et al., 1999; Pujol et al., 2006; Provenzale et al., 2007; Dubois et al., 2008; Giorgio et al., 2008; Lebel et al., 2008; Shaw et al., 2008; Tamnes, Ostby, Fjell, et al., 2010) that continues until early adulthood (Paus et al., 1999; Blakemore, 2008), and does not proceed synchronically in all brain regions (Paus et al., 1999; Pujol et al., 2006; Dubois et al., 2008; Giorgio et al., 2008). To clarify these anatomical and behavioural correlations, studies have mainly focused on changes in white and grey matter.

Cortical thickness (grey matter layer), density, and volume are undergoing fundamental changes until being fully matured. An initially increase in volume during childhood is followed by a peak in adolescence and decline into adulthood (Giedd et al., 1999; Sowell et al., 1999, 2003. 2004; Lebel et al., 2008; Shaw et al., 2008, for a review see Blakemore, 2008). These processes are not homogeneous across brain areas and of nonlinear nature. Grey matter consists of neuronal cell bodies, dendrites and non myelinated axons of neurons, capillaries and glial cells. The inverted U-shaped changes in mental trajectory of grey matter volume are probably caused by dendritic outgrowth and synaptogenesis, followed by synaptic pruning (Blakemore, 2008; Giorgio et al., 2010).

The second brain tissue, the white matter, is composed of bundles of myelinated axons of neurons, and shows a steady linear increase in global volume during early childhood and adolescence, with a stabilization of this process into adulthood (Giedd et al., 1999; Paus et al., 1999; Dubois et al., 2006, 2008; Pujol et al., 2006; Ashtari et al., 2007; Giorgio et al., 2008; Lebel et al., 2008; Tamnes, Ostby, Fjell, et al., 2010). This development has been attributed to gradually processes of axonal myelination, and has been also demonstrated in post-mortem histological studies (Yakovlev & Lecours, 1967; Benes et al., 1994). Alternatively, it has been explained as due to increasing axonal calibre (Paus et al., 2008). These differences and asynchrony of maturation of white and grey matter structures of the different brain areas are associated with changes and age-related enhancement of children's behavioural performance (Barnea-Goraly et al., 2005; Beaulieu et al., 2005; Cantlon et al., 2011).

Little is known how changes in the developing brain influence and improve language processing. Pujol and colleagues (2006) examined one hundred children from birth to three years of age and described in their study the myelination process in the brain. They found an early myelination in the sensorimotor and in Heschl's gyrus (HG) before the changes spreads to language related areas, that is, temporo-frontal regions. A recent study by Leroy and colleagues (2011) revealed that in one to four-month-old infants the maturation of the ventral STS is still behind the inferior frontal areas. Comparing adults to seven-year-old children, Brauer and colleagues (2011) found differences in fractional anisotropy (FA), i.e. a measure that indicates the directionality of water diffusion along fiber tracts. They reported a higher FA in adults compared to children mainly in perisylvian regions in STG/STS and left inferior frontal areas. Higher FA values are suggested to reflect increasing organization of white matter tracts, and therefore an increased myelination status of these regions (Beaulieu & Allen, 1994). Brauer and colleagues (2011) supported this suggestion with functional data indicating that in seven-year-olds the ventral pathway that connects Broca's area (BA 45) with the temporal cortex is recruited for language processing because of the immaturity of the dorsal connection between Broca's area (BA 44) and the temporal areas. Assuming that there are two dorsal fiber connections, dorsal pathway I connecting the temporal cortex with the PMC, and dorsal pathway II connecting the posterior STG/STS with BA 44, a structural connectivity analysis by Perani and colleagues (2011) found evidence that the later fiber tract connection is not present at birth. Comparing the data of adults and two-month-old infants in a DTI analysis, they found the ventral pathway, as well as the dorsal pathway going to the PMC are present at birth, whereas the dorsal pathway connecting to BA 44 was not detectable. Other recent studies focusing on the maturation of white matter fiber bundles in infants and children support this view since they found the dorsal connection via the SLF to develop late and slowly (Zhang et al., 2007; Lebel et al., 2008). Focusing on the AF, previous studies showed that also this fiber tract is not fully developed in infants aged one to four-month-olds (Dubois et al., 2006, 2008). A subdivision of specific language functions that are supported by either the dorsal or the ventral pathway, introduced in detail in chapter 1.2, is still a matter of debate (Friederici, 2009a, Friederici, 2009b).

Preliminary evidence from developmental MRI studies confirmed that brain areas have to mature across infancy, childhood and adolescence, and that changes in terms of temporal development are brain area-specific. Connections have to mature to improve exchange of information between different brain regions. Further studies have to identify the exact pathways and maturation process to possibly find explanations for children's cognitive, social and motor development.

Part II

METHODOLOGY

2

INTRODUCTION

The structural and functional organisation in the developing brain and consequently the development of cognitive skills in infants and children are in the research focus of developmental cognitive neuroscience. Investigation and localisation of neural structures, which undergo developmental changes, is facilitated by a number of functional neuroimaging techniques. A method frequently applied in developmental studies due to its non-invasive characteristics is the electroencephalography (EEG). EEG refers to evoked measurement of electric potentials and offers a good temporal resolution in the range of milliseconds. An equal good temporal resolution provides magnetoencephalography (MEG) that measures the magnetic fields originating from the brain, but additionally, this method is considered to be superior when it comes to source localization. Positron emission tomography (PET) provides a detailed image of the brain activity, but has the disadvantage that injection of a radioactive tracer is necessary. Recently, near infrared spectroscopy (NIRS) in babies and infants and magnetic resonance imaging (MRI) in children became in vogue in developmental neuroscience, because of its good spatial resolution and non-invasive nature. Particularly technological advances in MRI provide an excellent insight in brain functional and structural changes during childhood and adolescence. This method served as the main technology for the research that is presented in this thesis. Therefore, the following chapter gives a brief introduction of the history and technical base of functional and structural MRI methods used in the experiments.

2.1 Magnetic resonance imaging

Magnetic resonance imaging is a method that provides an insight into the human body without using X-rays or radioactive tracers. As the name implies MRI uses a magnetic field and radio waves. The technique based on a physical phenomenon called Nuclear Magnetic Resonance (NMR) Spectroscopy and was independently described by the research groups of Felix Bloch (1946), at Stanford University, and Edward Purcell (1946), at Harvard University, and they were therefore jointly awarded the Nobel Prize in Physics in 1952. The method was mainly used for chemical analyses, rather than biological until the 1970s when a study by Raymond Damadian (1971) revealed that animal tissue samples emit different NMR signals. However, NMR was still a technique to measure the total energy absorbed and emitted by the entire sample, but no images were supplied so far, because an approach to extract spatial information about the tissue was not developed at this particular time. This status changed not even two years later, when Paul C. Lauterbur (1973) induced spatial gradients in the magnetic filed to extract besides only single dimension of NMR spectroscopy also second dimensional information from the sample, namely the spatial orientation. Lauterbur further developed the process by acquiring data using more gradients in succession. His achievements led to the creation of MR images. Further development by Peter Mansfield (1977), such as echo-planar imaging (EPI), improved the technique and made the process faster and therefore feasible for clinical purpose and consequently also for research. For the contribution and improvements of the MRI technique, Lauterbur and Mansfield jointly received the Nobel Prize in Physiology or Medicine in 2003.

Physical bases of MRI

MRI imaging focuses on the magnetic signal from hydrogen nuclei (^{1}H) in water (H_2O) that is one of the most abundant elements in the human body. The underlying principle of MRI is the creation of a strong magnetic field to align the magnetization of atomic nuclei and induce changes in their nuclear spin.[1] A Spin is a quantum mechanical term that describes atomic nuclei with a magnetic moment and angular momentum. The MRI takes advantage of the fact that the hydrogen nucleus consists of one single proton only (positively charged particles) that has the intrinsic characteristic of rotating around itself what creates the magnetic moment. Originally, until a strong external magnetic field is applied a spin is orientated randomly, but exposed to static magnetic field (called B0) it aligns itself parallel or antiparallel to the magnetic field to adopt either a low-energy state or high-energy state. This rotation for the magnetization is known as “gyroscopic precession”. The alignment of the protons to the magnetic field results in a net magnetization (longitudinal), and each proton starts its precession around an imaginary axis between the poles of the external magnetic field, the so-called Larmor precession. Correspondent to that, the specific frequency of this rotation is known as Larmor frequency ($\omega 0 = \gamma B0$). Thus, the gyromagnetic ratio (γ), proportionality constant, is for a proton 42.56 MHz per Tesla, resulting in a Larmor frequency for a 1.5 Tesla magnet of 63.8 MHz.

By applying now an oscillating electric pulse (RF pulse) at the same Larmor frequency in a perpendicular angle to B0, the protons will start a precession around the axis of this applied magnetic field (B1); a process known as (RF-)excitation that modifies the energy level of the system and the phases of the spin. Roughly speaking two things are observable, the former longitudinal magnetization decreases and net magnetization is tipped into the transverse plan, and the spin vectors are forced to move in phasic coherently. These processes started by the excitation pulse create a MR signal.

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[1] The following descriptions are based on Buxton (2009), and Huettel, Song, and McCarthy (2004).

However, the signal decays over time due to a phenomenon called spin relaxation. Once B1 is turned off at the end of a 90° pulse, the protons return into the previous longitudinal magnetization (time parameter is called T1 relaxation), start to precesses around B0 again, and fall back into a lower energy status. Simultaneously, spins start do diphase (time parameter is called T2 relaxation), and the spin system gradually loses energy absorbed during the excitation. These two relaxation parameters (T1 and T2) can be used to generate MR signals, because the values of the parameter are dependent of the given sample (such as a water, fat, or bone). Both T1 and T2 are mutually independent, and differ in time. While the MR signal decays due to T2 relaxation already after 100-300 ms, the T1 relaxation takes place within 0,5 to 5 sec (T2 « T1). A third measure of relaxation time is T2*. This parameter depends of accumulated phase differences as T2, but additionally, is influenced of local magnetic field inhomogeneities that are caused amongst other factors by the presence of deoxygenated haemoglobin. The deoxygenated haemoglobin on the other hand is especially important for drawing conclusions about the intensity of the oxygen metabolism in that specific area, which in turn is seen as an indicator of increased neural activity in this area and is the basis of functional MRI (describted in more detail in the following section).

The strength of the MR signal is constrained by these relaxation processes, and those in turn limit the time window within data collection is possible. Therefore, a series of excitation pulses must be applied several times to collect the data. To acquire data of a three-dimensional image MRI predominantly uses a combination of three steps: Slice selection, phase encoding, and frequency encoding. This process can be depicted (nevertheless it is arbitrary) by imaging the three spatial directions as an x, y, and z-axis in a coordination system; whereat usually the z-axis describes the slice selection, the x-axis the frequency encoding, and the y-axis relates to the phase encoding. In a first step a slice of the sample is selected, by applying a magnetic gradient additional to the external magnetic field at the same time as the RF pulse.

It excites only the protons in one selected slice and does not strongly affect spins of other slides by choosing a specific frequency range of the RF pulse. The next two steps are closely related and aim to encode the spatial information of the signal itself. First, a phase gradient pulse sequence is briefly applied along the y-axis to slightly adjust the precession. The consequence of this second step is that hydrogen atoms get out of their synchronicity with each other to be distinguishable in the xy-axis. In the next step, an additional static gradient field is turned on during the time of data acquisition. Similarly as the process for slice selection, a specific range of Larmor frequencies are applied to encode the signal terms of frequency. Due to this gradient frequency differences occur that enables to locate the signal along the x-axis. Finally, using the inverse Fourier transformation permits to reconstruct the desired MR image represented in the acquired data matrix (k-space). An overview on MRI and detailed description of the physical, mathematical and technical principals can be found e.g. in Buxton (2009), and Huettel et al. (2004).

2.1.1 Functional magnetic resonance imaging

Magnet resonance imaging does not only measure differences between tissues, functional MRI can also measure changes in the blood oxygenation of the brain in relation to time. These differences of the blood oxygenation level are used to make interferences about underlying neuronal activity.[2] It should be pointed out that fMRI cannot measure this activity in a direct way; it creates images of physiological activity what seem to correlate with neural activity. Nevertheless, this method offers the great possibility to infer which brain structures are involved in e.g. specific cognitive or motoric tasks. The underlying idea is to construct the images of the brain activity based upon blood-oxygenation-level dependent (BOLD) contrast. Increased neuronal activity goes along upon other facts with an increase in blood flow. The first one who investigated this was Seiji Ogawa and his colleagues in the late 1980s. Ogawa

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[2] The following descriptions are based on Buxton (2009), and Huettel et al. (2004).

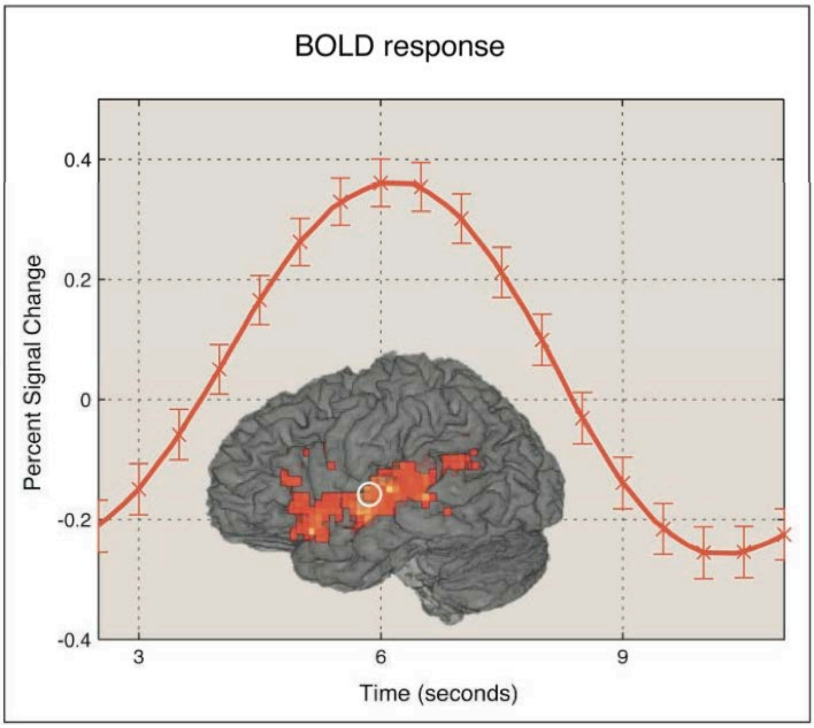

Figure 2.1: Illustration of the BOLD hemodynamic response (adapted from Brauer (2009)).

used fMRI to measure the blood flow and the underlying metabolic processes that require the supply of oxygen. Oxygen is transported mainly within the red blood cells (erythrocytes) by binding the oxygen molecules to the haemoglobin molecules (oxyhaemoglobin). Depending on the content of oxygen, haemoglobin molecules vary in their magnetic properties. Oxyhaemoglobin is diamagnetic (no net spin), and desaturated haemoglobin molecules (deoxyheamoglobin) are paramagnetic, and therefore magnetically susceptible. This fact and the previous finding that deoxyhaemoglobin influence T2* values due to local inhomogenities in the magnetic field were used by Ogawa and colleagues (1990). They observed for gradient echo images a signal loss in brain areas in which deoxygenated blood circulated (i.e. voxel appear darker on the image) and vice versa in areas with a high volume of oxyhaemoglobin an increase of the measured MR signal on T2* images (i.e. voxel appear brighter).

Thus, activation in the brain requires oxygen and therefore an increased regional cerebral blood flow (CBF) is observable. However, much more oxygen is delivered than is finally absorbed what leads to a reduction of the oxygen extraction fraction (OEF). The fact, that the oxygen metabolic rate (CMRO2) increases less than the blood flow caused an accumulation of oxygenated blood in the venous. This observation concerning the blood flow and the local increase of the MR signal due to deoxygenated haemoglobin produce the BOLD effect. The BOLD signal can be localized within a range of millimetres, but compared to other imaging techniques such as EEG the temporal response is rather slow, peaking at around 6 sec after a stimulus onset (see Figure 2.1).

The basic principles of fMRI are well investigated, however, the exact connection between these processes (such as CBF and metabolic process) and the neural activity are still not understood completely. There is an ongoing debate about these relationships and other possible underlying reasons, but will not be discussed here. Nevertheless, neither legitimate criticism about the still unclear connection nor the fact that fMRI has a comparatively slow temporal resolution could detract the fact that functional magnetic resonance imaging is a remarkable technique with a good spatial resolution that is non invasively and go without the injection or exposure with any radiation. It is an innovative method to shed light on the question of involved underlying brain structures and therefore, used in the studies that are described in detail in the next chapters.

2.1.2 Diffusion-weighted imaging and diffusion tensor imaging

Magnetic resonance imaging also provides a method to investigate the neuroanatomical structure of the brain. Magnetic resonance diffusion-weighted imaging (DWI) detects the microscopic motion of water molecules in the brain.[3] This technique can be used to visualize major fiber tracts in the brain by measuring the motion,

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[3] The following descriptions are based on Johansen-Berg & Behrens, 2009, and Mori, 2007.

so-called diffusion along white matter axons. Molecules such as the water molecules diffuse randomly in a fluid (this is called intra-voxel incoherent motion, or Brownian motion). Diffusion-weighted imaging is based on the fact that in biological tissues such as the white matter of the brain, water molecules cannot freely diffuse (isotropic diffusion). They are restricted in terms of their direction of the diffusion by the structure of the surrounding tissue. In e.g. the white matter, the water molecules diffuse mainly along myelinated axonal fiber bundles and thus, it results in a so-called anisotropic diffusion. Information about the direction of the anisotropy axis in a voxel obtained in a DWI scan can deduce the underlying structures of the sample, such as white matter tracts.

Measuring a whole brain sample and recording all possible orientations would be too time consuming. Therefore, a mathematical model is used that calculates on the basis of only a few orientation directions, and possible fiber angles the extent of anisotropy. One of these models is called diffusion tensor imaging (DTI) that estimates local diffusion properties. This imaging method calculates tensors by using information about local changes in anisotropic diffusion inside of the brain. It measures whether or not water molecules diffuse in a certain direction (fractional anisotropy), and determines the direction of a particular diffusion to extract information about axonal anatomy.

One way to measure diffusion in the brain is, described in simple terms, the application of a pulsed magnetic field gradient that creates a linear magnetic field inhomogeneity. That results in a weaker or completely loss of the MR signal as a result of differences in precession of the protons and thus, a dephasing of spin coherence. In a diffusion-weighted imaging sequence another strong gradient is applied with the same magnitude but in the opposite direction to rephase the spins. A signal elicits because of the diffusion of the water molecules, they move out of their former position and experience now a different gradient strength compared to the first gradient. Thus, the still existing dephasing causes a loss of the diffusion-weighted

MR signal. Diffusion tensor images are yielded now by acquiring one image without gradients (b = 0) and then a number of images with applied diffusion gradient that collects information about a number of chosen orientations. In general, six diffusion images are measured along six independent axes, since six constants are needed to calculate a diffusion ellipsoid that represents a single tensor. A tensor is a symmetric 3x3 matrix of three eigenvectors and three eigenvalues that describe the direction and distance of diffusion in a given time. Fractional anisotropy (FA) values describe the degree of anisotropy and are calculated from the eigenvalues of the diffusion tensor.

So far, DTI provides an excellent possibility to study in vivo white matter pathways and their anatomical integrity. The method is still prone to false positive and false negative findings caused by e.g. axonal crossings, but nevertheless, being aware of these problems DTI provides a further step to understand the relationship between structural neuroanatomy and functional activity in the brain.

Part III

EMPIRICAL INVESTIGATION

3

RESEARCH QUESTIONS

The present dissertation takes a closer look at the neural basis of syntactic processing of German speaking children at the age of five to six years old. The specific goal of the study was to examine the use of case-marking information when assigning thematic roles to the sentential arguments in canonical and non canonical sentences. It is currently unknown what underlying neural basis supports the processing of syntactically complex sentences in the developing brain. Do the same temporo-frontal networks found in adults support syntactic processes in children? So far, very little is known about the neural networks that are involved in the processing of specific language cues per se. Based on prior findings in behavioural and functional imaging studies in children, it was hypothesised that children at this age show a significant poorer behavioural performance in non canonical object-initial sentences compared with adults. Furthermore, children at this age are expected to be sensitive to case-marking information, but do not reliable use this information for sentence comprehension. Interestingly, recent developmental studies found high interindividual differences (Ettinger-Veenstra et al., 2010; Yeatman et al., 2010; Nuñez et al., 2011). The fMRI studies reported relations between language proficiency in children and activation in the left frontal brain areas. These led to the following central research questions:

- What are the neural underpinnings of processing syntactically more complex sentence in children at the age of five to six-years? Are similar brain areas involved as found in adults?

- Can individual differences in the functional data be explained by individual language proficiency?

- How does the language proficiency influence the strategies used for thematic role assignment in object-initial sentences?

- At this age, white matter structures in the developing brain are not completely myelinated. Do differences in fractional anisotrophy (FA) within language related brain areas correlate with language proficiency?

These questions were addressed in a series of experiments, utilizing behavioural, functional imaging (fMRI), and structural imaging (DWI) methods.

4

BEHAVIOURAL DATA

The behavioural session was assessed for several crucial reasons. First, to be able to possibly exclude participants from the subsequent fMRI study due to performance results below an expected range in the language tests, due to left-handedness, or a poor result in the audiometry. Second, receptive grammatical development was assessed to gain a general overview about the level of language competence, and most importantly, to obtain behavioural correlates for the subsequent functional data collection. Third, previous behavioural comprehension studies with German-speaking children reported a relatively late acquisition of case-marking information as a cue to assign thematic roles in a sentence (Chan et al., 2009; Dittmar et al., 2008; Lindner, 2003; Primus & Lindner, 1994; Schaner-Wolles, 1989). According to their findings, German children do not detect the strength of the case-marking cue before the age of five to six years. Nevertheless, findings from an ERP-study by Schipke and colleagues (2012) suggest that children at the age of 4;6 are already sensitive to case-marking information, although they do not use it for sentence interpretation. Moreover, even thought the results showed that 6-year-olds still do not perform above chance in non canonical sentences, the ERP effects indicated that the underlying processes are already similar to adults.

In the present study, children were tested in a paradigm consisting of two different types of sentence structures. A (1) canonical structure where the subject of the sentence preceded the object and a (2) non canonical sentence structure where the object was in the initial position. Thereby, sentential arguments were unambiguously case-marked. Children's performance was assessed in order to evaluate their competence in accomplishing sentence comprehension of non canonical sentences compared with adults, who were tested using the same paradigm.

4.1 Methods

4.1.1 Participants

Children Thirty children (12 female and 18 male) were recruited form the local Kindergartens of Leipzig and the Infant Database of the Max Planck Institute for Human Cognitive and Brain Sciences in Leipzig. All participants came from monolingual German families and were between 4;08 and 6;10 years of age (mean age: 5;09). According to parental information, no child had any known hearing deficits or neurological, medical, or psychological diseases. No child was left-handed but eight children were ambidextrous (modified version of Oldfield, 1971). Prior to their participation, parental informed consent was obtained for all children.

Adults Twenty-two adult participants (11 female and 11 male) took part in the experiment. All participants were native speakers of German (age range: 21 to 33; mean age: 25.1). All were right-handed, as assessed by a German version of the Edinburgh Handedness Inventory (Oldfield, 1971). These participants reported having no known hearing deficits or neurological problems.

4.1.2 Procedure

The behavioural testing procedure for the children encompassed a total of 1-1.5 hours and was distributed over 2 days. A first testing session was conducted before the fMRI data acquisition to assess language skills, handedness, hearing, and also included the mock scanner training. In a second behavioural session which was scheduled right after the fMRI experiment, all children participated in a picture-matching test that was related to the presented stimuli in the scanner.

The behavioural testing procedure for the adults comprised only the post-scanner picture-matching test. Handedness score was acquired in a previous study.

Pre-scan behavioural testing (only children)

In the first session a receptive language development test, the TROG-D (Fox, 2008) was employed. This test is a measure of verbal comprehension of syntax standardized for 3 to 10-year-olds; it uses a multiple-choice format to assess the receptive grammatical development of children. The child sat together with the experimenter in a separate room and was asked to choose one out of four pictures, which depicts the sentence spoken by the experimenter.

Post-scan behavioural testing (children & adults)

Material

For the behavioural part of the experiment, 24 sentences were used. The sentences were of the same type that were successfully applied in a previous behavioural and ERP study by Schipke and colleageus (in press). The sentences had the following structures:

1a Der Igel küsst den Frosch.
[the hedgehog]$_{NOM}$ kisses [the frog]$_{ACC}$

The hedgehog kisses the frog.

1b Den Frosch küsst der Igel.

[the frog]$_{ACC}$ kisses [the hedgehog]$_{NOM}$

The hedgehog kisses the frog.

Using this type of sentence, the aim was to investigate the acquisition of the case-marking cue for argument interpretation. Other cues (e.g., animacy and prosody for argument interpretation) were controlled. Nouns and their combining transitive verbs were chosen after a pre-test with 30 children (ten 3-year-olds, ten 5-year-olds, and ten 6-year-olds) to ensure that all children knew the relevant words and named every actor and its action consistently.

In the behavioural part of the study 12 sentences with a (1a) subject-initial structure and 12 sentences with an (1b) object-initial structure were used. All nouns corresponding to animals, were masculine, thus belonging to the strong declination type. In German, nominative and accusative are unambiguously case-marked for masculine nouns only, by the case-marking of the definite article preceding the noun. Thus, in our experiment, all nominal constituents in a sentence were unambiguously marked for accusative or nominative by the definite article. For the behavioural test sentences, the following six nouns and six verbs were used:

Nouns: Igel (hedgehog), Hund (dog), Tiger (tiger), Vogel (bird), Käfer (beetle), Frosch (frog)

Verbs: ziehen (to pull), küssen (to kiss), waschen (to wash), malen (to paint), tragen (to carry), kämmen (to comb)

Every animal occurred equally as often as an actor, as an undergoer, and in interaction with other animals.

Corresponding pictures were created using Adobe illustrator and featured two animals engaging in a particular action. Animals were controlled for size and position within the picture frame. The illustration of the action performed by one of the two animals was counterbalanced in order to equally show the actor (agent) to the right or to the left of the undergoer (patient). Thus, each picture card contained two pictures in a counterbalanced order aligned on the horizontal axis, i.e., a picture corresponding to the respective test sentence and another picture with the actor and undergoer in a reversed version.

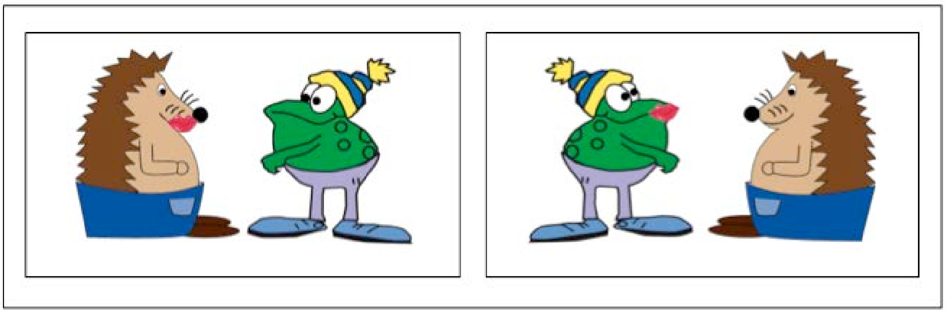

Figure 4.1: Picture-matching task.

Procedure

The behavioural picture-matching test was carried out after the scan session. Children sat together with the experimenter in a separate room and first familiarized themselves with the animal pictures by naming each animal separately. Next, the task was introduced: "Now, I am going to show you a picture card with two pictures on it. I am going to ask you to find a picture for me". Then the first picture card was presented on the table and the experimenter would ask the child: "Show me . . . " followed by the test sentence. All test sentences were taken from the experimental material of the scanner session. Number of correct pointing was counted. The experimenter repeated each test sentence maximally twice. The order of the test sentences was pseudo-randomized.

The behavioural testing procedure for adult participants included only the post-scan picture test and was conducted similarly to the children testing.

4.2 Results

4.2.1 Children

In the receptive language test (TROG-D), 18 children performed within the expected T-score of 50 ± 10 and eleven children performed above this mean result for this age group, one child performed even below the expected t-score. In the behavioural picture-matching task conducted after the scanner session, participants had on average 80.4% (SD 12.4%) correct responses. Mean accuracy for the subject-initial condition on the picture task was 95.1% (SD 7.4%) and for the object-initial condition 66.7% (SD 23.2%), suggesting a significant advantage for subject-initial sentences ($t(29) = 6.2$, $p < .001$). Importantly, however, children performed significantly above chance in both conditions (subject-initial: $t(29) = 33.4$, $p < .001$; object-initial: $t(29) = 3.9$, $p < .001$). Mean accuracy for subject-initial sentences was correlated with age (Pearson $r = .46$, $p = .01$), while for object-initial sentences it was not ($r = -.09$, n.s.). Due to these results, children were divided by median on their age in a younger and older subgroup. No differences were found between these two groups in their performance in the TROG-D ($t(28) = 1{,}73$, n.s.) and in the picture matching task (subject-initial: $t(28) = -1.71$, n.s.; object-initial: $t(28) = .25$, n.s.).

Additionally, on the whole group level ($n = 30$), significant correlations were found between the results of the TROG-D and the performance in the post-scan picture test; percentile rank in the TROG-D and mean accuracy for picture task in general ($r = .36$, $p = .05$) and for object-initial sentences ($r = .44$, $p = .01$).

4.2.2 Adults

In the post-scanning picture-matching task, adult had on average 98.9% (SD 3.7%) correct responses, and as expected, participants performed significantly above chance in both sentence conditions (99.6% correct responses in subject-initial: $t(21) = 131.1$,

$p < .001$; 98.1% correct responses in object-initial: $t(21) = 39.5$, $p < .001$). No significant difference was found between the two sentence conditions ($t(21) = 1.7$, n.s.).

Hence, adults and children performed in both conditions above chance. Nevertheless, independent t-tests revealed a significant difference between the performance of adults and children in both conditions (for subject-initial: $t(33.45) = 3.2$, $p = .003$; object-initial: $t(33.66) = 7.1$, $p < .001$), with the adults outperforming the children.

4.3 Discussion

A first behavioural test was administered before the scan session in order to assess the general receptive grammatical development of the children. Twenty-nine children showed typical language development as obtained by the standardized values of the TROG-D and were included in the subsequent functional MRI data sample. Based on low scores on the language test one child had to be excluded from the subsequent fMRI study. Furthermore, 37% of the children in the current study performed above the expected mean in the TROG-D which indicates that their receptive grammatical skills are overall above average in their age group.

A second behavioural test (a picture-matching task) was conducted which focused especially on children's ability to deal with object-initial sentences. The behavioural results suggest that the children are able to process case-marking information even in object-initial sentences. However, their responses were less accurate in object-initial (66,7%) as compared to subject-initial sentence constructions (95,6%). Thus, it seems that five to six-year-olds have not yet completely reached the developmental level to solely rely on case-marking information; the results suggest a significant advantage for a subject-initial sentence structure at this age. In spite of these results, children performed above chance level in both conditions. This result is in contrast to other studies (Lindner, 2003; Schipke et al., 2012), where children were found to perform not significantly above chance level for object-initial sentences until the age of seven years. Despite the similarities between the present study and the study by Schipke and colleagues (in press), the present study differed with respect to the age groups. The group of children in the present study was, on average, somewhat older and had with 26 months an expanded age range. A division into a younger and an older subgroup of the tested children revealed no differences in their performance in the behavioural tests (TROG-D and picture matching task). Besides, Schipke and colleagues (2012) also stated that children at the age of six years seem to be able to use case-marking cues for comprehension, but did just not reach the significance level to be considered above chance. The differences between their results and the present results suggest a smooth transition in their performance enhancement around the age of five to six years.

As expected, in the post-scan picture-matching test, adults performed perfectly in subject-initial (99.6%) as well as in object-initial sentences (98.1%). No significant differences were found in their performance between different types of sentence structure. Only two participants made mistakes in the picture test at all, while 91% of the adult participants performed without any mistake. This finding indicates that these short object-initial sentences are not challenging enough for adults.

Our findings in the performance of the children indicate that five to six-year-olds are already sensitized to case-marking cues, but they have not yet completely integrated these language markers into their grammatical knowledge. Thus, they do not entirely rely on these language cues for sentence interpretation. A positive correlation between their performances in the object-initial sentences in the picture-matching test and the TROG-D indicates that a general grammatical knowledge is important to use case-marking information for sentence interpretation in German. The results reveal a still existing development gap in children at this age that has to be overcome to achieve adult-like performance.

5

FMRI STUDY IN ADULTS

The first functional MRI experiment aimed to investigate sentence processing in adults and furthermore, served as a control for the fMRI study in children. Adults are far beyond the level of acquiring case-marking cues for argument interpretation in sentences. Using morphological cues like case-marking information of the German article declension is assumed to be an inherent process for sentence understanding. The sentences used in this study were mainly developed for sentence processing in children and were successfully applied in a previous behavioural and ERP study in pre-school children (Schipke et al., 2012). For adults, the sentence paradigm consisting of one verb and two arguments was hypothesized to be minimal challenging and therefore, the activation differences between the conditions were expected to be less pronounced.

An extensive amount of data from fMRI studies exists investigating syntactic processing in adults. Most studies examined processing of syntactic complexity by varying the argument hierarchies in languages which provide additional information relevant for argument interpretation (e.g., case-marking). The studies report that syntactic processes are mainly subserved by the left inferior frontal gyrus (IFG) and the left superior temporal gyrus and sulcus (STG/STS). Both areas show stronger activation for the processing of grammatically more complex sentences (e.g., scrambling) than sentences with canonical word order (Röder et al., 2002; Ben-Shachar et al., 2004; Bornkessel et al., 2005; Grewe et al., 2005; Friederici, Fiebach, et al., 2006; Obleser et al., 2011). Interestingly, imaging data also indicate that activation within the left IFG (BA 44) increases parametrically with syntactic complexity, as operationalized by the number of permutations of case-marked arguments in a sentence (Friederici, Fiebach, et al., 2006).

Other fMRI studies found evidence that this area is activated by syntactic complexity in adults and children (Bornkessel et al., 2005; Friederici, Fiebach, et al., 2006; Nuñez et al., 2011; Röder et al., 2002; Yeatman et al., 2010). However, this effect was not replicated in all of the studies and often only ROI analysis could reveal activation differences in this region (Ben-Shachar et al., 2004; Yeatman et al., 2010). Besides, the present fMRI experiment utilized a passive listening task that had the advantage of targeting relatively normal language processing and excluded task-specific processes that could interfere with the data collection. Nevertheless, many fMRI studies in adults that found stronger activation for the processing of grammatically more complex sentences predominantly included an active task already during the scan session (e.g., a comprehension task in Ben-Shachar et al., 2004; Bornkessel et al., 2005; Friederici, Fiebach, et al., 2006; or error detection in Röder et al., 2002). Due to these reasons, a subsequent ROI analysis focusing on the left IFG was conducted to unveil the predicted difference in the contrast of object-initial compared to subject-initial.

5.1 Methods

5.1.1 Participants

Twenty-two adults (11 female and 11 male) that took already part in the behavioural picture-matching task were participants in the fMRI study after giving informed consent. All adults were native speakers of German, were between 21 and 33 years of age (mean age: 25.1), were right-handed, as assessed by a German version of the Edinburgh Handedness Inventory (Oldfield, 1971), and had normal hearing. No participant had any history of neurological or psychiatric disorders. The study was approved by the Research Ethics Committee of the University of Leipzig, Germany.

5.1.2 Stimulus material

For the fMRI experiment, the same sentences as in the behavioural picture-matching test were used. In addition, another six pretested transitive verbs (schieben (to push), kratzen (to scratch), schlagen (to hit), fangen (to catch), beißen (to bite), and treten (to kick) were included making a total of 96 test sentences: 24 in the subject-initial condition (1a) and 24 in the object-initial condition (1b). Furthermore, in order to minimize the predictability of the type of sentences structure 24 ungrammatical sentences with a double nominative (1c), and 24 ungrammatical sentences with a double accusative (1d) were included in the presentation. Thus, if a sentence starts e.g. with the definite article “den”, the participant could not predict which sentence structure is presented; in this example there is a fifty percent chance of an object-initial and a double accusative condition, respectively. See the following examples:

1a Der Igel küsst den Frosch.

[the hedgehog]$_{NOM}$ kisses [the frog]$_{ACC}$

The hedgehog kisses the frog.

1b Den Frosch küsst der Igel.

[the frog]$_{ACC}$ kisses [the hedgehog]$_{NOM}$

The hedgehog kisses the frog.

1c *Der Igel küsst der Frosch.

[the hedgehog]$_{NOM}$ kisses [the frog]$_{NOM}$

*The hedgehog kisses the frog.

1d *Den Frosch küsst den Igel.

[the frog]$_{ACC}$ kisses [the hedgehog]$_{ACC}$

*The hedgehog kisses the frog.

Participants were presented with mildly child-directed spoken sentences. All stimuli were recorded in a soundproof chamber by a female trained native speaker of German. After recording, sentences were digitized (44.1 kHz/16bit sampling rate, mono) and normalized in root mean squared amplitude. The last noun phrase was afterwards cross-spliced to assure comparability and to avoid prosodic cues. The resulting audio files had a mean duration of 2368 milliseconds (SD = 134 ms), and did not differ between the conditions (t(46) $<$ n.s.).

5.1.3 Procedure

All participants were briefed on the experiment, and any questions were answered outside the scanner. They got a written instruction that it was a study of language processing and that they would hear simple sentences about various animals acting with each other. The participants knew that they would listen to stimuli for a children experiment and that the sentences could be grammatically correct or incorrect. To ensure attentive listening, they were told to listen to the sentences carefully because afterwards they had to answer questions about the sentences and the involved actions and animals.

An experimental session consisted of 120 events lasting 6 seconds each (i.e. 3 scans of TR = 2000 milliseconds (ms)), resulting in 16 minutes duration per session. Within each 6 seconds event (except for 24 null events, that was a silent baseline), a single sentence was presented. All participants completed 24 sentences per condition (subject-initial, object-initial, double nominative, and double accusative sentence structure) plus 24 null events (silent baseline). All events were presented in an event-related, pseudo-randomized design according to the following constraints:

1. No more than two consecutive events belonging to the same stimulus condition;
2. No more than four consecutive events containing either correct or incorrect stimuli.

Stimulus onset was jittered randomly relative to the beginning of the first scan of each single event either 0, 400, 800, 1200 or 1600 ms to facilitate for measurements to be taken at numerous time points along the BOLD signal curve, thus systematically reading the signal and increase the resolution of the BOLD response (Miezin et al., 2000). The stimuli were presented acoustically via headphones while a screensaver (a rotating cube) that didn't involve any kind of human or animal action was presented via LCD display glasses.

5.1.4 Data acquisition and analysis

Data acquisition

Twenty-six axial slices (3 mm thickness, 1 mm inter-slice distance, field of view (FOV) 19.2 cm, data matrix 64x64 voxels, in plane resolution of 3 x 3 mm) were acquired every 2 seconds (s) during functional measurements (BOLD sensitive gradient echo-planar-imaging (EPI) sequence, time repetition (TR) = 2 s, time echo (TE) = 30 ms, flip angle 90°, acquisition bandwidth = 100 kHz) with a 3 Tesla scanner (Siemens TimTrio, Germany).

After functional imaging, a T1-weighted 3D magnetization-prepared rapid gradient-echo (MP-RAGE) sequence (data matrix 256 x 256, TR = 1.48 s, TE = 3.46 ms, inversion time (TI) = 7.4 s, flip angle 10°, bandwidth 190 kHz, space resolution 1 x 1 x 1.5 mm) was acquired with a non-slice-selective inversion pulse followed by a single excitation of each slice. These anatomical data were used to co-register functional images before normalized to a chose representative brain image of one of the adult participants. This brain was previously rotated into the stereotactic coordinate system and transformed to a standard size (Talairach & Tournoux, 1988). Therefore, it served as a template for normalization and anatomical ROI definition.

Data analysis

Functional imaging data processing was performed using the software package LIPSIA (Lohmann et al., 2001). This software package contains tools for pre-processing, co-registration, ROI-definition, statistical evaluation, and visualization of fMRI data. Functional data were entered into a distortion correction using a field-map scan and corrected for motion artefacts. Movement correction was allowed up to 3 mm (= one voxel). Subjects were excluded if head movement exceeded this range. To correct for the temporal offset, data were corrected for slicetime acquisition differences using cubic-spline interpolation. Low frequency signal changes and baseline drifts were removed by applying a temporal high pass filter to remove frequencies below 1/70 Hz. A spatial smoothing filter with a kernel of 6.0 mm^3 FWHM was applied.

The anatomical images acquired during the functional session and previously rotated into the stereotactic coordinate system and were transformed to a standard size by linear scaling and then co-registered with the reference brain by an additional non-linear normalization known as 'demon matching' (Thirion, 1998). The transformation parameters obtained from these steps were subsequently applied to the preprocessed functional images after aligning the data with the individual anatomical image that serves as reference data set by performing a rigid, affine linear transformation registration with six degrees of freedom (3 rotational, 3 translational).

Using the software package LIPSIA, the statistical evaluation was based on a least-squares estimation using the general linear model for serially autocorrelated observations (Friston et al., 1994). The design matrix was generated with a synthetic hemodynamic response function (Josephs et al., 1997; Friston et al., 1998) and their temporal and dispersion derivatives. To take the autocorrelation of the data into account for statistical evaluation, a two-pass whitening procedure was performed (Worsley et al., 2002). Movement correction parameters were included into the model as regressors. For each participant, four contrast images were generated to represent the main effects of each of the conditions (subject-initial, object-initial, double nominative, and double accusative) contrasted with a baseline (null events), and a fifth contrast was generated to represent the effect of object-initial sentences compared to subject-initial sentences.

Subsequent random-effects group analysis consisted of a one-sample t-test across the contrast images of all participants to indicate whether observed effects were significantly distinct from zero. The resulting t-statistics were transformed to standard normalized distribution. To protect against false-positive activations, a multiple comparison correction tested for cluster size (number of voxel) and the minimal p-value per cluster, based on Monte Carlo simulations. The Monte Carlo simulation generates voxels at a rate equal to the significance criterion specified, proportional to the total number of voxels in the dataset. It calculates a cluster size that corresponds to the true false-positive rate for these conditions. A combination of single voxel probability thresholding on the one hand, and cluster-size and cluster-z-value thresholding on the other hand, was used to take account of the possibility that even small clusters may be true activations if the effect is strong enough (Lohmann et al., 2008). Using 1000 iterations, a minimum cluster size at $z > 3.09$ was determined in order to arrive at a false positive cluster probability of $p < .05$. Following this protocol, the statistical threshold was then applied to all voxels in the data. Thus, a cluster was qualified as being significant if it was either larger than 999 mm^3 (37 voxel) or had a maximum of $z > 3.09$, or both, resulting at a corrected p-value of $p < .05$.

Region of interest analysis

A subsequent region of interest (ROI) analysis focused on the left IFG. Prior fMRI studies found evidence that this area is activated by syntactic complexity in adults and children (Röder et al., 2002; Bornkessel et al., 2005; Friederici, Fiebach, et al., 2006; Yeatman et al., 2010; Nuñez et al., 2011), and significant differences in the contrast of object-initial compared to subject-initial were expected. However, this effect was not replicated in all studies and often only ROI analysis could unveil activation differences in this region (Ben-Shachar et al., 2004). Because the focus of the present study was on Broca's area, the cytoarchitectonic probabilistic maps of the Juelich database (Amunts et al., 1999) were used to build two regions of interest for BA 44 and BA 45. These ROIs were thresholded to p = .05 to avoid an overlap of these two areas. These two ROIs were analyzed by direct statistical comparison between the object-intial and the subject-initial (factor *word order*). To do so, the percent signal change (PSC) was calculated per condition as a function of time (averaged across all subjects) and analyzed for mean PSC per condition in a time window from 3 to 10 s post stimulus onset (also averaged across all subjects) in a repeated-measures GLM including Greenhouse-Geisser correction.

5.2 Results

5.2.1 Baseline contrasts

When contrasted with a silent baseline, the subject-initial and the object-initial condition activated similar networks in the whole brain analysis. Table 5.1 describes the region of activation, Brodmann areas, Talairach coordinates for the peak activation, number of active voxels, and peak z-value. Bilateral clusters of activation were found in the STG/STS, premotor cortex (PMC), IFG, superior parietal cortex (SPC), occipital cortex (OC), brainstem, thalamic regions and striatum (Figure 5.1A & 5.1B). Both conditions elicited cluster of activation in the left IFG in BA 44, additionally the object-initial condition activated BA 45, an activation that is part of the large left STG/STS cluster and therefore not separately listed in the table. Strong and extensive bilateral activation in the STG/STS was also observed in both violation sentences contrasted with a silent baseline (Figure 5.1C & 5.1B). Additional areas of activation included the PMC bilaterally, the striatum, cerebellum, and the left IFG. In sentences with a double nominative marked article additional activation was

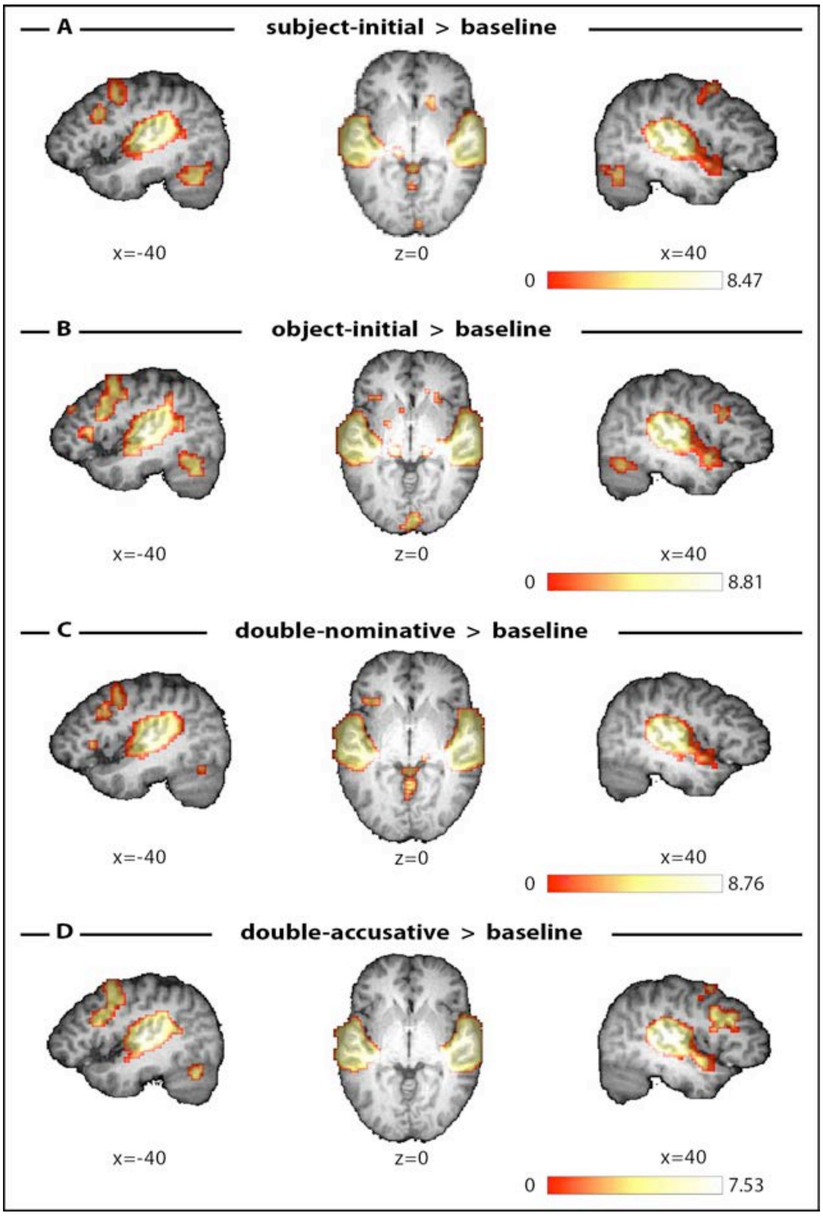

Figure 5.1: ***Main effects contrasted with baseline (null events) in adults.*** *Effects mapped on the best brain. Observed activation for (A) subject-initial sentences, (B) object-initial sentences, (C) for double-nominative sentences, (D) double-accusative sentences. All activation thresholded to p =.05, corrected.*

Table 5.1: Overview of significant clusters (in mm^3), random-effects contrast, thresholded to p < .05, corrected. Peaks in a bigger cluster are reported, if they are bigger than 81 mm^3 (3 voxel). If a region has more than one peak, just the one with the highest z-value is reported. Location is described in Talairach coordinates. Table shows following contrasts in adults: (a) subject-initial > baseline, (b) object-initial > baseline.
Ant = anterior, CC = cingulate cortex, IFG = inferior frontal gyrus, MI = primary motor cortex, OC = occipital cortex, PCC = posterior cingulate cortex, PMC = premotor cortex, post = posterior, SPC = superior parietal cortex, STG = superior temporal gyrus.

region	**BA**	**X**	**Y**	**Z**	**cluster-size**	**z-value**
a. subject-initial > baseline						
right STG	22	53	-16	3	43956	8.48
left STG	22	-55	-25	6	51057	7.76
right cerebellum		2	-43	3	837	4.93
left PMC	6	-46	-4	48	3861	4.62
left cerebellum		-40	-67	-27	6750	4.60
right PMC	6	47	-4	42	1485	4.49
brain stem		-13	-28	0	1134	4.07
right caudate		14	23	6	3672	4.04
left caudate		-19	23	12	1458	3.90
left IFG	44	-40	14	27	2079	3.74
right SPC	7	2	-76	45	2187	3.71
b. object-initial > baseline						
right STG	22	56	-16	3	48330	8.81
left STG	22	-46	-22	6	54756	8.23
right cerebellum		8	-85	-21	14445	5.31
left cerebellum		-37	-67	-27	9099	4.91
brain stem		-13	-28	0	3213	4.86
right SPC	7	2	-82	51	1431	4.82
right ant. thalamus		11	-1	9	7776	4.68
right PCC	23	23	-22	33	1404	4.64
left PMC	6	-4	2	57	2754	4.62
left IFG	44	-40	14	21	12771	4.57
right PMC	6	8	14	48	2376	4.40
left caudate		-13	23	6	4239	3.92
left SPC	7	-4	-82	54	81	3.83
left OC	18	-4	-100	0	81	3.73

observed in the left IFG, in BA 45, the frontal operculum (FO), and in the isthmus of cingulate gyrus (Table 5.2).

Table 5.2: Overview of significant clusters (in mm^3), random-effects contrast, thresholded to p < .05, corrected. Peaks in a bigger cluster are reported, if they are bigger than 81 mm^3 (3 voxel). If a region has more than one peak, just the one with the highest z-value is reported. Location is described in Talairach coordinates. Table shows following contrasts in adults: (c) double nominative > baseline, and (d) double accusative > baseline.
Ant = anterior, CC = cingulate cortex, IFG = inferior frontal gyrus, MI = primary motor cortex, OC = occipital cortex, PCC = posterior cingulate cortex, PMC = premotor cortex, post = posterior, SPC = superior parietal cortex, STG = superior temporal gyrus.

region	BA	X	Y	Z	cluster-size	z-value
c. double nominative > baseline						
right STG	22	56	-19	3	47574	8.76
left STG	22	-37	-28	9	56673	8.18
left PMC	6	-4	2	57	2565	4.66
right CC	29	2	-52	0	1458	4.34
right PMC	6	2	2	57	2241	4.17
left cerebellum		-7	-91	-18	540	4.14
left ant. insula		-25	20	6	1755	4.02
right caudate		23	17	6	1080	3.98
left CC	29	-4	-43	-3	162	3.71
right cerebellum		2	-79	-9	162	3.25
d. double accusative > baseline						
right STG	22	56	-16	3	42822	7.53
left STG	22	-55	-25	6	57726	7.18
left PMC	6	-4	2	54	2403	4.91
right putamen		26	26	9	2187	4.61
right PMC	6	47	17	24	4536	4.51
left cerebellum		-10	-82	-27	2295	4.31
right MI	4	47	-1	42	1728	4.12
left putamen		-22	5	15	1566	4.06
right cerebellum		14	-85	-18	702	3.56

5.2.2 Direct contrast

In a direct comparison of object-initial versus subject-initial sentences no activation differences were found after applying the threshold criterion of 999 mm^3 or a maximum of $z > 3.09$.

5.2.3 Regions of interest analysis

Table 5.3 shows the results of a region of interest analyses focusing on the left IFG, the two ROIs (cytoarchitectonic probabilistic maps of BA 44 and BA 45) were analysed by direct statistical comparison between the object-intial and the subject-initial sentences. Mean percent signal change in this brain region indicated that sentences with object-initial structure elicited a stronger hemodynamic response than subject-initial sentences. In a repeated-measure analyses with factors *ROI*, and *word order*, a significant main effect of factor *ROI* (F(1,21) = 7.3, p = .01) and a significant interaction of factor *ROI* by *word order* (F(1,21) = 4.3, p = .05) was found. A closer examination revealed also a significant main effect of *word order* in BA 44 (t(21) = –2.2, p = .04).

Table 5.3: (a.) Results of repeated-measures GLM in adults for region of interest analysis in Broca's area with within-subject factors ROI (BA 44 and BA 45) and word order (subject-initial vs. object-initial), (b.) and post-hoc paired T-tests.

ROI	**effect**	**Df**	**f-value**	**p-value**
a.				
IFG	*ROI* (BA 44 & BA 45)	1,21	7.3	.01
	word order	1,21	3.3	n.s.
	*ROI * word order*	1,21	4.3	.05
b.				
BA 44	*word order*	21	-2.2	.04
BA 45	*word order*	21	-.18	n.s.

5.3 Discussion

The first study investigated the processing of case-marking and argument structures in adults. The behavioural testing already indicated that adults are not challenged to understand these relatively simple object-initial sentences designed for a study in children. Therefore it is not surprising that no differences in their performance were found in the behavioural testing between the two sentence structures. The whole brain results of the imaging study confirm this expectation resulting from the behavioural findings.

In the first place, the conditions were contrasted with a silent baseline to get a general overview about the underlying processes indicated by their location in the brain. In imaging studies in adults and children, it is an appropriate procedure to test a condition to a silent baseline or a noise condition (Wong et al., 2002; Schön et al., 2000; Brauer & Friederici, 2007; Nuñez et al., 2011; Badcock et al., 2012). Nevertheless, the interpretation of these results should be judged cautiously, because they do not indicate any statistical differences between the conditions. Therefore, in the present study a direct comparison of the two correct sentence conditions was conducted in a subsequent step.

Both correct conditions (subject-initial sentences and the object-initial sentences) contrasted with a silent baseline revealed similar activation (Figure 5.1A & 5.1B), which was observed mainly bilaterally along the entire STG/STS, a typical activation for auditory encoding (Scott et al., 2000; Giraud & Price, 2001; Liebenthal et al., 2005). Additionally, the object-initial sentences revealed a stronger involvement of the left IFG. This activation is in line with previous findings that found IFG activation for language processes. However, although extensively studied, the functions supported by IFG and its' subparts are still debated (Just et al., 1996; Stromswold et al., 1996; Friederici, Fiebach, et al., 2006, Friederici et al., 2010; Grodzinsky & Santi, 2008; Rogalsky & Hickok, 2011). Activation for the correct conditions was mainly found in Broca's area, a brain region found to subserve different kinds of cognitive processes. While some researchers claim that this area is relevant for syntactic processes (Caplan et al., 2000, 2008; Makuuchi et al., 2009; Friederici et al., 2010; for an overview see Grodzinsky & Friederici, 2006), others propose it is partly related to working memory mechanisms that are associated with language processes (Fiebach et al., 2004, 2005), or simply rehearsal (Rogalsky & Hickok, 2011). In addition, the left IFG can be divided into several subregions which are associated with different aspects of sentence processing: whereas BA 44 is linked to syntactic structure building (Friederici, 2002), BA 45/47 is associated supporting semantic processes (Bookheimer, 2002; Friederici, 2002; Hagoort, 2005). More recently, BA 45 has been subdivided receptor-architectonically in an anterior portion (45a) and a posterior portion (45b) with the latter bordering area 44 (Amuts et al., 2010). Considering that object-initial sentences are expected to be syntactically more complex than subject-initial sentences in general, an increased activation in the left IFG for object-initial sentence contrasted with a baseline was predicted. And indeed, a more pronounced activation in the left IFG for object-initial sentences was observed in BA 44 as well as in BA 45. However, in the subject-initial condition, the results also indicated an activation peak in BA 44, but not in BA 45. Nevertheless, these observations were not confirmed in the direct comparison between the both conditions as no activation differences were found in a direct contrast on whole brain level. Thus, the direct comparison confirmed the behavioural findings that adults are already highly proficient in processing these simple object-initial sentences.

Strong and extensive bilateral activation in the STG/STS was also observed in both violation sentences contrasted with a silent baseline (Figure 5.1C & 5.1D). Additional areas of activation included the PMC bilaterally, the striatum, the cerebellum, and the left IFG. In sentences with a double nominative marked article additional activation was observed in the left IFG, in BA 45, left anterior insula and in the isthmus of cingulate gyrus. Interestingly, the cluster of activation comprising the left anterior insula and the frontal operculum (FO) was found in the violation paradigm with double nominative and in the object-initial condition only. The frontal operculum has been found activated in imaging studies involving executive functions such as error monitoring (for a review see Taylor et al., 2007) or articulatory rehearsal processes (Fiez et al., 1996; Price et al., 2003; Hurschler et al., in press). However, it was also activated in studies focusing in syntactic encoding and processing of syntactic structure (Friederici et al., 1999, 2000, 2003, 2006). Thus, the observed activation in the FO in object-initial and double nominative sentences could be associated with a local structure building process that is apparently more challenging in non canonical sentences and in sentences with a violated syntactic structure. Therefore, the findings are in line with previous imaging studies that found the FO more activated in sentences containing a syntactic violation compared to syntactically correct sentences (Friederici et al., 2003, 2006, Brauer & Friederici, 2007). Friederici and colleagues (2003) also observed a cluster of activation for the main effect in syntactically correct sentences (compared to baseline), which did not pass the critical cluster size threshold. Furthermore, FO activation was found in studies that compared grammatically correct sentences with word lists (Friederici et al., 2000); those did not include functional words and therefore, the lists did not provide the opportunity to process single words of the lists as possible word combination (e.g. noun phrases, adjective phrase). However, the role of the FO as an indicator for structure building is still discussed controversially (see Rogalsky & Hickok, 2011), and Friederici (2011) argued that many studies failed to find the FO activated for local structure building, because it is a rather automatic process in adults. The findings in the present study raise the question why the second violation sentence condition including a double accusative did not also elicit an increase in activation in that region. A potential explanation comes form the ERP-literature on speech processing. In a study in adults by Frisch and Schlesewsky (2005), the processing of interrogative sentences with a double accusative and a double nominative marked argument was investigated. The authors observed a more pronounced negativity around 400 ms (N400) in sentences with a double accusative than in sentences with a double nominative. Frisch and Schlesewsky suggested that an accusative is thematically more marked than a nominative and therefore, the thematic integration problem is more salient. This conclusion was supported by their speeded-acceptability judgment task: double accusatives were judged as being incorrect more accurately than double nominatives. The authors explained the differences in the N400 effect "by the fact that the accusative is thematically more marked, as it is always [+ dependent]. By contrast, the thematic variability of nominative-marked argument is greater, since they can be either [+ dependent] or [- dependent]." (pp. 494). Consequently, only the nominative can receive the assignment as actor or as undergoer in the transitive event. An accusative marked argument, however, has always the function as undergoer [+ dependent]; and thus, in the first place, there is never a possibility to solve the hierarchizing problem in transitive sentences. Finally, an attempt to perform a hierarchical structure building is also bound to fail in sentences with double nominative used in the present study, but apparently, that failure of the structure building is not as fast to detect in sentences with double nominatives. Unfortunately, due to the poor temporal resolution of fMRI, this hypothesis of temporal processing differences (detection of double nominative > detection of double accusative) could not be proved in this current study.

An effect of syntactic complexity was expected in the left IFG. The fact that the expected activation in this region was not found in the whole brain analysis can be explained by various factors. First, as already above-mentioned, the sentences were designed for a study in children. It seems that the used sentences were too simple to elicit significant differences between the conditions in the adult brain. Second, previous fMRI studies in adults also failed to find Broca's area to be activated for syntactic processes, and were only successful using a region of interest approach (Ben-Shachar et al., 2004). Lastly, many fMRI studies in adults predominantly included an active task already during the scanning session (e.g., a comprehension task in Bornkessel et al., 2005; Friederici, Fiebach, et al., 2006; or error detection in Röder et al., 2002), which is assumed to increase activation differences during sentence processing (Love et al., 2006). However, using the cytoarchitectonic probabilistic maps of the Juelich database (Amunts et al., 1999), the results of a region of interest analysis for BA 44 and BA 45 yielded a significant main effect of *ROI* and a significant interaction between *word order* and *ROI*. As in previous studies, the effect for *word order* turned out to be significant only in BA 44. These results, i.e. a stronger activation for the processing of the more complex object-initial sentences, confirmed the hypotheses that syntactic processes are subserved by Broca's area and are in line with previous studies reporting a stronger activation for the processing of syntactically more complex sentences (Ben-Shachar et al., 2003; Bornkessel et al., 2005; Fiebach et al., 2005; Grewe et al., 2005; Friederici, Fiebach, et al., 2006; Grodzinsky & Santi, 2008; Obleser et al., 2011). The findings suggest that Broca's area, more precisely BA 44, is involved in syntactic structure processing and shows highly sensitivity that can be observed in child-oriented stimuli.

6

FMRI STUDY IN CHILDREN

The second fMRI experiment aimed to investigate the neural basis of syntactic processing in German children using the same stimulus set already applied in the study in adults. The specific goal of that study was to examine the use of case-marking in order to identify “who is doing what to whom” in a sentence. As already pointed out, assigning the role of the arguments in a sentence, German children could theoretically use other cues such as word order, animacy, pragmatic, contextual, or prosodic information. It was assumed and supported by the behavioural testing that children in contrast to adults are challenged by the object-initial structure of the presented sentences. Although behavioural findings indicated that German children do not develop this ability before the age of 7;0 (Lindner, 2003; Schipke et al., 2012), the behavioural results of the present study suggest that even younger children are aware of case-markings and are able to apply them. So far, we know little about the neural networks involved in the processing of syntactically more complex sentences in young children. Up to date, no fMRI study investigated the processing of unambiguously case-marked sentences with subject-initial and object-initial structure in German children at the age of five to six years.

Findings in fMRI studies suggest that sentence processing in children between the ages of 7 to 16 years involves the same brain areas as found in studies investigating syntactic processing in adults (Brauer & Friederici, 2007; Yeatman et al., 2010; Nuñez et al., 2011). However, the studies in children often failed to find significant results at the group level, indicating a high variance in language proficiency. Hence, one aim of this experiment was to shed light on the processing of syntactically complex sentences in the developing brain. Furthermore, a closer look at Broca's area should provided additional information concerning the involvement of this area in syntactic processes in five to six-year-olds.

6.1 Methods

6.1.1 Participants

Data were collected from thirty children who took already part in the behavioural study. Before their participation, parental informed consent was obtained for all children. The data of eight children were excluded due to the following reasons: low scores on a language development test for reception of grammar (TROG-D, Fox, 2008) (one child), and movement artefacts (seven children). The final sample for the fMRI experiment consisted of twenty-two children (nine female). The age ranged from 4;08 to 6;08 years old (mean age 5;09). All children were monolingual German speakers and had no neurological, medical, or psychological disorders and no contraindications to obtaining an MRI scan. No child was left-handed but six children were ambidextrous (modified version of Oldfield, 1971). Group statistics with and without these six children did not suggest that this group was an outlier; therefore these data remained in the final analysis. The study was approved by the Research Ethics Committee of the University of Leipzig, Germany.

6.1.2 Stimulus material

For the fMRI experiment, the same sentences as in the behavioural picture-matching test were used, that were exactly the same sentences already used in the fMRI experiment in adults. Once again, 96 test sentences were presented to the children in the scanner: 24 sentences in the subject-initial condition, 24 sentences in the object-initial condition. Additionally, sentences with a violated sentence structure including 24 sentences with two identically case-marked definite articles in nominative and 24 sentences with double accusative were presented in order to minimize the predictability of the type of sentence structure.

6.1.3 Procedure

All children participated in a previous testing session to assess language skills, handedness, and hearing. All children included in the final fMRI sample showed normal language development as assessed by the TROG-D.

To familiarize the children with the experimental setting and scanner noise, each child underwent a simulated scanner session in a mock MR scanner. Stimuli similar to, but not identical to, the experimental stimuli were used for familiarization. To practice lying still in the scanner, each child got verbal and visual feedback via headphones and a motion sensor during the session. Each child was given a clear instruction before the practice scan and was reminded that there would be a post-scanning survey with specific questions about the sentences they heard.

Before the actual fMRI session, children had the chance to accustom themselves to the environment and the scanner. They were reminded to lie still and listen to the sentences, and that after the scanner session, they had to answer test questions about the sentences that they would hear in the scanner. The test procedure including behavioural and fMRI data acquisition encompassed a total of 2-3 hours and was distributed over 2 days. The scanning session was scheduled on average two weeks after the behavioural session that also included the mock scanner training.

All children completed a 16 minute run consisting of 120 events: 24 sentences per condition (subject-initial, object-initial, double nominative, and double accusative sentence structure) plus 24 null events, presented in an event-related, pseudo-randomized design according to the following constraints:

1. No more than two consecutive events belonging to the same stimulus condition;
2. No more than four consecutive events containing either correct or incorrect stimuli.

The 120 events lasted 6 seconds each (i.e. 3 scans of TR = 2000 ms), with a randomly varied onset jitter of 0, 400, 800, 1200 or 1600 ms. The stimuli were presented acoustically via headphones while a screensaver (a rotating cube), that didn't involve any kind of human or animal action, was presented via LCD display glasses. The screensaver was presented to keep the children interested and also minimize potential anxiety from darkness. Additionally, the LCD display glasses disguised the scan environment.

6.1.4 Data acquisition and analysis

Data acquisition

Twenty-six axial slices (3 mm thickness, 1 mm inter-slice distance, FOV 19.2 cm, data matrix 64x64 voxels, in plane resolution of 3 x 3 mm) were acquired every 2 s during functional measurements (BOLD sensitive gradient EPI sequence, TR = 2 s, TE = 30 ms, flip angle 90°, acquisition bandwidth = 100 kHz) with a 3 Tesla scanner (Siemens TimTrio, Germany).

After functional imaging, a T1-weighted 3D magnetization-prepared rapid gradient-echo (MP-RAGE) sequence (data matrix 256 x 256, TR = 1.48 s, TE = 3.46 ms, TI = 7.4 s, flip angle 10°, bandwidth 190 kHz, space resolution 1 x 1 x 1.5 mm) was acquired with a non-slice-selective inversion pulse followed by a single excitation of each slice. These anatomical data were used to co-register functional images before normalized to a chosen representative brain image of one of the children participants.

This brain was previously rotated into the stereotactic coordinate system and transformed to a standard size (Talairach and Tournoux, 1988). Therefore, it served as a template for normalization and anatomical ROI definition.

Data analysis

Functional imaging data processing was performed using the software package LIPSIA (Lohmann et al., 2001). This software package contains tools for pre-processing, co-registration, ROI-definition, statistical evaluation, and visualization of fMRI data. Functional data were entered into a distortion correction using a field-map scan (only one child was analysed without this latter step, because no field-map scan was available) and corrected for motion artefacts. Movement correction was allowed up to 3 mm (= one voxel). Subjects were excluded if head movement exceeded this range. To correct for the temporal offset, data were corrected for slicetime acquisition differences using cubic-spline interpolation. Low frequency signal changes and baseline drifts were removed by applying a temporal high pass filter to remove frequencies below 1/70 Hz. A spatial smoothing filter with a kernel of 6.0 mm^3 FWHM was applied.

The anatomical images acquired during the functional session were previously rotated into the stereotactic coordinate system and were transformed to a standard size by linear scaling and then co-registered with the reference brain by an additional non-linear normalization known as 'demon matching' (Thirion, 1998). The transformation parameters obtained from these steps were subsequently applied to the preprocessed functional images after aligning the data with the individual anatomical image that serves as reference data set by performing a rigid, affine linear transformation registration with six degrees of freedom (3 rotational, 3 translational).

Using the software package LIPSIA, the statistical evaluation was based on a least-squares estimation using the general linear model for serially autocorrelated observations (Friston et al., 1994). The design matrix was generated with a synthetic hemodynamic response function (Friston et al., 1998; Josephs et al., 1997) and their temporal and dispersion derivatives. To take the autocorrelation of the data into account for statistical evaluation, a two-pass whitening procedure was performed (Worsley et al., 2002). Movement correction parameters were included into the model as regressors. For each participant, four contrast images were generated to represent the main effects of each of the conditions (subject-initial, object-initial, double nominative, and double accusative) contrasted with a baseline (null events), and furthermore, one contrast image was generated to represent the effect of object-initial sentences compared to subject-initial sentences.

Subsequent random-effects group analysis consisted of a one-sample t-test across the contrast images of all participants to indicate whether observed effects were significantly distinct from zero. The resulting t-statistics were transformed to standard normalized distribution. To protect against false-positive activations, a multiple comparison correction tested for cluster size (number of voxel) and the minimal p-value per cluster, based on Monte Carlo simulations. The Monte Carlo simulation generates voxels at a rate equal to the significant 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. A combination of single voxel probability thresholding on the one hand, and cluster-size and cluster-z-value thresholding on the other, was used to take account of the possibility that even small clusters may be true activations if the effect is strong enough (Lohmann et al., 2008). Using 1000 iterations, a minimum cluster size at $z > 3.09$ ($p < .001$) was determined in order to arrive at a false positive cluster probability of $p < .05$. Following this protocol, the statistically computed statistical threshold was then applied to all voxels in the data. Thus, a cluster was qualified as being significant if it was either larger than 837 mm^3 (31 voxel) or had a maximum of $z > 3.09$, or both, resulting at a corrected p-value of $p < .05$.

Region of interest analysis

A subsequent region of interest (ROI) analysis focused on the left IFG, because a significant difference in the contrast of object-initial compared to subject-initial was expected. Other fMRI studies found evidence that this area is activated by syntactic complexity in adults and children (Röder et al., 2002; Bornkessel et al., 2005; Friederici, Fiebach, et al., 2006; Yeatman et al., 2010; Nuñez et al., 2011). However, this effect was not replicated in all studies and often only ROI analysis could unveil activation differences in this region (Ben-Shachar et al., 2004). The representative brain image of one of the children previously used for co-registration served as a template to define the ROIs. They were anatomically defined using a Lipsia tool (vledit) to draw two ROIs based on anatomy, covering two subregions of Broca's area in the left IFG, i.e. BA 44 and BA 45, respectively (Figure 6.3A). The areas were identified by visual inspection of the macrostructural information of the brain. For BA 44, the opercular part of the IFG was selected between precentral gyrus, lateral fissure, inferior frontal sulcus, and ascendant ramus. For BA 45, the triangular part of the IFG was selected between inferior frontal sulcus, lateral fissure, ascendant ramus, and horizontal ramus. Regions of interest were analyzed by direct statistical comparison between the object-initial and the subject-initial condition (factor *word order*). To do so, the percent signal change (PSC) was calculated per condition as a function of time (averaged across all subjects) and analyzed for mean PSC per condition in a time window from 3 to 10 s post stimulus onset (also averaged across all subjects) in a repeated-measures GLM including Greenhouse-Geisser correction.

6.2 Results

6.2.1 Baseline contrasts

The main effects of subject-initial and object-initial conditions (compared to baseline) revealed a similarly activated network in both conditions, including the STS/STG bilaterally, and bilateral thalamic regions. Additional cluster of activation for the object-initial condition were found in the anterior and posterior cingulate gyrus, and the left IFG (Table 6.1, Figure 6.1A & 6.1B).

In the sentences with a violated structure a similar picture is observed in both conditions. Sentences with a double nominative as well as sentences with a double accusative activated areas bilaterally in the STG/STS, the thalamus, and isthmus of the cingulate gyrus, and cerebellum (Table 6.1, Figure 6.1C & 6.1D). Additionally, sentences containing a double nominative induced an increase in brain activity in the left IFG and the ACC bilaterally.

6.2.2 Direct contrast

The direct comparison of object-initial and subject-initial sentences revealed two large cluster of activation. The area of activation comprised the IPC, particularly the supramarginal gyrus (SMG) and angular gyrus (AG); posterior STG (pSTG); and mainly the right hemispheric part of the ACC (Table 6.1, Figure 6.2).

6.2.3 Regions of interest analysis

The repeated-measures GLM focusing on the left IFG showed a marginally significant interaction of *ROI* by *word order* effect in the group including 22 children (F(1, 21) = 3.7, p = .07). As displayed in Figure 6.3A, it seemed that there is increased activation for object-initial compared to subject-initial sentences in BA 44, but no differences were found in a statistical comparison of these two regions (BA 44 & BA 45) (Table 6.2).

6.3 Follow-up survey

At some week's distance to the scan session (on average 2.5 month after the fMRI), children were invited again to the institute or were visited at home for a follow-up

Table 6.1: Overview of significant clusters (in mm^3), random-effects contrast, thresholded to p < .05, corrected. Peaks in a bigger cluster are reported, if they are bigger than 81 mm^3 (3 voxel). If a region has more than one peak, just the one with the highest z-value is reported. Location is described in Talairach coordinates. Table shows following contrasts for the group of all children: (a) subject-initial > baseline, (b) object-initial > baseline, (c) double nominative > baseline, (d) double accusative > baseline, and (e) object-initial > subject-initial.
ACC = anterior cingulate cortex, IFG = inferior frontal gyrus, IPC = inferior parietal cortex, PCC = posterior cingulate cortex, post. = posterior, STG = superior temporal gyrus.

region	**BA**	**X**	**Y**	**Z**	**cluster-size**	**z-value**
a. subject-initial > baseline						
right STG	22	55	-15	9	37125	7.73
left STG	22	-44	-24	9	40797	7.22
left post. thalamus		-14	-27	0	1377	4.40
right post. thalamus		13	-27	0	756	4.11
b. object-initial > baseline						
right STG	22	52	-15	9	48789	7.61
left STG	22	-44	-24	9	58995	7.43
left IFG	45	-47	18	21	1755	4.68
left PCC	23	-5	-51	18	675	4.03
left ACC	24	-14	3	30	1458	3.82
right PCC	23	1	-48	21	432	3.53
right ACC	24	1	-9	30	162	3.49
c. double nominative > baseline						
right STG	22	55	-15	9	49356	8.19
left STG	22	-53	-15	9	68067	7.69
left ACC	24	-8	21	30	783	3.71
right ACC	24/32	1	21	27	648	3.57
d. double accusative > baseline						
right STG	22	52	-15	9	45144	7.66
left STG	22	-41	-24	9	56187	7.49
brain stem		1	-21	9	108	3.60
e. object-initial > subject-initial						
right ACC	24/32	16	21	33	1728	4.76
left IPC	40/39	-47	-57	39	1728	4.02

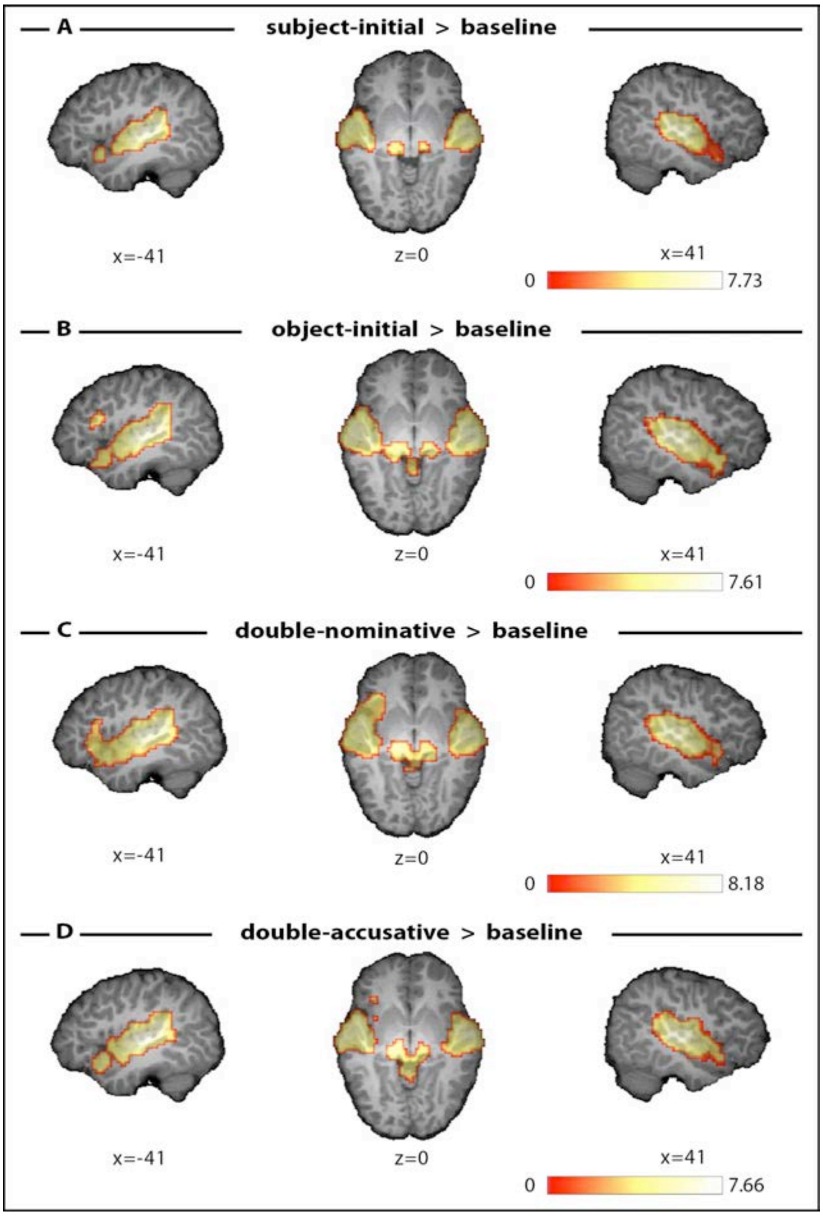

Figure 6.1: ***Main effects contrasted with baseline (null events) in all children.*** *Effects mapped on the best brain. Observed activation for (A) subject-initial sentences, (B) object-initial sentences, (C) for double-nominative sentences, (D) double-accusative sentences. All activation thresholded to p =.05, corrected.*

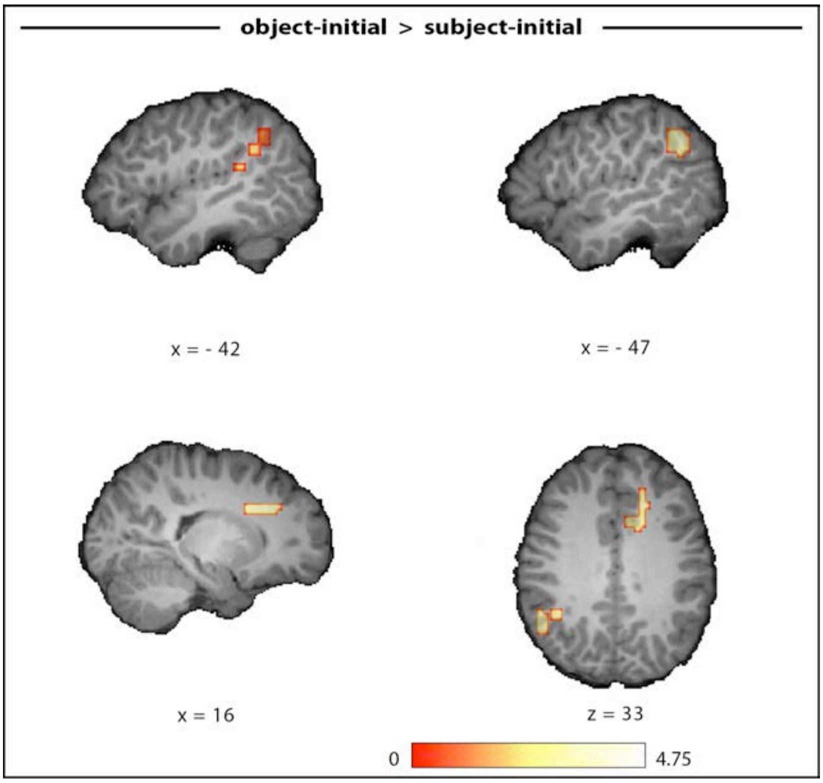

Figure 6.2: ***Effect for object-initial sentences contrasted with subject-initial sentences in all children.*** *Observed activation for object-initial vs. subject-initial sentences in all children mapped on the best brain. All activations are thresholded to p = .05, corrected.*

Table 6.2: Region of interest analysis. Results of repeated-measures GLM for a specific ROI with within-subject factors ROI (BA 44 vs. BA 45) and word order (subject-initial vs. object-initial) in ***all children****.*

ROI	**effect**	**Df**	**f-value**	**p-value**
IFG	*ROI* (BA 44 & BA 45)	1,21	2.998	n.s.
	word order	1,21	.081	n.s
	*ROI * word order*	1,21	3.72	.068

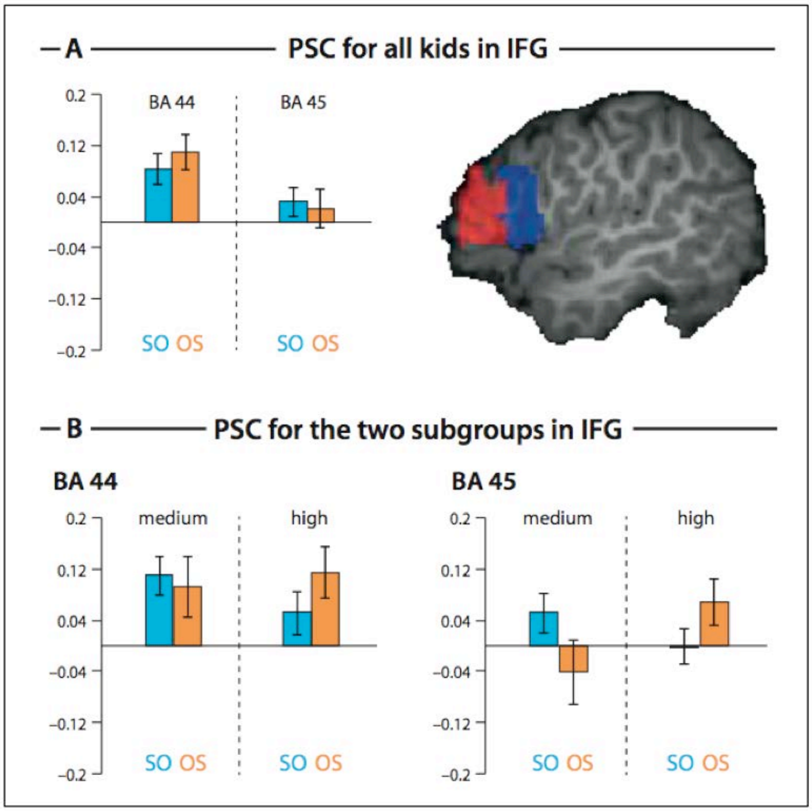

Figure 6.3: ***Results of region of interest analyses in left IFG in all children and in subgroups.*** *Adopted from Knoll et al., 2012. Original legend reads: (A) Percent signal changes (PSC) for a 3–10 s averaged time window for the two subregions of the left IFG (BA 44 and BA 45) in all children. Error bars represent ± 1 between- subjects Standard error of the mean (SEM). Figure shows anatomical defined IFG ROIs (BA 44 in blue and BA 45 in red). (B) Percent signal changes for a 3–10 s averaged time window for the two subgroups (medium and high-performing children) in BA 44 and BA 45. Error bars represent ±1 between-subjects Standard error of the mean (SEM). Blue bars refer to subject- initial sentences (SO) and orange bars to object-initial sentences (OS).*

survey. Children were again confronted with the sentences they had heard during the scan session. The testing served as a supplementary measure how the group of tested children dealt in general with all four sentences conditions (subject-initial and object-initial sentences and the sentences with a violated structure with double nominative and double accusative), because only the two grammatical correct sentences could be tested in the picture-matching test. Besides, additional information should be obtained for interpretation of the overall results of the study.

Introductorily, the instructor reminded the child that it should imagine a fairy tale context, in which e.g. also the small bird could play with the big tiger. Then, the sentences were read to the children and they had to decide which of the sentences were correct. Children performed in all four conditions significantly above chance (subject-initial: 74% (SD 28%), t(21) = 4.0, $p < .001$; object-initial: 66% (SD 31%), t(21) = 2.5, $p < .02$; double nominative: 65% (SD 35%), t(21) = 2.1, $p < .05$; double accusative: 66% (SD 33%), t(21) = 2.2. $p < .04$). Results confirmed the findings of the post-scanner picture-matching task that children perform above chance in subject-initial and object-initial sentences. Furthermore, also the violation conditions was tested and the findings indicated that children at this age are also able to correctly evaluate grammatically incorrect sentences. Additionally, significant correlations were found between the overall results of the follow-up survey and the performance (raw score) in the TROG-D (Spearman-rho = .69, $p < .001$) and in mean accuracy in the picture-matching task (Pearson r = .71, $p < .001$).

6.4 Discussion

The current fMRI study investigated the processing of case-marking and argument structure in children. The behavioural results already showed that children are indeed sensitive to case-marking information and use it for sentence interpretation. As expected, a strong activation for both correct conditions in contrast to a silent baseline was found in the STG/STS bilaterally, areas which are suggested to mirror auditory encoding (Scott et al., 2000; Giraud & Price, 2001; Liebenthal et al., 2005), and bilateral thalamic regions. Sentences with an object-initial structure showed additional activation in the anterior and posterior cingulate gyrus and the left IFG. This latter activation is generally in agreement with previous studies that found IFG activation for language processes (Just et al., 1996; Stromswold et al., 1996; Friederici, Fiebach, et al., 2006, 2010; Grodzinsky & Santi, 2008; Rogalsky & Hickok, 2011). Considering that object-initial sentences have a more complex syntactic structure, the activation in the left IFG for object-initial sentence was predicted. However, contrary to expectations the activation was observed in BA 45 and not in BA 44 as reported in studies in adults (Bornkessel et al., 2005; Friederici, Fiebach, et al., 2006; Rogalsky et al., 2008). In general, Brodmann's area 45 is associated supporting semantic processes (Bookheimer, 2002; Friederici, 2002; Hagoort, 2005). Moreover, Brauer and colleagues (2011) propose that this area is more engaged during sentence processing in children than in adults, possibly because the dorsal white-matter pathway that is assumed to connect BA 44 to the temporal region is not yet fully matured at this age. Rather, a ventral pathway targeting BA 45 might serve as the supporting connection within the language network, as reflected by increased functional activation in BA 45 in children (Brauer et al., 2011).

The present results specify this concept; enhanced activation in BA 45 might reflect a different strategy used by children compared to those used by adults. While adults rely on case-marking information as a cue in processing object-initial sentences to assign the thematic roles to the arguments, children at this age are not at this proficiency level yet. Their performance in the post-scan picture-matching task for the object-initial condition was, though above chance, significantly below their performance for the subject-initial condition. Thus, the current data support the view that the children are aware of case-marking as a cue, but they have not yet completely integrated this knowledge in order to use it reliably in sentence processing. Instead, they seem to rely on other information (i.e., semantic cues) for sentence interpretation. Indeed, Chapman (1978) argued that preschool children derive the meaning of a sentence through world knowledge rather than from syntactic structure. An evidence for such a strategy stems from reports provided by the children after they completed the picture-matching task. When being asked about the sentences they just listened to, a few children refused some sentences due to their semantic content ("You cannot comb a bird. The bird has no hair."; "You cannot touch the hedgehog, it has spines."). Earlier fMRI studies in adults found the left BA 45 more activated for sentences containing real-world knowledge violations compared to those that did not (Hagoort et al., 2004).

A direct comparison of object-initial sentences versus subject-initial sentences revealed left hemispheric activation in the IPC (comprising particularly the SMG and the AG) as well as the posterior STG. This finding is in line with previous studies which found an increased activation in the IPC and posterior STG during sentence processing in children and adults (Booth et al., 2000; Ahmad et al., 2003; Yeatman et al., 2010). Recently it was suggested that also children recruit the posterior STG for syntactically complex sentences. For example, Yeatman and colleagues (2010) found activation in this area for syntactically complex versus easy sentences, and several findings in adults point in this direction (Friederici et al., 2009; Newman et al., 2010; Santi & Grodzinisky, 2010). Additionally, contrasting object-initial sentences to subject-initial sentences elicited activation in a second brain region, the anterior cingulate cortex (ACC). The ACC has been typically found in studies investigating cognitive control, for example conflict monitoring during cognitive tasks (Carter et al., 1998; Barch et al., 2001; Botvinick et al., 2001, 2004). Activation in this area is usually enhanced when participants produce errors or detect a salient violation of expectancy. With regard to the present experiment, ACC activation is interpreted as reflecting violation of expectancy, as a canonical subject-initial was expected, but was not presented.

Looking into the activation of the violation conditions, a similar activation pattern was found. Sentences with a double nominative as well as a double accusative activated areas bilaterally in the STG/STS, the thalamus, and isthmus of the cingulate gyrus and left FO. The double nominative condition revealed additional activated areas in the left IFG and ACC bilaterally. Following the hypothesis that was proposed for the previous experiment in adults, activation in the FO mirrors syntactic processes. The question is, whether the FO activation in children can also be explained by local structure building processes or by a general violation processing (Brauer & Friederici, 2007). The IFG activation in the double nominative condition is not in line with this argumentation. If the accusative was the more salient marker and therefore faster to detect (Frisch & Schlesewsky, 2005), this would implicate that the children have not identify this violation and try to build a local structure in the double nominative condition. This would be contrary to the findings in the two correct conditions (contrasted with baseline), where activation in the IFG reached only significance in the object-initial structure. If the children did not detect the double nominative, a subject-initial structure should be the preferred reading. However, speculations should be viewed with caution because baseline contrasts and no direct contrasts between the conditions are presented here. Nevertheless, further studies are needed to address this point. So far no functional imaging study is published that investigates the underlying structures involved in the processing of case-marking violations.

Furthermore, a region of interest analysis for BA 44 and BA 45 was conducted in order to investigate the effect of syntactic complexity in children. Only a marginal interaction could be found between the factors *word order* and *ROI*. However, no significant effect of *word order* could be found in one of the subregions in Broca's area.

In summary, comparing syntactically complex sentences to a baseline, the predicted involved IFG activation could be found, but was observed in BA 45. The findings suggest a broad heterogeneity related to sentence processing in five to six-year-old children. Enhanced activation in BA 45 might reflect a different strategy used by children compared to adults. It might be that children use semantic information to assign thematic roles in the sentences, a view that is also supported by statements made by the children. Furthermore, the direct contrast between object-initial and subject-initial sentences revealed activation in IPC and ACC. While the IPC involvement is in line with previous studies investigating sentence processing, the ACC activation is attributed to executive functions such as prediction errors. In order to get a better understanding of the underlying processes, a subsequent data analysis is presented in the following chapter. It presents a closer look at the single-subject data to provide additional information concerning the individual developmental level.

7

INTERINDIVIDUAL DIFFERENCES

Recently, many developmental studies (Ettinger-Veenstra et al., 2010; Yeatman et al., 2010; Nuñez et al., 2011) reported high individual differences in their group of tested children. Nuñez and colleagues (2011) found a relation between syntactic proficiency and activation in the left frontal brain areas. Additionally, Yeatman and colleagues (2010) found a higher involvement of the IFG in children with better receptive language skills.

Based on these previous findings, a closer look at the single-subject data should provide additional information concerning the individual developmental level in the tested children of the actual fMRI study. And in fact, a closer inspection revealed two distinct patterns of activation. A subgroup of children (n = 11) showed the predicted increased activation for object-initial sentences compared to subject-initial sentences, while a second subgroup (n = 11) showed the reversed effect with stronger activation for subject-initial compared to object-initial sentences. Importantly, each child showed suprathreshold activation in only one of these two contrasts. Thus, children could be unambiguously classified on the basis of their activation patterns.

Due to reported correlation of brain activity and behavioural and language skills (Ettinger-Veenstra et al., 2010; Yeatman et al., 2010; Nuñez et al., 2011), statistical tests were conducted post-hoc to identify the factor that could explain the different activation pattern. One factor seems to be the children's performance in the TROG-D (t(20) = -2.3, p = .03). One subgroup had an average performance of 61% and the other subgroup 82%. Based on this result, children were divided by median split depending on their result in the TROG-D (10 children below median and 10 children above median). Two-sample t-tests were conducted but did not reveal differences in medium and high-performing group for sex (t(18) = .00, n.s.), age (t(18) = .94, n.s.), or results of the post-scan behavioural picture-matching task (t(18) = -.89, n.s.). Importantly, however, the performance in the object-initial sentences in the picture-matching test was found significantly above chance level only for the subgroup that performed high in the TROG-D (t(9) = 4.5, p < .001; t(9) = 1.4., n.s.).

Given the performance differences in the grammatical knowledge of these two subgroups, the fMRI data was reanalysed in order to uncover the neural differences in the subgroups. Maybe different grammatical knowledge of these two subgroups could explain why especially Broca's area was not as strongly involved in syntactic processes as predicted.

7.1 Methods

7.1.1 Participants

As already mentioned, the aim of this investigation was to shed light on the individual differences in the previously tested group of children. Therefore participants were the same as in the previous fMRI study. Due to a correlation between the activation in the contrast of word order (object-initial vs. subject-initial sentences) and the performance in the receptive language test, the children were divided into two groups by median split on their performance results in the TROG-D. Two participants laid with their performance exactly in the median and were therefore excluded from the group. The final sample consisted of twenty children (eight female), range 4;08 to 6;08 years old (mean age medium-performer: 5;11; mean age high-performer: 5;07).

7.1.2 Data acquisition and analysis

In order to investigate interindividual differences in the children, the data acquired in the fMRI study were reanalysed. Functional imaging data processing (pre-processing, co-registration, ROI-definition, statistical evaluation, and visualization of fMRI data) was performed following the protocol of the former fMRI study in all children.

Statistical evaluation of the data was based on a least-squares estimation using the general linear model for serially autocorrelated observations (Friston et al., 1994). The design matrix was generated with a synthetic hemodynamic response function (Friston et al., 1998; Josephs et al., 1997) and their temporal and dispersion derivatives. A two-pass whitening procedure was also performed to take the autocorrelation of the data into account. Movement correction parameters were included into the model as regressors. For each participant, five contrast images were generated to represent the main effects of each of the conditions (subject-initial, object-initial, double nominative, and double accusative) contrasted with a baseline (null events), and furthermore, a fifth contrast image was generated to investigate the direct effect of object-initial sentences compared to subject-initial sentences.

Subsequent random-effects group analysis for both groups separately consisted of a one-sample t-test across the contrast images of all participants in the median and high-performing group, respectively, were performed to indicate whether observed effects were significantly distinct from zero. The resulting t-statistics were transformed to standard normalized distribution. To protect against false-positive activations, a multiple comparison correction tested for cluster size (number of voxel) and the minimal p-value per cluster, based on Monte Carlo simulations. Using 1000 iterations, a minimum cluster size at $z > 3.09$ was determined in order to arrive at a false positive cluster probability of $p < .05$. Following this protocol, the statistically computed statistical threshold was then applied to all voxels in the data. Thus, a cluster was qualify as being significant in the group of the medium-performing children if it was either larger than 837 mm^3 (31 voxel) or had a maximum of $z > 3.09$, or both. In the group of high-performing children, a cluster had to be larger than 837 mm^3 (31 voxel) or had a maximum of $z > 3.09$, or both, as qualified of being significant. In both groups the presented results are at a corrected p-value of $p < .05$

Region of interest analysis

Subsequent ROI analysis focused on the left IFG were conducted for both subgroups. The same ROIs used for the analyses in all children were analyzed by direct statistical comparison between the object-initial and the subject-initial condition. To do so, the percent signal change (PSC) was calculated per condition as a function of time (averaged across all subjects of the medium-performing group and the high-performing group, respectively) and analyzed for mean PSC per condition in a time window from 3 to 10 s post stimulus onset (also averaged across all subjects of each group separetely) in a repeated-measures GLM including Greenhouse-Geisser correction with within-factors *ROI* (BA 44 and BA 45), *word order* (object-initial and subject-initial), and between factor *group* (medium-performers and high-performers).

7.2 Results

7.2.1 Baseline contrasts

Medium-performing children

In the group of the medium-performing children, the main effects of subject-initial (compared to baseline) revealed a widely spread activation in the STG/STS bilaterally. Additionally to this cluster that was also observed in the object-initial

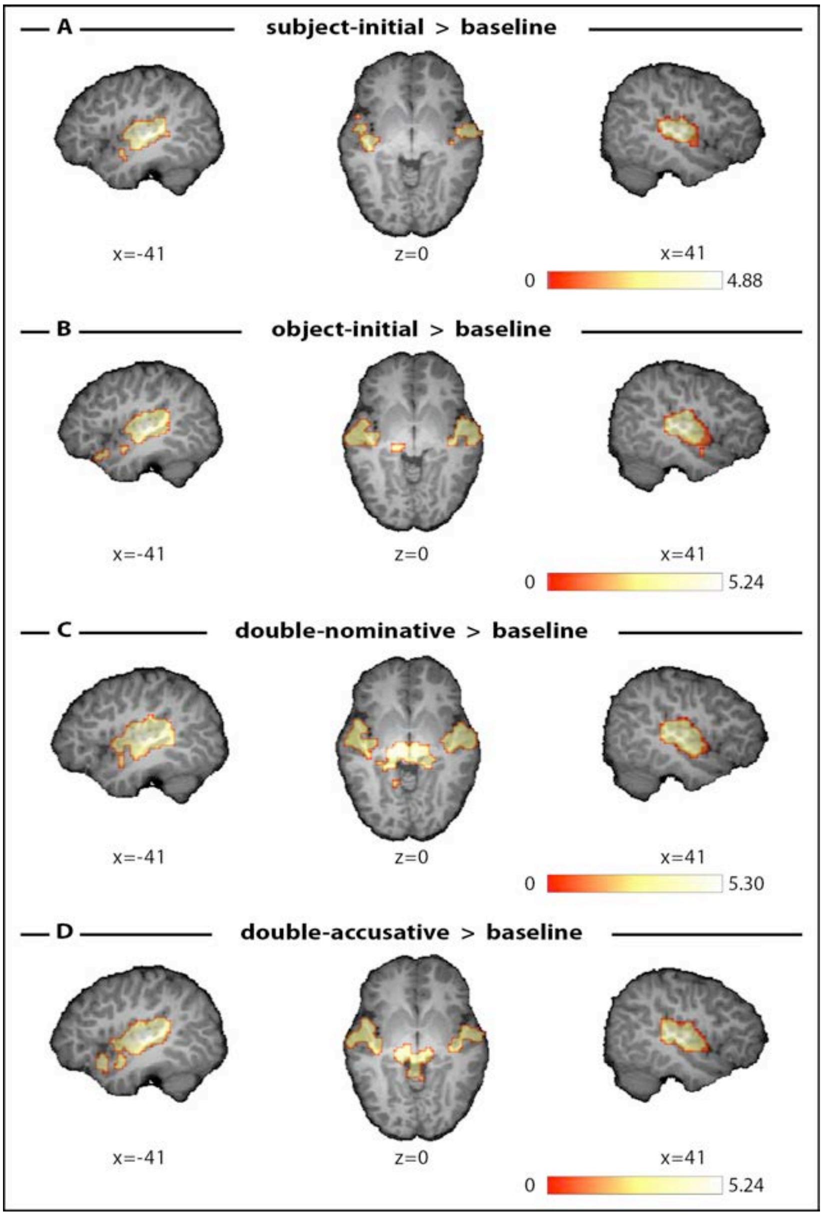

Figure 7.1: ***Main effects contrasted with baseline (null events) in medium-performers.*** *Effects mapped on the best brain. Observed activation for (A) subject-initial sentences, (B) object-initial sentences, (C) for double-nominative sentences, (D) double-accusative sentences. All activation thresholded to p =.05, corrected.*

Table 7.1: Overview of significant clusters (in mm^3), random-effects contrast, thresholded to $p < .05$, corrected. Peaks in a bigger cluster are reported, if they are bigger than 81 mm^3 (3 voxel). If a region has more than one peak, just the one with the highest z-value is reported. Location is described in Talairach coordinates. Table shows following contrasts for ***medium-performing children****: (a) subject-initial > baseline, (b) object-initial > baseline, (c) double nominative > baseline, (d) double accusative > baseline, and (e) object-initial > subject-initial.*
ACC = anterior cingulate cortex, DLPFC = dorsolateral prefrontal cortex, IFG = inferior frontal gyrus, PHG = parahippocampal gyrus, PMC = premotor cortex, post = posterior, STG = superior temporal gyrus, TP = temporal pole.

region	**BA**	**X**	**Y**	**Z**	**cluster-size**	**z-value**
Medium performing group (n=10)						
b. object-initial > baseline						
right STG	22	52	-18	12	14931	4.88
left STG	22	-41	-24	9	16254	4.78
b. object-initial > baseline						
right STG	22	52	-18	12	22140	5.24
left STG	22	-41	-24	9	24381	5.17
right ACC	24/32	16	24	36	999	4.10
left post. thalamus		-17	-24	0	1053	3.68
c. double nominative > baseline						
left post. thalamus		-11	-24	3	33912	5.31
right STG	22	55	-15	9	29214	5.24
left cerebellum		-5	-36	-6	594	3.54
right caudate		1	3	9	81	3.33
d. double accusative > baseline						
left STG	22	-41	-24	9	24381	5.25
right STG	22	52	-18	12	19602	5.14
left TP	38	-44	15	-12	783	4.59
left cerebellum		-5	-42	-6	3132	4.48
right post. thalamus		1	-27	0	2673	4.39

sentences, this condition with a more syntactically complex sentence structure activated the right ACC and the left posterior thalamic region. In the violation conditions (both compared to baseline) revealed a similarly activated network in both conditions, including a widely spread activation in the STS/STG bilaterally, bilateral posterior thalamic regions, brainstem, and distinctly different strong activation in the isthmus of cingulate gyrus (Figure 7.1). Brain activation in the left STG extended slightly to the temporal pole in the double accusative sentences. Results are summarized in Table 7.1.

High-performing children

Results of the group of the high-performing children are shown in Table 7.2 and are illustrated in Figure 7.2. Activation for the subject-initial contrasted with a baseline included suprathreshold activation in bilateral STG/STS. Brain activation of the main effect of object-initial sentences enclosed bilaterally clusters of activation in the STG/STS, thalamic regions, isthmus of cingulate gyrus, brainstem, and cerebellum. Activation in the left hemisphere was found in the IFG, AG, and parahippocampal gyrus (PHG).

In the sentences with a double nominative bilaterally activation was observed in STG/STS, and IFG (BA 45), that extended in the left IFG to BA 44 and the frontal pole (FP). The double accusative revealed activation bilateral in the STG/STS, isthmus of the cingulate gyrus, and cerebellum. Left hemispheric activation was found in the IFG, anterior insula, PMC, and, primary motor cortex (MI), as well as right hemispheric cluster of activation in the PHG, the AG, and the superior parietal cortex (SPC).

7.2.2 Direct contrast

Medium-performing children

In a direct comparison of object-initial and subject-initial sentences no activation

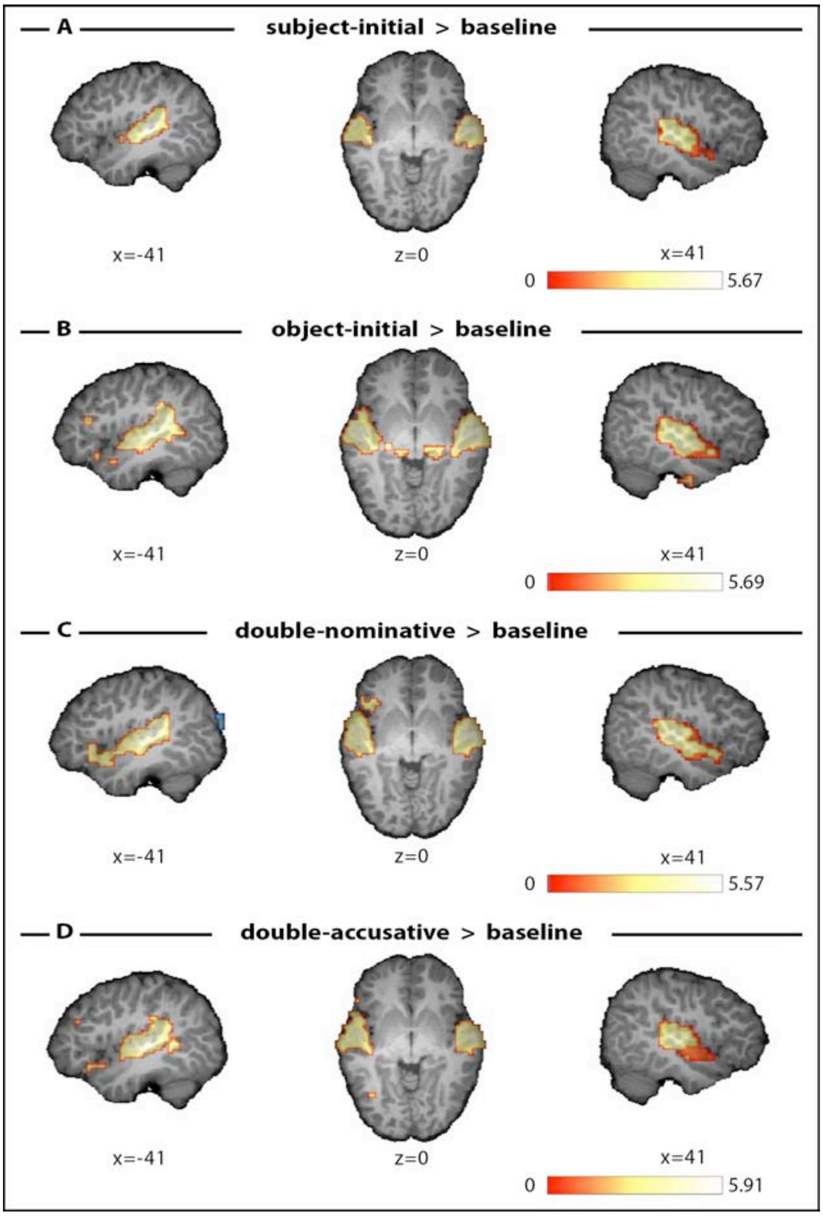

Figure 7.2: ***Main effects contrasted with baseline (null events) in high-performers.*** *Effects mapped on the best brain. Observed activation for (A) subject-initial sentences, (B) object-initial sentences, (C) for double-nominative sentences, (D) double-accusative sentences. All activation thresholded to p =.05, corrected.*

Table 7.2: Overview of significant clusters (in mm^3), random-effects contrast, thresholded to $p <$ .05, corrected. Peaks in a bigger cluster are reported, if they are bigger than 81 mm^3 (3 voxel). If a region has more than one peak, just the one with the highest z-value is reported. Location is described in Talairach coordinates. Table shows following contrasts for ***high-performing children****: (a) subject-initial > baseline, (b) object-initial > baseline, (c) double nominative > baseline, (d) double accusative > baseline, and (e) object-initial > subject-initial.*
ACC = anterior cingulate cortex, DLPFC = dorsolateral prefrontal cortex, IFG = inferior frontal gyrus, PHG = parahippocampal gyrus, PMC = premotor cortex, post = posterior, STG = superior temporal gyrus, TP = temporal pole.

region	BA	X	Y	Z	cluster-size	z-value
Medium performing group (n=10)						
b. object-initial > baseline						
left STG	22	-41	-29	12	24219	5.67
right STG	22	52	-8	3	21087	5.57
b. object-initial > baseline						
left STG	22	-47	-32	15	37179	5.69
right STG	22	55	-8	0	33345	5.45
left cerebellum		-8	-47	-15	513	4.07
left IFG	44	-44	13	21	1080	3.89
c. double nominative > baseline						
left STG	22	-56	-8	9	33264	5.57
right STG	22	52	-8	6	25488	5.43
d. double accusative > baseline						
left STG	22	-47	-20	6	35289	5.91
right STG	22	46	-26	9	22437	5.46
right PHG	36	22	4	-27	324	4.78
left PMC	6	-11	4	-27	135	4.75
left cerebellum		-20	-71	-9	945	3.83
left IFG	44	-50	28	15	1242	3.81
e. object-initial > subject-initial						
left DLPFC	9/46	-35	34	12	4455	4.74
right ACC	24	16	22	33	1620	4.64

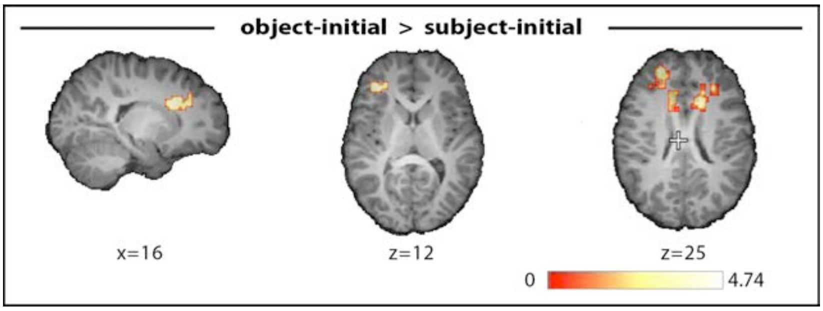

Figure 7.3: ***Effect for object-initial sentences contrasted with subject-initial sentences in high-performers.*** *Observed activation for object-initial vs. subject-initial sentences in all children mapped on the best brain. All activations are thresholded to p b .05, corrected.*

differences were found after applying the threshold criterion of 837 mm^3 or a maximum of $z > 3.09$.

High-performing children

In the group of high-performing children the direct contrast between object-initial and subject-initial sentences revealed activation in the frontal lobe area in the left dorsolateral prefrontal cortex (DLPFC) and in the cingulate cortex in the ACC (Table 7.2, Figure 7.3).

7.2.3 Regions of interest analysis

A post-hoc repeated-measures GLM was performed with the within-subject factors *ROI* (BA 44 vs. BA 45) and *word order* (subject-initial vs. object-initial) and the new between-subject factor *group* (Table 7.3). This analysis showed a tendency of a main effect of factor *ROI* (F(1,18) = 4.0, p = .06), a significant interaction of factor *word order* by *group* (F(1, 18) = 5.6, p = .03) and a marginally significant threefold interaction of factor *RO*I by *word order* by *group* (F(1, 18) = 4.2, p = .06). A closer examination revealed a significant interaction of *word order* by *group* in BA 45 (F(1,18) = 7.0, p = .02; Figure 6.3B). Based on our prediction that only high-performing children would show an adult-like pattern of higher activation in

Table 7.3: (a.) Region of interest analysis. Results of repeated-measures GLM for specific ROIs with within-subject factors ROI (BA 44 vs. BA 45) and word order (subject-initial vs. object-initial) and with between-subject factor group (medium-performers vs. high-performers), (b.) planed post-hoc paired T-tests in BA 44 in medium-performers, (c.) and planed post-hoc paired T-tests in BA 44 in high-performers

ROI	effect	Df	f-value	p-value
a.				
IFG	*ROI* (BA 44 & BA 45)	1,18	4.00	.061.
	*ROI * group*	1,18	1.01	n.s.
	word order	1,18	.059	n.s.
	*word order * group*	1,18	5.61	.029
	*ROI * word order*	1,18	2.93	n.s.
	*ROI * word order * group*	1,18	4.19	.056
b. normal-performers				
BA 44	*word order*	9	.48	n.s.
c. high-performers				
BA 44	*word order*	9	-1.20	.077

object-initial compared to subject-initial sentences in BA 44, planned t-tests were conducted. The results suggest a trend towards higher activation for object-initial sentences compared to subject-initial sentences solely in high-performing children (BA 44: high-performing subgroup, t(9) = -2.0, p = .077; medium-performing subgroup, t(9) = .48, n.s.).

Subsequent analysis

In order to test the assumption that only the high-performers show a adult-like pattern of activation in the IFG, a repeated-measure GLM was performed. Therefore, anatomical ROIs for the two subregions of Broca's area (BA 44 & BA 45) were defined for the adult template image (same approach was used as described in section 6.1.4). Comparing the medium-performing group to the adults from the previous fMRI study, significant differences were found for the interaction of *ROI* by *group* (F(1,30) = 9.4, p = .01), *word order* by *group* (F(1,30) = 5.7, p = .02) and for the threefold interaction of *ROI* by *word order* by *group* (F(1,30) = 4.3, p =.05).

In contrast, comparing the high-performing group to the adults solely a significant main effect of *word order* was found (F(1,30) = 9.3, p = .01). These results confirm the assumption that only the high-performing group employs adult-like sentence comprehension strategies that are reflected in the left IFG.

7.3 Discussion

Based on the results described above, a follow up study investigated the processing of case-marking and argument structures in children with a high grammatical knowledge and a medium grammatical knowledge. The latter group showed a similar pattern of activation in all four sentence structures. In general, a widely spread activation in the STG/STS bilaterally was found, which is suggested to mirror auditory encoding (Scott et al., 2000; Giraud & Price, 2001; Liebenthal et al., 2005). Particularly the more complex object-initial sentences additionally activated the right ACC what was suggested to mirror executive functions such as error detection (Barch et al., 2001; Botvinick et al., 2001, 2004; Carter et al., 1998). Subcortical regions such as the bilateral thalamus were observed in object-initial and in sentences with violation structure. The results already indicated that no differences were to expect in a direct contrast between object-initial and subject-initial sentences which was confirmed in a statistical test.

A more differentiated picture was found in children with high grammatical knowledge, who showed the typical activation for auditory encoding in the STG/STS bilaterally in response to subject-initial sentences (Scott et al., 2000; Giraud & Price, 2001; Liebenthal et al., 2005). Object-initial sentences additionally activated the left IFG and thalamic regions. This IFG activation was found in BA 44 and supported the hypotheses that already young children consult this area for syntactic processes (Röder et al., 2002; Ben-Shachar et al., 2004; Bornkessel et al., 2005; Grewe et al., 2005; Friederici, Fiebach, et al., 2006; Obleser et al., 2011). Interestingly, the results point in the direction that involvement of this region could be correlation with grammatical knowledge. A direct comparison of object-initial sentences and subject-initial sentences revealed a widely spread pattern of activation comprising mainly the ACC and left dorsolateral prefrontal cortex (DLPFC) that extended also to the region in the left IFG found in the object-initial sentence (contrasted with baseline). Activation in the DLPFC has been associated with increased short-term memory load in adults and children (Fletcher & Henson, 2001; Narayanan et al., 2005; Jolles et al., 2011), increased syntactic memory demands (Caplan et al., 2000) and executive control of working memory (WM), especially in processes that require the reorganization of information that had to be maintained (Miller & Cohen, 2001; Barbey et al., in press). With reference to the manipulation in this study, object-initial sentences require the prediction of a subject and a verb in order to build a grammatical sentence: a process that is assumed to be costly in terms of syntactic working memory (Gibson, 1998). The activation in the ACC underpins the previous interpretation of an expectancy violation for a canonical subject-initial sentence structure.

Activation found in the two violation conditions was quite similar. Both revealed bilateral STG/STS regions and the left IFG, BA 44. As in the adult data, activation in the FO for double nominative sentences was observed, but not in sentences with a double accusative. Therefore, this condition revealed activation in premotor and primary motor cortex regions as well as subcortical areas.

Interestingly, differences between the two subgroups (divided by their language abilities) were found in the left IFG. These findings are supported by prior developmental studies that reported correlations between language skills and IFG activation strength (Yeatman et al., 2010; Nuñez et al., 2011). Importantly, only the group with a high grammatical knowledge showed a pattern of activation in an adult-like manner with stronger activation in the Broca's area for object-initial sentences compared to subject-initial sentences (Bornkessel et al., 2005; Friederici, Fiebach, et al., 2006; Rogalsky et al., 2008). In order to test this assumption directly, both groups of children were compared to adults. While the medium-performing group showed activation differences compared with adults, the high-performing group did not. These results confirmed the assumption that only the high-performing group employs adult-like sentence comprehension strategies that are reflected in the left IFG.

The results suggest a considerable amount of heterogeneity related to sentence processing within five to six-year-olds, and that this heterogeneity is directly reflected in differential patterns of the frontal cortex activation. It seems that some children already use case-marking information for sentence interpretation reliably by this age, while others do not. The data indicate that different strategies are employed when it comes to using case-marking information for sentence processing, depending on the children's grammatical knowledge. Only one subgroup, namely the group with high grammatical knowledge showed differences in the direct contrast between non canonical object-initial sentences and canonical subject-initial sentences. The more demanding non canonical sentence structure revealed activation in left frontal areas. Moreover, a different pattern of activation was found in a ROI analysis focusing on the left IFG, suggesting that this area is more sensitive to sentence structure comprehension itself. Only the high-performing subgroup showed an adult-like pattern of activation in the left IFG (Friederici, Fiebach, et al., 2006; Rogalsky et al., 2008); that is a stronger activation for syntactically complex sentences in contrast to canonical sentences. Thus, it seems that the experiment has pinpointed a pivotal phase when children are already sensitized to grammatical cues but differ in their individual ability to integrate them for successful sentence comprehension.

8

DWI STUDY IN CHILDREN

The DWI study investigated the maturation in the developing brain and the structural differences in children which could be related to their language performance. Prior studies provided evidence that maturation of the brain is a dynamic process during infancy, childhood and adolescence (Giedd et al., 1999; Paus et al., 1999; Pujol et al., 2006; Provenzale et al., 2007; Dubois et al., 2008; Giorgio et al., 2008; Lebel et al., 2008; Shaw et al., 2008) and continuous until early adulthood (Paus et al., 1999; Blakemore, 2008; Lebel et al., 2008). Most importantly, these structural changes do not proceed synchronically in all brain regions (Paus et al., 1999; Pujol et al., 2006; Dubois et al., 2008; Giorgio et al., 2008; Lebel et al., 2008). Given these, the investigation of maturation and changes in the brain of children and adolescents appears to be an important parameter in the explanation of cognitive, motor, sensory, and executive development. In previous studies, the focus has been mostly on changes in grey and white matter. Grey matter consists of neuronal cell bodies, dendrites and non-myelinated axons of neurons, capillaries and glial cells. Studies focusing on cortical grey matter thickness, density, and volume found fundamental changes from childhood to adulthood (Giedd et al., 1999; Sowell et al., 1999, 2003, 2004; Lebel et al., 2008; Shaw et al., 2008; for a review see Blakemore, 2008).

The current study focused on the second tissue, namely the white matter which is composed of bundles of myelinated axons of neurons. White matter is found to be crucially involved in two points. First, white matter pathways interconnect particular brain regions and second, as part of the respective brain area, white matter supports overlying structures in the cerebral cortex (Wakana et al., 2004; Lazar, 2010; for latest review see Dell'Acqua & Catani, 2012). Studies reported a steady linear increase in global white matter volume during early childhood and adolescence, with a stabilization of this process into adulthood (Paus et al., 1999; Giedd et al., 1999; Dubois et al., 2006, 2008; Pujol et al., 2006; Ashtari et al., 2007; Giorgio et al., 2008; Lebel et al., 2008; Muftuler et al., 2012). Interestingly, language related areas were found to myelinate later than sensorimotor areas and Heschl's gyrus (HG) (Pujol et al., 2006).

A popular approach to study white matter changes is to investigate differences in fractional anisotropy (FA), which measures the directionality of the diffusion of water molecules along white matter fiber tracts and regional white matter tissue (Johansen-Berg & Behrens, 2009; Mori, 2007). Lebel and colleagues (2008) measured FA in 10 predefined brain regions to assess brain development in 202 healthy subjects aged 5 to 29 years. They reported a non-linear pattern of maturation and confirmed that fronto-temporal connections seem to develop slower than other connections. A study which compared seven-year-old children with adults found differences in FA mainly in perisylvian regions in the STG/STS and the left IFG (Brauer et al., 2011). Higher FA values are suggested to mirror increasing organization of white matter tracts, and therefore an increased myelination level in this region. Interestingly, positive correlations of FA and general intellectual abilities, i.e. verbal abilities in children were reported in several studies (Schmithorst et al., 2005; Tamnes, Ostby, Fjell, et al., 2010). Tamnes and colleagues (2010) found verbal abilities in children, adolescents and adults correlated with white matter microstructure, primarily in the left hemisphere, in the cingulum-cingulate gyrus and bilaterally in the superior longitudinal fasciculus. Schmithorst and colleagues (2005) also reported positive correlations of FA with IQ scores, but mainly bilaterally in white matter association areas comprising frontal areas and occipito-parietal areas.

The present study focused on white matter in BA 44 and in BA 45 in the left IFG, whereas the right IFG and a whole brain analysis served as control regions. FA values were extracted and analysed in order to identify areas that undergo developmental changes that could explain language performance in five to seven-year-olds.

8.1 Methods

8.1.1 Participants

Data were collected from eighteen children who took already part in the fMRI study. Before their participation, parental informed consent was obtained for all children. The data of one child had to be excluded from further analysis due to extensive movements in the scanner during data acquisition (movement artefacts in $< 30\%$ of the data). The final sample consisted of seventeen children (seven female), ranges from 5;00 to 7;03 years (mean age 6;02). All children were monolingual German speakers and had no neurological, medical, or psychological disorders and no contraindications to obtaining an MRI scan. No child was left-handed (modified version of Oldfield, 1971).

8.1.2 Procedure

The DWI session took place on average four month after the fMRI session. Therefore, the children were previously invited to a training mock session to get used to the procedure again. The data acquisition was conducted while the child was awake. An animated cartoon that was presented via LCD display glasses to the children should guarantee that they were entertained during the thirty minutes scanning time.

8.1.3 Data acquisition and analysis

Data acquisition

The experiment was carried out on a 3 Tesla scanner (Siemens TimTrio, Germany). The diffusion-weighted imaging data and a high-resolution T1-weighted image were obtained with a 12-channel head array coil. Diffusion-weighted images were acquired with a twice-refocused spin echo-planar-imaging sequence (Reese et al., 2003), TE = 100 ms, TR = 9300 ms, image matrix 128 x 128, and FOV = 220 x 220 mm, providing 60 diffusion-encoding gradient directions with a b-value of 1000 $\mathrm{s/mm^2}$. Acquisition of the data started with one image without any diffusion weighting (b0 image with b-value = 0 $\mathrm{s/mm^2}$) and one b0 image after each block of ten diffusion-weighted images as reference for offline motion correction. The interleaved measurement of 65 axial slices with 1.7 mm thickness (no gap) covered the entire brain. Averaging two acquisitions reduced random noise in the data. Furthermore, fat saturation was employed together with 6/8 partial fourier imaging, and parallel acquisition with acceleration factor 2.

T1-weighted structural images were acquired in a previous session on the same 3 Tesla scanner. A MP-Rage image was acquired (data matrix 256 x 256, TR = 1.48 s, TE = 3.46 ms, inversion time (TI) = 7.4 s, flip angle 10°, bandwidth 190 kHz, space resolution 1 x 1 x 1.5 mm) with a non-slice-selective inversion pulse followed by a single excitation of each slice.

Data analysis

Data processing was performed using the software package LIPSIA (Lohmann et al., 2001) and FSL (S. M. Smith et al., 2004). Diffusion-weighted data was first cleaned manually by removing volumes with movement artefacts. Data of one participant had to be excluded from further analysis due to important movement during the scan session; more than 30% of the data of this participant had to be cleaned of movement artefacts. T1-weighted structural images were then rotated into the Talairach space and images were “brain peeled”, i.e. non-brain tissue was removed from the images. Images without diffusion weighting distributed in the whole acquisition sequence were used to estimate motion correction parameters using rigid-body transformation (Jenkinson et al., 2002). In a next step, motion correction of the diffusion-weighted images was carried out and combined with a global registration to the T1-weighted structural image. The registered images were interpolated to the new reference frame with an isotropic voxel resolution (1 mm) and the two corresponding acquisitions and gradient directions were averaged. In a last step, for each voxel, a diffusion tensor was fitted to the data. Using Tract-Based Spatial Statistics (TBSS; S. M. Smith et al., 2006), part of FSL, a voxel wise statistical analysis of the diffusion-weighted data was carried out. It started by running registration for each individual image to all other images separately to find the most representative image to achieve the best alignment possible. After determination of the best target all other images were aligned to this one by a nonlinear registration and were transformed finally into MNI152 standard space. After the registration, the mean fractional anisotropy (FA) skeleton image was calculated and thresholded with a value of 0.25 (Tamnes, Ostby, Walhovd, et al., 2010; Taddei et al., 2012)

In order to test for correlation of white matter in the left IFG and behavioural performance, two region of interest (BA 44 and BA 45) were selected. Both regions were anatomically defined using the MNI template of FSL, the same template on which the data was registered previously. The areas were identified by visual inspection of the macro structural information of the brain. For BA 44, the opercular part of the IFG was selected between precentral gyrus, lateral fissure, inferior frontal sulcus, and ascendant ramus. For BA 45, the triangular part of the IFG was selected between inferior frontal sulcus, lateral fissure, ascendant ramus, and horizontal ramus. Additionally, the IFG in the right hemisphere was chosen as a control region. Both anatomically defined regions were flipped on the x-axis and checked for agreement with the structure of the MNI template. Using FSL implemented tools, the FA skeleton was masked with each of the four ROIs separately and then the mean FA value for each subject was extracted from the masked FA image. Additionally, FA value for each subject was extracted from the whole brain FA skeleton. SPSS was used to perform a Pearson's correlation between the FA values, age and the children's performance in the behavioural testings' (TROG-D and the follow-up survey).

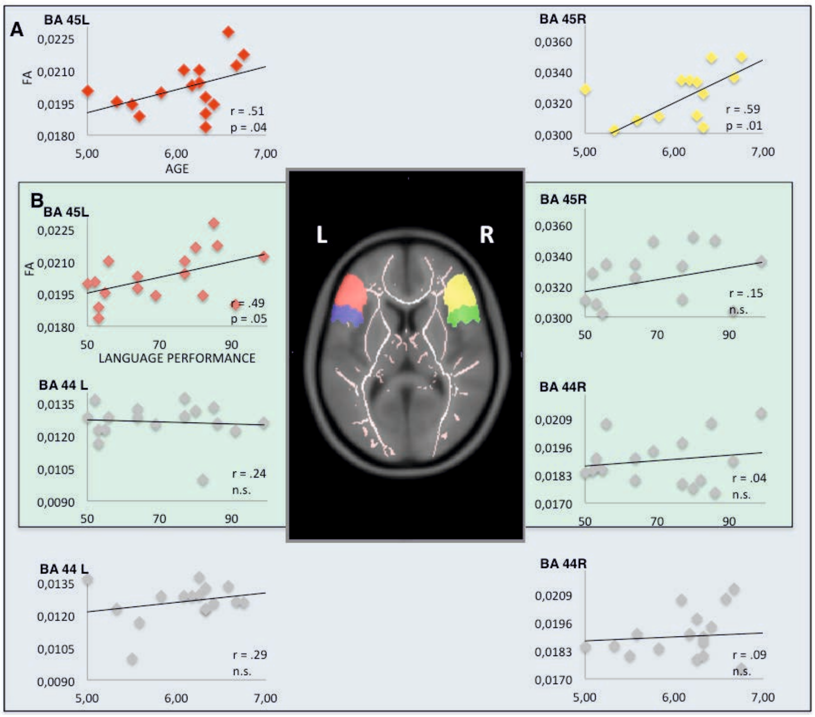

Figure 8.1: Figure shows correlations in four IFG ROIs: left BA 44 (blue) and BA 45 (red) and right BA 44 (green) and right BA 45 (yellow). (A) Correlation of FA and age. (B) Correlation of FA and language performance.

8.2 Results

Figure 8.1 shows the correlation plots of the FA values in four ROIs (left BA 44 and BA 45 and right BA 44 and 45) and age and language performance, respectively. No significant correlations with age were found in the whole brain FA (Person r = .43, n.s.) and left BA 44 (r = .29, n.s.) and right BA 44 (r = .09, n.s.). Age positively correlated with BA 45 in the right (r = .58, p = .01) and left hemisphere (r = .51, p = .04). The performance in the TROG-D did not show any correlation effect (whole brain (r = -.01, n.s.), left BA 44 (r = .05, n.s.), left BA 45 (r = .31, n.s.), right BA 44 (r = .21, n.s.), and right BA 45 (r = .25, n.s.), but the performance in the follow-up survey (see section 6.3.) was found to be positively correlated with FA in BA 45 in the left hemisphere (r = .49, p = .05). No correlations were found with FA in the other three IFG regions (right BA 45: r = .15, n. s.; left BA 44: r = .24, n. s.; right BA 44: r = .04, n.s.) and on whole brain level (r = .15, n. s.).

8.3 Discussion

The current study was set out to investigate structural changes in the left and right inferior frontal gyrus that specify the current results and support the interpretation of the findings in the functional imaging data in children. Fractional anisotropy was calculated in white matter pathways on whole brain level and in four regions of interests. The focus was on the left IFG (BA 44 and BA 45); whereas the right IFG (BA 44 and BA 45), and the whole brain structure analyses were used as control. A positive correlation with age was found in FA values in BA 45 in both the left and right hemisphere. If the assumption is correct that increased FA values mirror an increasing myelination process (Yakovlev & Lecours, 1967; Benes et al., 1994), the results indicate a significant maturation process in the left and right BA 45 within the age range of five to seven years of life.

Interestingly, only the left IFG (BA 45) covaried positively with language skills. Considering that especially the left IFG was found to be involved in sentence processing this finding provides further evidence that this area is (1) linked with language proficiency, and might indicate that it is (2) not fully developed in children at the age of five to seven years. This could also explain the poor performance in language/sentence processing compared to adults (chapter 4). A previous study investigating the ability of older adults (age range 64-76) to acquire syntactic knowledge in an artificial language learning found a positive correlation between the grammar learning ability and the FA in the left and right IFG (BA 44 and BA 45 combined) as well as in tracts originating in the left IFG (Antonenko et al., 2012). Other studies suggest a correlation of language tasks and underlying white matter changes in bilateral language-related areas in adults (Obler et al., 2010; Stamatakis et al., 2011). However, not all studies reported a bilateral correlation. Flöel and colleagues (2009) reported that rule-based grammar acquisition in adults was positively correlated only within left-hemispheric white matter structures of the IFG (BA 44 and BA 45 combined). Positive correlations of FA with general intellectual abilities were reported in studies in the developing brain (Schmithorst et al., 2005; Tamnes, Ostby, Fjell, et al., 2010). Correlations were mainly bilateral in white matter association areas comprising the SLF, frontal areas and occipito-parietal areas. The current results indicate that maturation of white matter microstructure in the IFG (BA 45) is related to children's language proficiency, i.e. grammatical knowledge.

These results raise the question why no correlation is found between language skills and the left BA 44 in the present study. Is it due to a general difference between children and adults or due to a difference in the function of BA 44 and BA 45? Previous DWI studies do not provide sufficient information for answering this question as they report correlation between language skills and Broca's area, but not in BA 44 and BA 45 separately (Flöel et al., 2009; Obler et al., 2010; Stamatakis et al., 2011; Antonenko et al., 2012). However, the results from the current fMRI analysis (chapter 6) might shed light on this question. Investigating sentence processing of object-initial sentences compared to subject-initial sentences, a strong involvement of BA 45 was found across all children, but not of BA 44. A closer look at the single-subject fMRI data indicated an in general higher variance in the left IFG with respect to an involvement of BA 45 and BA 44. As the same children were tested in the DWI-study, the diversity may also be reflected in the underlying white matter structure. This assumption is supported by the results found in the two subgroups (chapter 7), as in the fMRI analysis high performing children, but not medium-performing children, showed an adult-like effect in BA 44. Thus, the finding that no correlation between white matter underlying left BA 44 and the language skill was found in the overall group may be caused by high structural differences in the 17 children. Unfortunately, because only six high performing children of the fMRI study took part in the DWI-study, no separate analyses could be conducted for high-performers and medium-performers. A follow-up study should scrutinize this open question with a larger sample.

Taken together, the structural analysis clearly showed that age correlated positively with underlying white matter structures in the IFG (BA 45) bilaterally. Grammatical knowledge showed a left-hemispheric IFG (BA 45) correlation in FA values. The result indirectly demonstrates that language proficiency might be reflected in different maturational stages of white matter microstructure in the left IFG in five to seven-year-old children.

Part IV

GENERAL DISCUSSION AND FUTURE DIRECTIONS

9

General discussion

There are still many open questions concerning the fundamental processes and changes that children undergo until achieving adult-like language performance. The current dissertation provides a small but fascinating new insight into the structural and functional organization in the brains of five to six year-old German speaking children. Different methodologies and data acquisition techniques were used in order to investigate acquisition and processing of case-marking and word order information during sentence comprehension. In the following sections, a summary of the main findings is provided. Thereby, empirical findings will be compared to previous data in order to discuss possible consequences and future directions.

9.1 Summary

Before participating in a functional MRI experiment, children between the ages of 4;08 and 6;10 were tested in a **behavioural session** (chapter 4) in order to assess their receptive grammatical development (using the TROG-D) and to obtain behavioural correlates for the subsequent functional data collection. A picture-matching task was conducted to evaluate the children's level of proficiency in processing sentences with different syntactic complexity. The stimulus set consisted of sentences with two different types of structures, a (1) canonical structure where the subject of the sentence preceded the object and a (2) non canonical sentence structure where the object was in the initial position. All noun phrases were unambiguously case-marked by their masculine definite article, which indicated the subject or object status in the sentence. The results showed evidences for a clear advantage for subject-initial sentences as compared to object-initial sentences, but in both conditions children performed above chance level. Importantly, the results suggest that children at the age of five to six are not just sensitive to case-marking information, but also use this information in sentences to assign thematic roles. Nevertheless, their responses were less accurate in object-initial sentences, which indicates that they have not yet achieved the proficiency level to solely rely on case-marking; there is still a developmental gap to overcome before reaching the performance shown in subject-initial structures. Even though children showed an impressive performance of 96% correct responses in this latter condition, they performed still significantly poorer than adults, who were also tested with the same paradigm. In spite of these results, the question of why other studies reported that children were not able to use case-marking information until the age of seven (Lindner, 2003; Schipke et al., 2012) still exists. Considering that in the present study the tested group had an expanded age range (from 4;8 to 6;8), a post-hoc division into a younger (4;8 to 5;9) and an older (6;0 to 6;8) subgroup of the tested children was performed. No differences were found between the five and six-year-olds in their performance in the behavioural tests (TROG-D and picture matching task).

These results support the assumption that children are aware of the case-marking cue but do not rely exclusively on it for sentence interpretation. Certainly, it indicates that there is a smooth transition in performance enhancement in children around the ages of five to seven years.

The **first functional MRI experiment** (chapter 5) investigated processing of case-marking information in syntactically complex sentences in adults and served as a control for the children study. The same type of sentences which had already been used successfully in the behavioural testing was presented, but the material was extended. The extension included correct subject and object-initial sentences and also incorrect sentences with two arguments marked as nominative and two arguments marked as accusative, respectively. These additional two conditions were implemented in order to minimize the predictability of the sentence structure. Both the results from the behavioural pre-testing and fMRI revealed that these simple object-initial sentences were not challenging enough for adults to create significant differences to the subject-initial sentences. In the fMRI study in both grammatically correct conditions a similar activation pattern was observed. Contrasted with a silent baseline, both sentence types activated the entire STG/STS bilaterally and the left IFG. Even though the main contrast (condition vs. baseline) suggested a more pronounced activation in the left IFG for object-initial sentences, a direct comparison between these two conditions (object-initial vs. subject-initial) did not reveal significant activation differences at whole brain level. In contrast to a silent baseline an extensive activation in the STG/STS bilaterally as well as activation in the PMC bilaterally, the striatum, cerebellum and the left IFG was elicited by both violation structures. Interestingly, a cluster of activation with peak in the left anterior insula comprising also the FO and extended to the IFG was found in the double nominative condition and in the object-initial condition solely. The frontal operculum is assumed to be involved in local structure building (Friederici et al., 1999, 2000, 2003, 2006), articulatory rehearsal processes (Fiez et al., 1996; Price et al., 2003; Hurschler et al., in press), and executive functions such as error monitoring (for a review see Taylor et al., 2007). Thus, enhanced involvement of the FO in object-initial and double nominative sentences could be associated with a local structure building process that is apparently more challenging in non canonical sentences and in sentences with a violated sentence structure. The missing FO activation in the second violation condition (double accusative) can be explained by more salient characteristics of accusative markers. A study by Frisch and Schlesewsky (2005) indicated that the perception of a double nominative is somewhat delayed and its detection is not as fast as in the double accusative condition. Most importantly, focusing on Broca's area, a region of interest analysis revealed that higher processing demands for object-initial sentences can also be found in adults. A significant effect for sentence complexity was found for BA 44 in Broca's area. This finding is consistent with previous fMRI studies that reported a stronger activation for syntactically more complex sentences (Ben-Shachar et al., 2003, 2004; Bornkessel et al., 2005; Fiebach et al., 2005; Grewe et al., 2005; Friederici, Fiebach, et al., 2006; Grodzinsky & Santi, 2008; Obleser et al., 2011). The present results support the general assumption that Broca's area is involved in syntactic structure processes, and moreover, especially BA 44 seems to be highly sensitive to this process.

The **second functional MRI experiment** (chapter 6) examined the role of the IFG and other areas in the processing of case-marking information and argument structure in children. The same stimulus set as in the adult study was used. The behavioural results already indicated that children are sensitive to case-marking information and use it for sentence interpretation. As expected, activation for all four conditions contrasted with a silent baseline (Figure 6.1) was observed mainly bilaterally along the STG/STS. Object-initial sentences led to activation in the IFG, i.e. in BA 45. Activation in the left IFG was predicted for more syntactically complex non canonical structures. However, the canonical subject-initial sentences did not activate this region. Contrary to prior studies (Bornkessel et al., 2005; Friederici, Fiebach, et al., 2006; Rogalsky et al., 2008) and the results from the present study in adults, the complexity effect was observed in BA 45 for children, and not in BA 44. BA 45 is argued to be more engaged during sentence comprehension in young children than in adults (Brauer et al., 2011), possibly due to the fact that the dorsal white-matter pathway that connects BA 44 and the temporal region is not yet fully matured at this age. The authors suggested that a ventral temporo-frontal connection targeting BA 45 might serve as connection supporting the children's language network for sentence processing, as reflected by stronger activation in BA 45. Nevertheless, the present study specifies this view and suggests that enhanced BA 45 activation might reflect a different strategy used by children compared to adults. Children have not reached the proficiency level to fully rely on case-marking information as adults do; an assumption supported by the behavioural results (experiment 1). Additionally, activation of BA 45 points to semantic processes (Bookheimer, 2002; Friederici, 2002; Hagoort, 2005) and further evidence for this hypothesis is delivered by the children themselves. When being asked about the sentences, a few children refused some sentences due to their semantic content. Moreover, a direct comparison of object-initial sentences and subject-initial sentences revealed left-lateralized activation in the IPC extending to posterior STG as well as in the right-hemispheric ACC. Activation in the IPC is in line with previous studies investigating sentence processing (Booth et al., 2000; Ahmad et al., 2003; Yeatman et al., 2010) and has been attributed to aspects of phonological working memory during sentence comprehension (L. Meyer et al., in press). ACC activation has previously been attributed to executive functions such as conflict monitoring and prediction error (Carter et al., 1998; Barch et al., 2001; Botvinick et al., 2001). In the region of interest analysis, focusing on Broca's area, only a marginal interaction effect of *word order* (subject-initial vs. object-initial) by *ROI* (BA 44 vs. BA 45) was found.

Taken together, this experiment suggests a broad heterogeneity related to sentence processing in five to six-year-old children. Interestingly, enhanced activation in BA 45 might reflect a different strategy used by children compared to adults. To clarify this assumption, which is supported by many recent developmental studies reporting high individual differences in their group of tested children (Ettinger-Veenstra et al., 2010; Yeatman et al., 2010; Nuñez et al., 2011), a closer look at the single-subject data was subsequently taken to provide additional information concerning the individual developmental level.

A **subsequent data analysis** (chapter 7) asked about the role of the IFG and other involved areas in processing case-marking information in syntactically complex sentences in two subgroups of the tested children. The children were split by their performance in the receptive grammatical language test, resulting in a medium and a high-performing group. Interestingly, only high-performers showed an above chance behavioural performance in the object-initial sentences in the picture-matching task. The fMRI results also revealed differences between both groups, while no fundamental processing differences between object-initial and subject-initial sentences were found in the medium-performing group, left prefrontal areas showed higher activation for the more demanding complex object-initial compared to subject-initial sentences in the high-performing group. These left prefrontal areas included the DLPFC extending to the IFG and the ACC (bilaterally). DLPFC activation has been observed for increased short-term memory load (Fletcher & Henson, 2001; Narayanan et al., 2005; Jolles et al., 2011), increased syntactic memory demands (Caplan et al., 2000) and for executive control of working memory (Miller & Cohen, 2001; Barbey et al., in press). In the present study, the processing of object-initial sentences is assumed to be more costly in terms of syntactic working memory (Gibson, 1998), since object-initial structures require the prediction of a subject and a verb. Most importantly, only the group with high grammatical knowledge showed an adult-like pattern of activation in the left IFG (Friederici, Fiebach, et al., 2006; Rogalsky et al., 2008); that is a larger activation for more complex sentences in contrast to canonical sentences, whereas the medium-performing subgroup did not.

The data indicate that different strategies are employed when it comes to using case-marking information for sentence processing, depending on the children's grammatical knowledge. If they are not advanced enough to rely on case-marking information solely (medium-performers), they seem to rely instead on additional cues, for instance semantic cues, to process sentences. Moreover, patterns of activations in the left IFG seem to indicate the degree to which adult-like sentence comprehension strategies are already employed.

A **DTI study** in children asked about structural changes in the left IFG in order to explain children's language performance. Regions in the right IFG and a whole brain mask served as control areas. Fractional anisotropy (FA) was calculated in white matter structures underlying these regions. Previous studies provided evidence that structural changes do not precede synchronically in all brain regions (Paus et al., 1999; Pujol et al., 2006; Dubois et al., 2008; Giorgio et al., 2008). Besides, FA of white matter microstructure of the IFG was found to be positively correlated with language performance in adults (Flöel et al., 2009; Obler et al., 2010; Stamatakis et al., 2011; Antonenko et al., 2012). In the present study, age positively correlated with the underlying white matter structures in the IFG bilaterally (BA 45) as measured by FA. Importantly, grammatical knowledge was positively correlated only in the left IFG, whereas the right IFG did not reveal any correlation effects. The result suggests that language proficiency might be reflected in different maturational stages of white matter microstructure in the left IFG.

9.2 Conclusion

Taken together, the functional and structural data presented in this thesis show that there is a considerable amount of heterogeneity within the five to seven-year old group of children related to sentence processing, and that this heterogeneity is directly reflected in differential patterns of functional activation and in structural differences in the left inferior frontal gyrus. While some children already reliably use case-marking information for sentence interpretation at this age, others do not. Interestingly, the results indicate that they instead rely on additional cues, such as semantic information, to process syntactically more complex sentences. The functional and behavioural data indicate that different strategies are employed when it comes to process case-marked object-initial sentences, depending on the children's receptive grammatical knowledge.

An effect for object-initial sentence processing in the overall group was reflected in ACC activation, an area that is commonly attributed to executive functions (e.g. processing prediction errors) and in the left IPC, an area related to phonological working memory that has been previously found in studies focusing on syntactic complexity in children. Importantly, the left IFG seems to indicate the degree to which adult-like sentence comprehension strategies are already employed. While medium-performing children do not reliably use case-marking cues for syntactic integration processes, high-performing children do so. In contrast to medium-performing children the language system of high-performing children is not challenged by subject-initial sentence constructions anymore. Only object-initial sentence involve the left IFG. The structural data support this view by revealing increased FA in the left IFG, which correlates with grammatical knowledge. Thus, it seems that the present experiments have pinpointed a pivotal phase of language development during which children are already sensitive to grammatical cues but differ in their individual ability and brain structural foundation when it comes to using these cues to integrate them for successful sentence comprehension.

9.3 Open questions and future directions

There are still many research questions to be answered in the future. An interesting question is, which language skills exactly correlate with the underlying white matter structure of BA 45 and BA 44, measured by FA. Reviewed studies in adults (Flöel et al., 2009; Obler et al., 2010; Stamatakis et al., 2011; Antonenko et al., 2012) and the current study in children utilized various language tasks (artificial grammar learning, word retrieval, naming test, accuracy rating of syntactic structures) in order to correlate behavioural language performance with underlying white matter structures of Broca's area. Further studies should take a closer look at correlations in FA in Broca's area within different language domains such as syntax, semantics, or prosody. Additionally, previous studies, which found correlations in FA in the left IFG and language performance in adults (artificial grammar learning, word retrieval, naming test) focused on the whole Broca's area and not on the subregions independently (Flöel et al., 2009; Obler et al., 2010; Stamatakis et al., 2011; Antonenko et al., 2012). A subsequent study should concentrate on language correlations in white matter structures in Broca's areas, BA 44 and BA 45 separately. Previous findings in functional MRI studies indicated that these two areas support different language processes. Whereas BA 44 is often associated with syntactic structure building (Friederici, 2002), BA 44/45 is considered to be sensitive to thematic role assignment and supporting computation of syntactic movement (Osterhout & Nicol, 1999), and BA 45/47 is associated supporting semantic processes (Bookheimer, 2002; Friederici, 2002; Hagoort, 2005). Correlations in different language tasks and FA in the different areas in the left IFG could provide further evidence for a clear functional separation of BA 44 and BA 45.

A follow up fMRI study could test the formulated hypothesis based on the findings in the fMRI study. It is hypothesized that children in the medium-performing subgroup do not reliably use case-marking information, and search for additional language cues such as semantics for sentence interpretation (Chapman, 1978). They might turn to semantic information of the verb in order to assign the thematic roles to the sentential arguments ("You cannot comb a bird. The bird has no hair."). A possibility to test the strength of semantic influence in sentence processing in preschool children is to create a stimulus set without semantic verb information. Previous studies have already employed this kind of stimuli successfully in behavioural testing. Dittmar and colleagues (2008, 2011) presented sentences with nonsense verbs (such as e.g. weefing, tamming and baffing) in order to investigate the use of case-marking information in children. The present results of the fMRI study in children show that both groups (medium and high-performers) use case-marking information. However, the data indicates that different strategies are employed when it comes to process case-marked object-initial sentences, depending on the children's receptive grammatical knowledge. A functional imaging study should adopt these sentences with subject-initial and object-initial sentence structure including nonsense verbs. Thus, children are forced to use case-marking information for sentence interpretation, because semantic verb information is excluded. An fMRI study using this paradigm could shed light on the question of whether the activation found in the left IFG indeed indicates different strategies in children; medium-performers use case-marking and semantic information, while high-performers rely on case-marking solely. Alternatively, if the findings point in the same direction as the present study, it might indicate that the processing of morphosyntactic information in medium-performing children is supported by different brain areas (BA 45 vs. BA 44) compared to the findings in high-performing children and in adults.

A third fascinating research question is to investigate the developmental state of white matter fiber pathways in children. Brauer and colleagues (2011) argue for an immature status of the dorsal fiber tracts of the arcuate fasciculus and superior longitudinal fasciculus in children compared to adults. Perani and colleagues (2011) found evidence that the dorsal fiber tract connection is not fully maturated at birth, rather the dorsal connection from the STG/STS terminates in the premotor cortex. These findings indicate that the dorsal connection between temporal regions and the PMC and BA 44, respectively, maturates with increasing age. Considering that two dorsal pathways are assumed, one pathway (I) connecting the temporal regions with the PMC and the other pathway (II) linking the temporal regions with BA 44, a subsequent study should focus on the maturational level of these two dorsal pathways independently. In consideration of the fact that the second dorsal pathway (II) is assumed to manage syntactic processes (Friederici, Balhmann, et al., 2006; Gow, 2012), it should be investigated whether different maturation levels of dorsal pathway II can explain language performance in children. Based on Brauer and colleagues (2011) it is suggested that the developmental state of white matter in this dorsal connection (II), targeting BA 44, might be positively correlated with syntactic language skills.

The presented experiments in this thesis are a step towards specifying the underlying brain mechanisms and structures involved in syntactic processes in the developing brain. Most importantly, the findings indicate a pivotal phase in language development between the ages of five to seven years. However, further research has to scrutinize the interrelation of behavioural, functional and structural development to understand the underlying processes involved in language acquisition and processing.

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A.1 Abbreviations

ACC	accusative
AF	arcuate fasciculus
AG	angular gyrus
ANOVA	analysis of variance
ANT	anterior
BA	brodmann area
BG	basal ganlia
BOLD	blood-oxygen-level-dependent
CC	corpus calosum
DAT	dative
DTI	diffusion-tensor imaging
ECFS	extreme caspule fiber system
EEG	electroencephalography
EPI	echo planar imaging
ERP	event-related brain potential

FA	fractional anisotropy
FO	frontal operculum
fMRI	functional magnetic resonance imaging
FOV	field of view
FWHM	full width at half maximum
GLM	general linear model
HG	heschl's gyurs
IFG	inferior frontal gyrus
IPC	inferior parietal cortex
KHZ	kilo hertz
MEG	magnetoencephalography
MI	primary motor cortex
MNI	Montreal Neurological Institute
MP-RAGE	magnetization-prepared rapid gradient echo
MR	magnetic resonance
MRI	magnetic resonance imaging
MS	millisecond
MFG	middle frontal gyrus
MTG	middle temporal gyrus
NOM	nominative
OP	occipital cortex
PAC	primary auditory cortex
PMC	premotor cortex
POST	posterior
PSC	percent signal change
PT	planum temporale
ROI	region of interest
RT	reaction time

SEM	standard error of the mean
SFG	superior frontal gyrus
SLF	superior longitudinal fasciculus
SMG	supramarginal gyrus
SNR	signal-to-noise ratio
SPC	superior parietal cortex
STG	superior temporal gyrus
STS	superior temporal sulcus
TBSS	tract-based spatial statistics
TE	echo time
TI	inversión time
TR	repetition time
UF	uncinate fasciculus

A.2 Stimuli

01a Der Käfer trägt den Frosch.
02a Der Frosch trägt den Käfer.
03a Der Vogel kämmt den Hund.
04a Der Hund kämmt den Vogel.
05a Der Tiger zieht den Igel.
06a Der Igel zieht den Tiger.
07a Der Tiger küsst den Frosch.
08a Der Frosch küsst den Tiger.
09a Der Käfer wäscht den Hund.
10a Der Hund wäscht den Käfer.
11a Der Igel malt den Vogel.
12a Der Vogel malt den Igel.
13a Der Käfer kratzt den Vogel.
14a Der Vogel kratzt den Käfer.
15a Der Igel schlägt den Käfer.
16a Der Käfer schlägt den Igel.
17a Der Frosch schiebt den Igel.
18a Der Igel schiebt den Frosch.
19a Der Hund fängt den Frosch.
20a Der Frosch fängt den Hund.
21a Der Tiger beißt den Hund.
22a Der Hund beißt den Tiger.
23a Der Vogel tritt den Tiger.
24a Der Tiger tritt den Vogel.

01b Den Frosch trägt der Käfer.
02b Den Käfer trägt der Frosch.
03b Den Hund kämmt der Vogel.
04b Den Vogel kämmt der Hund.
05b Den Igel zieht der Tiger.
06b Den Tiger zieht der Igel.
07b Den Frosch küsst der Tiger.
08b Den Tiger küsst der Frosch.
09b Den Hund wäscht der Käfer.
10b Den Käfer wäscht der Hund.
11b Den Vogel malt der Igel.
12b Den Igel malt der Vogel.
13b Den Vogel kratzt der Käfer.
14b Den Käfer kratzt der Vogel.
15b Den Käfer schlägt der Igel.
16b Den Igel schlägt der Käfer.
17b Den Igel schiebt der Frosch.
18b Den Frosch schiebt der Igel.
19b Den Frosch fängt der Hund.
20b Den Hund fängt der Frosch.
21b Den Hund beißt der Tiger.
22b Den Tiger beißt der Hund.
23b Den Tiger tritt der Vogel.
24b Den Vogel tritt der Tiger.
01c Der Käfer trägt der Frosch.
02c Der Frosch trägt der Käfer.
03c Der Vogel kämmt der Hund.
04c Der Hund kämmt der Vogel.
05c Der Tiger zieht der Igel.
06c Der Igel zieht der Tiger.
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08c Der Frosch küsst der Tiger.
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15d Den Käfer schlägt den Igel.
16d Den Igel schlägt den Käfer.

17d Den Igel schiebt den Frosch.

18d Den Frosch schiebt den Igel.

19d Den Frosch fängt den Hund.

20d Den Hund fängt den Frosch.

21d Den Hund beißt den Tiger.

22d Den Tiger beißt den Hund.

23d Den Tiger tritt den Vogel.

24d Den Vogel tritt den Tiger.

Selbständigkeitserklärung

Hiermit versichere ich, dass ich die vorliegende Arbeit in allen Teilen selbständig verfasst und keine anderen als die angegebenen Hilfsmittel benutzt habe. Ich versichere weiterhin, dass die aus fremden Quellen direkt oder indirekt übernommenen Gedanken in der Arbeit als solche kenntlich gemacht worden sind.

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