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*How the Brain Attunes to Sentence Processing
Relating Behavior, Structure, and Function*

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HOW THE BRAIN ATTUNES TO SENTENCE PROCESSING

Relating Behavior, Structure, and Function

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Preface

The human brain is an impressive organ. It perfectly stands for the evolutionary accomplishment in humans by its high complexity and its striking adaptability. Especially the elaboration of the cerebral cortex allows for the highly specialized cognitive processes necessary, for example, for language, consciousness, and culture. Brain development during ontogeny results from a dynamic interplay of nature and nurture and modern neurobiological methods provide the remarkable opportunity to observe genetic variations as well as adjustments caused by experience. Both gene expressions and environmental input are essential for the lifelong process of brain maturation although brain plasticity, and with it its adaptability, decreases with age.

Language is one of the most impressive skills humans acquire. It enables us to articulate our needs and believes, it serves our social and cultural interchange, it helps us expressing our feelings, it shapes our thoughts, and only with language we are able to detach from here and now. Despite its complexity, children acquire a language incredibly fast. However, language acquisition progresses from being implicit, effortless, and unconscious to being more explicit, effortful, and conscious. Thus, the older we get, the harder it is to acquire, for example, the pronunciation or the grammatical aspects of a new language.

As the phylogenetic evolutionary development of the brain has been associated with the evolvement of language, it is also very likely that the

ontogenetic maturation, especially of the cerebral cortex, can be related to language acquisition. However, evidence for a direct link between cortical maturation, brain function during language processing, and language performance is rare. Therefore, the current thesis investigates the tripartite relation among behavior (= language performance and cognitive prerequisites), brain structure (= gray matter probability), and brain function (= brain activation).

Part I of the thesis provides an introduction into all three related aspects. Chapter 1 gives an overview about brain structural and brain functional maturation. Chapter 2 describes theoretical considerations and empirical evidence of sentence processing in adults and chapter 3 summarizes previous findings of children's sentence processing. In addition, the latter two chapters discuss the influence of verbal working memory capacities as a cognitive prerequisite for sentence processing.

Part II introduces the methods at hand: functional magnetic resonance imaging and the voxel-based morphometry analysis (chapter 4 and 5). Thereby special challenges in the application of these methods on a children's sample are presented in detail.

The empirical part III starts with an outline of the research questions and is followed by the description of four studies (chapter 6). Study I investigates the relation between verbal working memory capacity and sentence processing skills in children (chapter 7)¹. Study II examines whether gray matter maturation can be linked to sentence processing

skills in children (chapter 8)² and study III addresses different activation patterns during adults' and children's sentence processing (chapter 9)³. Study IV creates a symbiosis of the previous three studies by relating the brain activation pattern found in participants of this study to the language performance, verbal working memory capacities, and the degree of structural maturation (chapter 10)³. In chapter 11, the current findings are summarized and discussed in the overall framework. Open questions are proposed as future research directions.

¹Chapter 7 is a modified version of Fengler & Friederici (in prep.).

²Chapter 8 is a modified version of Fengler, Meyer & Friederici (2015).

³Sections of chapter 9 and 10 are modified versions of Fengler, Meyer, & Friederici (under review).

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PART I

INTRODUCTION

1 BRAIN MATURATION

1.1 Structural maturation

Even though the brain is not fully developed at birth, it already contains ~100 billion neurons. Numerous creations of neurons and their migration to different parts of the brain mark brain development in fetal stages. As soon as neurons have reached their target site and got aggregated to the neuronal structure around them, they start growing axons and dendrites to finally form synapses among one another. Thereby they start to establish rudimentary local neural networks. All these progressive changes appear early in life and induce a brain volume at age 6 that is already 90% the brain volume of adults (e.g. Courchesne et al., 2000; Lenroot & Giedd, 2006; Reiss, Abrams, Singer, Ross, & Denckla, 1996). Next to dendritic growth, axonal growth, and myelination of axons, particularly synaptic exuberance leads to brain volume increase after birth (Innocenti & Price, 2005). At this age, the amount of local connections exceed even those of the adult brain. Afterwards synaptic pruning gains

increased importance and with it neuronal density starts to decrease. Synaptic density peaks in different cortices at different time scales (Huttenlocher & Dabholkar, 1997). These peaks are associated with developmental cognitive milestones. For example, the formation of synaptic contacts in the dorsolateral prefrontal cortex reaches its maximum after 15 months, the age when infants acquire the notion of object permanence (for a more detailed discussion, see Diamond, 2002). In sum, brain maturation is characterized by progressive changes such as neurogenesis, synaptogenesis, axonal and dendritic growth as well as myelination which are opposed by concurrent regressive changes like cell death and synaptic pruning (for a review, see Stiles & Jernigan, 2010). These processes together are the basis for the lifelong brain alterations.

Early in life, progressive changes prevail. Nonetheless, gray matter volume already starts to decrease during early childhood while white matter increases until the fourth decade (Lebel, Walker, Leemans, Phillips, & Beaulieu, 2008). As changes in synaptic density, the loss of gray matter volume is region-specific (Lenroot & Giedd, 2006) following a functional maturation sequence whereas primary sensorimotor brain areas mature first and higher-order association areas such as the frontal and parietal cortical regions last (Gogtay et al., 2004). Again the question arises whether changes in gray matter maturation can be related to individual differences in behavior. For instance, Shaw et al. (2006) were interested in whether changes of the cortical thickness are correlated with

the individual intelligence quotient of their participants. To answer this question, they tested 307 children and adolescents. They found that those participants who showed the latest peaks in cortical thickening in various regions were the most intelligent and, since the prefrontal cortex showed a relatively late maturation in these subjects, they suggest that “the prolonged phase of prefrontal cortical gain in the most intelligent might afford an even more extended ‘critical’ period for the development of high-level cognitive cortical circuits” (Shaw et al., 2006: 678). Following these previous findings, it appears that brain development is a highly dynamic process that follows region-specific patterns and individual-specific developments.

1.2 Brain plasticity and critical phases

The pronounced dynamic character of brain development provides the basis for the plasticity of the brain. Brain plasticity stands for the brain’s remarkable ability to change and adapt to experience. However, these dynamic processes might occur during particular periods in time during which experience may have the greatest impact on the brain development.

With respect to specific phases of heightened plasticity during brain development, it is distinguished between critical and sensitive periods. A critical period describes a “strict time window during which experience provides information that is essential for normal development and

permanently alters performance” (Hensch, 2005: 877). During this critical phase, specific input is required to stimulate the development of a particular neural circuit (Hensch & Bilimoria, 2012). Without the required input, the circuit will be left unstimulated and its specific function will be permanently lost. The less stringent sensitive period is “a limited time during development, during which the effect of experience on brain function is particularly strong” (Hensch, 2005: 877). Experience during this time window has the highest impact on the neural circuits’ development. However, these particular circuits may be also shaped later but with much more effort and to a lesser degree (Hensch & Bilimoria, 2012).

Language acquisition consists of multiple overlapping critical and sensitive periods. An early critical time window during the first year of life involves phonetic and prosodic perception. During this critical phase, specific input is required to stimulate the development of neural circuits which are committed to phonetic and prosodic properties of the native-language speech to maximize the efficiency of language processing (Kuhl, 2004, 2010; Kuhl & Rivera-Gaxiola, 2008). In addition to this early critical time window, language acquisition underlies a sensitive period during which language input has the greatest impact on grammar development. This sensitive period appears to cease around late childhood and may explain why language learning after childhood must rely on more explicit, effortful, and conscious learning mechanisms and rarely results in native-like grammatical proficiency (Johnson & Newport, 1989; Zevin, Datta, &

Skipper, 2012). Data providing evidence for a clear relationship between brain structural maturation and the ceasing of the sensitive periods for language acquisition, however, are rare and thus will be addressed by this thesis.

1.3 Functional maturation of language-relevant areas

Recent developmental functional neuroimaging studies provide evidence for the early engagement of the perisylvian areas in language processing in newborns (Perani et al., 2011) and during the first months of life (Dehaene-Lambertz et al., 2006; Dehaene-Lambertz, Dehaene, & Hertz-Pannier, 2002). So far, functional imaging studies with children used paradigms focusing on testing language processing on two linguistic levels: Studies on word-level investigated brain activation related to word generation (Brown et al., 2005; Holland et al., 2001; Karunanayaka et al., 2010), semantic decision (Balsamo, Xu, & Gaillard, 2006), single word processing (Schlaggar et al., 2002), and object identification (Schmithorst, Holland, & Plante, 2007). Studies on sentence-level examined passive listening (Ahmad, Balsamo, Sachs, Xu, & Gaillard, 2003; Dehaene-Lambertz et al., 2002; Dehaene-Lambertz, Hertz-Pannier, & Dubois, 2006; Lidzba, Schwilling, Grodd, Krägeloh-Mann, & Wilke, 2011; McNealy, Mazziotta, & Dapretto, 2010; Schmithorst, Holland, & Plante, 2006), active response story processing (Vannest et al., 2009), and sentence violation detection (Brauer & Friederici, 2007). While the

acquisition of the lexicon is a lifelong process that is dependent on experience, grammar acquisition depends on specific input within a specified time window. However, the above mentioned studies on sentence-level did not test sentences of different complexities but rather sentence processing in general. Therefore, they cannot distinguish whether changes in activation with age can be attributed to grammatical or lexical/semantic aspects.

Up to now, functional imaging studies in preschool children that contrasted the processing of simple and complex sentences did not generally detect a complexity-related increase of activity in the left inferior frontal gyrus (IFG; Knoll, Obleser, Schipke, Friederici, & Brauer, 2012; Yeatman, Ben-Shachar, Glover, & Feldman, 2010). Knoll et al. (2012) could only show the emergence of complexity-sensitive activation for high performing children. In addition, only at the end of the 10th year of age, children show syntax-related activation segregated from semantic aspects (Skeide, Brauer, & Friederici, 2014). In adults, the IFG has been found to show increased activity while processing complex sentences with moved or scrambled constituents as well as nested structures (for a review, see Friederici, 2011). So far, it remains unclear when and how the left IFG attunes to syntactic complexity. The absence of an increase of activation in children compared to adults can be explained in two ways: On the one hand, the left IFG may not be specifically engaged in syntactic processing yet leading to alternative processing strategies in children's

sentence comprehension. For example, behaviorally German-speaking children were shown to initially rely on semantic cues like animacy in sentence-interpretation and only later proceed to make use of grammatical cues (Lindner, 2003). This could be a result of immature fiber tracts that transport information between brain regions involved in language processing such as the IFG and posterior cortical language regions (Brauer et al. 2011; Perani et al. 2011). On the other hand, findings by Brauer et al. (2007) indicate that children compared to adults show generally higher activation for processing syntactically and semantically incorrect sentences in inferior frontal regions. Following this result, an increase of activity with respect to complexity might not be observed since simple sentences engage the left IFG already to a high degree, perhaps due to less proficiency.

To answer the open questions about the functional attunement of the syntax-relevant regions, different age groups need to be functionally investigated by well controlled sentence material focusing on syntactic complexity. Since it has been proposed that recursion constitutes the fundamental property of syntax (Hauser, Chomsky, & Fitch, 2002), center-embedded sentences provide appropriate material for a functional study. In addition, performance data must be collected and be related to the functional data to conclude about different processing strategies in different age groups.

2 SENTENCE PROCESSING IN ADULTS

2.1 The processing of hierarchical sentence structures

Recent approaches suggest recursion to be the fundamental property of the human language faculty (Hauser et al., 2002). Although recursion has often been defined as embedding a phrase within another phrase, there is no single, universally accepted definition of recursion. However, a definition by Jackendoff and Pinker (2005) highlights the aspect of embeddedness in recursion as “a procedure that calls itself, or to a constituent that contains a constituent of the same kind” (Jackendoff & Pinker, 2005: 203). The authors assume that language needs to be recursive to enable the expression of recursive thoughts. More specifically, diplomatic speech, perlocutionary acts as well as prospective memory and cognition have been proposed as reasons for recursion in speech acts (Coolidge, Overmann, & Wynn, 2011). Therefore, it comes as no surprise that the strong version of recursion as in multiple hierarchical center-embedding (Coolidge et al., 2011) emerged with the

advent of written language, with Aristotle, Cicero, and Livy in the Greek and Latin stylistic tradition of 'periodic' sentence composition (Karlsson, 2007). Nonetheless, strings with two or three levels of center-embedding are extremely rare (Karlsson, 2007) and, if used at all in spoken language, frequently misunderstood (Bach, Brown, & Marslen-Wilson, 1986). They are read with the same intonation as a list of random words (Miller, 1962), they cannot be easily memorized (Foss & Cairns, 1970; Miller & Isard, 1964), they are difficult to paraphrase (Hakes & Foss, 1970; Larkin & Burns, 1977), they are difficult to comprehend (Blaubergs & Braine, 1974; Hakes, Evans, & Brannon, 1976; Hamilton & Deese, 1971; Wang, 1970), and they are judged to be ungrammatical (Marks, 1968). A very well documented phenomenon, the grammatical illusion effect, is that triple embedded sentences such as "The apartment that the maid who the service had sent over was cleaning every week was well decorated." (examples from Frazier, 1985) are rated more acceptable when the intermediate verbal phrase is omitted like in "*The apartment that the maid who the service had sent over was well decorated." (for further discussion, see Gibson & Thomas, 1999). This finding has been attributed to a possible pruning of the verbal phrase due to too high memory costs and thus this phenomena may be related to extrinsic memory limitations (Miller & Chomsky, 1963) such as limits on stack depth (Marcus, 1980), limits on the number of allowed sentence nodes (Kimball, 1973), limits on partially complete sentence nodes in a given sentence (Stabler, 1994), and limits

on the amount of activation available for storing intermediate processing products as well as executing production rules (Just & Carpenter, 1992). More specifically, the syntactic prediction locality theory (SPLT) assumes different costs at different incomplete syntactic relationships (Gibson, 1998). During sentence processing, two different components load on syntactic heads that need to be integrated into the sentence structure: a memory cost component that stores the structure processed so far and an integration cost component that integrates the current word into the structure. With the number of embeddings, costs on both components increase. While in non-embedded sentence structures complete subclauses can be stored separately, hierarchically embedded sentence structures contain multiple interrupted subclauses. Their simultaneous storage protracts the structure being processed and thus increases the memory cost. In addition, due to the interruption by other subclauses, the integration of nouns and verbs into the overall sentence meaning is delayed which increases the integration costs. These concepts are elaborated in the dependency locality theory (DLT; Gibson, 2000). In this theory, Gibson (2000) assumes that integration costs can be calculated by the number of new discourse referents between two dependent elements and that storage costs are the number of predicted syntactic heads. According to these ideas, the complexity of embedded sentences is increased by both the interruption of subclauses that increases the amount of predicted heads as well as intervening noun phrases which

protract the long-distance dependency between noun phrases and their corresponding verbs. The phenomenon of grammatical illusion is explained by difficulties in structural integration which is the greatest at the verb of the first relative clause in sentences since it is not coindexed with a nominal noun phrase but a noun phrase empty-category (like 'who' or 'that', see the example from Frazier, 1985 mentioned above). Therefore, its omission results in the greatest reduction of memory costs and counteracts most effectively the excess of verbal working memory capacities. Moreover, verbal working memory load can also be decreased by semantics that can facilitate possible chunking which reduces verbal working memory costs (Hudson, 1996) like in "The window (which) the ball (that) the boy threw hit broke." compared to "The tiger (which) the lion (that) the gorilla chased killed was ferocious." (examples from Hudson, 1996: 20).

The assumption that processing difficulties with hierarchical center-embedded sentence structures can be mainly attributed to the excess of verbal working memory capacities is supported by numerous studies. For example, selective verbal short-term memory deficits result in difficulties processing center-embedded sentences, while the processing of non-canonical sentence structures is preserved (Papagno, Cecchetto, Reati, & Bello, 2007). Compared to younger subjects, older subjects whose computational capacities are reduced show poorer performance in the repetition of center-embedded sentences (Baum, 1993). And better

ratings for triple embedded sentences in which the intermediate verbal phrase is omitted compared to ratings for the grammatical version have not only been reported in English but in other languages like French as well (Gimenes, Rigalleau, & Gaonach, 2009).

However, in German this effect could not be replicated (Vasishth, Suckow, Lewis, & Kern, 2010) and cross-linguistic differences have been found in processing center-embedded sentences that cannot be explained by mere verbal working memory overload: While English-speaking participants prefer a strategy of interpretation based on word order, Italian-speaking participants rely on agreement information (Bates, 1999). Therefore, it has been suggested that limitations on the processing of center-embedded sentences stem from interactions between linguistic experience and intrinsic constraints on learning and processing (Christiansen & MacDonald, 2009). This assumption is supported by the finding that processing strategies/preferences can change as a function of second language learning within 3 months (Davidson & Indefrey, 2009).

2.2 The processing of hierarchical sentences in the adults' brain

Humans attempt to extract inherent hierarchical, sequential structures whenever we attend to sequential events (Fiebach & Schubotz, 2006). In a next step, structural expectations are formed by combining these extracted structures with preexisting knowledge. The processing of

hierarchical center-embedded sentence structures requires the interaction of differential domain-specific and domain-general components: First, the processing of these sentences involves the syntactic computation of the structural hierarchy of the sentence probably based on stored structural templates (Fiebach & Schubotz, 2006). Second, it involves verbal working memory as sentence material that cannot be integrated into the overall sentence meaning immediately needs to be stored by a non-syntactic verbal working memory component to establish long-distance dependencies. And finally, to determine who is doing what to whom, semantic and syntactic information has to be integrated to assign thematic roles to their corresponding noun phrases.

Since the segregation of these differential aspects of hierarchical center-embedded sentence processing is quite challenging, the interpretation of functional brain activation patterns evoked by multiple embedded sentences is widely diverse. The first study using functional magnetic resonance imaging (fMRI) to investigate the processing of center-embedded sentence was conducted by Just, Carpenter, Keller, Eddy, & Thulborn (1996). The authors compared non-embedded, center-embedded subject-relative clauses, and center-embedded object-relative clauses. In this study, increased activation in relation to sentence complexity could be observed in the bilateral IFG and the bilateral superior temporal gyri (STG) extending to the middle temporal gyrus (MTG). This increase of activation was suggested to reflect higher computational

demands in general. Around the same time, a study using positron emission tomography (PET) directly contrasted center-embedded and right-branching relative clauses (Stromswold, Caplan, Alpert, & Rauch, 1996). Authors of this study found increased activation in the left pars opercularis (PO) of the left IFG which was associated with greater memory load in processing center-embedded sentences. A similar fMRI study using Japanese sentences attributed activation in the left IFG to syntax-related processing, while activation of the posterior part of the left frontal lobe (Brodmann area (BA) 6/9) and the left inferior parietal area (BA39/40) has been interpreted to reflect thematic role assignment (Inui et al., 1998).

Although a review of current imaging studies reveals that the left IFG has been found to be activated in all studies investigating center-embedded sentences, authors differ in their functional interpretation. Some suggest its engagement to reflect syntactic processing (Inui et al., 1998; Peelle, McMillan, Moore, Grossman, & Wingfield, 2004; Santi & Grodzinsky, 2010), others interpret its activation as increased working memory demands (Caplan, Chen, & Waters, 2008; Cooke et al., 2001; Stromswold et al., 1996). To segregate syntax-related aspects from verbal working memory, Makuuchi et al. (2009) contrasted hierarchical center-embedded sentences with non-embedded sentence structures (syntactic complexity) as well as sentences with a long distance between dependent syntactic elements and sentences with a short distance (working memory load). Both contrasts reveal an increase of activation in left frontal areas.

However, while the syntactic complexity (number of embeddings) appears to engage the left PO, working memory load taxes a region located slightly more superior in the left inferior frontal sulcus (IFS). In addition, contrasting hierarchical center-embedded sentences with non-embedded sentence structures also revealed an increase of activation in the left superior temporal sulcus (STS) extending to the STG which is suggested to reflect the integration of lexical-semantic and syntactic information for thematic role assignment during sentence comprehension (Friederici, Makuuchi, & Bahlmann, 2009) since a similar posterior cortical activation has not been found in artificial grammar studies that do not involve semantic aspects (Friederici, 2004b; Friederici, Bahlmann, Heim, Schubotz, & Anwender, 2006; Opitz & Friederici, 2004). An overview of functional imaging studies investigating center-embedded sentences can be found in Table 1.

Table 1. Activation patterns found for center-embedded sentence structures

Authors	Contrast	Coordinates [Talairach]	Region	Interpretation
Just et al. 1996	SR > baseline OR > baseline	No information	Bilateral IFG Bilateral STG / MTG	Computational demands
Stromswold et al. 1996¹	CE > RB	46.5, 9.8, 4.0	Left PO	Working memory load
Inui et al., 1998	CE > RB	No information	Broca's area	Syntactic processing
		No information	Left posterior frontal lobe and left IPL	Thematic role assignment
	CE > baseline	-68; -44; 8 -68; -44; 12 -64; -56; 8	Left pSTC	Sustaining comprehen- sion
	Long > short	56, -24, 0 48, -64, 16	Right pSTC	Short-term memory
Cooke et al. 2001		-56, 12, -4	Left IFG	Cognitive resources required to maintain long- distance syntactic dependencies during the comprehen- sion of grammatically complex sentences
	OR long > OR short	48, -64, 16	Right pSTC	
Peelle et al. 2004²	SR > Baseline	-28, -68, 40	Left pPL	
		4, 11 – 11	Right MFG	
	OR > Baseline	-32, -72, 29	Left IPL	
		12, -40, -25	Right cerebellum	
	OR > SR	-44, 15, -7	Left IFG	

2.2 The processing of hierarchical sentences in the adults' brain

Makuuchi et al. 2009 ³	CE > NE	-45, 6, 24	Left PO	Syntactic hierarchy building
	Long CE > short CE	-45, 27, 27	Left IFS	Syntactic working memory
Caplan et al. 2008	CE > RB	-52, 13, 9	left PO	Increased rehearsal and phonological storage
		-55, 8, 38	Left MFG	
		-39, -58, 29	Left STG	
		-55, -16, 3		
		-48, -35, -1	Left MTG	
		-16, -46, 40	Left precuneus	
		-18, 59, 2	Left MFG	Cognitive control
		38, -56, 40	Right SMG	
		33, -44, 42		
		33, 13, 32	Right MFG	
		-19, 8, 57	Left SFG	
		-1, 31, 41	Right SFG	
-9, 36, 1	Left ACG			
-45, 9, 36	Left IFS			
Friederici et al. 2009 ³	CE > NE	60, -45, 9	Right STS	Thematic role assignment
		-48, -54, 12	Left STS/STG	
		42, 0, 42	Right PMA	
		57, 15, 18	Right PO	
Santi & Grodzinsky, 2010	CE > RB	-41, 10, 31	Left IFG	Syntactic complexity
		48, 20, 36	Right IPS	
		-52, -34, 2	Left STG	

¹PET-study; ²only cortical structures reported; ³MNI coordinates; CE = center-embedding; RB = right-branching; OR = object-relative clause; SR = subject-relative clause; NE = no embedding; IFG = inferior frontal gyrus; STG = superior temporal gyrus; MTG = middle temporal gyrus; PO = pars opercularis; IPL = inferior parietal lobe; pSTC = posterior superior temporal cortex; pPL = posterior parietal lobe; MFG = middle frontal gyrus; SMG = supramarginal gyrus; SFG = superior frontal gyrus; ACG = anterior cingulate gyrus; IFS = inferior frontal sulcus, STS = superior temporal sulcus; PMA = premotor area; IPS = inferior precentral sulcus.

2.3 Neurocognitive models of sentence comprehension

Based on evidence from patient studies, structural imaging studies, and functional imaging studies, Friederici (2002) proposed a model of auditory sentence comprehension which was refined in Friederici (2004a) and Friederici (2011; Figure 1).

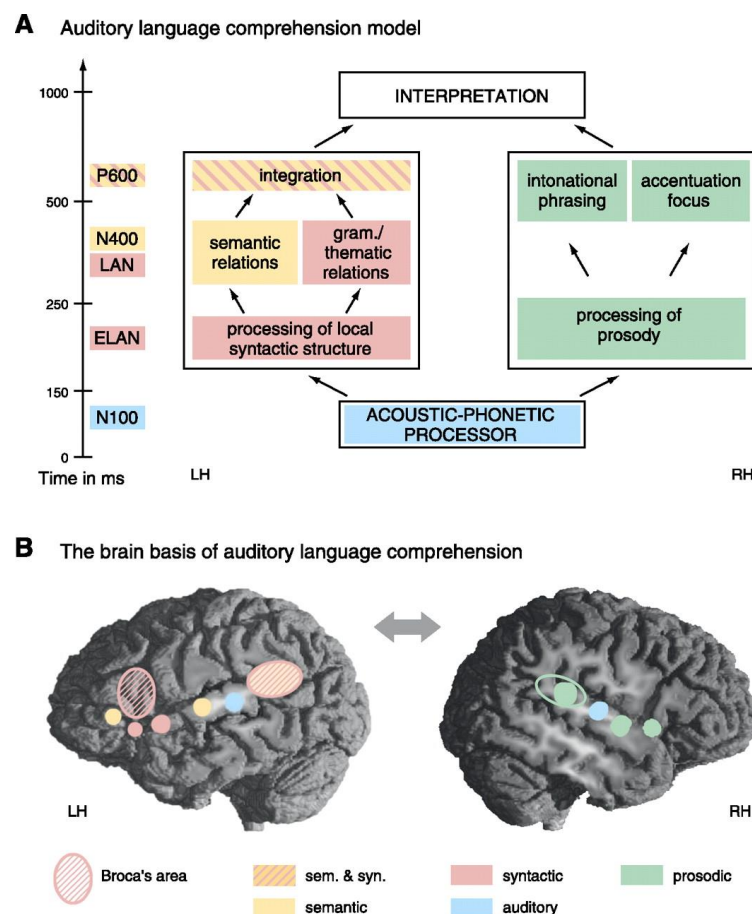


Figure 1. Neurocognitive model of sentence comprehension. (Figure adapted from Friederici 2011).

According to this model, the acoustic-phonetic processor that is located in the primary auditory cortex transfers information to the left anterior STG and the left frontal operculum (FOP). These two areas are seen as a network for local phrase structure building. In a second phase, two independent and parallel working paths engage regions of the left hemisphere that process semantic and grammatical/thematic information which are subsequently integrated to obtain a compatible interpretation. While semantic processing is suggested to be located in the MTG, complex syntactical processing is proposed to involve the left IFG. The integration of semantic and syntactic information is assumed to engage the posterior STG. During sentence processing, these three phases interact with prosodic information provided by the right hemisphere. With respect to the specific role of the left IFG in sentence processing, Friederici (2011) proposes different functions for different areas within this region. Based on cytoarchitectonical work and connectivity data, Broca's area can be subdivided into BA 44 (PO), BA 45 (pars triangularis) and BA 47, whereby only BA 44 is suggested to support syntactic structure building whereas BA 44/45 is assumed to support thematic role assignment and BA 45 /47 semantic processes.

The distinguishable functions of the first phase and the second phase are suggested to be mediated by differential structural connections that transfer information between specific language-relevant brain areas (see Figure 2). Local phrase structure building is assumed to be supported

by the uncinate fasciculus which connects the FOP and the anterior STG. The extreme capsule fiber system connects BA 45, the temporal cortex, and the occipital regions and is suggested to transfer semantic information. Next to these two ventral pathways, two dorsal pathways are additionally assumed to be involved in sentence processing: the arcuate fasciculus and the superior longitudinal fasciculus which are running in parallel and, so far, hardly distinguishable with the given available methods but which differ in their termination points.

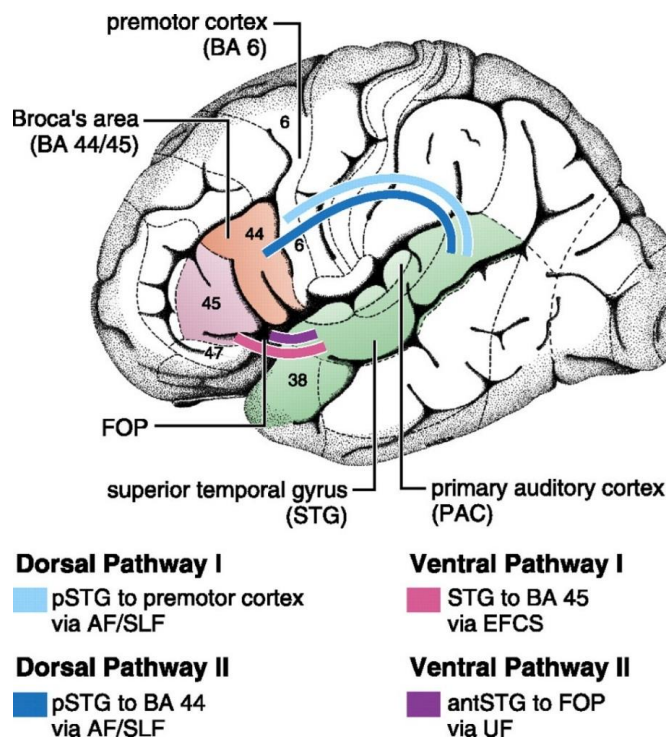


Figure 2. Fronto-temporal language regions and their structural connections. (Figure adapted from Friederici, 2011). BA = Brodmann area; AF = arcuate fasciculus; SLF = superior longitudinal fasciculus; EFCS = extreme capsule fiber system; UF = uncinate fasciculus; STG = superior temporal gyrus; FOP = frontal operculum; p = posterior; ant = anterior.

Connections between the dorsal premotor cortex and the posterior MTG/STG are already detectable in newborns (Perani et al., 2011) and are proposed to be involved in sensory-to-motor mapping and thus in speech repetition. Fiber tracts that connect BA 44 and the posterior STG are not even mature by age 7 yet (Brauer, Anwander, & Friederici, 2011) and are assumed to be involved in higher order language processing (for a review, see Friederici & Gierhan, 2013). Together, these four different pathways form a cortical circuit which enables bottom-up, input-driven processes via the ventral pathways and top-down, predictive processes via the dorsal connections (Friederici, 2012).

With respect to verbal working memory, two different brain regions are proposed: one located in the frontal and one in the parietal cortex. First, in the frontal cortex activation in the left IFS is proposed to reflect increased demands in syntactic working memory (Friederici, 2011). Second, activation in temporo-parietal regions has been found to reflect phonological working memory (Leff et al., 2009) and memory demanding sentence processing (Meyer, Obleser, Anwander, & Friederici, 2012; Novais-Santos et al., 2007).

A meta-analysis with studies on verbal working memory (see Figure 3) supports the dissociation of functionally different aspects of verbal working memory (Meyer et al., 2012): While storage in sentence processing and non-sentence processing engages temporo-parietal regions, prefrontal regions are activated during the (re-) ordering and

subvocal rehearsal of elements. Chunking based on sentential syntactic and semantic information alleviates rehearsal demands and therefore results in decreased activation in verbal working memory-related brain areas (Bonhage, Fiebach, Bahlmann, & Mueller, 2014).

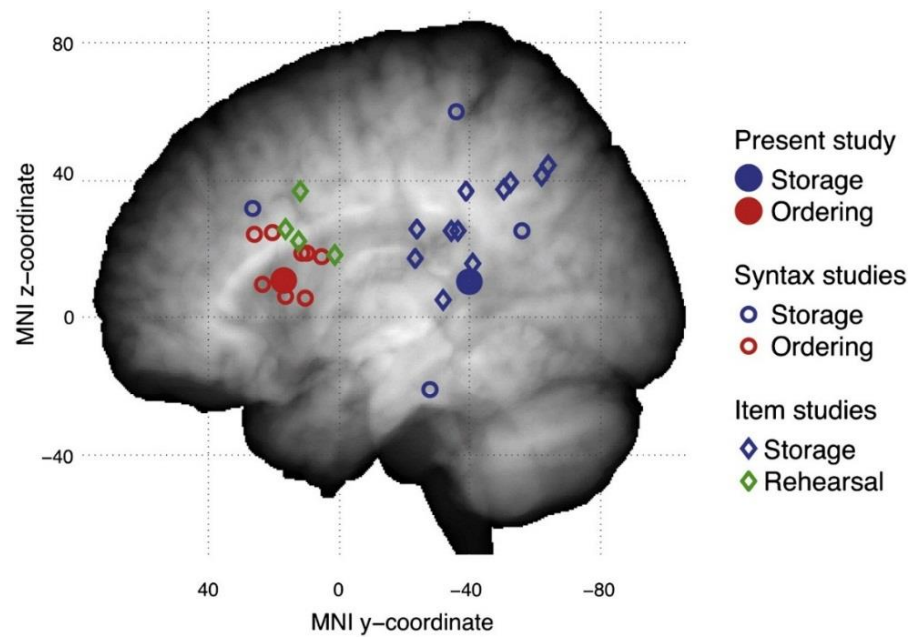


Figure 3. Meta-analysis of studies on verbal working memory. (Figure adapted from Meyer et al. 2012). Circles mark sentence-processing studies, diamonds mark non-sentence-processing studies; Storage is marked in blue, ordering is marked in red, and rehearsal is marked in green.

3 SENTENCE PROCESSING IN CHILDREN

3.1 Development of processing hierarchical sentence structures

The observation that children have problems in comprehending relative clause sentences has been subject to numerous debates about the acquisition of language-specific and domain-general abilities. Sheldon (1977) was one of the first researchers who reported on children's comprehension of subject- and object-relative clauses. She suggested that although both adults and children rely on the same strategies in processing relative clauses, children rely more on a heuristic strategy which predicts that the head noun will occupy the same grammatical function in the relative clause as it does in the main clause. Tavakolian (1981) claimed that children's grammar lacks recursion within the noun phrase and that children are, therefore, unable to process relative clauses as noun modifiers. Instead, they use a conjoined analysis of the noun phrases. This hypothesis is in accordance with the production data

collected by Bloom and her colleagues (Bloom, Lahey, Hood, Lifter, & Fiess, 1980; Bloom, Rispoli, Gartner, & Hafitz, 1989; Bloom, Tackeff, & Lahey, 1984). They found that children during their third year of life begin to produce complex sentences by linking two separate propositions via conjunction. Only later they are able to produce hierarchical structures like complementation and relativization. However, contributing factors for this developmental shift are still unclear.

Extensive research on children has focused on the asymmetry of comprehending subject- and object-relative clauses. In formal accounts, object-relative clauses are more complex than subject-relative clauses because they involve longer movements of noun phrases which result in an increased distance between a filler and its gap. Thus, children's difficulties on object-relative clauses may be based either on the longer distance between dependent elements (Wanner & Maratsos, 1978) which demands a higher load on the verbal working memory or in their problems processing movement per se (Goodluck, Guilfoyle, & Harrington, 2006). Recent studies additionally point to the importance of input frequencies and discourse properties that reduce the asymmetry (Brandt, Kidd, Lieven, & Tomasello, 2009; Fox & Thompson, 1990). For example, German-speaking children were shown to perform even better on object-relative clauses compared to subject-relative clauses if they contain an inanimate head noun (Brandt et al., 2009). Nonetheless, independent of available contextual information, the processing of hierarchical sentence

structures requires the ability to keep sentence parts active while other parts are processed and this will not succeed if verbal working memory capacity does not suffice. Therefore, it is important to relate children's processing abilities of relative clauses to their limited verbal working memory capacities. However, before discussing this specific relation, the concept of working memory as well as developmental aspects will be introduced.

3.2 The concept of the working memory

In the literature, there exists no uniform definition of working memory. Nonetheless, according to Cowan (2010) most researchers would agree that working memory is the small amount of information that is kept in an easily retrievable state concurrently. In general, working memory is the part of consciousness that we are aware of and which allows us to store immediate memory. This information can be compared and related to information in our long-term memory and it can be evaluated with respect to our current goal. Relevant concepts about the working memory were mentioned first by Wilhelm Wundt (e.g. 1874, an overview of Wundt's work can be found in Scheerer, 1980). However, his work was never translated into English and thus is not accessible to the international research community. Therefore, James (1890) is associated with the first distinction between primary and secondary memory. From a neurophysiological perspective, Hebb (1949) proposed the notion of cell assembly describing

neural firing in the brain representing the temporarily active information storage in the working memory.

The proposition of the multi-component model of working memory (Baddeley & Hitch, 1974) is of major relevance for the understanding of the concept of working memory. The authors suggest different modules for the verbal and visual domain. In earlier work, they also proposed a central storage component that can hold abstract information. This component was later replaced by the central executive, a component that contains a collection of processes that act on the different information stored in the separate buffers (Baddeley, 1986). The episodic buffer, a buffer store that not only links the different components of the model but also links working memory to perception and long-term memory, was added as a fourth component (Baddeley, 2000).

Cowan (1988) offered an alternative model of information processing by proposing that the phonological and visuospatial stores are just considered as instances of the temporary activation of long-term memory, thereby holding some of the activated information in the focus of attention. Items concurrently held in the focus of attention can then be combined to form new and larger units. The term working memory is used to indicate a functional level at which activated memory, the focus of attention, and central executive processes work together in order to keep items temporarily in mind to assist in various cognitive tasks.

Working memory is limited in duration and capacity. Limitations of the working memory were first described by Miller (1956) who noticed that we can only recall a list of about seven items which resulted in the classical view of an average memory span of 7 ± 2 items. However, more recent work suggests that the classical view overestimates working memory capacity (Cowan, Nugent, Elliott, & Saults, 2000). The authors propose a limit of approximately 4 items if chunking and rehearsal is completely suppressed. Contrariwise, it could be shown that successful rehearsal and chunking can increase the amount of information that can be remembered (Ericcson, Chase, & Faloon, 1980). With respect to duration, human adults can remember items up to 10 to 18 seconds unless they are actively attended to or rehearsed (Peterson & Peterson, 1959). Whether the forgetting of information is due to a passive decay over time or whether it is induced by the interference of previously stored information (for discussion, see Jonides et al., 2008; Lewandowsky, Duncan, & Brown, 2004; Nairne, 2002; Oberauer & Kliegl, 2006) is still a matter of debate.

3.3 The development of the working memory

Working memory capacity increases continuously between early childhood and adolescence while the structure of correlations between different components remains largely constant (Gathercole, 1999; Gathercole, Pickering, Ambridge, & Wearing, 2004). The basic structure of the working memory, as proposed by Baddeley (2000), is assumed to

be in place by age 6 (Gathercole et al., 2004). However, the short-term memory in the verbal and visual domain develop independently from each other (Gathercole et al., 2004).

A matter of debate is whether age-related changes in working memory performance are driven by higher storage capacities due to changes in attentional control (Barrouillet, Gavens, Vergauwe, Gaillard, & Camos, 2009; Conlin, Gathercole, & Adams, 2005; Portrat, Camos, & Barrouillet, 2009) or by an increase of speed in general information processing (Bayliss, Jarrold, Baddeley, Gunn, & Leigh, 2005). The time-based resource-sharing model (Barrouillet, Bernardin, & Camos, 2004) assumes that processing and storage functions compete for the limited space or capacity (Case, Kurland, & Goldberg, 1982; Daneman & Carpenter, 1980) and that the age-related increase of working memory capacity can be explained by a strategy of attentional refreshing, the switch of attention to briefly reactivate decaying memory traces. In contrast, the task-switching account (Towse & Hitch, 1995; Towse, Hitch, & Hutton, 1998) assumes that individuals perform a rapid serial alternation between the processing and the storage phases and the authors propose that an increase in working memory capacity is only a by-product of an increase in processing speed. For example, Case et al. (1982) found that developmental increases in complex span performance were not due to increases in the overall capacity of working memory but were the result of increases in operational efficiency. Thus, faster and more efficient basic

processing operations enhance resources available for storage. Furthermore, Kail (1992) and Kail and Park (1994) demonstrate that an increase of processing speed does improve the articulation speed which in turn is related to better short-term memory performance.

Nonetheless, if the age-related increase of working memory capacities can be explained by the implementation of the attentional shifting strategy, older children should be able to maintain a higher cognitive load, and thus a higher number of items, independent of their duration. In contrast, if an increase in working memory capacities results due to an increase of processing speed, recall performance should highly depend on the duration of the items and not on their amount. Camos and Barouillet (2011) provide evidence that only both cognitive developments together can account for the developmental pattern observed in 6- and 7-year-old children. While in 6-year-old children, recall performance is sensitive to the raw duration but not to the cognitive load, the opposite pattern could be observed in 7-years-old. These findings suggest that 6-year-old children do not implement a strategy of maintenance yet and, therefore, their memory traces suffer time-based decay. This fits data suggesting that children before 7 years of age do not show reliable rehearsal (Flavell, Beach, & Chinsky, 1966; Vygotsky, 1986; Vygotsky 1962). Even though the spontaneous use of subvocal rehearsal is absent in younger children (Hitch et al., 1983), these mechanisms seem to be in

place and children can be encouraged to exploit them (Gathercole & Hitch, 1993).

In sum, while it has been shown that an increase of verbal working memory capacity can be related to both higher storage capacities and faster processing abilities, it remains an open question how improvements of these different domains more specifically relate to cognitive domains such as sentence processing. In the next section, it will be discussed how these developmental aspects of working memory development are assumed to influence the processing of complex sentences.

3.4 Verbal working memory and sentence processing in children

Verbal working memory capacity has been found to be related to children's grammatical competences as young as 3 years of age since their phonological short-term memory capacity predicts the quantity and quality of the spontaneous speech (Adams & Gathercole, 1995). More specifically, it relates to the mean length of utterance and to the amount of different sentence types that are produced in these children. In older children, it has been found that the verbal working memory capacities are related to the comprehension of relative clauses (Felser, Marinis, & Clahsen, 2003; Roberts, Marinis, Felser, & Clahsen, 2007; Weighall & Altmann, 2010) and passive structures (Montgomery, Magimairaj, & O'Malley, 2008). For these sentences, a better comprehension of high

span children could be attributed to the ability to reactivate the antecedent at a gap position (Roberts et al., 2007), different sentence attachment strategies (Felser et al., 2003), and a sensitivity to contextual cues (Weighall & Altmann, 2010). Since all these factors also contribute to a better comprehension of multiple embedded sentences, it is very likely that performance for these sentences is related to children's verbal working memory as well.

PART II

METHODOLOGY

4 FUNCTIONAL MAGNETIC RESONANCE IMAGING

fMRI is a non-invasive technique that allows for the assessment of human brain function over time by detecting blood flow differences. Cognitive demands induce neuronal activity and this neuronal response requires energy in the form of glucose and oxygen that is supplied by blood. However, although changes in the magnetic resonance (MR) signal are triggered by neuronal activity, only the metabolic demands following the activation are measured by fMRI. Thus, fMRI does not directly map neuronal activity but physiological activity that is correlated with neuronal activity. This relation allows for inferences about how different brain areas are involved in perceptual, motor, or cognitive processes. In this section, the neurobiological basis of fMRI measurements is introduced and preprocessing steps as well as statistical analyses of fMRI data are described.

4.1 The *BOLD*-contrast

FMRI analyses are based on T2*-weighted images, images that not only represent the interactions between spins (as T2-weighted images) but also inhomogeneities of the magnetic field. These blood-oxygenation-level dependent (BOLD) images are sensitive to the amount of deoxygenated hemoglobin present in brain regions. While oxygenated hemoglobin has no unpaired electrons and thus is diamagnetic, deoxygenated hemoglobin has a significant magnetic moment due to its unpaired electron which induces local magnetic field variations. As a result, an increased MR signal can be measured where the blood is highly oxygenated and a lower signal is measured where it is highly deoxygenated. Therefore, increased neuronal activity which comes along with oxygen consumption should result in more deoxygenated hemoglobin and, therefore, a decreased MR signal (Ogawa, Lee, Kay, & Tank, 1990). Paradoxically, the MR signal increases during neuronal activity. This means that more oxygen must have been supplied than is consumed. More specifically, it has been proposed that an overcompensating increase in blood flow allows for the increase of the amount of oxygenated hemoglobin and the decrease of the amount of deoxygenated hemoglobin which suppressed the MR signal (Fox, Raichle, Mintun, & Dence, 1988).

Changes in the MR signal triggered by neuronal activity are known as the BOLD hemodynamic response (HDR). Interestingly, this HDR does

only occur after 1 to 2 seconds after stimulus onset, although cortical neuronal responses occur within milliseconds. This lack of onset is represented by an initial negative-going dip of signal introduced by the amount of deoxygenated hemoglobin (see Figure 4).

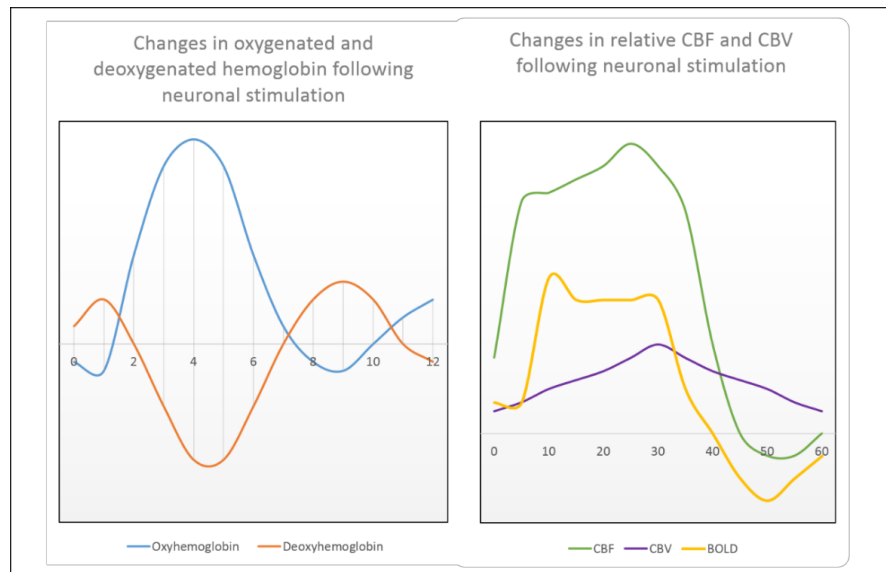


Figure 4. Origination of the BOLD-response. The ratio of oxygenated (in blue) and deoxygenated (in red) hemoglobin after neuronal stimulation is depicted in the left panel. Deoxygenated hemoglobin that reduces the MR signal is replaced by oxygenated hemoglobin. In the right panel, changes of the cerebral blood flow (CBF; in green) and the cerebral blood volume (CBV; in purple) after neuronal stimulation are depicted. Both processes together provide the blood supply underlying the BOLD-response (depicted in yellow).

According to this time course, only after 1 to 2 seconds more oxygen is supplied than extracted. The peak of the HDR typically occurs after 4 to 6 seconds after stimulus onset and is followed by an undershoot, which represents a higher amount of deoxygenated hemoglobin due to a combination of reduced blood flow and increased blood volume. Despite

data showing the remarkable correspondence between neuronal activity and the HDR, their exact relationship is still unclear (Logothetis, 2008; Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001).

4.2 Spatial resolution of fMRI

The spatial resolution describes the ability to distinguish changes in a map across different spatial locations (Huettel, Song, & McCarthy, 2008). While techniques such as electroencephalography (EEG) encounter the inverse problem, the impossibility of determining the localization of electrical sources within an object based on measurements of the electrical fields on its surface, fMRI can localize brain activity within the range of millimeters. The spatial resolution is defined by a voxel-size which depends on the field of view (FOV), the matrix size, and the slice thickness. To determine the appropriate voxel-size, following challenges need to be considered: The smaller the voxels, the more reduced is the signal compared to noise and the longer are the acquisition times. The larger the voxel, the greater is the partial volume effect which is the signal contribution of two or more tissue types.

FMRI in children is especially challenged by movement which most likely increases with acquisition time and results in a lower signal-to-noise ratio (SNR). To avoid this kind of artifact, a decision towards a higher spatial resolution with less acquisition time can be advantageous. For this study, a FOV of 192 mm, a matrix size of 64×64 voxels, and a slice

thickness of 3 mm was chosen to define voxels at a voxel-size of $3 \times 3 \times 3 \text{ mm}^3$.

4.3 Temporal resolution of fMRI

fMRI has an intermediate level of temporal resolution. While EEG can depict electrical field variations within a range of milliseconds, fMRI measures the delayed HDR following a neuronal response and is tied to the applicable repetition times (TR), the sampling rate at which an entire image can be acquired. The fMRI data of this thesis was sampled at a TR of 2 seconds. This time range does not allow for an appropriate modelling of the onset and shape of the HDR. Fortunately, the temporal resolution can be improved by an interleaved slice acquisition together with the introduction of a jitter, the randomly varying time between successive stimuli, which allows for the presentation of the events of interest at different time-points within a TR. In this thesis, jitters of 0, 400, 800, 1200 and 1600 milliseconds were used.

4.4 Preprocessing

fMRI analyses intend to extract the raw time course of each voxel's intensity and to compare each time course with the hypothesis. To do this, a voxel needs to be in the exact same location over this time course and the sampling of this voxel must occur in a regular known rate. However,

these assumptions are rendered by different sources of noise such as intrinsic thermal noise within the subject and the scanner electronics, the imperfection of the scanner, motion and physiological noise due to respiration and heart rate, variability in the neuronal activity associated with non-task-related brain processes, and changes in behavioral performance as well as cognitive strategies. Besides averaging across trials, training can improve the SNR. Therefore, children of the current studies were invited for a mockup session a couple of days before the actual data acquisition. During this session, they got introduced to the scanning and the experimental procedure. By verbal and visual feedback they were also trained to restrict their head motion as well as motion introduced by pressing the response buttons.

In order to prepare the collected fMRI data for the statistical analysis (see Figure 5), data was visually inspected for movement artifacts and data quality was assured by the mean intensity of slices. To improve the SNR, images with movement artifacts > 3 mm were excluded from further analyses.

The interleaved slice acquisition, where odd-numbered slices are acquired first and even-numbered slices second, was chosen to minimize excitation pulses upon adjacent slices and to improve the HDR. For this imaging technique, temporal interpolation is required to address the problem that adjacent parts of the brain are acquired at different time

points. The interpolation is based on the estimates of nearby time points of the amplitude of the MR signal at a single point within the TR.

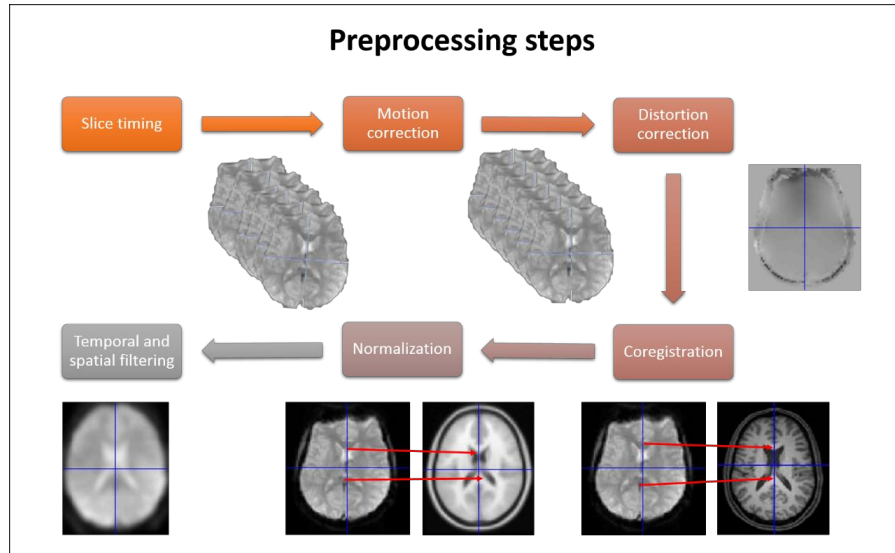


Figure 5. Flow chart of preprocessing steps of the fMRI analysis.

To adjust the time series of images to the same location, images were coregistered to the reference image which was the first acquired volume of the experiment. To align the images, rigid-body transformation was applied. This transformation translates and rotates the data according to 3 different parameters along the x-, y- and z-axes and planes without changing the size or shape of the brain. After the spatial interpolation, the resampled data represents the original data as there had been no head motion.

Since the SNR can also be reduced by inhomogeneities of the static magnetic field as well as the excitation field, a field map was acquired and applied to address geometric distortion as well as intensity variations. This field map contained information about the strength of the magnetic field at different spatial locations.

A challenging question, especially with respect to developmental data, is: How does the functional activity map to anatomy? To answer this question, here two different steps are used in the preprocessing procedure: First, functional images of each subject were linked to high-resolution structural images from the same subject and second, to compare between different subjects, images were normalized to a common template. As stereotaxic spaces, either the Talairach space (Talairach & Tournoux, 1988) or the MNI template are most widely used. However, normalization of children's data to an adult template can introduce deformations (Wilke, Schmithorst, & Holland, 2002) and increased variance in brain contours (Muzik, Chugani, Juhász, Shen, & Chugani, 2000). Only from 7 years of age, normalization to a standard adults' MR template is valid (Burgund et al., 2002; Kang, Burgund, Lugar, Petersen, & Schlaggar, 2003). To account for these normalization difficulties, it was decided to normalize all data to a template which represents the brain structure between early and advanced puberty (Fonov et al., 2011). Morphological differences of this pediatric template compared to the adult template correspond to maturational effects such

as corpus callosum thinning, flattening, and lengthening slightly in the anterior-posterior direction, the increase of lateral ventricles and the sulcal spaces widening, an increase of the white matter to gray matter ratio in the frontal lobe, an increase of the basal ganglia and the thalamus, an enlargement of the pons and a shift in the superior direction of the posterior part of the brain (cerebellum and occipital pole) as well as cerebellum widening.

In a last preprocessing step, spatial and temporal filters were applied to remove or retain different frequency components. The SNR of the data is decreased by system noise and physiological noise that causes fluctuations in the MR signal intensity over time and space (Huettel et al., 2008). While temporal filtering can improve the SNR, the threshold of the filter needs to be adjusted to ensure that the frequency of interest (the TR of 2 seconds) is not filtered. To avoid this, high-pass filtering is recommended (Woolrich, Ripley, Brady, & Smith, 2001). Spatial smoothing by a Gaussian filter spreads the intensity of each voxel in the image over nearby voxels (Huettel et al., 2008). This is done to account for functional similarities of adjacent brain regions as well as inter-subject variability. In addition, by spatial smoothing the validity of statistical tests can be improved since the amount of multiple comparisons in the statistical analysis is reduced. However, at the same time smoothing results in a lower spatial resolution which compounds the anatomical localization of functional effects. The width of the kernel size is specified

by its full width at half maximum values (FWHM). This measurement determines how many voxels are smoothed. While too little smoothing does not prevent rough and noise-like results, too much smoothing can lead to distributed and indistinct blobs. Therefore, the optimal kernel size should comply the expected size of effects.

4.5 Statistical modeling and analysis

Depending on the research question, either blocked or event-related designs are suitable in fMRI analyses. In blocked designs, all trials of one experimental condition are presented over a specific time interval. The depending measure of each block can then be compared amongst each other or to some baseline condition. While blocked designs are very sensitive to significant fMRI activity, they are relative insensitive to the shape of the HDR as well as the timing of the response (Huettel, 2008). Since this dissertation focuses on the relation between functional activity and performance, an event-related design of stimulus presentation is chosen. Therefore, stimuli are presented in a randomized order. Even though the detection power of this design is lower, the estimation of the time course is much better and it allows for the implementation of regressors such as reaction time and movement parameters, which are seen as confounds that especially challenge developmental data, into the design.

The general linear model (GLM) represents a class of statistical tests that assume that the experimental data are composed of the linear combination of different model factors along with uncorrelated noise (Huettel, 2008). Thereby the basic formula for the regression analysis is:

$$y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n + \varepsilon$$

The basic idea of this model is that the observed data in each voxel (y) is equal to a weighted combination (β) of model factors (x) plus an additive error term (ε). The design matrix (x) is composed of the different regressors representing each condition. Given the observed data and a specified set of regressors, the goal is to identify the combination of parameter weights that minimize the error term.

The design matrix of the functional experiment is depicted in the upper left panel in Figure 6. As regressors, correct and incorrect trials for each of the different sentence structures as well as movement parameters were included into the model. In a next step, changes of BOLD activation are extracted for each voxel and compared to each of these regressors (Figure 6, upper panel; ride sight). A beta weight is determined by the correspondence between the presentation of a specific condition and the BOLD activation pattern. Subsequently, the estimated betas can be compared between certain conditions for each voxel. Contrast files of the present dissertation were created by subtracting the complex baseline (correct trials of non-embedded sentence structures) from the regressors

representing the correct trials for simple and complex sentences. Corresponding T-values are summarized in statistical parametric maps.

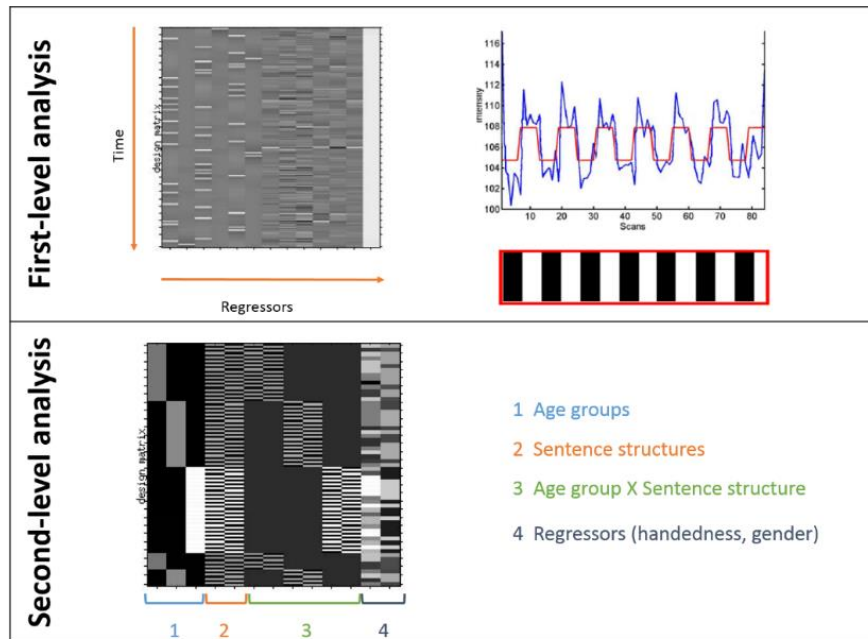


Figure 6. Statistical analysis of the preprocessed fMRI data. In the first-level analysis, a design matrix for each subject is computed (upper panel; left side). In a next step, the BOLD of each voxel is compared to the regressors of interest (upper panel; right side). A high beta is assigned to voxels of high correspondence. In a second-level analysis, a design matrix representing the statistical maps for each subject in each condition is created (lower panel).

Up to this processing step, comparisons between conditions are restricted to each individual subject. In a second-level analysis, activation patterns between subjects can be compared. In order to evaluate group effects, random effects can be computed by treating the experimental condition as a variable across subjects so that it could have a different effect on different subjects or by assuming that the experimental condition is fixed

across subjects with differences between subjects caused by noise (fixed effects analysis; Huettel, 2008). Since age group effects are hypothesized, a random-effects analysis was chosen whereby two contrast images for each subject were passed into a flexible factorial analysis (see Figure 6, lower panel).

A big challenge of fMRI analysis is the high amount of univariate t-tests for all voxels in the brain. Together, these t-tests lead to a considerable increased probability of false-positives which need to be addressed. The reduction of the α -level proportionally to the number of independent statistical tests, known as Bonferroni correction, is a standard strategy. However, this procedure might be too conservative and increase the probability of so-called type-II errors which may result in the missing of real activity. The methods at hand used in this thesis take the size of the cluster of active voxels into account. While the activation of single voxels might occur by chance alone, the activation of clusters more likely represent real effects. Therefore, two methods which consider the correction for multiple comparison on cluster level were implemented into the statistical analyses: the false-discovery rate (Benjamini & Hochberg, 1995) and the Monte Carlo simulation (NIMH Scientific and Statistical Computing Core, Bethesda, MD, USA).

5 VOXEL-BASED MORPHOMETRY

Voxel-based morphometry (VBM) is a sophisticated technique that analyzes differences in the local composition of brain tissue while discounting large scale differences in gross anatomy and position. Therefore, images are compared in a voxel-based manner after deformation fields have been used to spatially normalize them (see Figure 7). VBM is a simple comparison of gray matter or white matter partitions following segmentation (Ashburner & Friston, 2000). It offers an approach for in-vivo characterizations of the brain morphology and it allows for the investigation of the volume of different brain structures, dissociations between healthy and pathologic findings, the characterization of tumors or lesions, and the observation of developmental changes within and between subjects.

The following steps are implemented into the optimized VBM procedure: Based on each voxel's intensity, T1-weighted images are segmented into gray matter, white matter, and cerebral spinal fluid. This

segmentation is optimized by mapping the data onto tissue probability maps (TPMs) which encode prior probabilities representing the spatial distribution of tissue types in normal subjects. To further improve the segmentation procedure for the current study, differential TPMs according to each age group were implemented into the segmentation procedure.

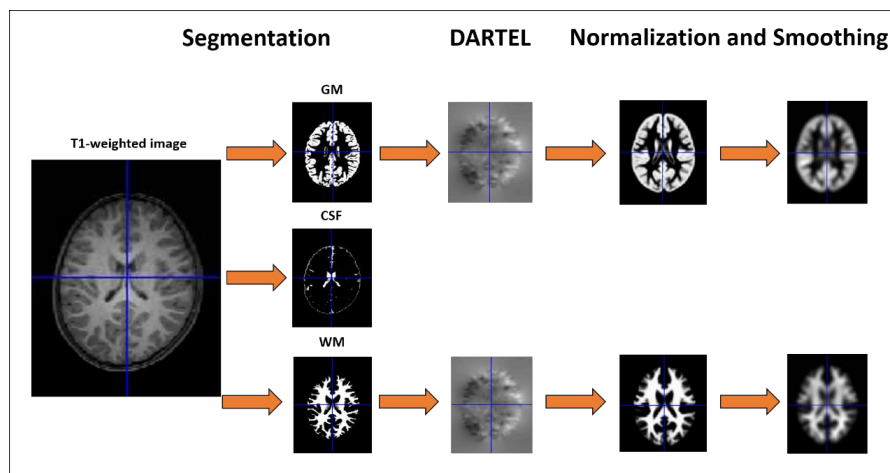


Figure 7. Preprocessing steps of the VBM analysis. T1-weighted images are segmented in gray matter (GM), white matter (WM), and cerebral spinal fluid (CSF) partitions. In a next step, images are coregistered and normalized using the diffeomorphic anatomical registration through exponentiated lie algebra (DARTEL) procedure. Finally, images are smoothed to decrease spatial noise.

A big challenge in comparing different groups is the registration of images despite local inter-individual gyrification (Bookstein, 2001). To address these registration difficulties, the segmented images are registered to the MNI space and further passed into the diffeomorphic anatomical registration through exponentiated lie algebra (DARTEL) procedure to create a common template based on the acquired data. DARTEL has the

advantage that resulting deformations are diffeomorphic, easily invertible, and can be rapidly computed. This technique involves the registration of images by minimizing differences between the image and the warped template, while also minimizing deformations used to warp the template (Ashburner, 2007). Deformations are then parametrized by so-called flow fields which are used to normalize each subject's data to the common template.

A matter of debate is whether the segmented data should be modulated or not. To compensate for the effect of global normalization, the spatially normalized gray matter can be multiplied by its relative volume before and after normalization. Without this adjustment, the gray matter probability (GMP) of the voxels can be thought of representing the relative concentration of gray matter in this image whereas with this adjustment, the GMP of the voxels reflects the gray matter volume. Since an increased variance of morphological properties in specific brain regions is expected for different age groups, modulation is applied to address these non-linear registration confounds. Before any statistical analysis, the modulated data are smoothed to filter spatial noise and optionally warped into a standard space.

PART III

EMPIRICAL

INVESTIGATION

6 RESEARCH QUESTIONS

Unlike other aspects of language, the ability to process complex sentences develops late. Brain maturation as well as verbal working memory expansion have been discussed as possible reasons. To determine the factors contributing to this functional development, the current dissertation investigates cognitive maturation in the verbal working memory domain as well as brain structural maturation and brain functional maturation in language-relevant brain areas in relation to behavior. The current thesis focusses on center-embedded sentence structures as research paradigm since their efficient processing requires both sufficient verbal working memory capacity (see ‘The processing of hierarchical sentence structures’) and the functional engagement of the frontal-temporal language network (see ‘The processing of hierarchical sentences in the adults’ brain’).

First, previous behavioral studies indicate that children’s verbal working memory capacity is associated with different processing

strategies for relative clauses (Felser et al., 2003; Roberts et al., 2007; Weighall & Altmann, 2010). However, while studies on verbal working memory development in general discuss different contributions of higher storage capacities due to changes in attentional control and an increase of processing speed, the relation of these differential aspects of verbal working memory to the processing of complex sentences has not been investigated so far. The processing of center-embedded sentences involves both the establishment of multiple hierarchies and long-distance dependencies. These different processes of sentence comprehension can be facilitated by increased storage capacities as well as increased processing speed (see ‘Verbal working memory and sentence processing in children’). However, previous developmental data indicate that these differential aspects of verbal working memory develop at different time-points (Camos & Barrouillet, 2011). These findings lead to following behavioral research questions:

1. How is restricted verbal working memory capacity related to the processing of center-embedded sentences in children?

And more specifically:

- a. Are qualitative changes in the correlations between different aspects of complex sentence processing and verbal working memory capacities between different age groups observable?

Second, brain maturation is discussed as another factor contributing to more efficient complex sentence processing (see ‘Brain plasticity and critical phases’). While this relation has already been found between sentence processing and white matter maturation (Brauer et al., 2011), it has not been shown between sentence comprehension and gray matter maturation yet. This lack of evidence results in the following brain structural research question:

2. Can we observe correlations between complex sentence processing skills and gray matter maturation in grammar-relevant brain areas?

Third, previous developmental imaging studies contrasting simple and complex studies revealed a functional immaturity especially of the left IFG (see ‘Functional maturation of language-relevant areas’). In the current thesis, the functional research question is not restricted to:

3. When and how does the left IFG functionally attune to syntactic complexity?

But more specifically addresses the following open issue:

a. Is the more mature activation pattern associated with better performance?

Finally, the tripartite relationship between brain structure, brain function, and behavioral performance will be discussed in detail to answer a more general developmental research question:

4. Do gray matter maturation and/or cognitive maturation predict the establishment of an adult-like brain activation pattern for complex sentence processing which in turn is associated with a better performance?

To address these different research questions, children between 5–6 years and children between 7–8 years as well as adults were investigated. To test the hypotheses, a series of behavioral, functional imaging (fMRI) and structural imaging (VBM) studies were conducted.

7 BEHAVIORAL STUDY: EMBEDDED SENTENCES AND VERBAL WORKING MEMORY

7.1 Introduction

The processing of hierarchical center-embedded sentences constitutes a big challenge to the human language parser. Center-embedded sentences are constructed by the embedding of phrases into phrases which result in increasing levels of hierarchy as well as the separation of noun phrases and their respective verbs. Successful interpretation of these sentence structures require the ability to store the complex noun phrase at the beginning of the sentence until it can be analyzed as the subject or the object of the main verb at the end (Slobin, 1973). These processes clearly depend on a certain amount of verbal working memory capacity (Gibson, 1998) which enables the processor to keep sentence parts active while other parts are processed. However, if the differential partial analyses exceed verbal working memory capacity, the analysis breaks down and noun phrases cannot be associated with their

corresponding verbs (Chomsky & Miller, 1963; Gibson, 1998; Miller & Chomsky, 1963).

The processing of center-embedded sentences involves two different types of cognitive capacities which are discussed as explanatory factors in working memory development. On the one hand, the interruption of sentences leads to the necessity to store the first noun phrase over a certain duration until it can be integrated with the final verb phrase into the overall sentence meaning. Therefore, the pure duration of the storage of the first noun phrase may exceed verbal working memory capacities and thus lead to specific problems interpreting those subclauses that contain such a long-distance dependency. On the other hand, the processing of center-embedded sentences requires the build-up of hierarchical syntactic structures. To do this, multiple incomplete subclauses need to be stored at the same time. Therefore, a successful interpretation of center-embedded sentences requires the ability to shift attention between the respective subclauses.

While the question of how differential verbal working memory capacities influence the processing of center-embedded sentence structures has been studied in adults of different age groups (Caplan, DeDe, Waters, Michaud, & Tripodis, 2011; Waters & Caplan, 2001) and patients (Papagno et al., 2007), it has not been examined in children yet. With respect to working memory development, it is suggested by the task-switching model (Towse & Hitch, 1995) that an increase in processing

speed during development leads to higher short-term memory capacities which in turn result in higher working memory abilities. Thus, the duration of storage is the critical factor in working memory-related tasks that is increased during development. Following this suggestion, children's digit span, the amount of numbers children can recall after verbal presentation of a random sequence of numbers, reflects the duration they are able to store verbal material and children with a lower digit span are hypothesized to show difficulties in processing long-distance dependencies in particular since this processing step requires the listener to store verbal material over a certain amount of time. In contrast, according to the time-based resource-sharing model (Barrouillet et al., 2004), children are predicted to be sensitive to the cognitive load of sentences. In this case, children's digit span reflects the amount of verbal material they are able to recall. Therefore, children with a lower digit span may be incapable of storing all differential subclauses and as a result fail to interpret the center-embedded sentences altogether since the structural hierarchy of the sentences cannot be constructed.

In order to test how restricted working memory capacities influence the processing of center-embedded sentences, children between 5 and 8 years were tested. In this age range, quantitative and qualitative changes in cognitive domains lead to significant increases in verbal working memory capacities (Camos & Barrouillet, 2011; Case et al., 1982; Gathercole et al., 2004). Sentence complexity was operationalized by the

amount of embedded sentences. It is hypothesized that children with a lower digit span show specific difficulties for double embedded sentence structures since these structures contain long-distance dependencies and they require the storage of three separate subclauses at the same time. Furthermore, to address the question whether limited verbal working memory capacity effects the establishment of long-distance dependencies, the structural hierarchy building or both, the interpretation of each subclause was tested separately.

7.2 Methods

7.2.1 Participants

To investigate the relation of verbal working memory capacity to the processing of center-embedded sentence structures, 22 children between 5 and 6 years (mean age = 5;10 years, range = 5;0 – 6;9 years), 22 children between 7 and 8 years (mean age = 8;0 years, range = 7;3 – 8;10 years) and 20 adults (mean age = 24;6 years, range = 18 – 32 years) were tested. Adults and children were recruited from the database of the Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig. All participants were healthy, monolingual German speakers who had normal hearing, normal or corrected-to-normal vision, and no known language impairment. The number of male and female subjects was equal. Parental consent was obtained for all children. Of the original sample (52 children

altogether), eight children had to be excluded because they showed a side bias or were too fidgety.

7.2.2 Materials

The experimental design of the sentence-picture verification task comprised sentences containing three subclauses but different levels of complexity: sentences without embedding (see Figure 8A), sentences with one embedding containing two coordinated relative clauses (see Figure 8B) and sentences with two embedded relative clauses (see Figure 8C). Eighteen sentences were constructed for each condition. In order to control for potential confounds, sentences across conditions contained an equal number of subclauses (3), pronouns (2), and verbs (3). Due to the coordination of subclauses, no embeddings and single embeddings contained one additional word (altogether 11 words) in comparison to double embeddings (altogether 10 words).

Sentences without embedded subclauses (see Figure 8A) were constructed as simple as possible to control for a general comprehension of three different subclauses. The transitive subclause appeared as the last one to avoid crossing dependencies (movement of the subject of a conjunct across the object of a previous one) which has been shown to cause difficulties in comprehension (Friedmann & Costa, 2010). Sentences with one embedded relative clause (see Figure 8B) involved a main clause headed by an intransitive verb whose complex subject noun

phrase was followed by two subject-relative clauses which in turn were coordinated. Similarly, sentences with two embedded relative clauses (see Figure 8C) involved a main clause headed by an intransitive verb whose complex subject noun phrase was followed by a subject-relative clause.

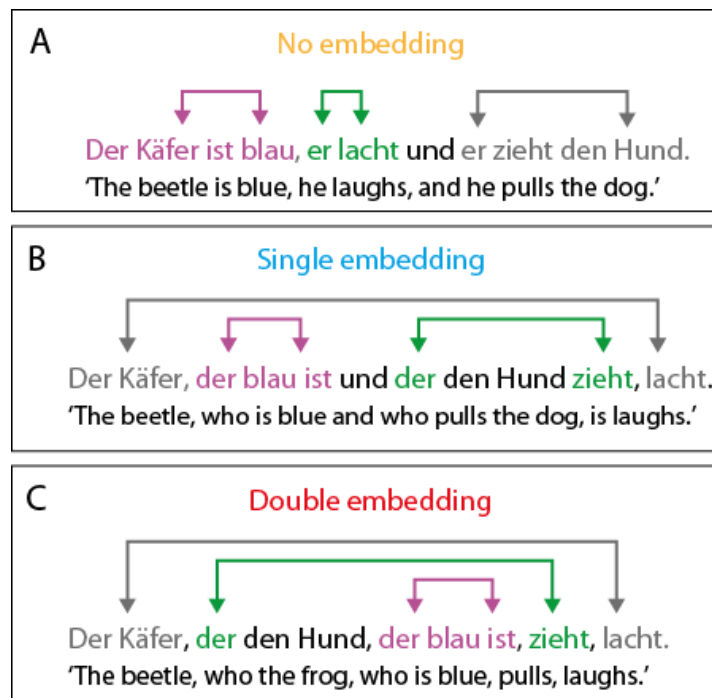


Figure 8. Overview of experimental conditions. Sentence complexity was manipulated by the number of embeddings. (A) No embeddings (marked in orange) only contained coordinated subclauses. (B) Single embeddings (marked in blue) contained two coordinated relative clauses embedded into one matrix clause. (C) Double embeddings (marked in red) contained two embedded relative clauses.

To create a second embedding, another subject-relative clause was constructed modifying the object of the previous relative clause. In order

to focus on children's ability of structural hierarchy building and since German-speaking children have problems in thematic role assignment until 7 years of age (Dittmar, Abbot-Smith, Lieven, & Tomasello, 2008), the canonical word order (subject-first) was used to restrict the complexity of the sentence material. Instead, the material intends to test whether participants can relate verbs to their corresponding subjects.

The semantic content of the sentences of the different conditions was held as constant as possible: Each sentence described a scene involving two interacting animals. One of the three subclauses described the color of one of the animals using a copula, the second subclause described the action involving the two animals by a reversible transitive verb, and the third subclause described the emotional expression (laughing/crying) of one of the animals by an intransitive verb. In German, case is marked by determiners preceding the noun. To ensure unambiguous marking for nominative and accusative, only masculine animate nouns were used.

Sentences were recorded by a trained female speaker, digitized (44.1 kHz/16 bit sampling rate, mono), and normalized according to the root-mean-square amplitude of all files. Corresponding pictures were created to test the comprehension of the particular subclauses (see Figure 9). Each picture pair depicted one correct and one incorrect interpretation. Thereby the divergent pictures displayed either referents in opposing colors (see Figure 9; upper panel), the opposite agent-patient relationship

(see Figure 9; middle panel) or opposing emotion expressed by the verbs (see Figure 9; lower panel). The presentation side of the correct picture was counterbalanced across conditions and participants.

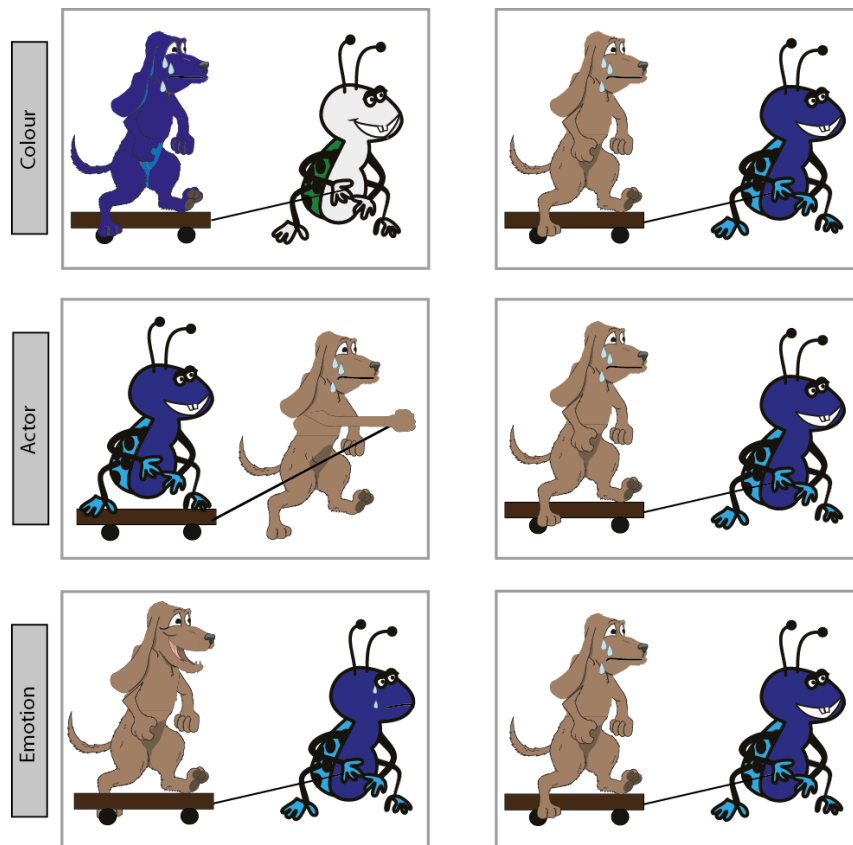


Figure 9. Pictures for each subclause. To test the comprehension of each subclause, different sets of picture were created.

7.2.3 Procedure

Stimuli were presented using the Presentation® software package (Neurobehavioral Systems, Inc., Albany, CA, USA). To set up a child-

friendly procedure, the experiment was introduced as a game. Participants were seated in front of a computer screen in a quiet room in our laboratory and briefly instructed how to play the game. During the introduction, they were made aware of that there were only tiny difference between the pictures. Pictures and the auditory sentence stimuli were presented simultaneously. Participants were instructed to choose the picture matching the sentence by pressing a button as fast as possible as soon as they detected the correct picture, even before the completion of the sentence. The buttons were fixed underneath each picture on the computer screen and participants were told to keep their thumbs on each button during the whole experiment. In order to familiarize participants to the procedure, three items containing the same sentence structure, but different lexical material than the test items, were presented. In case of any questions, the introduction was repeated until the task was clear. The 54 items of the test phase were presented without any break. A button press for one item initiated the presentation of the next one. Necessary repetitions of items were enabled by the experimenter but were not evaluated in further analyses. After the completion of the task, participants got positive feedback.

Subsequently, children's memory capacities were administered by the sequential processing scale of the Kaufman Assessment Battery for children (K-ABC; Kaufman, Kaufman, Melchers, & Preuss, 1994). Although only scores of the digit span test were included into further

analyses, the whole scale was tested to obtain data that can be compared to standardized values for each age group. These values were used to ensure that children, who participated in the study, normally develop in this cognitive domain.

7.3 Data analysis

Data analysis was performed using SPSS® (SPSS Inc., Chicago, IL, USA). To obtain the level of performance, the mean response accuracy for each sentence structure was calculated. Participants choosing one side of pictures more than 66.67% were excluded from further analyses, to eliminate any side biases. In order to test whether participants in each age group performed above chance for each sentence structure, Wilcoxon matched-pair signed-rank tests were used.

7.3.1 Performance data for the different sentence structures

The response data is not normally distributed. Therefore, non-parametric tests were computed to verify main effects and interactions between the two factors sentence structure (COMPLEXITY) and age group (AGE). While Kruskal-Wallis one-way analyses and Friedman's analyses of variances (ANOVAs) were used to test for main effects, adjusted rank transformations (ART; Leys & Schumann, 2010) had to be applied to test for possible interactions between the two factors. This procedure contains

the following steps: First, the respective marginal means have to be subtracted from each observation. Second, the adjusted raw data is transformed to a rank which, thirdly, is used for a subsequent factorial ANOVA.

7.3.2 Performance data for the different subclauses in double embeddings

Processing difficulties are predicted for double embedded sentences in particular since they involve both a complex hierarchy building and long-distance dependencies. While difficulties in syntactic hierarchy building are assumed to result in a breakdown of the analysis altogether, problems in establishing long-distance dependencies would be only pronounced in the specific subclause containing this feature. In order to test for performance differences between subclauses in double embedded sentences, mean response accuracy data for each subclause of the double embedded sentences were passed into the different kinds of ANOVAs.

7.3.3 Correlational analyses

Since the processing of center-embedded sentences highly taxes on verbal working memory in adults (Caplan et al., 2011; Waters & Caplan, 2001), it is assumed that performance of the children may be influenced

by their individual digit span as well. A Spearman's rho correlation was computed to test for the relationship between performance for each sentence structure and digit span. Since it is hypothesized that limitations in verbal working memory capacity could be related to difficulties in both the establishment of long-distance dependencies and structural hierarchy, stepwise regression analyses tested whether digit span predicts performance for the different subclauses in double embeddings, controlling for participants' age.

7.4 Results

The performance of each age group for each sentence structure was significantly above chance (see Table 2).

Table 2. Performance of each age group for each sentence structure against chance

	Z-values of no embeddings against chance	Z-values of single embeddings against chance	Z-values of double embeddings against chance
5-6-year-olds	-4.16	-4.13	-3.75
7-8-year-olds	-4.22	-4.16	-4.09
Adults	-4.38	-4.07	-4.13

Each age group performed above chance for each sentence structure. All $p < 0.001$.

7.4.1 Results for the different sentence structures

To determine main effects and interactions of the factors COMPLEXITY and AGE, different non-parametric computations were performed. A Kruskal-Wallis one-way analysis yielded a main effect of AGE ($\chi^2_2 = 35.83$, $p < 0.001$). A Friedman's ANOVA confirmed a main effect of COMPLEXITY ($\chi^2_2 = 42.48$, $p < 0.001$). However, a factorial ANOVA on ART data (see Data analysis) revealed an interaction between AGE X COMPLEXITY ($F_{4,183} = 11.08$, $p < 0.001$).

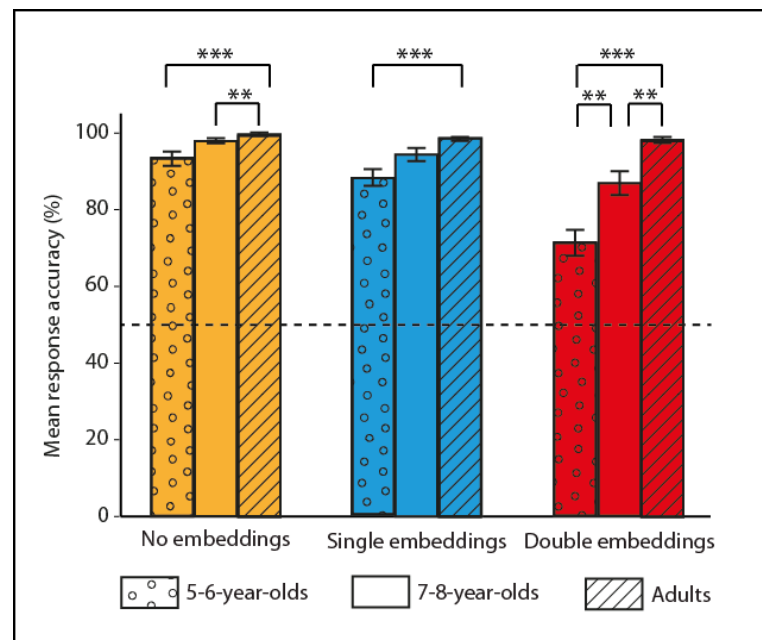


Figure 10. Overview of between-group comparisons of performance for each sentence structure. All age groups performed above chance (the dashed line marks the chance level). No embeddings are plotted in yellow, single embeddings are plotted in blue, and double embeddings are plotted in red. Dotted bars mark 5- and 6-year-olds, blank bars mark 7- and 8-year-olds, and dashed bars mark adults. All post-hoc between-group comparisons are Bonferroni-corrected (** = $p < 0.006$; *** = $p < 0.001$).

Between-group comparisons yielded main effects of AGE for all different sentence structures (no embeddings: $\chi^2_2 = 14.75$, $p < 0.01$; single embeddings: $\chi^2_2 = 15.67$, $p < 0.001$; double embeddings: $\chi^2_2 = 31.88$, $p < 0.001$). Direct comparisons between age groups showed significant differences between 5- and 6-year-old children and 7- and 8-year-old children for double embeddings ($Z = -3.06$; $p < 0.01$), between 7- and 8-year-old children and adults for no embeddings ($Z = -2.95$; $p < 0.01$) and double embeddings ($Z = -3.67$; $p < 0.001$), and between 5- and 6-year-old children and adults in all sentence structures (no embeddings: $Z = -3.68$; $p < 0.001$; single embeddings: $Z = -3.84$; $p < 0.001$; double embeddings: $Z = -5.18$; $p < 0.001$). A closer inspection of the results illustrated in Figure 10 revealed that age effects appear to be most pronounced in double embedded sentences.

7.4.2 Results for the different subclauses in double embeddings

ANOVAs testing whether processing difficulties for double embeddings in children arise from one of the subclauses in particular revealed a main effect of AGE ($\chi^2_2 = 31.88$, $p < 0.001$), a main effect of SUBCLAUSE ($\chi^2_2 = 14.75$, $p < 0.01$), and an interaction between AGE and SUBCLAUSE ($F_{4,183} = 5.73$, $p < 0.001$).

Subsequent Kruskal-Wallis one-way analyses yielded main effects of AGE for all different subclauses (first subclause: $\chi^2_2 = 29.53$, $p < 0.001$; second subclause: $\chi^2_2 = 26.07$, $p < 0.001$; third subclause: $\chi^2_2 = 15.46$, p

< 0.001, see Figure 11) and direct comparisons between age groups revealed significant improvements between 6 and 7 years for the first ($Z = -3.46$, $p < 0.01$) and the second subclause ($Z = -3.82$, $p < 0.001$) but not for the third subclause ($Z = -0.17$, $p = 0.87$). Performance for the third subclause only improved towards adulthood ($Z = -3.71$, $p < 0.001$). Performance differences between 5- and 6-year-old children and adults could be confirmed for all subclauses (first subclause: $Z = -4.93$, $p < 0.001$; second subclause: $Z = -4.15$, $p < 0.001$; third subclause: $Z = -3.43$, $p < 0.01$).

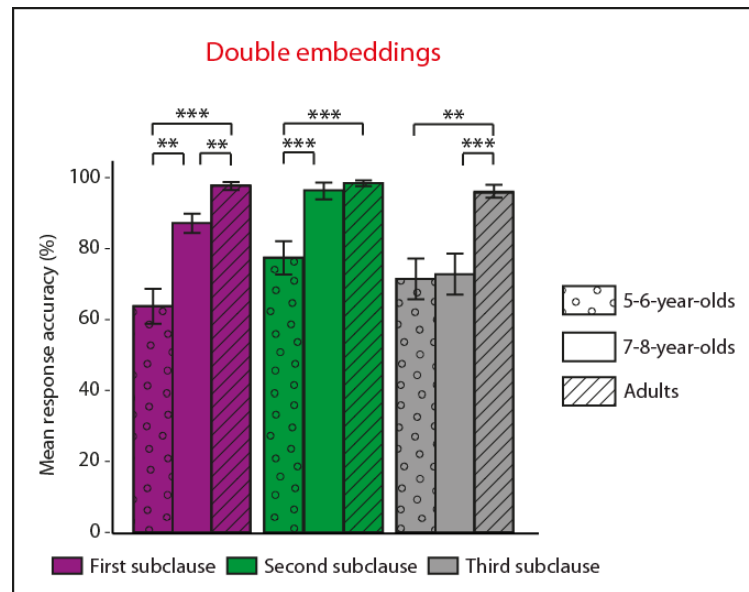


Figure 11. Between-group comparison of the performance for each subclause in double embedded sentences. Mean response accuracy rates for the first subclause are plotted in purple, for the second subclause are plotted in green, and for the third subclause are plotted in gray. Dotted bars mark 5- and 6-year-olds, blank bars mark 7- and 8-year-olds and dashed bars mark adults. All post-hoc between group comparisons are Bonferroni-corrected (** = $p < 0.002$; *** = $p < 0.001$).

7.4.3 Correlations with digit span

In a next step, it was tested whether performance in specific sentence structures is related to the individual verbal working memory capacity of children.

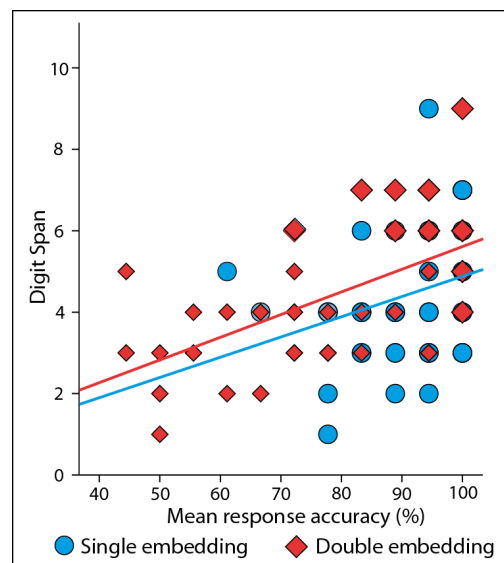


Figure 12. Correlation between digit span and mean response accuracy in children. A positive correlation could be found for single (marked in blue) and double embedded sentence structures (marked in red). However, only the correlation for double embeddings could be controlled for age effects.

As predicted, a spearman's rank correlation revealed that the performance for single ($\rho = 0.35$, $p < 0.05$) and double embeddings ($\rho = 0.62$, $p < 0.001$) in children is highly related to their digit span (see Figure 12). However, only the effect for double embeddings subsisted if data is controlled for age effects ($\rho_p = 0.47$, $p < 0.01$).

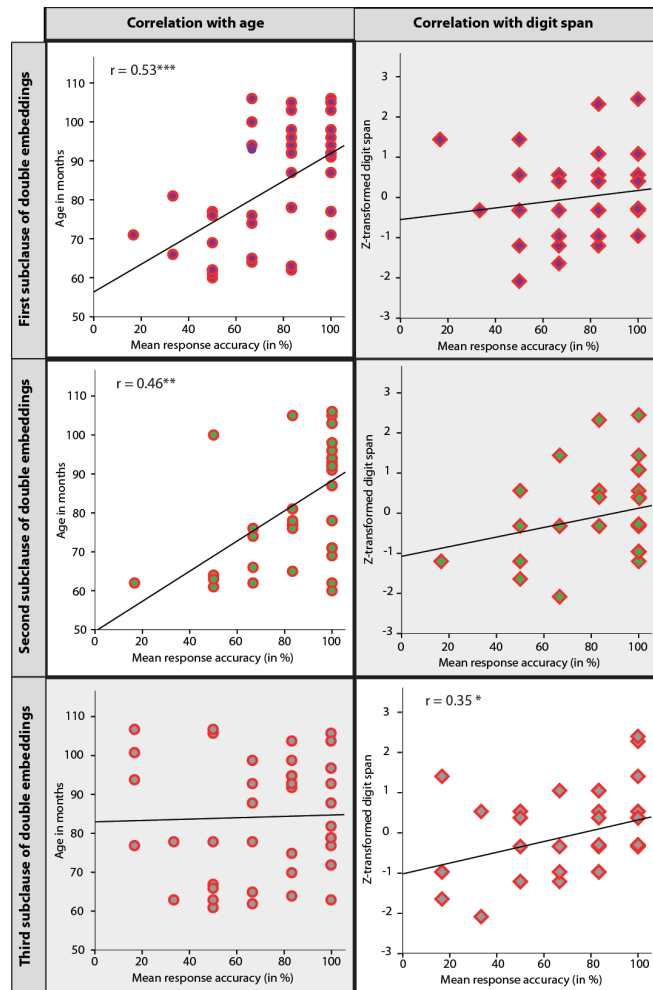


Figure 13. Results of the multiple regression analysis. Mean response accuracy of the first (purple) and the second subclause (green) is significantly predicted by age; mean response accuracy of third subclause (gray) is significantly predicted by digit span. Correlations with age are marked by circles; correlations with digit span are marked by squares.

Previous analyses indicate that both 5- and 6-year-old children and 7- and 8-year-old children show particular processing difficulties for the long-distance dependency in double embedded sentences (subclause 3). To test whether these specific processing difficulties in children are related to

restricted verbal working memory capacities, stepwise regression analyses on the response data of children for the different subclauses of double embeddings were performed. Age and standardized digit span values were entered as predictors in each analysis.

These analyses revealed that digit span is a significant predictor for the performance of the third subclause in double embeddings ($\beta = 0.35$, $p < 0.05$) which explains 12.2% of the variance ($F_{1,43} = 5.85$, $p < 0.01$). Performance of the first subclause is only predicted by age ($\beta = 0.53$, $p < 0.001$) which explains 28.2% of the variance ($F_{1,43} = 16.48$, $p < 0.001$) as well as performance of the second subclause ($\beta = 0.46$, $p < 0.01$) where age explains 20.8% of the variance ($F_{1,43} = 11.06$, $p < 0.01$). Correlational results are plotted in Figure 13.

7.4.4 Post-hoc analysis of children's linguistic knowledge

Considering that previous developmental research indicates that morphological information necessary for antecedent resolution cannot be reliably processed until 7 years of age (Dittmar et al., 2008; Schipke, Knoll, Friederici, & Oberecker, 2012), the observed age effect for the first subclause in double embeddings is hypothesized to be related to these kind of processing difficulties. To test whether processing difficulties of the first subclause in 5- and 6-year-old children may arise from missing linguistic knowledge, a post-hoc correlational analysis between scores of the German version of the Test for the Reception of Grammar (TROG-D;

Fox, 2006), a standardized language comprehension test, and mean response accuracy of the different subclauses in double embeddings was performed.

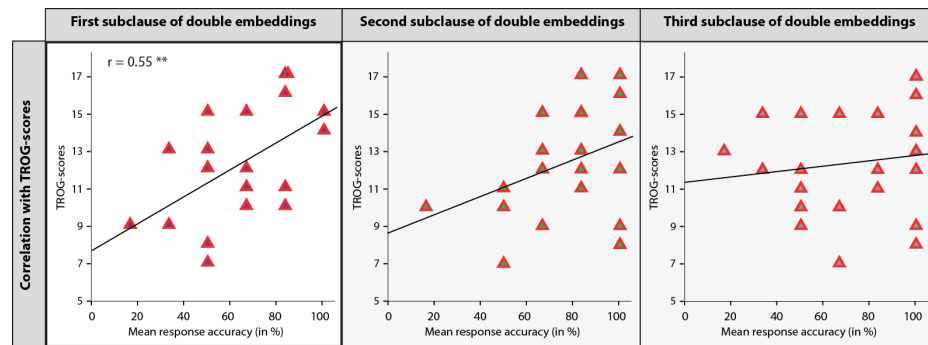


Figure 14. Correlation between TROG-scores and mean response accuracy rates for each subclause in double embeddings in 5- and 6-year-old children. The first subclause is marked in purple; the second subclause is marked in green; the third subclause is marked in gray. All post-hoc correlational analysis are Bonferroni-corrected ($** = p < 0.016$).

These analyses confirmed a correlation of mean response accuracy for the first subclause and general sentence comprehension ($r = .55$, $p < 0.01$, see Figure 14).

7.5 Discussion

This study sought to investigate the relation between verbal working memory capacity in children and the processing of multiple center-embedded sentences. The data suggest a clear relation between the processing of long-distance dependencies in double embedded sentence

structures and digit span in the children's group irrespective of their age: the higher the digit span, the better sentence processing (see Figure 12 and Figure 13). But nonetheless, qualitative changes of sentence processing can be observed between the age groups.

7.5.1 The processing of center-embedded sentences in different age groups

Previous research indicates that even adults have problems processing sentences that contain more than one level of embedding (e.g. Blaubergs & Braine, 1974; Foss & Cairns, 1970; Hakes & Cairns, 1970; Hakes et al., 1976; Hakes & Foss, 1970; Hamilton & Deese, 1971; Larkin & Burns, 1977; Marks, 1968; Miller, 1962; Miller & Isard, 1964; Wang, 1970). With respect to the causing factors of the sentence processing difficulties, memory limitations (e.g. Miller & Chomsky, 1963) and lack of experience (e.g. Christiansen & MacDonald, 2009; Vasishth et al., 2010) have been discussed (see 'The processing of hierarchical sentence structures'). In this study, responses of the adults did not differ between the different sentence structures (see Figure 10). This may be mainly attributable to the child-friendly paradigm with containing sentences of only two levels of embeddings and a canonical word order. Children, however, show a decrease of response accuracy with the number of embeddings.

Double embedded sentences pose a special challenge to the immature language parser (see Figure 10). A closer inspection of the

performance in these sentences revealed that in 5- and 6-year-old children the processing of double embedded sentence structures across subclauses leads to problems in the interpretation. In 7- and 8-year-old children, the performance pattern is more refined. Children of this age group show specific problems in double embedded sentence structures with subclauses that contain long-distance dependencies (see Figure 11). This points to their inability to keep the first noun phrase long enough active until it can be linked to its corresponding verb and may be attributed to restricted verbal working memory capacities. Since the focus of this study is on the relation between verbal working memory and the processing of center-embedded structures in children, its relation will be discussed in a separate section below. Compared to 7- and 8-year-old children, additional difficulties in 5- and 6-year-old children arise when processing the first and the second subclause in double embedded sentences (see Figure 11). Particularly the interpretation of the first subclause requires the ability to bind the pronoun to its antecedent.

However, since two noun phrases have been processed until then, children need to process case-marking information to be able to implement the correct assignment and as a result to establish the complete structural hierarchy of the sentence. The finding of processing difficulties for the first subclause in 5- and 6-year-old children and its correlation to language comprehension scores of the TROG-D (Fox, 2006) is in accordance with previous developmental research showing

that German-speaking children of this age group cannot reliably process morphological information yet (Dittmar et al., 2008; Schipke et al., 2012).

7.5.2 The relation between verbal working memory and the processing of center-embedded sentences in children

Previous studies attributed children's difficulties in processing relative clauses either to a non-adult-like processing strategy (Sheldon, 1977; Tavakolian, 1981) or to limitations in the cognitive capacities such as verbal working memory (Corrêa, 1995; Fragman, Goodluck, & Heggie, 2007; Kidd & Bavin, 2002; Kidd, Brandt, Lieven, & Tomasello, 2007). The influence of verbal working memory capacity on processing relative clauses plays an important role because it restricts computational resources for sentence processing. Studies investigating children's processing of relative clauses found verbal working memory capacity to be related to the ability to reactivate antecedents of moved components in object-relative clauses (Roberts et al., 2007) and the integration of contextual information that facilitate the interpretation of center-embedded sentences (Weighall & Altmann, 2010). In addition, it has been shown that restrictions of verbal working memory capacity might induce attachment preferences (Felser et al., 2003). Felser et al. (2003) found listening span to affect children's attachment strategies in ambiguous relative clauses like "The student photographed the fan of the actress who was looking happy." While low spanners appear to prefer a recency strategy (Gibson

et al., 1996) in which incoming material is attached to the most recently built sentence structure, children with a high listening span also use the predicate proximity strategy (Gibson et al., 1996) in which attachment closest to the head of the predicate phrase is favored. Different attachment strategies in relative clauses can be detected in sentences containing a pronoun that can be linked to two different noun phrases as potential antecedents. In the current study, the pronoun of the most embedded clause in double embedded sentences can be linked either to the subject noun phrase of the first interrupted subclause or to the object noun phrase of the second one. However, since the recency strategy does lead to the correct pronoun resolution, no relation to children's verbal working memory capacity should be expected. Nonetheless, if children are sensitive to the cognitive load of a sentence, as proposed by the time-based resource-sharing model (Barrouillet et al., 2004), the introduction of the third subclause may lead to the break-down of the sentence processing altogether if verbal working memory does not suffice to store all three subclauses and, therefore, should be related to children's verbal working memory capacity. Data of this study revealed that the performance for double embedded sentences in children is related to digit span (see Figure 12). However, correlational analyses for different subclauses confirmed that digit span only predicts performance of the third subclause, the subclause that contains the long-distance dependency (see Figure 13). Since digit span is not related to

performance of the other subclauses, the current data contradicts the time-based resource-sharing model. Nonetheless, it cannot be precluded that children may have implemented the recency strategy as default option which may have improved their performance results for the first subclause. The implementation of this strategy may also explain the early improvement for this subclause compared to the later improvement for the subclause containing the long-distance dependency. Secondly, improved performance for the first subclause may be also related to improvements in processing case-marking information. A correlational analysis of scores of the TROG-D (Fox, 2006) and mean response accuracy rate for the first subclause in double embeddings in 5- and 6-year-old children provides evidence for this assumption. Therefore, results of the current study suggest qualitative changes in processing the most embedded sentences between 6 and 7 years of age which may be related to the improvement of processing case-marking information and not to an increase of working memory capacity

Correlations between digit span and performance have been found for long-distance dependencies in double embedded sentences. This finding points to suggestions introduced by the task-switching model (Towse & Hitch, 1995). According to this model, high spanners may be able to associate the first noun phrase and the final verb phrase since they enact a higher processing speed and thus are able to process the complete sentence before the representation of the initial sentence

material has ceased. This interpretation is in accordance with findings by Montgomery et al. (2008) who found processing speed to be related to complex sentence processing. However, an open question remains how much the implementation of specific processing strategies such as subvocal rehearsal or chunking may, on the one hand, lead to an increase in digit span and, on the other hand, facilitate sentence processing. Several studies found that children before 7 years of age do not show reliable spontaneous rehearsal yet (Gathercole & Hitch, 1993; Gathercole et al., 2004) which can also explain processing difficulties with long-distance dependencies in embedded sentences in particular. Therefore, more detailed research is needed to investigate different subcomponents that facilitate verbal working memory capacities and their relation to complex sentence processing.

7.5.3 Limitations of this study

It should be noted that digit span only measures short-term memory capacities and thus represents a subcomponent of verbal working memory. To represent the entire verbal working memory skills, additional measurements of attention resources allocation, attentional control mechanisms, and speed processing features would be needed. At the time of the study, no standardized test for these subcomponents for children between 5–6 years existed. However, Montgomery et al. (2008) found that in older children between 6 and 12 years measurements of

these subcomponents highly correlate with each other. Therefore, here the digit span test of the K-ABC (Melchers et al., 1994), which is part of a standardized verbal working memory subscale, was chosen as a representative of verbal working memory measurements.

7.6 Conclusion

Data of this study show that children face a special challenge when processing multiple center-embedded sentence structures. Processing difficulties are correlated, on the one hand, with general language comprehension skills and, on the other hand, with verbal working memory, i.e. digit span. While the processing of the first subclause in double embedded sentences improves between 6 and 7 years and appears to be related to the improvement of processing case-marking information, the processing of long-distance dependencies in these sentences is highly correlated to children's verbal working memory and only improves later, possibly due to increases in processing speed.

8 STRUCTURAL MRI STUDY: GRAY MATTER AND GRAMMATICAL PROFICIENCY

8.1 Introduction

Brain development follows intrinsic, genetic, and molecular mechanisms but is also subject to external experience. Compared to other species, humans show a prolonged phase of brain functional specialization which allows the brain to be shaped by postnatal experience. This delayed time course in brain maturation provides more time for learning processes (Johnson, 2001). Brain volume drastically increases early in life and at 6 years of age, children have reached approximately 90% of the adult brain volume (Courchesne et al., 2000; Lenroot & Giedd, 2006; Reiss et al., 1996). This structural increase originates from exceeding progressive changes in the gray and white matter compartments. However, during preadolescence, the developmental pattern of gray matter is inverted and maturation is generally defined as a loss of gray matter density (Giedd et al., 1999; Gogtay et al., 2004; Sowell, Thompson, & Toga, 2004). Onset

and rate of gray matter loss is region-specific and follows a functional maturation sequence, starting with gray matter reduction in early-maturing primary sensorimotor areas, followed by gray matter reduction in late-maturing higher-order association areas (Gogtay et al., 2004). While progressive changes in the cortical development are assumed to provide the basis for neural plasticity and thus maximal learning opportunities (Johnson, 2001; Simonds & Scheibel, 1989), regressive changes in the cortex have been related to a decline of the brain's ability to adapt to environmental input during development (Huttenlocher, 2002).

Prior structural imaging work found initial evidence for the link between structural gray matter changes and the development of language performance in children: Infants' gray matter maturation of the right cerebellum and the right hippocampus was found to correlate with later language competence (Deniz Can, Richards, & Kuhl, 2013). The receptive and productive phonological skills of children between 5 and 11 years correlate with measurements of GMP in the left IFG (Lu et al., 2007). In teenagers between 12 and 17 years, gray matter of the left supramarginal gyrus (SMG) and left posterior temporal regions correlate with vocabulary knowledge (Richardson, Thomas, Filippi, Harth, & Price, 2010).

Frontal and parietal areas, which have been shown to be involved in language processing, show the onset of gray matter reduction during late childhood, more specifically between 7 and 12 years (Giedd et al., 1999; Sowell et al., 2003). This time range parallels the end of the

sensitive period for grammar acquisition which is assumed to be reflected by increasing effort in second language learning to gain a comparable grammatical proficiency as native speakers (Johnson & Newport, 1989). However, no study to date has linked these brain-structural changes of the brain regions relevant to sentence processing to the establishment of grammatical proficiency.

Therefore, the aim of this study is to investigate the interrelation between structural properties and the grammatical proficiency. To do this, whole-brain MR images from 60 children between 5 and 8 years were assessed and analyzed using VBM analyses. Grammatical proficiency was determined by scores of grammar-specific subtests of the German version of the TROG-D (Fox, 2006): Only sentences requiring specific morphological and syntactic knowledge were included into the analysis. In order to segregate the different contributions of grammatical knowledge and working memory capacity, a principal component analysis was run on the behavioral data of the participants. To allow for the investigation of a relation between these two factors and GMP, a multiple regression analysis was performed.

8.2 Methods

8.2.1 Participants

Children were recruited through letter announcements in local kindergartens and schools. Interested parents were invited for an informative meeting about the experiment and procedures. They gave written informed consent and children gave verbal assent prior to assessment and scanning. Participants were not included if they met following criteria: abnormal intelligence, any known neurological or psychiatric disease or disorder or medical treatment affecting the central nervous system, and clinical or technical contraindications to an magnetic resonance imaging (MRI) examination.

Table 3. Overview of participants.

	5–6 years	7–8 years	Total
Boys	13	11	24
Girls	15	10	25
Total	28	21	49

Eleven children had to be excluded from the study because of too much head movement during the anatomical scan or brain anomalies. In the end, data from 49 children (24 boys, 25 girls) could be analyzed (mean age: 6;9 years, age range: 5;3 - 8;5 years; for an overview of participants, see Table 3). The procedure and the protocol of the study were approved

by the Research Ethics Committee of the University of Leipzig (Leipzig, Germany).

8.2.2 Assessment of grammatical proficiency and working memory

Children's language comprehension skills were assessed by a German version of the TROG-D (Fox, 2006). This test is a standardized sentence comprehension test for children between 3 and 11 years. The comprehension of grammatical constructions of increasing complexity is assessed by 84 items. In this test, each grammatical construction comprises four test sentences that are auditorily presented. The child is asked to point to one out of four pictures whereby deflecting pictures depict either divergent lexical or grammatical interpretations.

Verbal working memory skills were determined by the Mottier test (Mottier, 1951). Children had to listen to nonwords with an increasing number of syllables and repeat them immediately after the presentation. For constant presentation, test items were recorded by a trained female speaker and subsequently digitized (44.1 kHz/16 bit sampling rate, mono), normalized in amplitude, and presented via headphones. To make the procedure more suitable for children, stimuli were presented in form of a repetition game. Thereto participants were introduced to a parrot on the screen who told them to repeat the items exactly the way he pronounced them. To prevent lexicalization of the nonwords during repetition, children were told that they cannot know the words they would hear since the

parrot speaks a foreign parrot language. Children's responses were recorded via a portable mini disk recorder (Sony, Ft. Myers, FL, USA). These tests and an abridged version of the test for handedness (Oldfield, 1971) were administered in close temporal proximity to the MRI scanning.

8.2.3 MRI acquisition procedures

During the scanning session, participants were presented a movie of their choice. Before scanning, children participated in a mock MRI scanner session to get accustomed to the scanning procedure and the scanner noise. A small sensor was fixated on the children's forehead to register movement and to send a signal to the computer to interrupt the movie whenever children started to move. Additionally, children got verbal feedback via the headphones.

Participants were scanned in a whole-body 3-T Magnetom Trio scanner (Siemens Healthcare, Erlangen, Germany) and a 12-channel head coil at the Max Planck Institute for Human Cognitive and Brain Sciences in Leipzig, Germany. MRI data was acquired by applying a T1-weighted 3D magnetization-prepared rapid gradient echo (MP-RAGE) sequence with selective water excitation and linear phase encoding. The magnetization preparation consisted of a non-selective inversion pulse. Following imaging parameters were used: inversion time (TI) = 740 ms; repetition time of the total sequence cycle (TR) = 1480 ms; repetition time of the gradient-echo kernel (snapshot FLASH) = 10 ms; TE = 3.46 ms;

alpha = 10°; bandwidth = 190 Hz/pixel; image matrix = 256 x 240; FOV = 256 mm x 240 mm; slab thickness = 192 mm; 128 partitions; 95% slice resolution; sagittal orientation; spatial resolution = 1 mm x 1 mm x 1.5 mm; 2 acquisitions. To avoid aliasing, oversampling is performed in the read direction (head-foot). The MRI sequence lasted about 6 minutes.

8.3 Data analysis

8.3.1 Confirmatory factor analysis

The TROG-D contains a big variety of sentences. Some of the sentences test the interpretation of a specific word form such as prepositions, other focus on morphological and syntactic aspects of sentence processing. The different sentences demand thereby a varying degree of working memory capacities. Since all these different aspects of sentence processing are known to involve differential brain areas (Makuuchi, Bahlmann, Anwender, & Friederici, 2009; Meyer et al., 2012; Novais-Santos et al., 2007), a more homogenous subset of sentences of the TROG-D was used. This subset only contained sentences which required specific knowledge about case marking and structural hierarchy building to allow for the correct interpretation of who is doing what to whom (for an overview of sentences see Table 4).

Table 4. Overview of sentences from the TROG-D.

Sentence structure	Example	Word order
Passive construction	Das Mädchen wird vom Pferd gejagt. The girl _{NOM} is chased by the horse _{ACC} .	SVO
Subject-relative clauses	Der Junge, der das Pferd jagt, ist dick. The boy _{NOM} , who _{NOM} the horse _{ACC} chases, is fat.	S ₁ S ₂ OV ₂ V ₁
	Das Mädchen jagt den Hund, der groß ist. The girl _{NOM} chases the dog _{ACC} , who _{NOM} is big.	S ₁ V ₁ OS ₂ V ₂
Sentences with 3 arguments	Die Frau malt dem Jungen das Mädchen. The woman _{NOM} paints the boy _{DAT} the girl _{ACC} .	SVO ₁ O ₂
Object-topicalized sentences	Den braunen Hund jagt das Pferd. The brown _{ACC} dog chases the horse _{NOM} .	OVS
Object-relative clauses	Der Junge, den der Hund jagt, ist groß. The boy _{NOM} , who _{ACC} the dog _{NOM} chases, is big.	S ₁ OS ₂ V ₂ V ₁

S = subject; V = verb; O = object; NOM = nominative; ACC = accusative; DAT = dative.

The interpretation of the selected sentences constitutes a big challenge for children for two reasons: On the one hand, children need to inhibit their preferential interpretation strategy of only following word order for thematic role assignment and, on the other hand, they need to be able to store the entire sentence to allow the processing of long-distance dependencies and potential reanalysis processes. To confirm that successful interpretation performance relies on these two different cognitive abilities, namely the inhibition of interpretation preferences and working memory abilities, a confirmatory factor analysis was computed applying the principle component analysis to extract the two factors. In order to control for general age effects, behavioral subscores for each

sentence structure were z-transformed according to the age group before the analysis. For rotation, the varimax criterion was used to prevent correlations between factors. To confirm that one of these factors represents working memory capacities, the individual factor scores were correlated with scores of the Mottier test.

8.3.2 VBM data processing

Before preprocessing, all T1-images were visually inspected for movement artifacts. The MRI data was analyzed with SPM 8 (Wellcome Department of Imaging Neuroscience, University College London) running in MATLAB 7 (Math-Works, Natick, MA, USA). Images were segmented into gray matter, white matter, and cerebral spinal fluid based on intensity values and a TPM representing brain structure of children between 5 and 8 years (Fonov et al., 2011). Non-brain tissue was removed and initial segmentations were registered into MNI space. The gray and white matter images were imported into DARTEL (Ashburner, 2007) and a template was created using the default parameters. The resulting flow fields containing the deformation information were subsequently used to normalize gray and white matter onto an age-specific template (Fonov et al., 2011). To obtain a measure of regional volume, images were modulated, resampled to $1.5 \times 1.5 \times 1.5 \text{ mm}^3$ voxel size and smoothed using an isotropic Gaussian kernel of 8 mm at FWHM.

8.3.3 Statistical analysis of the VBM data

The statistical analysis was also performed using the software package SPM 8 (Wellcome Department of Imaging Neuroscience, University College London). To control for different brain sizes, the total intracranial volume (TIV) was calculated by summing the unmodulated volumes of gray matter, white matter, and cerebral spinal fluid. For assessing the relationship between gray matter volume and behavioral covariates, scores of the different factors extracted by the principle component analysis were entered into a multiple regression analysis. In order to account for different brain sizes, potential sex differences (Tanaka, Matsui, Uematsu, Noguchi, & Miyawaki, 2012), and structural alterations due to handedness (Dos Santos Sequeira et al., 2006; Zetzsche et al., 2001), sex, TIV, and the quotient of handedness (Oldfield, 1971) were added as covariates of no interest into the analysis. The individual voxel p-value threshold was set to $p < 0.001$. An AFNI implemented Monte Carlo simulation (NIMH Scientific and Statistical Computing Core, Bethesda, MD, USA) ensured that a cluster size of 174 voxels protects against whole-volume type I error at $\alpha = 0.05$.

After an explanatory whole brain assessment, a small volume correction procedure was used to restrict the analysis to left IFG, a brain region which constantly has been shown to be involved in complex sentence processing (for a review, see Friederici, 2011). To ensure that only the relevant anatomical structures were included, a mask was

generated by the Wake Forest University Pickatlas (Maldjian, Laurienti, Kraft, & Burdette, 2003) based on the Talairach Daemon database (Lancaster et al., 2000). To correct for multiple comparisons, only clusters yielding a peak-level of $p < 0.05$, family-wise error-corrected for the search volume, are reported.

8.4 Results

8.4.1 Sentence interpretation and working memory

The principle component analysis on the different sentence structures of the TROG-D confirms two different factors underlying performance values. The appropriateness of the factor analysis and the distinction between these two factors are validated by the Bartlett's Test of Sphericity ($\chi^2_{10} = 44.74$, $p < 0.001$) and the Kaiser-Meyer-Olkin Measure (KMO = 0.68). While the first factor accounts for 45.5% of the variance in the observed variables, the second factor accounts for another 21% of variance.

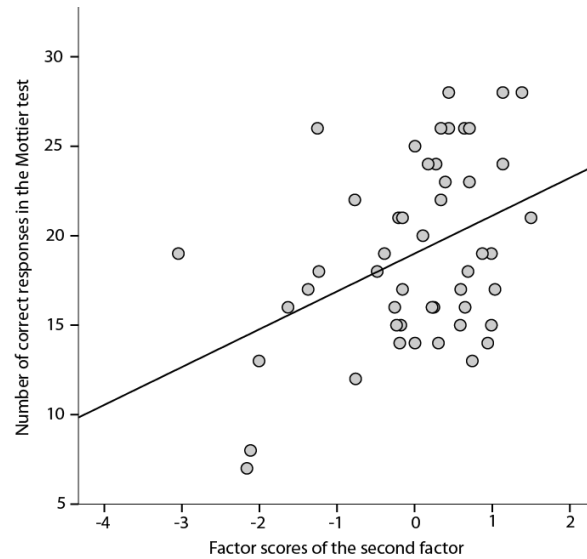
The following variables highly load on the first factor: passive constructions, subject-relative clauses, and object-topicalized sentences. Sentences with three arguments highly load on the second factor. Object-relative clauses load on both factors almost equally alike (see Table 5).

Table 5. Factor loadings after the principle component analysis.

	Factor 1	Factor 2
Passive constructions	0.743	0.080
Subject-relative clauses	0.763	-0.060
Sentences with three arguments	-0.063	0.910
Object-topicalized sentences	0.806	0.252
Object-relative clauses	0.511	0.619

Bold font marks factor loading > 0.5.

In order to confirm that one of these factors represents working memory-related aspects of sentence processing, correlations between factor scores and the values of the Mottier test were computed.

**Figure 15.** Correlation between factor scores for the second factor and scores of the Mottier test (Number of correct responses).

A significant correlation could be found for the second factor ($r = 0.41$, $p < 0.01$; see Figure 15) but not for the first factor ($r = 0.27$, $p = 0.60$), indicating that the second factor is related to verbal working memory.

8.4.2 Results of the voxel-based morphometry analysis

Table 6. Significant clusters for the positive correlation between the first factor and GMP.

Hemisphere	Region	MNI coordinate				Cluster size	z value
		BA	X	Y	Z		
Positive correlation between the first factor and GMP							
Left	ITG		-42	-16	-23		4.03
		20	-50	-18	-36	514	3.89
	Hippocampus		-33	-10	-15		3.50
Left	IFG	44/45	-56	20	19	24	3.36*
Positive correlation between the second factor and GMP							
Left	Parietal Operculum	13	-44	-24	21		4.40
		41	-44	-27	6	783	3.72
	STG	41	-46	-37	13		3.30

174 voxels threshold at $p < 0.001$ to achieve family-wise error control at $p < 0.05$; * = small volume corrected; BA = Brodmann area; MNI = Montreal Neurological Institute; GMP = gray matter probability; ITG = inferior temporal gyrus; IFG = inferior frontal gyrus; STG = superior temporal gyrus.

In a next step, it was examined whether individual scores of these different factors predict GMP. A multiple regression analysis considering the entire

brain revealed a positive relationship between the first factor and GMP in the left posterior inferior temporal gyrus (ITG; main peak at $x = -42$, $y = -16$, $z = -23$).

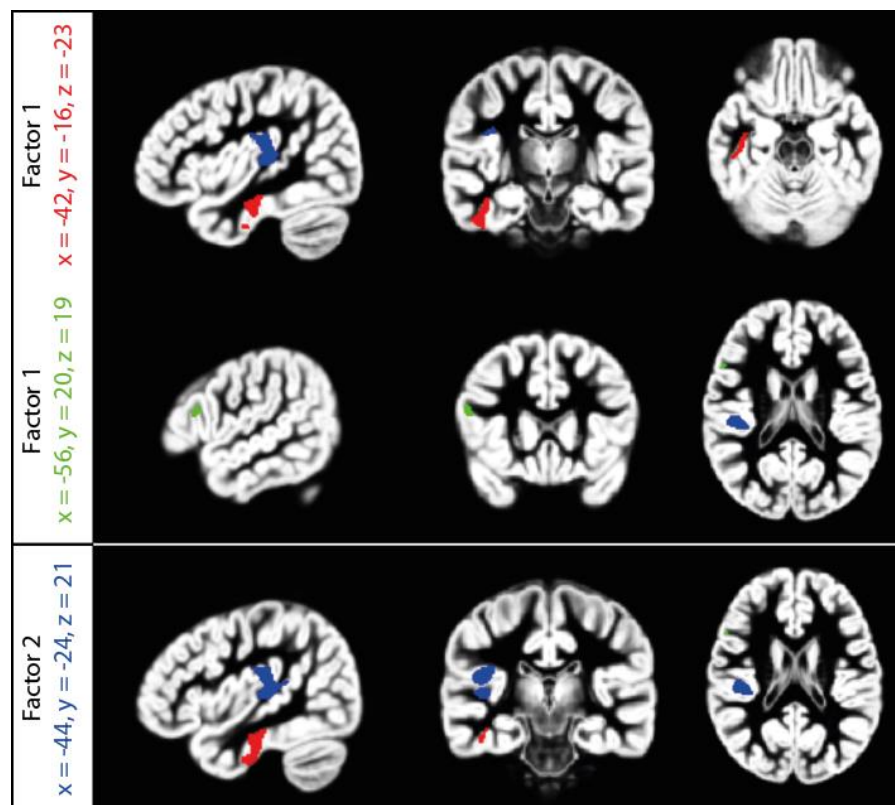


Figure 16. Results of the VBM analysis. Significant correlations are plotted on a template representing gray matter between 4 and 8 years; positive correlations could be found between the first factor and GMP in the left inferior temporal gyrus (in red) and in left inferior frontal gyrus (in green); a positive correlation between the second factor and GMP could be found in the left parietal operculum/superior temporal gyrus (in blue).

When the search volume is restricted to the left IFG, a positive correlation between GMP and the first factor was found as well (main peak at $x = -56$, $y = 20$, $z = 19$). A positive relationship between the second factor and

GMP was evident in the left parietal operculum extending to the left posterior superior temporal gyrus (main peak at $x = -44$, $y = -24$, $z = 21$). No negative correlations were observed. The full set of significant clusters can be found in Table 6 and in Figure 16.

8.5 Discussion

The principle component analysis confirms two factors contributing to the variance in the performance data. Passive constructions, subject-relative clauses, object-topicalized sentences, and object-relative clauses load on the first factor. In these sentences, word order is not a reliable cue for the interpretation. In general, listeners typically prefer to assign the agent role to the first noun phrase and the patient role to the second one. In German, subject and object noun phrases are differentially marked by case. Subject noun phrases are usually interpreted as the agent of the sentences, object noun phrase as the patient. The canonical word order in German follows the order: subject-verb-object. In canonical sentence structures, word order and case assignment provide congruent information about the thematic role assignment. However, word order, case assignment, and thematic role assignment are not congruent in passive constructions, object-topicalized sentences, and object-relative clauses. A special case are the subject-relative clauses which follow the canonical word order, but which require thematic role assignment for two subjects. Additionally, in some of these sentences (see Table 4), the

interruption of subclauses makes the assignment of noun phrases to their corresponding verbs more difficult. Children may not be able to identify and maintain the morphological information necessary assign the agent role to both subjects of these sentences and consequently rely on a plausible instead of a structural interpretation (Skeide, 2012). In sum, the correct thematic role assignment of all four types of sentences loading on the first factor mandatorily requires the processing of morphological case-marking. However, it has been shown that this morphological information cannot be reliably processed up to 7 years of age (Dittmar et al., 2008; Schipke et al., 2012). Due to these limitations, children between 5 and 8 years may still have difficulties processing these type of sentences which may have resulted in performance variance represented by the first factor.

The second factor contains loadings of sentences with three arguments and additionally loadings of object-relative sentences. A correlation between factor scores for this component and scores of the Mottier test (Mottier, 1951) confirms that this factor most likely represents working memory-related aspects of sentence processing that are especially represented by performance in these two type of sentences. The processing of case marking is likewise mandatory for sentences loading on this factor. However, if working memory is too restricted, not all arguments can be hold actively long enough to process all case-marking information and thus thematic roles may have to be assigned before conflicting information is evaluated. While in the sentences with three

arguments the amount of arguments may exceed storage capacities in general, object-relative clauses require the establishment of long-distance dependencies. To process these dependencies, the listener has to store the first noun phrase until the end of the sentence while processing a non-canonical relative clause. The processing of these sentences may fail, since storage capacities are limited in time and/or influenced by intervening sentence material. Consequently, factor scores of this factor are suggested to represent sentence processing differences due to differences in verbal working memory capacities.

The whole brain analysis reveals a positive relationship between GMP and scores of the first factor in the left posterior ITG and in the left hippocampus. If the search volume is restricted by small volume correction, another positive effect can be identified in the left IFG. In addition, a positive relationship between the second factor and GMP could be found in the left parietal operculum extending to the left posterior STG. Thus, the higher the values for each factor, the higher the GMP in these areas.

The positive correlation between GMP and behavioral performance is in line with previous studies showing gray matter thickening in left IFG and bilateral posterior perisylvian regions in children between 5 and 11 years (Sowell et al., 2004) as well as a positive correlation between the intelligence quotient and cortical volume especially in prefrontal areas in children between 5 and 17 years (Reiss et al., 1996). The exact underlying

neurophysiological mechanisms of GMP changes in the cortex are yet unclear. Values of gray matter measurements depend on the extent of the cortical surface, cortical thickness, and myelination in adjacent white matter (Hutton, Draganski, Ashburner, & Weiskopf, 2009; Mechelli, Price, Friston, & Ashburner, 2005). Gray matter changes during childhood can be induced by progressive changes such as an overgrowth of cell bodies (Petanjek, Judas, Kostović, & Uylings, 2008), dendritic sprouting (Simonds & Scheibel, 1989), and an overgrowth of synaptic connections (Huttenlocher & de Courten, 1987; Rakic, Bourgeois, Eckenhoff, Zecevic, & Goldman-Rakic, 1986) as well as by concurrent regressive changes such as synaptic pruning (Rakic et al., 1986). As mentioned earlier, progressive changes are assumed to provide the basis for maximal learning opportunities, especially in language-related areas (Johnson, 2011; Simonds & Scheibel, 1989).

Following these assumptions, increased GMP in the left IFG, left posterior ITG, and in the left parietal operculum extending to the posterior STG may provide a better basis for language learning mechanism and this can explain, why children with increased GMP perform better. In addition, it has been shown that trajectories of cortical maturation are associated with intelligence whereby more intelligent individuals show a prolonged phase of cortical increase (Shaw et al., 2006). Therefore, increased GMP may reflect a latter onset of gray matter reduction and

thus a higher plasticity in these areas which may result in an extended sensitive period.

In general, the processing of increased sentence complexity has been found to parallel increased activity in the left IFG (for a review, see Friederici, 2011). The left IFG can be subdivided in cytoarchitectonically distinct areas: the left PO and the left pars triangularis (Amunts et al., 1999; Brodmann, 1909). While the left PO has been suggested to be involved in structural hierarchy building, a combined activation of the left PO and the left pars triangularis has been assumed to support thematic role assignment (for a review, see Friederici, 2011). This assumption is supported by German studies that manipulated the word order and thus make thematic role assignment more difficult (Bornkessel, Zysset, Friederici, von Cramon, & Schlesewsky, 2005; Fiebach, Schlesewsky, Lohmann, von Cramon, & Friederici, 2005; Friederici, Fiebach, Schlesewsky, Bornkessel, & Cramon, 2006; Grewe et al., 2005; Röder, Stock, Neville, Bien, & Rösler, 2002). Studies of other languages that involved movement and activated the pars triangularis/pars opercularis provide additional evidence (Ben-Shachar, Hendler, Kahn, Ben-Bashat, & Grodzinsky, 2003; Ben-Shachar, Palti, & Grodzinsky, 2004; Caplan et al., 2008; Constable et al., 2004; Cooke et al., 2001; Just et al., 1996; Kinno, Kawamura, Shioda, & Sakai, 2008; Newman, Ikuta, & Burns, 2010; Santi & Grodzinsky, 2007, 2010; Stromswold et al., 1996).

The left pars triangularis and the left MTG are connected via ventral pathway through the extreme capsule fiber system (Frey, Campbell, Pike, & Petrides, 2008; Saur et al., 2008) and it has been suggested that the interaction between prefrontal and temporal areas is essential for the integration of contextual information (Dapretto & Bookheimer, 1999; Kaan & Swaab, 2002). The MTG and neighboring parts of the ITG are proposed to store lexical-semantic information (Crinion, Lambon-Ralph, Warburton, Howard, & Wise, 2003; Hickok & Poeppel, 2004, 2007; Leff et al., 2008). These regions become active while processing semantic sentence ambiguity (Rodd, Davis, & Johnsrude, 2005) and during semantic working memory tasks (Fiebach, Friederici, Smith, & Swinney, 2007) and they interact with working memory-related activation in prefrontal areas (Fiebach, Rissman, & D'Esposito, 2006). Taken these functional findings together, activation in left IFG reflects the detection and structural building of a non-canonical sentence structure which requires the consideration of contextual information provided by the ITG for thematic role assignment. Therefore, increased GMP in these areas may provide a better neurophysiological basis for the acquisition of these mechanisms guiding the processing of non-canonical sentence structure.

The second factor is assumed to reflect performance variance introduced by different verbal working memory capacities. Scores of this factor positively correlate with GMP in the left parietal operculum extending to the left posterior STG. This result is consistent with patient's

data showing that the structural integrity of the posterior STG after a stroke predicts both the auditory short-term memory capacity and the ability to comprehend spoken sentences (Leff et al., 2009). In addition, this finding fits data showing that inferior parietal regions and the posterior STG show increased activation while processing sentences with increased verbal working memory load (Meyer et al., 2012; Novais-Santos et al., 2007) which suggests that this area serves as a phonological buffer storing verbal material. Therefore, high GMP in this area may reflect higher storage capacities.

8.6 Conclusion

Results of this study show that at the end of the sensitive period for grammar acquisition, grammatical proficiency can be related to the underlying brain cortical structure. Differential cognitive abilities are thereby represented in different brain substrates: While the ability to assign thematic roles against a preferential interpretation strategy is positively correlated to GMP in the left ITG and IFG, verbal working memory-related performance of complex sentence comprehension is positively correlated to GMP in the left parietal operculum extending the posterior STG. However, it remains an open question whether the increased GMP reflects differential cortical prerequisites or differential trajectories of cortical development.

9 FUNCTIONAL MRI STUDY: EMBEDDED SENTENCES AND BRAIN ACTIVATION

9.1 Introduction

Recent developmental neuroimaging studies provide evidence for the early engagement of the left perisylvian areas in language processing during the first months of life (Dehaene-Lambertz et al., 2006). So far, studies on sentence-level focused on passive listening (Ahmad et al., 2003; Dehaene-Lambertz et al., 2006; Dehaene-Lambertz et al., 2002; Knoll et al., 2012; Lidzba et al., 2011; McNealy et al., 2010; Schmithorst et al., 2006), active response story processing (Vannest et al., 2009), sentence violation detection (Brauer & Friederici, 2007), sentence comparison (Nuñez et al., 2011), and sentence comprehension (Skeide et al., 2014; Yeatman et al., 2010). The attainment of grammatical proficiency related to complex sentence processing depends on specific input within a specified time window (Johnson & Newport, 1989). This study is sought to investigate functional activation related to sentence

processing in different age groups because the existence of a sensitive period for grammar acquisition points to fundamental changes in brain plasticity which may influence functional maturation of syntax-related brain regions. In addition, most of the above mentioned studies on sentence-level did not test sentences of different complexities but rather sentence processing in general. Therefore, they cannot distinguish whether changes in activation with age can be attributed to grammatical or lexical/semantic aspects. However, functional imaging studies in children that contrasted simple and complex sentences did not detect a related increase of activity in the left IFG (Knoll et al., 2012; Yeatman et al., 2010).

In adults, the left PO has been found to increase its activation with the complexity of natural language and artificial grammar sentences (e.g. Bahlmann, Schubotz, & Friederici, 2008; Bahlmann, Schubotz, Mueller, Koester, & Friederici, 2009; Friederici, Bahlmann, et al., 2006; Makuuchi et al., 2009; Opitz & Friederici, 2004, 2007, for a recent review, see Friederici, 2011), whereas a functional selectivity for sentence complexity in this region only emerges around the age of 6 years (Knoll et al., 2012). Furthermore, while adults show a dissociation of syntactic and semantic processing within the IFG (Newman et al., 2010), with the left PO being involved in syntactic processing and semantic processes involving more anterior parts of the IFG (for a review, see Friederici, 2011), children

around the age of 6 years do not yet show a similar segregation of activation in the IFG (Brauer & Friederici, 2007; Skeide et al., 2014).

However, the processing of complex sentences is not supported by the IFG alone but rather by a fronto-temporal network (for a review, see Friederici, 2011) including the posterior STG which is thought to support the integration of syntactic and semantic information as well as the inferior parietal lobe (IPL) known to subserve verbal working memory (Meyer et al., 2012). The posterior STG and the IPL have been observed to be involved in sentence processing in children (Brauer & Friederici, 2007; Knoll et al., 2012). Thus, there are indications for a functional language network that develops towards an adult-like system around the age of 6 years.

In order to test when and how the functional language network attunes to sentence processing, fMRI was used to assess subjects of different age groups (5–6 years, 7–8 years, and adults) during the processing of sentences of increasing complexity operationalized by the number of embeddings. Functional selectivity of activation is defined by an increase of activation in accordance to a sentence's complexity. Based on previous findings (Brauer et al., 2011; Knoll et al., 2012; Skeide et al., 2014; Yeatman et al., 2010), a development from non-selective to selective activation in syntax-relevant brain regions is hypothesized. To ensure the engagement of the entire language network for sentence processing, the functional analysis focused on the establishment of long-

distance dependencies since it has been shown to involve memory-related aspects of sentence processing as well (see 'Behavioral study: Embedded sentences and verbal working memory').

9.2 Methods

9.2.1 Participants

Children who participated in the structural MRI study reported above were also participating in the functional experiment. Parental consent and children's verbal assent was obtained prior to data acquisition. In total, 59 children and 21 adults (mean age: 27 years, standard deviation (SD): 44 months) took part in the experiment, all of whom were monolingual German speakers, right-handed (Oldfield, 1971), and had no neurological, medical, or psychological disorders. Twenty-one children had to be excluded after fMRI scanning due to excessive movement in more than 50 % of the trials and/or quitting (see Procedure; $n = 9$), no baseline brain activation in response to sound ($n = 4$), performance accuracy below 50 % (see Procedure; $n = 4$), performance below average on the standardized TROG-D ($n = 1$), constantly responding after the response time window (see Procedure; $n = 1$), or brain anomalies as verified by trained clinicians ($n = 2$). The final children sample consisted of 18 children between 5 and 6 years (mean age: 72.0 months, SD: 6 months) and 20 children between 7 and 8 years (mean age: 95.5 months, SD: 7 months).

All procedures were approved by the Research Ethics Committee of the University of Leipzig

9.2.2 Materials

As in the first study, sentence material (see Figure 17) consisted of sentences containing three subclauses arranged into different levels of syntactic complexity: sentences with coordinated main matrix clauses (baseline condition), sentences with one embedding containing two coordinated relative clauses (simple sentences), and sentences with two embedded relative clauses (complex sentences). In contrast to the behavioral study, sentences of the baseline condition followed the same order of subclauses as simple and complex sentences. This sentence structure was chosen to allow for the comparison of final words in the sentences. Twenty-two sets in the three conditions were constructed, yielding a full set of 66 sentences. Sentences were recorded by a trained female speaker, digitized (44.1 kHz/16 bit sampling rate, mono), and normalized according to the root-mean-square amplitude of all files. Average sentence duration was 5.2 s (SD: 0.5 s). Corresponding to each sentence, two pictures were created, focusing on the long-distance dependency between the sentence-initial subject and sentence-final verb.

Sentence and picture stimuli were controlled to avoid possible confounds and development of processing strategies during the experiment. As in the behavioral study, sentences across conditions

contained an equal number of clauses (3), pronouns (2), and verbs (3). Due to the coordination of subclauses, simple sentences contained one additional word (altogether 11 words) in comparison to complex sentences (altogether 10 words).

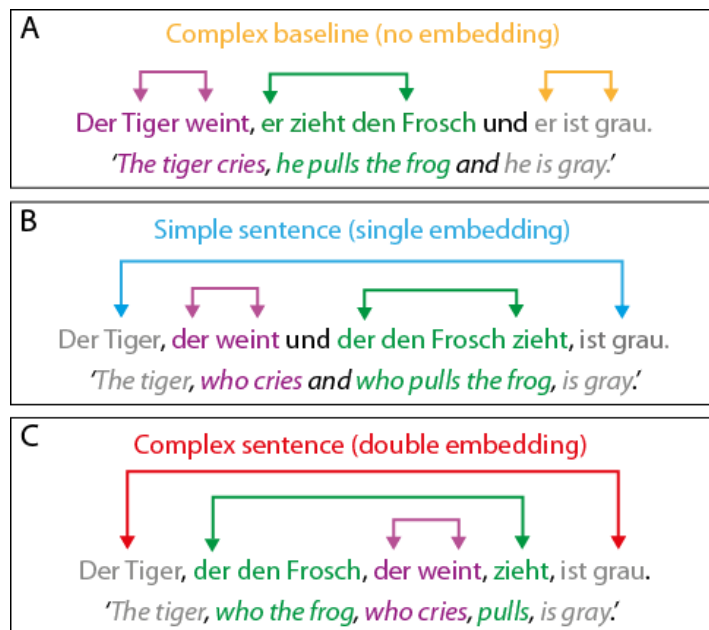


Figure 17. Exemplary sentence material for the fMRI-study. Sentence complexity was operationalized by the number of embeddings. (A) Complex baseline without embedding, (B) simple sentences contained a single embedding of two relative clauses and (C) complex sentences contained two embedded relative clauses.

To avoid semantic complexity effects, the content of the sentences of the different conditions was held as constant as possible: Each sentence described a scene involving two interacting animals. One of the three clauses described the color of one of the animals using a copula, the second clause described the action involving the two animals by a

reversible transitive verb, and the third clause described the emotional expression (laughing/crying) of one of the animals by an intransitive verb whereby the position of the first and the third subclause in the sentence was counterbalanced across stimuli (see Appendix). The coordinated sentences which contained the same amount of subclauses, words, verbs, and pronouns as embedded sentences were constructed as a high-level baseline that controlled for brain activations with respect to pronoun and verb processing: Additional pronoun–noun dependencies may affect brain activations during sentence processing (Fiebach et al., 2005; Santi & Grodzinsky, 2007), potentially interfering with the focus of the current study, that is, the assessment of brain activation related to the establishment of subject–verb dependencies during the processing of hierarchical sentences. By embedding relative clauses into superordinate clauses, the number of long-distance dependencies between the subject and the verb of a sentence and the sentence’s level of hierarchy was increased.

Pictures corresponding to each sentence stimulus were created focusing on the long-distance dependency between subject and verb (see Figure 18). To avoid the development of strategies, six filler items were included per sentence structure that tested comprehension performance of the other two subclauses and which were assigned to the implicit baseline in the fMRI analysis. Altogether, an experimental list contained

66 trials and 11 null events (6 s of a blank screen), from which an individual list was pseudo-randomized for each participant.

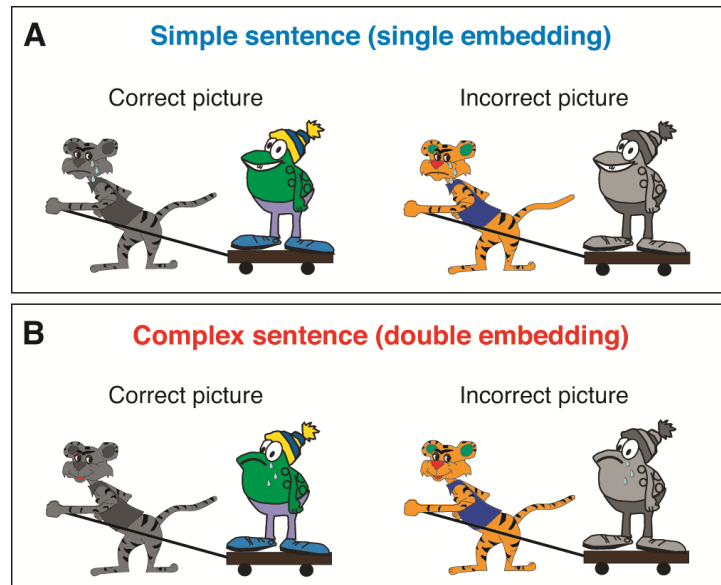


Figure 18. Picture sets of the fMRI study. In parallel to the auditory presentation of the simple and complex sentences, participants saw two pictures, one matching the stimulus sentence and one not matching the stimulus sentence (picture set A in parallel to the simple sentences; picture set B in parallel to the complex sentences). Participants indicated via button press which of these pictures was the correct one.

9.2.3 Procedure

During the experiment, sentences and pictures were presented using the Presentation® software package (Neurobehavioral Systems, Inc., Albany, CA, USA). Auditory stimuli were presented via air-conduction headphones; visual stimuli were presented via LCD display glasses (both VisuaStim XGA, Resonance Technology Inc., Northridge, CA, USA). To familiarize children with the scanning procedure, they were invited for a

training session one week prior to scanning. The training session involved stimuli of the same syntactic structure as the experimental items but contained different words, presented in a model scanner. In this session, children watched a movie before and after the experiment to simulate the time needed for anatomical data collection. Motion was controlled by a motion sensor and verbal as well as visual motion feedback was given. Before actual scanning, the experimenter presented printed examples of stimuli that were not presented during the experiment to remind children of and to familiarize adults with the procedure. The experimental procedure (see below) during actual scanning was the same as in the training session. Both training session and actual experiment started with an introduction during which volume acquisition was already started to allow for magnetic saturation effects to establish. An experimental trial started with a random onset jitter of 0, 400, 800, 1200, or 1600 ms length, after which an auditory sentence stimulus was presented. In parallel, two pictures were presented on the left and right side of the display glasses, one matching, the other picture mismatching the auditory stimulus. Participants held a button in each hand and were instructed to indicate via button press whether the left or right picture matched the sentence, whereby the response time window was limited to 4 s after stimulus offset. Presentation side of the correct picture was counterbalanced across conditions and participants. Each trial lasted 12 s, resulting in a total scanning time of approximately 22 minutes.

9.2.4 MRI data acquisition

During fMRI scanning, the response accuracy (i.e., correct versus incorrect response) and the reaction time (RT) for each trial were obtained. Anatomical and functional brain data were acquired with a whole-body 3-T Magnetom TIM TRIO scanner (Siemens Healthcare, Erlangen, Germany) with a 12-channel head coil. Functional data were acquired with a gradient-echo EPI sequence (TR = 2 s; echo time (TE) = 30 ms; flip angle = 90°; 26 slices; data matrix = 64 × 64 voxels; voxel size = 3 × 3 × 3 mm³; 1 mm gap; FOV = 192 mm; 484 volumes). Structural data were obtained with a T1-weighted magnetization-prepared rapid gradient echo 3D sequence with selective water excitation and linear phase encoding. This structural data acquisition conforms the data acquisition used in the MRI study.

9.3 Data analysis

9.3.1 Behavioral data

Sentence comprehension performance for each participant was quantified by calculating mean response accuracies and mean reaction times. To exclude that children performed at chance level, a one-sample t-test between the mean response accuracy and chance level performance (50 % correct responses) for each age group was performed. To account for potential speed–accuracy tradeoffs in the behavioral responses, Inverse

Efficiency Scores (IES), were calculated by dividing the log-transformed RT by accuracy (Townsend & Ashby, 1983), where higher values indicate less efficient processing. To determine potential performance differences between simple and complex sentences as well as the influence of age, a 2 (COMPLEXITY) \times 3 (AGE) ANOVA was run. To receive a score for behavioral selectivity for complexity to employ during correlation analyses (see below), IES for simple sentences was subtracted from IES for complex sentences, henceforth referred to as behavioral complexity score.

9.3.2 fMRI data

Analyses of fMRI data were performed using the SPM8 software package (Wellcome Department of Imaging Neurosciences, UCL, London, UK). Images were corrected for slice timing and the time series was realigned to the first image. Trials with excessive movement (> 3 mm in any direction) were excluded from statistical analysis (5–6-year-olds: 4.4 % of trials; 7–8-year-olds: 1.6 % of trials; adults: 0 % of trials). This also resulted in the exclusion of four participants from further analyses (see Participants). Before image normalization (gray matter segmentation-based procedure), functional images were co-registered to participants' anatomical images, then to a template appropriate from early to advanced puberty (Fonov et al., 2011) to keep normalization bias equal across age groups. Previous studies have shown that normalization to a standard

adults' MR template is valid only from 7 years of age (Burgund et al., 2002; Kang et al., 2003) but can drive spurious between-age-groups differences (Wilke et al., 2002) and increased variance in brain contours (Muzik et al., 2000) in younger age groups. Functional data were resampled to $2 \times 2 \times 2$ mm³ voxel size. A spatial smoothing filter with a kernel of 8.0 mm³ FWHM was applied. A temporal high-pass filter with a cut-off frequency of 1/100 Hz was used to remove low-frequency signal changes and baseline drifts. For statistical analyses, experimental epochs were modeled starting at the last word of each sentence, where the relationship between the initial subject and the sentence-final verb is established. For each participant, these events were passed into a GLM, creating a design matrix on the basis of a convolution with a canonical HDR function, yielding statistical parametric maps. Excluded error and movement trials as well as the six movement parameters for each scan were modeled as covariates of no interest. Two contrast images were generated to capture brain activity during the successful processing of the simple sentences and complex sentences, respectively, compared to the high-level baseline. Group statistics were computed from the two contrast images per participant, using a 2 (COMPLEXITY) \times 3 (AGE) random-effects model, as well as gender and the lateralization quotient from the handedness assessment as covariates of no interest. Statistical maps were thresholded at peak level $p < 0.001$ (uncorrected) with a cluster-level false discovery rate correction of $q < 0.05$.

9.3.3 ROI

Using MarsBar (available at <http://marsbar.sourceforge.net>), percentage signal change values inside four different regions of interest (ROIs) as defined by the group-peak activation clusters in the whole-brain analysis were calculated (see Results). To quantify each ROI's functional selectivity, the percent signal change of simple sentences was subtracted from complex sentences (see Figure 21)—henceforth referred to as functional complexity score. Values above zero indicate complexity-sensitivity, values at or below zero point to complexity-insensitivity. To investigate age-related changes of the functional selectivity for syntactic complexity in each ROI, an ANOVA across age groups on the functional complexity scores inside each ROI was computed. Planned comparisons with Bonferroni-corrected significance thresholds were run.

In a next step, it was tested whether age-related patterns in activation differences are driven by an age-related activation increase for the complex sentences or by an age-related activation decrease for the simple sentences or by both processes together, and whether this effect was specific to a single ROI or age group. To investigate this, the AGE X COMPLEXITY interaction was resolved by running between-subject analyses in each ROI for each condition. Again, planned comparisons with Bonferroni-corrected significance thresholds were run.

9.4 Results

9.4.1 Behavioral data

Performance accuracy was above chance across conditions and age groups (all $p < 0.001$; Figure 19A).

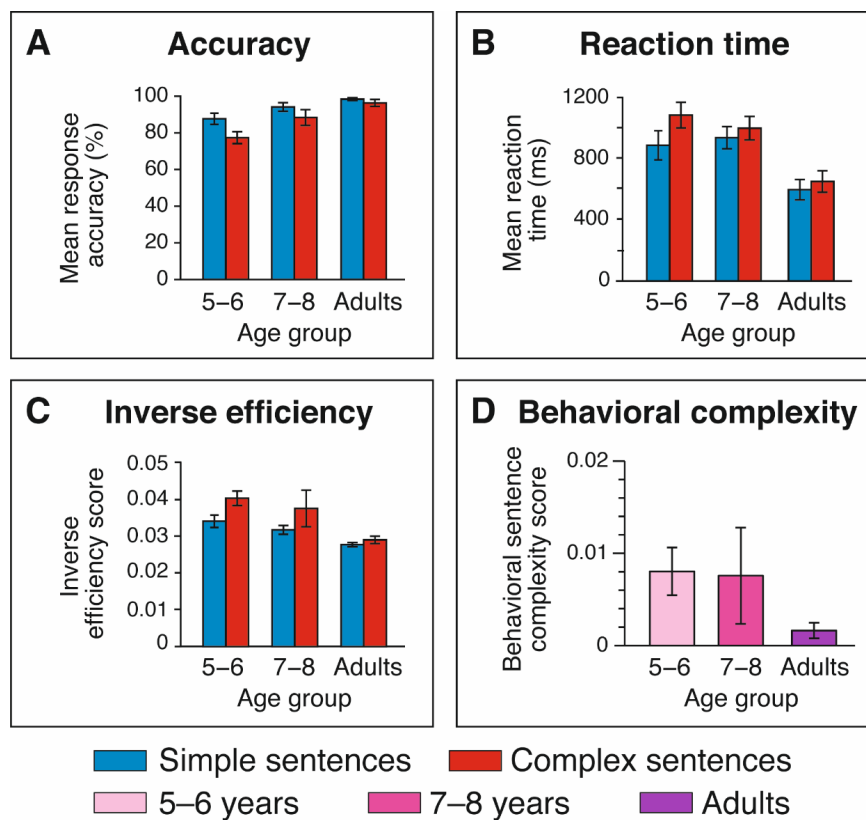


Figure 19. Behavioral results of the fMRI study. All age groups performed above chance. (A) Response accuracy (%) and (B) reaction times (ms). (C) Inverse Efficiency Scores (IES; considering potential speed–accuracy tradeoffs). Main effects of age and complexity were found, but no interaction. (D) Behavioral complexity scores are computed by subtracting IES for simple sentences from IES for complex sentences. Simple sentences are depicted in blue, complex sentences are depicted in red.

The 2 (COMPLEXITY) \times 3 (AGE) ANOVA on the IES (Figure 19C) yielded main effects of COMPLEXITY ($F_{1,56} = 9.07$, $p < 0.01$) and AGE ($F_{2,56} = 5.61$, $p < 0.01$), the latter driven by a significant difference between adults and children (5–6-year-olds versus adults: $t_{37} = 5.19$, $p < 0.001$; 7–8-year-olds versus adults: $t_{39} = 2.19$, $p < 0.05$). Between children groups, performance did not differ ($t_{36} = 0.76$, $p = 0.45$). The COMPLEXITY \times AGE interaction did not reach significance ($F_{2,56} = 1.17$, $p = 3.32$). In sum, performance accuracy decreased with sentence complexity but increased with age. Behavioral complexity scores did not differ between groups ($F_{2,56} = 1.14$, $p = 0.33$; Figure 19D).

9.4.2 FMRI data

The whole-brain analysis revealed a COMPLEXITY \times AGE interaction in the language-related left PO (main peak at $x = -32$, $y = 12$, $z = 28$), the left IPL extending to the left posterior STG (IPL/STG; main peak at $x = -36$, $y = -46$, $z = 38$), the cerebellum bilaterally (main peak at $x = 14$, $y = -78$, $z = -28$), and bilateral supplementary motor areas (SMA; main peak at $x = 0$, $y = 24$, $z = 48$). No significant main effects were obtained. For an overview of the results, see Figure 20 and Table 7.

Table 7. Significant clusters in the interaction between sentence complexity and age group.

Hemisphere	Region	BA	MNI coordinate			Cluster size (number of voxels)	Z-value
			X	Y	Z		
Left	IFG	44	-32	12	28		4.03
		44	-48	6	38	1146	4.03
		44	-52	10	24		3.95
Left	IPL	40	-36	-46	38		4.78
Left	STG	22	-58	-48	12	1781	4.01
Left	STG	22	-56	-36	6		3.96
Left	SMA	6	0	24	48		4.15
Right	SMA	6	8	4	46	629	3.64
Right	MCC	6	4	-20	46		3.43
	Cerebellum		14	-78	-28		4.70
			-44	-72	-28	4621	4.63
			-12	-66	-32		4.53

Peak level $p < 0.001$ uncorrected, FDR cluster corrected at $q < 0.05$; BA = Brodmann area; MNI = Montreal Neurological Institute; IFG = inferior frontal gyrus; IPL = inferior parietal lobe; STG = superior temporal gyrus; SMA = supplementary motor area; MCC = middle cingulate cortex.

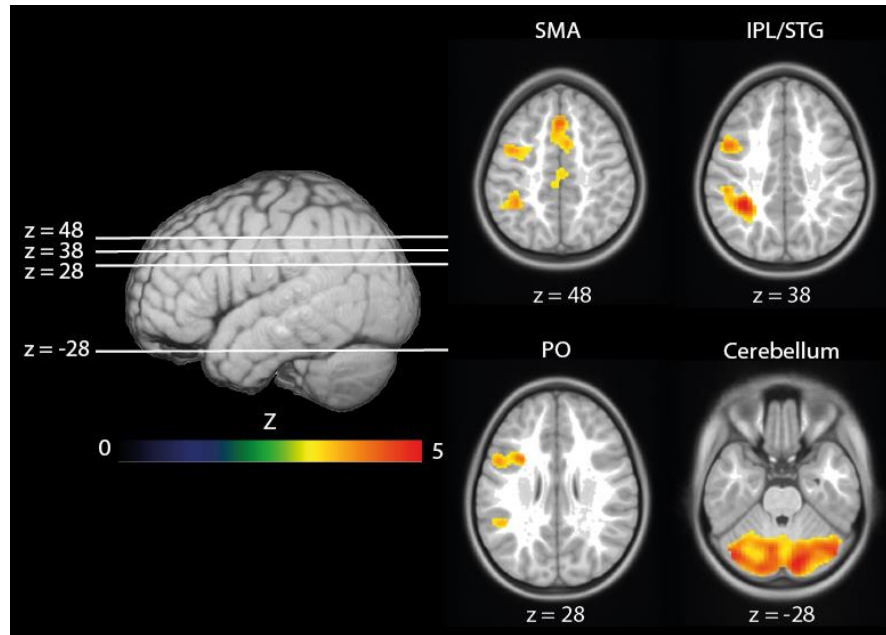


Figure 20. Whole-brain functional magnetic resonance imaging results. Results of the whole brain analysis revealed an interaction between age and sentence complexity in left pars opercularis (PO), left inferior parietal lobe extending to the posterior superior temporal gyrus (IPL/STG), cerebellum bilaterally, and bilateral supplementary motor areas (SMA; $p < 0.001$, corrected).

9.4.3 ROI

Across ROIs, functional complexity scores increased with AGE (left PO: $F_{2,56} = 7.80$, $p < 0.01$; left IPL/STG: $F_{2,56} = 12.48$, $p < 0.001$; Cerebellum: $F_{2,56} = 9.57$, $p < 0.001$; SMA: $F_{2,56} = 7.53$, $p < 0.01$; Figure 21). Significant differences between adults and both children groups across ROIs (Table 8) indicate that only adults show complexity-selective brain activity across ROIs.

9.4 Results

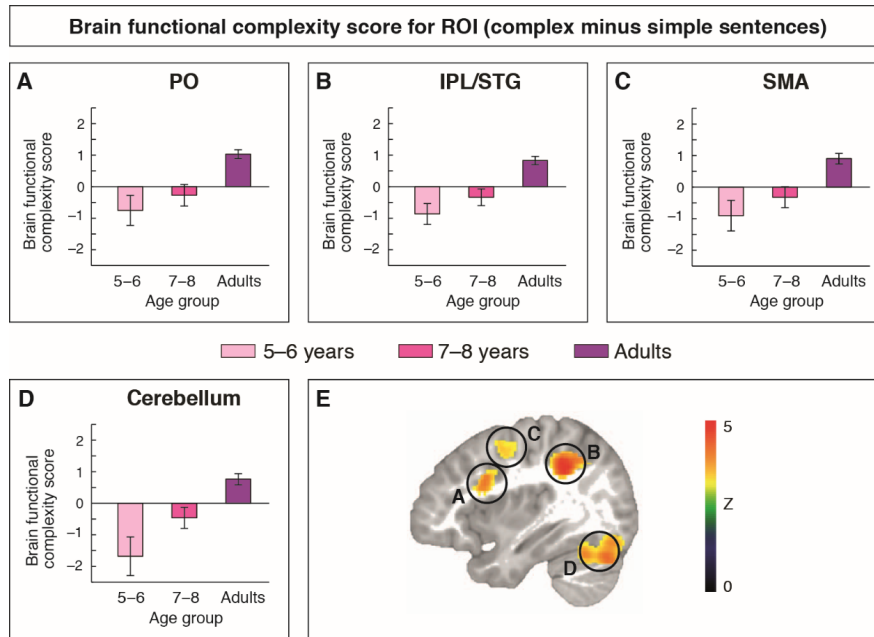


Figure 21. Results of the region-of interest analysis. Planned comparisons in each region of interest (ROI; A–D) on functional complexity scores (i.e., percent signal change for simple sentences subtracted from percent signal change for complex sentences; $p < 0.01$, corrected) indicate increased functional selectivity for syntactic complexity with age for all ROIs. (E) Neuroanatomical location of the ROIs.

Table 8. Comparison of functional complexity scores between age groups.

	Older children versus younger children	Adults versus younger children	Adults versus older children
Left PO	$t_{36} = 0.83$	$t_{37} = 3.85^{***}$	$t_{39} = 3.58^{**}$
Left IPL/STG	$t_{36} = 1.26$	$t_{37} = 5.06^{***}$	$t_{39} = 4.03^{***}$
SMA	$t_{36} = 1.01$	$t_{37} = 3.74^{**}$	$t_{39} = 3.36^{**}$
Cerebellum	$t_{36} = 1.80$	$t_{37} = 4.10^{***}$	$t_{39} = 3.30^{**}$

Functional complexity scores: percent signal change for simple sentences subtracted from percent signal change for complex sentences; PO = pars opercularis; IPL = inferior parietal lobe; STG = superior temporal gyrus; SMA = supplementary motor area; results are corrected for multiple comparisons; $**p < 0.004$; $***p < 0.001$.

A multivariate between-subject ANOVA on the percent signal change for each condition in each ROI (see Figure 22 and Table 9) revealed main effects of AGE in the PO ($F_{2,56} = 11.44$, $p < 0.001$) and in the SMA ($F_{2,56} = 6.69$, $p < 0.01$) for the simple sentences. In the left IPL/STG ($F_{2,56} = 5.15$, $p < 0.01$), the age effect was only present in the complex condition: Compared to both children groups, adults show decreased activity in left PO (5- and 6-year-olds versus adults: $t_{37} = 4.98$, $p < 0.001$; 7- and 8-year-olds versus adults: $t_{39} = 3.32$, $p < 0.006$) and compared to the 5- and 6-year-old children in the SMA ($t_{37} = 3.48$, $p < 0.001$) as well as increased activity in the left IPL/STG compared to 7- and 8-year-old children ($t_{39} = -3.45$, $p < 0.006$).

Table 9. Post-hoc comparisons of significant age effects on the percent signal change for each condition

	7-8 year olds versus 5-6 years olds	Adults versus 5-6 years old	Adults versus 7-8 years old
% signal change for simple sentences in the PO	$t_{36} = -1.49$	$t_{37} = -4.98^{***}$	$t_{39} = -3.32^{**}$
% signal change for simple sentences in the SMA	$t_{36} = -1.38$	$t_{37} = -3.48^{**}$	$t_{39} = -2.78$
% signal change for complex sentences in the left IPL/STG	$t_{36} = -0.09$	$t_{37} = 2.69$	$t_{39} = 3.45^{**}$

PO = pars opercularis; IPL = inferior parietal lobe; STG = superior temporal gyrus; SMA = supplementary motor area. Results are corrected for multiple comparisons; ** = $p < 0.006$; *** = $p < 0.001$.

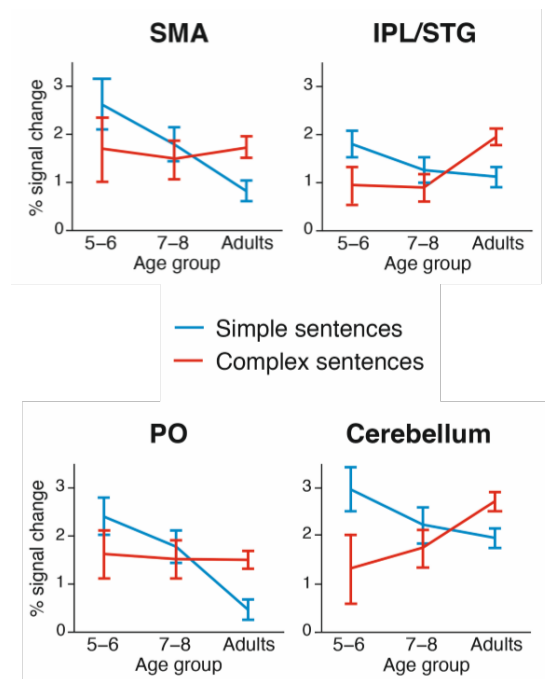


Figure 22. Post-hoc analyses in each region of interest on percent signal change for each condition. (blue = simple sentences; red = complex sentences) yield a decrease of activation with age for simple sentences in the left pars opercularis (PO), as well as an increase of activation with age for complex sentences in the left inferior parietal lobe extending to the posterior superior temporal gyrus (IPL/STG) and in the supplementary motor area (SMA).

9.4.4 Brain function in different ROIs

As the functional ROIs have been discussed as being part of different functional networks underlying sentence processing (Brauer, Anwander, Perani, & Friederici, 2013), post-hoc multiple regression analyses in each age group were computed to assess changes of the relationship between the activation patterns inside the PO and the other functional ROIs across age groups. For this analysis, the functional complexity score of PO was used as dependent variable and the functional complexity scores of the

IPL/STG, the cerebellum and the SMA as predictors. Results revealed different correlational patterns within the language network across development. In the youngest age group (5–6 years) the activation difference between complex and simple sentences was predicted by the activation in the SMA ($\beta = 0.93$, $p < 0.001$; $R^2 = 0.864$, $p < 0.001$). In the older children (7–8 years) it was partly predicted by activation in the SMA ($\beta = 0.55$, $p < 0.01$) and by activation in the IPL/STG ($\beta = 0.43$, $p < 0.05$, $R^2 = 0.864$, $p < 0.001$). In adults activation in PO was completely predicted by activation in the IPL/STG ($\beta = 0.91$, $p < 0.001$, $R^2 = 0.831$).

9.5 Discussion

For adults, a well-described network in the left hemisphere including the PO, the IPL, and the posterior STG was found to support sentence processing. For all these regions, a functional attunement towards an adult-like selectivity for complex sentences across development was observed. The attunement towards an adult-like language development is reflected in the development of the relation between the different brain regions within the language network. While the activation in PO is predicted by the functional activation of the IPL/STG in adults, it is predicted by the functional activation of the SMA in the 5–6-year-olds. The older children represent an intermediate pattern with activation in both regions predicting the activation in PO. This finding could be related to the developmental changes in the structural connectivity between these

regions (Brauer et al., 2013). While in adults, the left PO, IPL, and posterior STG are structurally connected via a dorsally located pathway consisting of the superior longitudinal and arcuate fasciculi (Friederici & Gierhan, 2013) which have been proposed to play a major role in the processing of complex sentences in adults (Friederici, 2011; Meyer, Cunitz, Obleser, & Friederici, 2014; Meyer et al., 2012; Wilson et al., 2011), this connection is not detectable in newborns (Perani et al., 2011), and still immature by the age of 7 (Brauer et al., 2011, 2013). In children, however, the ventrally located white matter pathways connecting the temporal lobe to the frontal lobe are well established early in life, with one sub-component terminating in the prefrontal cortex, the premotor cortex, and the superior frontal gyrus reaching out to the SMA (Brauer et al., 2013). Functional activation finding in the different brain regions will be discussed separately below.

9.5.1 The pars opercularis

The current fMRI data revealed that only adults show complexity-selective activation in the PO. The data are in line with earlier work reporting the left PO to be involved in the processing of syntactically complex structures in adults (Bahlmann et al., 2008; Makuuchi et al., 2009; Opitz & Friederici, 2004, 2007), more specifically in structural hierarchy building (for a review, see Friederici, 2011). The functional activation observed in children can be related to earlier studies showing that sentence processing generally

leads to higher, more diffuse activation in the prefrontal cortex in children compared to adults (Brauer & Friederici, 2007; Durston et al., 2006; Lidzba et al., 2011). The absence of a functional selectivity of the left PO in the present study may be due to the demanding center-embedded sentences used here, as compared to short object-first sentences used by Knoll et al. (2012) who showed a development towards a functional selectivity of the left PO for complex sentences in 6-year-olds, although only in a high performing subgroup.

Interestingly, a comparison of the functional activation between adults and children for each condition revealed that the functional selectivity develops by a decrease of activation for simple sentences. Since performance also generally increases with age (see Behavioral data), it appears that the more efficient processing of simple sentences in adults is related to decreased activation in the left PO. Increased activation in children can reflect additional compensatory processing strategies as proposed for the finding of increased activation in the left IFG for non-native German speakers in response to correct and syntactically incorrect sentences (Rüschemeyer, Fiebach, Kempe, & Friederici, 2005) or it can be attributed to reduced verbal working memory capacities and thus higher processing demands as postulated for adult low spanners who show increased activity in the left PO during processing sentence ambiguity (Fiebach, Vos, & Friederici, 2004). Moreover, despite an increase of performance for complex sentence processing, activation

stays constant across age groups. These findings suggest that adults require less activity in the PO to gain higher efficiency in structural hierarchy building.

9.5.2 The IPL/STG

In the left IPL/STG, functional selectivity for sentence complexity is also only evident in adults. However, in contrast to the PO, functional selectivity of the IPL/STG emerges from an activation increase for syntactically complex sentences (Figure 22). While the IPL is assumed to support verbal working memory (Leff et al., 2009; Meyer et al., 2012; Novais-Santos et al., 2007), the left posterior STG has been proposed to be involved in integrating semantic and syntactic information into an overall sentence meaning (for a review, see Friederici, 2011). The latter argument is based on the finding that the posterior STG only becomes active in paradigms using sentence material but not in artificial grammar paradigms (Bahlmann et al., 2008; Friederici et al., 2009; Opitz & Friederici, 2004, 2007). The current finding of the missing increase of activation for complex sentences in the IPL/STG in the children's groups may reflect the absence of a verbal working memory strategy that appears to facilitate complex sentence processing in adults. In the developmental psycholinguistic literature, it is discussed whether children's difficulties in processing relative clauses can indeed be attributed to working memory limitations (Felser et al., 2003; Roberts et al., 2007; Weighall & Altmann,

2010). Findings of the behavioral study of this thesis additionally support this suggestion.

9.5.3 The SMA

The SMA shows complexity-selective activation in adults but rather a selectivity for simple sentences in children (see Figure 21). The developmental pattern of functional activation in the SMA parallels that of the PO: Functional activity for simple sentences decreases with age, while activation for complex sentences does not differ significantly between age groups (see Figure 22). Interestingly, the activation of the SMA predicts the activation of the PO in children and thus appears to be part of the language network in children. Functionally, the SMA has been suggested to be involved in temporal sequencing in adults (Coull, Cheng, & Meck, 2011), more specifically in the prediction of dynamics in auditory and visual sequences (Schubotz, 2007). Children appear to have difficulties with the extraction of pure statistical regularities from sequential structures in speech perception, showing increased pre-SMA activity only when provided with additional prosodic cues (McNealy et al., 2010).

The peak of the current interaction in the SMA is located in the pre-SMA, which is rostral to the vertical line intersecting the anterior commissure that has been suggested to separate the rostral pre-SMA from the caudal SMA-proper (Lehéricy et al., 2004; Picard & Strick, 2001; Schwartze, Rothermich, & Kotz, 2012). Activity of the pre-SMA may relate

to the sequential ordering of the hierarchical sentence structure, as the pre-SMA has been found active during the processing of hierarchical sentences (Makuuchi, Bahlmann, & Friederici, 2012), during the processing of abstract items in the non-language domain (Bahlmann et al., 2009; Hanakawa et al., 2002), abstract rule processing in the verbal domain (Bunge, Kahn, Wallis, Miller, & Wagner, 2003), and working memory tasks (Honey, Bullmore, & Sharma, 2000; LaBar, Gitelman, Parrish, & Mesulam, 1999; Ravizza, Hazeltine, Ruiz, & Zhu, 2011).

9.5.4 The cerebellum

The cerebellum also showed a complexity-selective activation only in adults (see Figure 21). Interestingly, activation differences did not reach significance for simple or for complex sentences between age groups (see Figure 22). Therefore, the development towards the adult-like pattern does not depend on changes for a particular condition. This region is connected to the prefrontal, parietal, and temporal cortices via cortico-ponto-cerebellar and dentate-thalamo-cortical pathways (Schmahmann, 1996). The cerebellum has been shown to be involved in the modulation of a broad spectrum of linguistic functions (for a review, see Murdoch, 2010), more specifically in the generation of internal representations of the temporal structure of spoken sentences (Kotz & Schwartz, 2010). This is of particular interest with respect to the present results, as in German, it has been found that the embeddedness of spoken sentences

entails the embeddedness of prosodic domains as marked by clausal boundary tones (Féry & Schubö, 2010). The increased cerebellar activity in the current study might thus reflect the application of timing and sequencing schemes provided by prosodic features to facilitate verbal working memory storage of embedded clauses.

The higher activation for simple compared to complex sentences in the cerebellum for children may reflect either the inability to exploit prosodic features in the complex sentences and/or the missing cooperation between the cerebellum and the IPL/STG. However, since both brain structures are essential for generating timing and sequencing schemes which in turn facilitate the sequential ordering of hierarchical sentence structures, the activation pattern in the cerebellum may be mirrored by the SMA which in turn is related to the activation in PO in the younger children. Further research manipulating prosodic features in the sentence presentation may help to clarify the relation of the activation in the cerebellum and the SMA.

9.6 Conclusion

Adults and children activated a qualitatively comparable network of language-relevant brain regions while processing center-embedded sentences: the left PO, the left IPL/STG, the bilateral supplementary motor areas, and the cerebellum. However, only adults show a functional selectivity of these regions marked by an increase of activation parallel to

the increase of sentence complexity. Furthermore, the current data indicate that the functional selectivity of language-relevant brain regions develops across age groups either by a decrease of activation for simple sentences (in the PO and SMA), by an increase of activation for complex sentences (in the IPL/STG) or by the interplay of both developmental patterns (in the cerebellum). In addition, the development towards an adult-like language processing system is reflected in changes of the relation between the activation in different brain regions within the language network. Nonetheless, it remains open whether these qualitative changes mirror different cognitive strategies and/or structural maturational effects.

10 COMBINED FUNCTIONAL MRI AND STRUCTURAL MRI STUDY

10.1 Introduction

The observed differential sensitive periods for specific aspects of language acquisition suggest fundamental time windows for neural plasticity in language-relevant brain regions. Seminal studies on the relationship between brain maturation and language development found that receptive and productive phonological skills of children between 5 and 11 years correlate with measurements of GMP in the left IFG (Lu et al., 2007), and gray matter of the left SMG and left posterior temporal regions correlate with vocabulary knowledge in teenagers between 12 and 17 years (Richardson et al., 2010). In general, during development, gray matter density decreases with higher-order association areas decreasing later than lower-order sensorimotor regions (Gogtay et al., 2004). More specifically, the onset of gray matter loss in those frontal and parietal brain regions that are involved in complex sentence processing in adults (for

review, see Friederici 2011) can be observed between 7 and 12 years (Giedd et al., 1999; Sowell et al., 2003). To date, only the MRI study of this thesis has linked the brain-structural properties of those brain regions relevant to sentence processing to the establishment of grammatical proficiency. It could be shown that the ability to assign thematic roles against a preferential interpretation strategy is positively correlated to GMP in the left ITG and IFG, working memory-related performance in complex sentence processing is positively correlated to GMP in the left parietal operculum extending the posterior STG.

Nevertheless, it is unclear whether the maturation of cortical gray matter constrains the functional attunement of language-relevant brain areas to sentence processing. While developmental trajectories from children-like to adult-like functional activation patterns have been described with respect to brain-functional changes and with respect to brain-structural changes, descriptions of the tripartite relationship between brain structure, brain function, and behavioral performance are rare. From the two studies investigating the tripartite relationship during development in school age, one focused on orthographic naming (Lu et al., 2009) and the other used a sentence comparison paradigm (Nuñez et al., 2011).

It is hypothesized that gray matter maturation of the language-relevant brain regions in the left hemisphere across age groups can predict the establishment of adult-like brain activation patterns for complex

sentence processing, and that more mature activation patterns are associated with better performance. In addition, because the processing of complex sentences is memory-demanding, and verbal working memory expansion has been found to be a crucial predictor of children's sentence processing skills (Felser et al., 2003; Montgomery et al., 2008; Roberts et al., 2007; Weighall & Altmann, 2010; as well as in the 'Behavioral study' of the current thesis), it is hypothesized that the activation pattern for complex sentence processing can partially be predicted by an increase of verbal working memory capacity.

To test these hypotheses, the following measurements were taken: First, individual participants' verbal working memory capacity was assessed by a digit span test (Tewes 2003). Second, to evaluate whether brain-structural maturation underlies brain-functional maturation, a VBM analysis was conducted to extract the GMP inside those ROIs that showed increased functional activation during sentence processing as revealed in the fMRI study reported above, and those reported in the literature to support sentence processing (Friederici 2011). Finally, GMP and behavioral data on verbal working memory capacity and sentence comprehension were used as predictors for the functional brain results.

10.2 Methods

Participants and procedures were the same as in the MRI and fMRI study. In contrast to the MRI study, structural data of adults were analyzed as well.

10.3 Data analysis

10.3.1 MRI data analysis

Structural brain data were analyzed using VBM to quantify region-specific cortical maturation. Images were resampled to $1 \times 1 \times 1 \text{ mm}^3$ and segmented into gray matter, white matter, and cerebro-spinal fluid based on intensity values and TPMs. Because TPMs generated from adult images can misclassify children's data (Altaye, Holland, Wilke, & Gaser, 2008), different maps for adults (ICBM atlas) and children groups (age-appropriate maps from the NIHPD-database; Fonov et al., 2011) were used. The gray and white matter segments were then iteratively matched onto a template generated from their own mean by employing DARTEL (Ashburner, 2007). To avoid the non-linear warping to obscure regional GMPs, GMP values were corrected for the relative amount of warping, then resampled to $1.5 \times 1.5 \times 1.5 \text{ mm}^3$ voxel size and smoothed using an isotropic Gaussian kernel of 8 mm^3 at FWHM. In a final step, each participant's GMP was averaged across each of the four ROIs derived

from the functional analysis (see 'Functional MRI study: Embedded sentences and brain activation').

10.3.2 Correlational analysis

Separate correlational analyses were run to determine the relationships between functional selectivity and gray matter maturation versus functional selectivity and the performance level. This was done as performance for simple and complex sentences is highly correlative ($r = 0.635$, $p < 0.001$) and thus cannot be properly orthogonalized (see below). To determine whether more selective functional activation is related to more efficient processing, a partial correlation analysis was run between the mean brain functional complexity score across all four ROIs and IES performance scores for each condition. Thereby correlations were controlled for the mean percent signal change across ROIs for each condition and age.

To assess the differential relationships between an area's functional selectivity, structural maturation of the underlying gray matter, performance differences between conditions, and verbal working memory, a multiple regression analysis was computed in each ROI, treating functional complexity scores as dependent variable and GMP, behavioral complexity scores, and digit span as predictors, controlling for participants' age. Prior to statistical analysis, the predictors were orthogonalized using principal component analyses to arrive at non-

correlated regressors based on the individual factor loadings (see Table 10).

Table 10. Factor loadings after the orthogonalization of gray matter probability, digit span, performance, and age

		Factor 1	Factor 2	Factor 3	Factor 4
Left PO	GMP	0.92	-0.18	0.09	-0.33
	Digit Span	-0.17	0.95	-0.11	0.23
	Performance	0.07	-0.12	0.99	0.23
	Age	-0.37	0.27	-0.08	0.89
Left IPL/STG	GMP	0.95	-0.12	-0.01	-0.29
	Digit Span	-0.12	0.96	-0.14	0.23
	Performance	-0.00	-0.12	0.99	-0.07
	Age	-0.36	0.28	-0.09	0.88
Cerebellum	GMP	0.96	-0.12	0.04	-0.26
	Digit Span	-0.12	0.95	-0.14	0.24
	Performance	0.04	-0.12	0.99	-0.07
	Age	-0.30	0.28	-0.08	0.91
SMA	GMP	0.99	0.27	-0.08	0.01
	Digit Span	0.08	0.95	-0.13	0.28
	Performance	-0.07	-0.12	0.99	-0.08
	Age	0.01	0.07	-0.07	0.96

GMP = gray matter probability; PO = pars opercularis, IPL = inferior parietal lobe; STG = superior temporal gyrus; SMA = supplementary motor area; **bold** font marks maximum factor loading.

10.4 Results

10.4.1 Brain function – behavior

Partial correlational analyses indicate a negative relationship between brain functional complexity scores and IES for both simple ($r_p = -0.38$, $p < 0.01$) and complex sentences ($r_p = -0.32$, $p < 0.05$). Therefore, the higher the functional selectivity across ROIs, the more efficient appears sentence processing in both conditions. This effect is independent of age.

10.4.2 Brain function – brain structure

Table 11. Results of the multiple regression analysis.

	Left PO (β)	Left IPL/STG (β)	Cerebellum (β)
GMP	-0.264*	-0.297*	-0.123
Digit span	0.215	0.283*	0.294*
BCS	-0.004	-0.073	0.024
Age	0.348**	0.397**	0.421**
Model fit	$R^2 = 0.237^{**}$	$R^2 = 0.331^{***}$	$R^2 = 0.279^{**}$

PO = pars opercularis; IPL = inferior parietal lobe; STG = superior temporal gyrus; GMP = gray matter probability; BCS = behavioral complexity score; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

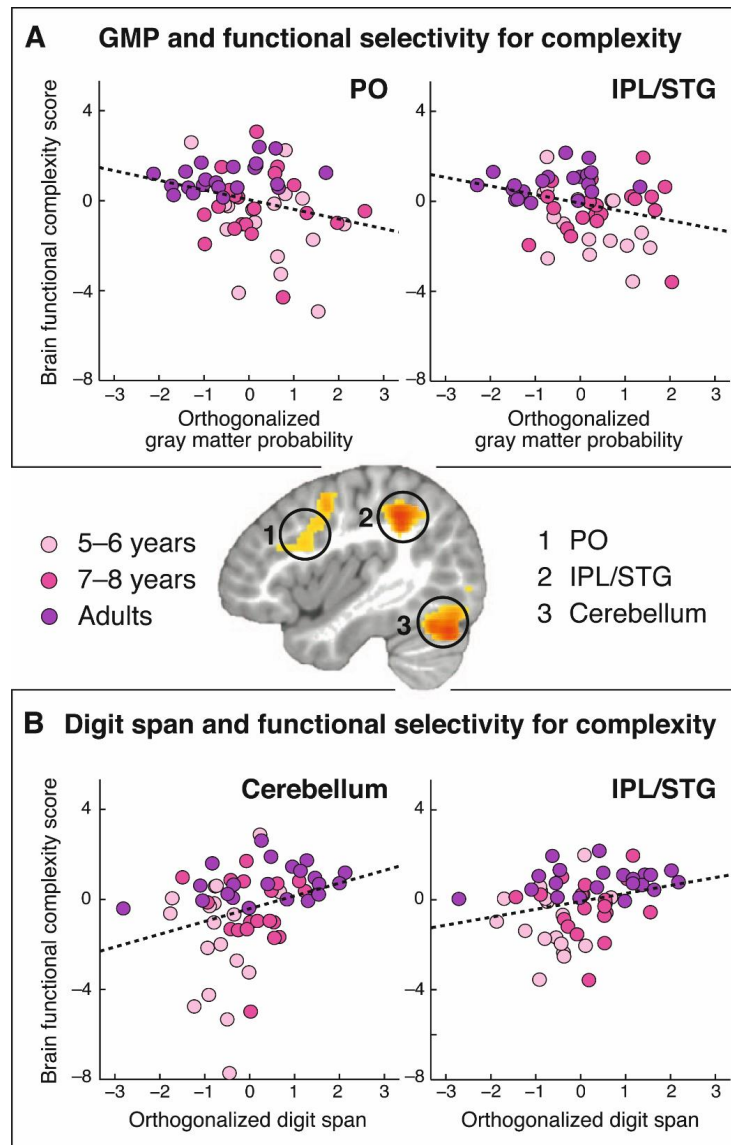


Figure 23. Results of the multiple regression analysis. Multiple regression analyses indicate that while the brain functional selectivity for sentence complexity in the left pars opercularis (PO) is predicted by gray matter probability (A, left panel) and the activation pattern in the cerebellum is predicted by digit span (B, left panel), the functional selectivity for sentence complexity in the inferior parietal lobe extending to the posterior superior temporal gyrus (IPL/STG) is predicted by both factors (A, right panel and B, right panel; all $p < 0.05$; light pink = 5–6 years; pink = 7–8 years; purple = adults; functional complexity score = percent single change for simple sentences subtracted from the percent signal change for complex sentences.)

Multiple regression analyses indicate that in the left PO and in the left IPL/STG, increased GMP was accompanied by decreased functional complexity scores (PO: $\beta = -0.26$, $p < 0.05$, IPL/STG: $\beta = -0.29$, $p < 0.05$). Moreover, increased brain functional complexity scores were accompanied by increased digit span in the left IPL/STG ($\beta = 0.28$, $p < 0.05$), and the same was found for the cerebellum ($\beta = 0.29$, $p < 0.05$; see Figure 23 and Table 11). No correlation could be found the SMA.

10.5 Discussion

The present analyses sought to establish the missing link between the brain-functional attunement of language-relevant areas to sentence processing and the underlying brain-structural changes from childhood to adulthood. Furthermore, the aim of these analyses was to characterize the relationship between the emergence of the crucial behavioral skills required for the processing of complex sentences, considering behavioral performance during sentence processing, verbal working memory, and the functional brain activation during complex sentence processing.

As hypothesized, the observed changes in children's GMP in the left PO can be related to this area's functional attunement to complex sentences, that is, from complexity-insensitive activation in children to complexity-sensitive activation in adults. The functional attunement of the IPL/STG rather reflects an interplay between gray matter maturation and verbal working memory capacity. However, as proposed in the functional

study, missing functional selectivity of the entire network comprised by the left PO, IPL, and posterior STG in children might be related to its immature interregional structural connectivity (see ‘Functional MRI study: Embedded sentences and brain activation’) because maturation of white matter fiber tracts close to the vicinity of the cortex can be reflected in GMP measurements as well (see below a more detailed discussion).

As expected, the development towards a brain-functional selectivity for syntactic complexity within the observed neural network is correlated with sentence processing performance: the higher the brain functional selectivity for complexity, the more efficient is sentence processing. This finding indicates that the functional attunement towards complex sentence processing of these brain regions parallels the improvement of behavioral performance. Furthermore, the current results may suggest that the structural maturation of PO and IPL/STG contributes to the attunement of the functional connectivity, as does children’s verbal working memory capacity. Again the different brain regions will be discussed separately below.

10.5.1 The pars opercularis

In addition to the age-dependent changes in the functional activation pattern, the current analyses show that the establishment of the adult-like functional selectivity for complex sentences is predicted by a reduction of the PO’s GMP across age groups (Figure 23). The apparently immature

brain morphology in children's PO suggests a fundamental role of cortical maturation in the functional attunement to complex sentence processing. As already discussed in the MRI study, the exact neurophysiological substrate of GMP changes in the cortex is still unclear, because, on the one hand, GMP depends on different brain structural properties such as the extent of the cortical surface, cortical thickness, and myelination in adjacent white matter (for a review, see Mechelli et al., 2005) and, on the other hand, brain maturation during childhood is characterized by progressive changes and concurrent regressive changes. Nonetheless, previous data indicates that GMP in frontal areas starts to decline between 9 and 12 years of age (Giedd et al., 1999; Tanaka et al., 2012), when the sensitive period for language acquisition is assumed to cease and language learning becomes more effortful (Hensch & Bilimoria, 2012; Lenneberg, 1967). However, while the data clearly suggest that neural plasticity of the PO plays a crucial role in the region's functional attunement to complex sentence processing, more work is necessary to better understand the underlying neurophysiological mechanisms.

10.5.2 The IPL/STG

The positive correlation between brain-functional selectivity and verbal working memory (digit span) in the left IPL/STG in this study provides support that both IPL and posterior STG support the processing of verbal working memory-intensive sentences—possibly with the posterior STG

responsible for integration processes and IPL supporting verbal working memory as such. This interpretation is in line with the processing demands posed by the sentence material: In the complex double embeddings, the first noun phrase can only be linked to its verb after seven words, potentially exceeding participants' available verbal working memory capacity (Gibson, 1998). The interpretation also converges on brain data which indicate that children between 7 and 12 years of age do not show selective activation of frontal and parietal areas during verbal working memory tasks (Thomason et al., 2009).

As in the left PO, GMP reduction in the left IPL/STG is associated with the attunement towards the adult-like activation pattern (Figure 23). Therefore, structural maturation appears to provide the basis for a specific engagement of the IPL/STG during the processing of sentences with high verbal working memory demands. Gray matter development has been found to follow similar trajectories in frontal and parietal regions (Giedd et al., 1999). The late onset of gray matter decrease in both regions occurs simultaneously with the maturational increase of the dorsal white matter fiber tracts (Brauer et al., 2011, 2013) connecting the posterior STG with the PO passing through the IPL (Catani, Jones, & Ffytche, 2005). The correlational data suggest that the development of the cortical language network for complex sentence processing depends not only on specific brain regions but, moreover, on interregional processes between the left PO and the left IPL/STG.

10.5.3 The cerebellum

As mentioned in the fMRI study, the increased cerebellar activity is suggested to reflect the application of timing and sequencing schemes provided by prosodic features to facilitate verbal working memory storage of embedded clauses. This suggestion is in line with findings showing that the interchange between the right inferior posterior cerebellum and the left temporo-parietal cortex contributes to verbal working memory (Chen & Desmond, 2005a, 2005b; Desmond, Gabrieli, Wagner, Ginier, & Glover, 1997). The correlation of functional selectivity of both the cerebellum and the IPL/STG with digit span performance supports the relationship between these regions' functions and verbal working memory.

10.6 Conclusion

Data of this correlational study show that the attunement of the entire network towards an adult-like activation pattern during sentence processing is differentially predicted by region-specific gray matter changes and partly by inter-individual differences in verbal working memory capacity. Gray matter reduction and the development of brain functional selectivity for complex sentence processing, especially in frontal and parietal areas, emerges only after the age of 7–8 years, that is, at the end of the sensitive period for grammar acquisition. The closure

of this specific time window may be related to the observed brain-functional changes from child-like to adult-like pattern

11 GENERAL DISCUSSION AND FUTURE DIRECTIONS

The current dissertation investigated the tripartite relationship between cognitive, brain structural, and brain functional maturation which enables more efficient complex sentence processing. Different methodologies and data acquisition techniques were used to investigate the processing of center-embedded sentences in 5- and 6-year-old children, 7- and 8-year-old children as well as adults. The collected data give insights about the complex interplay of these different domains which is illustrated by a schematic overview in Figure 24. Findings of the fMRI study indicate that language-relevant brain areas such as the left PO, the left IPL/STG, the SMA, and the cerebellum show a functional attunement towards an adult-like selectivity for complex sentences across development which is either driven by an activation decrease of for simple sentences, an activation increase for complex sentences or both (see Figure 24, bottom row; middle picture). This functional attunement in the different brain areas is differentially related to cognitive maturation, structural, and functional

maturation whereby verbal working memory predicts the activation pattern in the left IPL/STG and the cerebellum (see Figure 24, top row) and GMP predicts the activation pattern in the left PO and the IPL/STG (see Figure 24, bottom row, left picture).

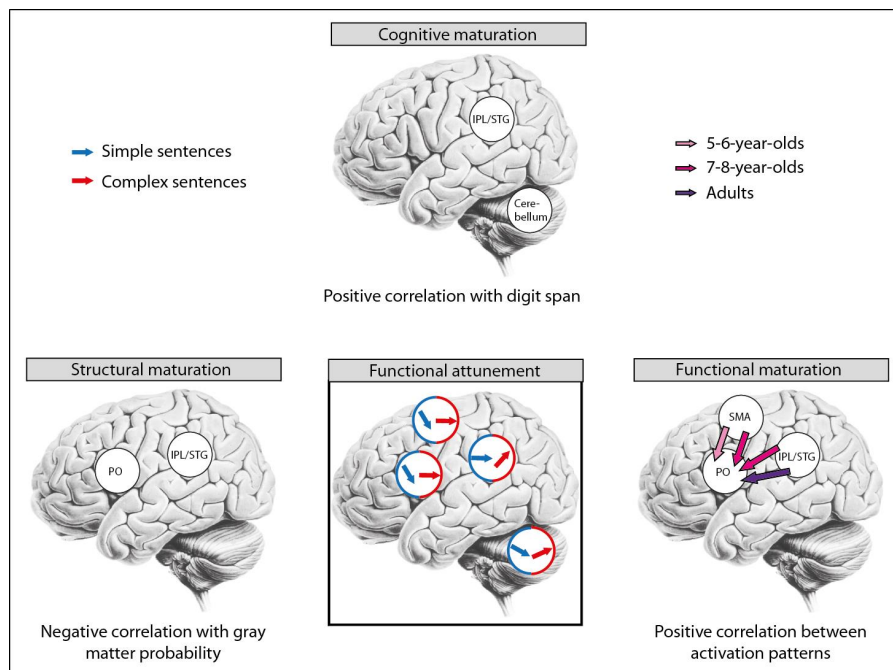


Figure 24. The tripartite relationship of cognitive, structural, and functional maturation. The framed picture depicts the functional attunement of the left pars opercularis (PO), the left inferior parietal lobe extending to the superior temporal gyrus (IPL/STG), the supplementary motor area (SMA), and the cerebellum. Changes of activation with age for simple sentences are depicted in blue, for complex sentences in red. The functional attunement is associated with structural maturation in the PO and IPL/STG (left picture in the bottom row) and cognitive maturation in the IPL/STG and the cerebellum (top row). The functional activation pattern of the PO in 5- and 6-year-old children is correlated to the functional activation pattern in the SMA (right picture in the bottom row; depicted in light pink), in 7- and 8-year-old children to the activation pattern in the SMA and the IPL/STG (depicted in dark pink) and in adults to the activation pattern in the IPL/STG (depicted in purple).

Furthermore, the activation pattern of the left PO is predicted by the functional activation of the IPL/STG in adults, it is predicted by the functional activation of the SMA in the 5–6-year-olds, and it represents an intermediate pattern with activation in the IPL/STG and SMA predicting the activation in PO in older children (see Figure 24, bottom row, right picture). In the following section, main findings of the different studies and remaining open question will be summarized.

11.1 The relation of verbal working memory capacities and complex sentence processing

While previous studies indicate that children's verbal working memory capacity is associated with different processing strategies for relative clauses (Felser et al., 2003; Roberts et al., 2007; Weighall & Altmann, 2010), differential contributions of higher processing speed (Bayliss et al., 2005) and/or changes in attentional control (Barrouillet et al., 2009; Conlin et al., 2005; Portrat et al., 2009) that increase storage capacities for processing complex sentences have not been investigated so far. The first study sought to investigate children's processing of multiple center-embedded sentences in relation to their verbal working memory capacities and thus to determine cognitive prerequisites which can interact with activation patterns for complex sentence processing as illustrated in Figure 24 (top row) . This study found that children between 5 and 8 years show difficulties in processing double embedded sentence and that these

processing difficulties are closely related to their digit span and thus verbal working memory capacities. Moreover, the results provide evidence for qualitative changes in complex sentence processing across different age groups. While successful processing of double embedded sentences appear to depend on syntactic-morphological processing skills for structural hierarchy building in the younger group, verbal working memory capacity seems to effect particularly the processing of long-distance dependencies in double embedded sentences in the older group.

The time-based resource-sharing model (Barrouillet et al., 2004) suggests that an increase of verbal working memory capacity is associated with a strategy of attentional refreshing which allows for a higher cognitive load. Following this suggestion, children with increased verbal working memory capacities were thought to have higher capacities for processing multiple interrupted sentences which facilitate the structural hierarchy building. In contrast, the task-switching account (Towse & Hitch, 1995; Towse et al., 1998) proposes that an increase in verbal working memory capacities is a by-product of an increase in processing speed. Following this proposal, children with insufficient verbal working memory capacities due to too slow processing speed would not able to process the whole sentence before it ceases. Therefore, particularly the processing of long-distance dependencies within the embedded sentences should be effected. The finding that insufficient verbal working memory in children is only associated with establishment of long-distance

dependencies and not with structural hierarchy building provides evidence for the latter account.

Nonetheless, it remains an open question which specific subcomponent of verbal working memory leads to improvements in processing double embedded structures. Cowen et al. (2000) proposed that the short-term memory can only store up to 4 items. Following the author's suggestion, the representation of the whole double embedded sentence necessarily requires chunking and rehearsing abilities. However, reliable spontaneous rehearsal cannot be found in children before 7 years of age (Gathercole & Hitch, 1993; Gathercole et al., 2004). To solve the open question whether an increase of processing speed or the implementation of additional processing strategies effect the establishment of long-distance dependencies, future studies need to implement measurements of simple memory span, complex memory span, and processing speed as possible performance predictors, as well as articulatory suppression tasks.

Further evidence may be provided by functional imaging studies. Previous studies indicate that children show not only higher activation but also a qualitatively different activation pattern compared to adults in different processing domains (Brauer & Friederici, 2007; Durston et al., 2006; Lidzba et al., 2011). While the former can indicate differences in processing efficiency (Schlaggar et al., 2002), the latter finding is associated with different processing strategies (Brauer & Friederici, 2007;

Skeide et al., 2014). A comparison of functional activation patterns evoked by processing double embedded sentences between different age groups can reveal quantitative and/or qualitative differences of activation. While the former finding may reflect differences in processing efficiency, the latter finding may be associated with different processing strategies.

11.2 Gray matter maturation in grammar-relevant brain areas

In order to be able to reliably interpret activation differences, structural maturation has likewise to be taken into account because it influences activation patterns just as well as performance differences. The current thesis has been confined to the investigation of gray matter maturation because previous structural imaging data already provide evidence for correlations between differential activation patterns for sentence processing and white matter maturation (Brauer et al., 2011), but correlations between functional activation for complex sentence processing and gray matter maturation have not been investigated so far.

However, before relating structural and functional maturation with respect to the processing of double embedded sentences (as illustrated by Figure 24, bottom row, left picture), the second study aimed at investigating the structural maturation of brain areas involved in sentence comprehension in general. It was found that the ability to assign thematic roles against a preferential interpretation strategy was positively

correlated to GMP in the left ITG and IFG, whereas performance for sentences that highly load on verbal working memory capacities was positively correlated to GMP in the left parietal operculum extending to the posterior STG. The left IFG has been proposed to be involved in structural hierarchy building (for a review, see Friederici, 2011), the left ITG may be involved in processing and integrating contextual information for thematic role assignment since this region has been suggested to store lexical-semantic information (Crinion et al., 2003; Hickok & Poeppel, 2004, 2007; Leff et al., 2008). Higher GMP in the left parietal operculum extending to the posterior STG may reflect higher storage capacities for verbal materials (Fiebach et al., 2005; Leff et al., 2009; Meyer et al., 2012; Novais-Santos et al., 2007).

The finding that a better performance is associated with a higher GMP is in line with previous developmental studies indicating that cortical maturation between 5 and 11 years complies with gray matter thickening (Sowell, Thompson, Leonard, et al., 2004) and that the later cortical thickness peaks, the more intelligent participants are because a prolonged maturation allows for an extended critical phase (Shaw et al., 2006). However, it remains an open question whether children with a lower GMP in the present study are either in a less maturational state or if they passed an abridged sensitive phase for language acquisition. Only longitudinal data can answer this open issue. To understand the underlying physiological processes that drive the cortical maturation, the combination

of different techniques is required. VBM measurements depend on the extent of the cortical surface, cortical thickness, and myelination in adjacent white matter (Hutton et al., 2009; Mechelli et al., 2005). To disentangle contributions of these different processes, a combination of T1- and T2-weighted images as well as cortical thickness analyses are needed. However, even all in-vivo techniques together cannot depict the actual physiological mechanisms such as the growth of cell bodies, dendritic sprouting, the establishment of synaptic connections, and synaptic pruning. To gain insight into these processes, a comparison with ex-vivo data bases is required.

11.3 The functional attunement to complex sentence processing

Previous developmental data indicate that functional selectivity of the left IFG only emerges at the age of 6 (Knoll et al., 2012). Besides the left IFG, the processing of center-embedded sentences additionally requires the engagement of brain areas which are assumed to be involved in working memory-related aspects of sentence processing (Makuuchi et al., 2009) as well as the integration of syntactic and semantic information for thematic role assignment (Friederici et al., 2009). The emergence of functional selectivity in these areas and the age at which children are able to recruit the entire fronto-temporal language network has not been described so far. To capture the effect of restricted verbal working memory

capacities, the functional analyses were restricted to the long-distance dependency within the embedded sentences. A comparison of functional activation patterns for single and double embedded sentences between 5- and 6-year-old children, 7- and 8-year-old children, and adults reveals that all age groups engage a qualitatively comparable network of the left PO, the left IPL/STG, the SMA and the cerebellum. However, functional selectivity of these regions was only observable in adults (see Figure 24, bottom row; middle picture). Moreover, interrelations of activation patterns between brain areas differ between age groups: In adults the activation in the left PO is predicted by the functional activation of the IPL/STG, in 5- and 6-year-olds it is predicted by the functional activation of the SMA. In 7- and 8-year-olds both regions predict the activation of the left PO (see Figure 24, bottom row, right picture). These qualitative activation differences are in accordance with structural imaging data of white matter tracts, which reveal that the dorsal fiber tracts that connect the left IPL/STG and the left PO only mature around 7 years of age (Brauer et al., 2011) and may indicate that children use different processing strategies compared to adults.

A closer inspection of age differences in each area revealed that functional selectivity differentially emerges in each of these regions. While in the left PO and the SMA, activation for simple sentences decreases with age, the activation for complex sentences in the left IPL/STG increases. These differential activation patterns point to the relation of

different factors that contribute to the development of functional selectivity in each of these regions. Based on findings of the first study showing that the processing of double embedded sentences is related to verbal working memory capacities, an increased activation in the left IPL/STG for complex sentences in adults might reflect the application of a verbal working memory-related strategy which facilitates complex sentence processing and which might not be accessible for children yet. The decrease of activation for simple sentences in the left PO could be either related to processing efficiency which increases with age and/or structural maturation. The latter assumption is supported by studies that found that synaptic pruning is related to a decline in metabolic activity (Chugani, 1998; Chugani, Phelps, & Mazziotta, 1987). However, the second study of this thesis indicated that a higher GMP is associated with a better sentence comprehension in children. Thus, whereas a negative relation between functional selectivity and GMP would reflect an age-related maturational effect, a positive correlation across age groups would provide evidence for different brain structural prerequisites which may result in different processing skills.

To solve this question of the complex interplay between these different factors, a fourth study analyzed the relationship of cognitive, structural and functional maturation.

11.4 The tripartite relationship between cognitive, brain structural, and brain functional maturation

Correlational analyses of the fourth study indicate that the GMP in the left PO and the left IPL/STG is correlated to the observed activation pattern: the higher the functional selectivity of these regions, the lower the GMP (see Figure 24, bottom row, left picture). Thus, gray matter maturation across age groups appears to have an important impact on the observed functional activation pattern. Since gray matter loss of these regions has been found to begin between 7 and 12 years (Giedd et al., 1999; Sowell et al., 2003), a lower GMP in participants of this study most likely reflects a more mature state of the underlying cortical brain structure whereas the positive correlation between GMP and sentence comprehension in the children's sample of the MRI study may reflect different structural prerequisites and/or different time courses of sensitive periods. However, VBM is a technique which classifies a voxel to either gray or white matter based on its intensity. Therefore, white matter maturation close to the vicinity of the cortex may influence the measured intensities and thus GMP in this area may partly reflect white matter changes. According to this methodological limitation, it cannot be precluded that an increase of myelination in the adjacent white matter dorsal fiber tracts (Brauer et al. 2011, 2013) connecting the posterior STG with the PO passing through the IPL (Catani et al. 2005) can partly explain the reduction of GMP. Myelination of fiber tracts results in higher conduction velocity, which

allows for a faster transfer of neuronal signals. As proposed by the findings of the first study, the resulting increase in processing speed may be associated with an increased verbal working memory capacity which facilitates the processing of the long-distance dependencies in double embeddings. To answer this open question whether the negative relation between GMP and functional selectivity is purely related to gray matter maturation, white matter maturation or both, the implementation of additional analyses using diffusion-weighted data is required.

Furthermore, it was found that the functional selectivity of the left IPL/STG and the cerebellum is positively related to the participant's digit span (see Figure 24, top row). While the IPL/STG has been shown to be directly associated with verbal working memory-related aspects of sentence processing (Fiebach et al., 2005; Leff et al., 2009; Meyer et al., 2012; Novais-Santos et al., 2007), the cerebellar activity has been proposed to rather indirectly represent verbal working memory-related aspects by reflecting the application of timing and sequencing schemes provided by prosodic features to facilitate the storage of embedded clauses. Moreover, the additional correlation of the functional selectivity with GMP in the IPL/STG points to the structural maturation as basis for a specific engagement of the IPL/STG during the processing of sentences with high verbal working memory demands

In sum, these findings show that the functional selectivity of brain areas involved in complex sentence processing are differentially

associated with either brain structural maturation, cognitive maturation, or both. But does a higher selectivity associated with these processes result in more efficient complex sentence processing? As expected, the development towards a brain-functional selectivity for syntactic complexity within the observed neural network is correlated with sentence processing performance: Thus, the functional attunement towards complex sentence processing of these brain regions driven by differential maturational processes parallels the improvement of behavioral performance.

References

- Adams, A. M., & Gathercole, S. E. (1995). Phonological working memory and speech production in preschool children. *Journal of Speech and Hearing Research, 38*(2), 403–414.
- Ahmad, Z., Balsamo, L. M., Sachs, B. C., Xu, B., & Gaillard, W. D. (2003). Auditory comprehension of language in young children: Neural networks identified with fMRI. *Neurology, 60*(10), 1598–1605.
- Altaye, M., Holland, S. K., Wilke, M., & Gaser, C. (2008). Infant brain probability templates for MRI segmentation and normalization. *NeuroImage, 43*(4), 721–730.
- Amunts, K., Schleicher, A., Bürgel, U., Mohlberg, H., Uylings, H. B., & Zilles, K. (1999). Broca's region revisited: Cytoarchitecture and intersubject variability. *The Journal of Comparative Neurology, 412*(2), 319–341.
- Ashburner, J. (2007). A fast diffeomorphic image registration algorithm. *NeuroImage, 38*(1), 95–113.
- Ashburner, J., & Friston, K. J. (2000). Voxel-Based Morphometry—The Methods. *NeuroImage, 11*(6), 805–821.
- Baddeley, A. D. (1986). *Working memory*. Oxford: Oxford University Press.
- Baddeley, A. D. (2000). The episodic buffer: A new component of working memory? *Trends in Cognitive Sciences, 4*(11), 417–423.
- Baddeley, A. D., & Hitch, G. (1974). Working memory. In G. H. Bower (Ed.), *Psychology of learning and motivation: Advances in research and theory* (Vol. 8, pp. 47–89). New York: Academic Press.
- Bahlmann, J., Schubotz, R. I., & Friederici, A. D. (2008). Hierarchical artificial grammar processing engages Broca's area. *NeuroImage, 42*(2), 525–534.

- Bahlmann, J., Schubotz, R. I., Mueller, J. L., Koester, D., & Friederici, A. D. (2009). Neural circuits of hierarchical visuo-spatial sequence processing. *Brain Research*, 1298, 161–170.
- Balsamo, L. M., Xu, B., & Gaillard, W. D. (2006). Language lateralization and the role of the fusiform gyrus in semantic processing in young children. *NeuroImage*, 31(3), 1306–1314.
- Barrouillet, P., Bernardin, S., Camos, V., & Pierre. (2004). Time constraints and resource sharing in adults' working memory spans. *Journal of Experimental Psychology. General*, 133(1), 83–100.
- Barrouillet, P., Gavens, N., Vergauwe, E., Gaillard, V., & Camos, V. (2009). Working memory span development: A time-based resource-sharing model account. *Developmental Psychology*, 45(2), 477–490.
- Bates, E. (1999). Processing complex sentences: A cross-linguistic study. *Language and Cognitive Processes*, 14(1), 69–123.
- Baum, S. R. (1993). Processing of center-embedded and right-branching relative clause sentences by normal elderly individuals. *Applied Psycholinguistics*, 14(01), 75–88.
- Bayliss, D. M., Jarrold, C., Baddeley, A. D., Gunn, D. M., & Leigh, E. (2005). Mapping the developmental constraints on working memory span performance. *Developmental Psychology*, 41(4), 579–597.
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, 57(1), 289–300.
- Ben-Shachar, M., Hendler, T., Kahn, I., Ben-Bashat, D., & Grodzinsky, Y. (2003). The neural reality of syntactic transformations: Evidence from functional magnetic resonance imaging. *Psychological Science*, 14(5), 433–440.

- Ben-Shachar, M., Palti, D., & Grodzinsky, Y. (2004). Neural correlates of syntactic movement: Converging evidence from two fMRI experiments. *NeuroImage*, 21(4), 1320–1336.
- Blaubergs, M. S., & Braine, M. D. (1974). Short-term memory limitations on decoding self-embedded sentences. *Journal of Experimental Psychology*, 102(4), 745–748.
- Bloom, L., Lahey, M., Hood, L., Lifter, K., & Fiess, K. (1980). Complex sentences: Acquisition of syntactic connectives and the semantic relations they encode. *Journal of Child Language*, 7(2), 235–261.
- Bloom, L., Rispoli, M., Gartner, B., & Hafitz, J. (1989). Acquisition of complementation. *Journal of Child Language*, 16(1), 101–120.
- Bloom, L., Tackeff, J., & Lahey, M. (1984). Learning to in complement constructions. *Journal of Child Language*, 11(2), 391–406.
- Bonhage, C. E., Fiebach, C. J., Bahlmann, J., & Mueller, J. L. (2014). Brain signature of working memory for sentence structure: Enriched encoding and facilitated maintenance. *Journal of Cognitive Neuroscience*, 26(8), 1654–1671.
- Bookstein, F. L. (2001). “Voxel-based morphometry” should not be used with imperfectly registered images. *NeuroImage*, 14(6), 1454–1462.
- Bornkessel, I., Zysset, S., Friederici, A. D., von Cramon, D. Y., & Schlesewsky, M. (2005). Who did what to whom? The neural basis of argument hierarchies during language comprehension. *NeuroImage*, 26(1), 221–233.
- Brandt, S., Kidd, E., Lieven, E., & Tomasello, M. (2009). The discourse bases of relativization: An investigation of young German and English-speaking children’s comprehension of relative clauses. *Cognitive Linguistics*, 20(3), 539–570.

- Brauer, J., Anwender, A., & Friederici, A. D. (2011). Neuroanatomical prerequisites for language functions in the maturing brain. *Cerebral Cortex*, 21(2), 459–466.
- Brauer, J., Anwender, A., Perani, D., & Friederici, A. D. (2013). Dorsal and ventral pathways in language development. *Brain and Language*, 127(2), 289-295
- Brauer, J., & Friederici, A. D. (2007). Functional Neural Networks of Semantic and Syntactic Processes in the Developing Brain. *Journal of Cognitive Neuroscience*, 19(10), 1609-1623.
- Brodmann, K. (1909). *Vergleichende Lokalisationslehre der Grosshirnrinde in ihren Prinzipien dargestellt auf Grund des Zellenbaues*. Leipzig: Barth.
- Brown, T. T., Lugar, H. M., Coalson, R. S., Miezin, F. M., Petersen, S. E., & Schlaggar, B. L. (2005). Developmental changes in human cerebral functional organization for word generation. *Cerebral Cortex*, 15(3), 275–290.
- Bunge, S. A., Kahn, I., Wallis, J. D., Miller, E. K., & Wagner, A. D. (2003). Neural circuits subserving the retrieval and maintenance of abstract rules. *Journal of Neurophysiology*, 90(5), 3419–3428.
- Burgund, E. D., Kang, H. C., Kelly, J. E., Buckner, R. L., Snyder, A. Z., Petersen, S. E., & Schlaggar, B. L. (2002). The feasibility of a common stereotactic space for children and adults in fMRI Studies of development. *NeuroImage*, 17(1), 184–200.
- Camos, V., & Barrouillet, P. (2011). Developmental change in working memory strategies: From passive maintenance to active refreshing. *Developmental Psychology*, 47(3), 898–904.
- Caplan, D., Chen, E., & Waters, G. (2008). Task-dependent and task-independent neurovascular responses to syntactic processing. *Cortex*, 44(3), 257–275.

- Caplan, D., DeDe, G., Waters, G., Michaud, J., & Tripodis, Y. (2011). Effects of age, speed of processing, and working memory on comprehension of sentences with relative clauses. *Psychology and Aging, 26*(2), 439–450.
- Case, R., Kurland, D. M., & Goldberg, J. (1982). Operational efficiency and the growth of short-term-memory span. *Journal of Experimental Child Psychology, 33*(3), 386–404.
- Catani, M., Jones, D. K., & Ffytche, D. H. (2005). Perisylvian language networks of the human brain. *Annals of Neurology, 57*(1), 8–16.
- Chen, S. H. A., & Desmond, J. E. (2005a). Cerebrocerebellar networks during articulatory rehearsal and verbal working memory tasks. *NeuroImage, 24*(2), 332–338.
- Chen, S. H. A., & Desmond, J. E. (2005b). Temporal dynamics of cerebro-cerebellar network recruitment during a cognitive task. *Neuropsychologia, 43*(9), 1227–1237.
- Chomsky, N., & Miller, G. A. (1963). Introduction to the formal analysis of natural languages. In R. D. Luce, R. R. Bush, & E. Galanter (Eds.), *Handbook of mathematical psychology* (pp. 269–321). New York: Wiley.
- Christiansen, M. H., & MacDonald, M. C. (2009). A usage-based approach to recursion in sentence processing. *Language Learning, 59*(607), 126–161.
- Chugani, H. T. (1998). A critical period of brain development: studies of cerebral glucose utilization with PET. *Preventive Medicine, 27*(2), 184–188.
- Chugani, H. T., Phelps, M. E., & Mazziotta, J. C. (1987). Positron emission tomography study of human brain functional development. *Annals of Neurology, 22*(4), 487–497.

- Conlin, J. A., Gathercole, S. E., & Adams, J. W. (2005). Children's working memory: Investigating performance limitations in complex span tasks. *Journal of Experimental Child Psychology*, 90(4), 303–317.
- Constable, R. T., Pugh, K. R., Berroya, E., Mencl, W. E., Westerveld, M., Ni, W., & Shankweiler, D. (2004). Sentence complexity and input modality effects in sentence comprehension: An fMRI study. *NeuroImage*, 22(1), 11–21.
- Cooke, A., Zurif, E. B., Devita, C., Alsop, D., Koenig, P., Detre, J., ... Grossman, M. (2001). Neural basis for sentence comprehension: Grammatical and short-term memory components, 94(5), 80 –94.
- Coolidge, F. L., Overmann, K. A., & Wynn, T. (2011). Recursion: What is it, who has it, and how did it evolve? *Wiley Interdisciplinary Reviews: Cognitive Science*, 2(5), 547–554.
- Corrêa, L. M. S. (1995). An alternative assessment of children's comprehension of relative clauses. *Journal of Psycholinguistic Research*, 24(3), 183–203.
- Coull, J. T., Cheng, R.-K., & Meck, W. H. (2011). Neuroanatomical and Neurochemical Substrates of Timing. *Neuropsychopharmacology*, 36(1), 3–25.
- Courchesne, E., Chisum, H. J., Townsend, J., Cowles, A., Covington, J., Egaas, B., ... Press, G. A. (2000a). Normal brain development and aging: Quantitative analysis at in vivo MR imaging in healthy volunteers. *Radiology*, 216(3), 672–682.
- Cowan, N. (1988). Evolving conceptions of memory storage, selective attention, and their mutual constraints within the human information-processing system. *Psychological Bulletin*, 104(2), 163–191.
- Cowan, N. (2010). Multiple concurrent thoughts: The meaning and developmental neuropsychology of working memory. *Developmental Neuropsychology*, 35(5), 447–474.

- Cowan, N., Nugent, L. D., Elliott, E. M., & Saults, J. S. (2000). Persistence of memory for ignored lists of digits: Areas of developmental constancy and change. *Journal of Experimental Child Psychology*, 76(2), 151–172.
- Crinion, J. T., Lambon-Ralph, M. A., Warburton, E. A., Howard, D., & Wise, R. J. S. (2003). Temporal lobe regions engaged during normal speech comprehension. *Brain*, 126(5), 1193–1201.
- Daneman, M., & Carpenter, P. A. (1980). How children and adults detect their own comprehension errors. *Bulletin of the Psychonomic Society*, 16(3), 150–150.
- Dapretto, M., & Bookheimer, S. Y. (1999). Form and content: Dissociating syntax and semantics in sentence comprehension. *Neuron*, 24(2), 427–432.
- Davidson, D. J., & Indefrey, P. (2009). Plasticity of grammatical recursion in German learners of Dutch. *Language and Cognitive Processes*, 24(9), 1335–1369.
- Dehaene-Lambertz, G., Dehaene, S., & Hertz-Pannier, L. (2002). Functional neuroimaging of speech perception in infants. *Science*, 298, 2013–2015.
- Dehaene-Lambertz, G., Hertz-Pannier, L., & Dubois, J. (2006). Nature and nurture in language acquisition: Anatomical and functional brain-imaging studies in infants. *Trends in Neurosciences*, 29(7), 367–373.
- Dehaene-Lambertz, G., Hertz-Pannier, L., Dubois, J., Mériaux, S., Roche, A., Sigman, M., & Dehaene, S. (2006). Functional organization of perisylvian activation during presentation of sentences in preverbal infants. *Proceedings of the National Academy of Sciences of the United States of America*, 103(38), 14240–14245.

- Deniz Can, D., Richards, T., & Kuhl, P. K. (2013). Early gray-matter and white-matter concentration in infancy predict later language skills: A whole brain voxel-based morphometry study. *Brain and Language*, 124(1), 34–44.
- Desmond, J. E., Gabrieli, J. D., Wagner, A. D., Ginier, B. L., & Glover, G. H. (1997). Lobular patterns of cerebellar activation in verbal working-memory and finger-tapping tasks as revealed by functional MRI. *The Journal of Neuroscience*, 17(24), 9675–9685.
- Diamond, A. (2002). Normal development of prefrontal cortex from birth to young adulthood: Cognitive functions, anatomy, and biochemistry. In D. T. Stuss & R. T. Knight (Eds.), *Principles of frontal lobe function* (pp. 466–503). Oxford: Oxford University Press.
- Dittmar, M., Abbot-Smith, K., Lieven, E., & Tomasello, M. (2008). German children's comprehension of word order and case marking in causative sentences. *Child Development*, 79(4), 1152–1167.
- Dos Santos Sequeira, S., Woerner, W., Walter, C., Kreuder, F., Lueken, U., Westerhausen, R., ... Wittling, W. (2006). Handedness, dichotic-listening ear advantage, and gender effects on planum temporale asymmetry – A volumetric investigation using structural magnetic resonance imaging. *Neuropsychologia*, 44(4), 622–636.
- Durstun, S., Davidson, M. C., Tottenham, N., Galvan, A., Spicer, J., Fossella, J. A., & Casey, B. J. (2006). A shift from diffuse to focal cortical activity with development. *Developmental Science*, 1, 1–8.
- Ericcson, K. A., Chase, W. G., & Faloon, S. (1980). Acquisition of a memory skill. *Science*, 208, 1181–1182.
- Felser, C., Marinis, T., & Clahsen, H. (2003). Children's processing of ambiguous sentences: A study of relative clause attachment. *Language Acquisition*, 11(3), 127–163.

- Féry, C., & Schubö, F. (2010). Hierarchical prosodic structures in the intonation of center-embedded relative clauses. *The Linguistic Review*, 27(3), 293–317.
- Fiebach, C. J., Friederici, A. D., Smith, E. E., & Swinney, D. (2007). Lateral inferotemporal cortex maintains conceptual-semantic representations in verbal working memory. *Journal of Cognitive Neuroscience*, 19(12), 2035–2049.
- Fiebach, C. J., Rissman, J., & D'Esposito, M. (2006). Modulation of inferotemporal cortex activation during verbal working memory maintenance. *Neuron*, 51(2), 251–261.
- Fiebach, C. J., Schlesewsky, M., Lohmann, G., von Cramon, D. Y., & Friederici, A. D. (2005). Revisiting the role of Broca's area in sentence processing: Syntactic integration versus syntactic working memory. *Human Brain Mapping*, 24(2), 79–91.
- Fiebach, C. J., & Schubotz, R. I. (2006). Dynamic anticipatory processing of hierarchical sequential events: A common role for Broca's area and ventral premotor cortex across domains? *Cortex*, 42(4), 499–502.
- Fiebach, C. J., Vos, S. H., & Friederici, A. D. (2004). Neural correlates of syntactic ambiguity in sentence comprehension for low and high span readers. *Journal of Cognitive Neuroscience*, 16(9), 1562–1575.
- Flavell, J. H., Beach, D. R., & Chinsky, J. M. (1966). Spontaneous verbal rehearsal in a memory task as a function of age. *Child Development*, 37(2), 283–299.
- Fonov, V., Evans, A. C., Botteron, K., Almli, C. R., McKinstry, R. C., & Collins, D. L. (2011). Unbiased average age-appropriate atlases for pediatric studies. *NeuroImage*, 54(1), 313–327.

- Foss, D. J., & Cairns, H. S. (1970). Some effects of memory limitation upon sentence comprehension and recall. *Journal of Verbal Learning and Verbal Behavior*, 9(5), 541–547.
- Fox, A. V. (2006). *TROG-D. Test zur Überprüfung des Grammatikverständnisses. Handbuch. Das Gesundheitsforum*. Idstein: Schulz-Kirchner Verlag.
- Fox, B. A., & Thompson, S. A. (1990). A discourse explanation of the grammar of relative clauses in English conversation. *Language*, 66(2), 297–316.
- Fox, P. T., Raichle, M. E., Mintun, M. A., & Dence, C. (1988). Nonoxidative glucose consumption during focal physiologic neural activity. *Science*, 241, 462–464.
- Fragman, C., Goodluck, H., & Heggie, L. (2007). Child and adult construal of restrictive relative clauses: Knowledge of grammar and differential effects of syntactic context. *Journal of Child Language*, 34(2), 345–380.
- Frazier, L. (1985). Syntactic complexity. In D. R. Dowty, L. Karttunen, & A. M. Zwicky (Eds.), *Natural language parsing: Psychological, computational, and theoretical perspectives* (pp. 129–189). Cambridge: Cambridge University Press.
- Frey, S., Campbell, J. S. W., Pike, G. B., & Petrides, M. (2008). Dissociating the human language pathways with high angular resolution diffusion fiber tractography. *The Journal of Neuroscience*, 28(45), 11435–11444.
- Friederici, A. D. (2002). Towards a neural basis of auditory sentence processing. *Trends in Cognitive Sciences*, 6(2), 78–84.
- Friederici, A. D. (2004a). Lateralization of auditory language functions: A dynamic dual pathway model. *Brain and Language*, 89(2), 267–276.

- Friederici, A. D. (2004b). Processing local transitions versus long-distance syntactic hierarchies. *Trends in Cognitive Sciences*, 8(6), 245–247.
- Friederici, A. D. (2011). The brain basis of language processing: From structure to function. *Physiological Reviews*, 91(4), 1357–1392.
- Friederici, A. D. (2012). The cortical language circuit: From auditory perception to sentence comprehension. *Trends in Cognitive Sciences*, 16(5), 1–7.
- Friederici, A. D., Bahlmann, J., Heim, S., Schubotz, R. I., & Anwander, A. (2006). The brain differentiates human and non-human grammars: Functional localization and structural connectivity. *Proceedings of the National Academy of Sciences of the United States of America*, 103(7), 2458–2463.
- Friederici, A. D., Fiebach, C. J., Schlesewsky, M., Bornkessel, I. D., & von Cramon, D. Y. (2006). Processing linguistic complexity and grammaticality in the left frontal cortex. *Cerebral Cortex*, 16(12), 1709–1717.
- Friederici, A. D., & Gierhan, S. M. (2013). The language network. *Current Opinion in Neurobiology*, 23(2), 250–254.
- Friederici, A. D., Makuuchi, M., & Bahlmann, J. (2009). The role of the posterior superior temporal cortex in sentence comprehension. *Neuroreport*, 20(6), 563–568.
- Friedmann, N., & Costa, J. (2010). The child heard a coordinated sentence and wondered: On children's difficulty in understanding coordination and relative clauses with crossing dependencies. *Lingua*, 120(6), 1502–1515.
- Gathercole, S. E. (1999). Cognitive approaches to the development of short-term memory. *Trends in Cognitive Sciences*, 3(11), 410–419.

- Gathercole, S. E., & Hitch, G. J. (1993). Developmental changes in short-term memory: A revised working memory perspective. In A. F. Collins, S. E. Gathercole, M. A. Conway & P. E. Morris (Eds.), *Theories of memory* (pp. 189–209). Hove (UK): L. Erlbaum Associates.
- Gathercole, S. E., Pickering, S. J., Ambridge, B., & Wearing, H. (2004). The structure of working memory from 4 to 15 years of age. *Developmental Psychology*, 40(2), 177–190.
- Gibson, E. (1998). Linguistic complexity: Locality of syntactic dependencies. *Cognition*, 68(1), 1–76.
- Gibson, E. (2000). The dependency locality theory: A distance-based theory of linguistic complexity. In A. Marantz, Y. Miyashita, & W. O'Neil (Eds.), *Image, Language, Brain* (pp. 95–126). Cambridge, MA: MIT Press.
- Gibson, E., & Thomas, J. (1999). Memory limitations and structural forgetting: The perception of complex ungrammatical sentences as grammatical. *Language and Cognitive Processes*, 14(3), 225–248.
- Giedd, J. N., Blumenthal, J., Jeffries, N. O., Castellanos, F. X., Liu, H., Zijdenbos, A., ... Rapoport, J. L. (1999). Brain development during childhood and adolescence: A longitudinal MRI study. *Nature Neuroscience*, 2(10), 861–863.
- Gimenes, M., Rigalleau, F., & Gaonach, D. (2009). When a missing verb makes a French sentence more acceptable. *Language and Cognitive Processes*, 24(3), 440–449.
- Gogtay, N., Giedd, J. N., Lusk, L., Hayashi, K. M., Greenstein, D., Vaituzis, A. C., ... Thompson, P. M. (2004). Dynamic mapping of human cortical development during childhood through early adulthood. *Proceedings of the National Academy of Sciences of the United States of America*, 101(21), 8174–8179.

- Goodluck, H., Guilfoyle, E., & Harrington, S. (2006). Merge and binding in child relative clauses: The case of Irish. *Journal of Linguistics*, 42(3), 629–661.
- Grewe, T., Bornkessel, I., Zysset, S., Wiese, R., von Cramon, D. Y., & Schlesewsky, M. (2005). The emergence of the unmarked: A new perspective on the language-specific function of Broca's area. *Human Brain Mapping*, 26(3), 178–90.
- Hakes, D. T., & Cairns, H. S. (1970). Sentence comprehension and relative pronouns. *Perception & Psychophysics*, 8(1), 5–8.
- Hakes, D. T., Evans, J. S., & Brannon, L. L. (1976). Understanding sentences with relative clauses. *Memory & Cognition*, 4(3), 283–290.
- Hakes, D. T., & Foss, D. J. (1970). Decision processes during sentence comprehension: Effects of surface structure reconsidered. *Perception & Psychophysics*, 8(6), 413–416.
- Hamilton, H. W., & Deese, J. (1971). Comprehensibility and subject-verb relations in complex sentences. *Journal of Verbal Learning & Verbal Behavior*, 10(2), 163–170.
- Hanakawa, T., Honda, M., Sawamoto, N., Okada, T., Yonekura, Y., Fukuyama, H., & Shibasaki, H. (2002). The role of rostral Brodmann area 6 in mental-operation tasks: An integrative neuroimaging approach. *Cerebral Cortex*, 12, 1157–1170.
- Hauser, M. D., Chomsky, N., & Fitch, W. T. (2002). The faculty of language: What is it, who has it, and how did it evolve? *Science*, 298, 1569–1579.
- Hebb, D. O. (1949). *The organization of behavior: A neuropsychological theory*. New York: Wiley.
- Hensch, T. K. (2005). Critical period plasticity in local cortical circuits. *Nature Reviews Neuroscience*, 6(11), 877–888.

- Hensch, T. K., & Bilimoria, P. M. (2012). Re-opening windows: Manipulating critical periods for brain development. In *Cerebrum: The Dana forum on brain science* (Vol. 2012).
- Hickok, G., & Poeppel, D. (2004). Dorsal and ventral streams: A framework for understanding aspects of the functional anatomy of language. *Cognition*, 92(1-2), 67–99.
- Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience*, 8(5), 393–402.
- Hitch, G.J. & Halliday, M.S. (1983). Working memory in children. *Philosophical Transactions of the Royal Society London Series B*, 302, 325-340.
- Holland, S. K., Plante, E., Weber Byars, A., Strawsburg, R. H., Schmithorst, V. J., & Ball, W. S. (2001). Normal fMRI brain activation patterns in children performing a verb generation task. *NeuroImage*, 14(4), 837–843.
- Honey, G. D., Bullmore, E. T., & Sharma, T. (2000). Prolonged reaction time to a verbal working memory task predicts increased power of posterior parietal cortical activation. *NeuroImage*, 12(5), 495–503.
- Hudson, R. (1996). The difficulty of (so-called) self-embedded structures. Working paper in *Linguist*, 8, 283–314.
- Huettel, S. A., Song, A. W., & McCarthy, G. (2008). *Functional magnetic resonance imaging* (2nd edition). Sunderland, Mass: Sinauer Associates.
- Huttenlocher, P. R. (2002). *Neural plasticity the effects of environment on the development of the cerebral cortex*. Cambridge, MA: Harvard University Press.
- Huttenlocher, P. R., & Dabholkar, A. S. (1997). Regional differences in synaptogenesis in human cerebral cortex. *The Journal of Comparative Neurology*, 387(2), 167–178.

- Huttenlocher, P. R., & de Courten, C. (1987). The development of synapses in striate cortex of man. *Human Neurobiology*, 6(1), 1–9.
- Hutton, C., Draganski, B., Ashburner, J., & Weiskopf, N. (2009). A comparison between voxel-based cortical thickness and voxel-based morphometry in normal aging. *NeuroImage*, 48(2), 371–380.
- Innocenti, G. M., & Price, D. J. (2005). Exuberance in the development of cortical networks. *Nature Reviews Neuroscience*, 6(12), 955–965.
- Inui, T., Otsu, Y., Tanaka, S., Okada, T., Nishizawa, S., & Konishi, J. (1998). A functional MRI analysis of comprehension processes of Japanese sentences. *Neuroreport*, 9(14), 3325–3328.
- Jackendoff, R., & Pinker, S. (2005). The nature of the language faculty and its implications for evolution of language (Reply to Fitch, Hauser, and Chomsky). *Cognition*, 97(2), 211–225.
- James, W. (1890). *The principles of psychology*. New York: H. Holt and Company.
- Johnson, J. S., & Newport, E. L. (1989). Critical period effects in second language learning: The influence of maturational state on the acquisition of English as a second language. *Cognitive Psychology*, 21(1), 60–99.
- Johnson, M. H. (2001). Functional brain development in humans. *Nature Reviews Neuroscience*, 2(7), 475–483.
- Johnson, M. H. (2011). Interactive Specialization: A domain-general framework for human functional brain development? *Developmental Cognitive Neuroscience*, 1(1), 7–21.
- Jonides, J., Lewis, R. L., Nee, D. E., Lustig, C. A., Berman, M. G., & Moore, K. S. (2008). The mind and brain of short-term memory. *Annual Review of Psychology*, 59, 193–224.

- Just, M. A., & Carpenter, P. A. (1992). A capacity theory of comprehension: Individual differences in working memory. *Psychological Review*, 99(1), 122–149.
- Just, M. A., Carpenter, P. A., Keller, T. A., Eddy, W. F., & Thulborn, K. R. (1996). Brain activation modulated by sentence comprehension. *Science*, 274, 114–116.
- Kaan, E., & Swaab, T. Y. (2002). The brain circuitry of syntactic comprehension. *Trends in Cognitive Sciences*, 6(8), 350–356.
- Kail, R. (1992). Processing speed, speech rate, and memory. *Developmental Psychology*, 28(5), 899–904.
- Kail, R., & Park, Y. S. (1994). Processing time, articulation time, and memory span. *Journal of Experimental Child Psychology*, 57(2), 281–291.
- Kang, H. C., Burgund, E. D., Lugar, H. M., Petersen, S. E., & Schlaggar, B. L. (2003). Comparison of functional activation foci in children and adults using a common stereotactic space. *NeuroImage*, 19(1), 16–28.
- Karlsson, F. (2007). Constraints on multiple center-embedding of clauses. *Journal of Linguistics*, 43(02), 365–392.
- Karunanayaka, P., Schmithorst, V. J., Vannest, J., Szaflarski, J. P., Plante, E., & Holland, S. K. (2010). A group independent component analysis of covert verb generation in children: A functional magnetic resonance imaging study. *NeuroImage*, 51(1), 472–487.
- Kaufman, A. S., Kaufman, N. L., Melchers, P. & Preuss, U. (1994). *K-ABC: Kaufman-assessment battery for children* (2. Aufl.). Amsterdam: Swets & Zeitlinger.
- Kidd, E., & Bavin, E. L. (2002). English-Speaking children's comprehension of relative clauses: Evidence for constraints on development, 31(6), 599–617.

- Kidd, E., Brandt, S., Lieven, E., & Tomasello, M. (2007). Object relatives made easy: A cross-linguistic comparison of the constraints influencing young children's processing of relative clauses. *Language and Cognitive Processes*, 22(6), 860–897.
- Kimball, J. (1973). Seven principles of surface structure parsing in natural language. *Cognition*, 2(1), 15–47.
- Kinno, R., Kawamura, M., Shioda, S., & Sakai, K. L. (2008). Neural correlates of noncanonical syntactic processing revealed by a picture-sentence matching task. *Human Brain Mapping*, 29(9), 1015–1027.
- Knoll, L. J., Obleser, J., Schipke, C. S., Friederici, A. D., & Brauer, J. (2012). Left prefrontal cortex activation during sentence comprehension covaries with grammatical knowledge in children. *NeuroImage*, 62(1), 207–216.
- Kotz, S. A., & Schwartz, M. (2010). Cortical speech processing unplugged: A timely subcortico-cortical framework. *Trends in Cognitive Sciences*, 14(9), 392–399.
- Kuhl, P. K. (2004). Early language acquisition: Cracking the speech code. *Nature Reviews Neuroscience*, 5(11), 831–843.
- Kuhl, P. K. (2010). Brain mechanisms in early language acquisition. *Neuron*, 67(5), 713–727.
- Kuhl, P. K., & Rivera-Gaxiola, M. (2008). Neural substrates of language acquisition. *Annual Review of Neuroscience*, 31, 511–34.
- LaBar, K. S., Gitelman, D. R., Parrish, T. B., & Mesulam, M. (1999). Neuroanatomic overlap of working memory and spatial attention networks: A functional MRI comparison within subjects. *NeuroImage*, 10(6), 695–704.

- Lancaster, J. L., Woldorff, M. G., Parsons, L. M., Liotti, M., Freitas, C. S., Rainey, L., ... Fox, P. T. (2000). Automated Talairach atlas labels for functional brain mapping. *Human Brain Mapping, 10*(3), 120–131.
- Larkin, W., & Burns, D. (1977). Sentence comprehension and memory for embedded structure. *Memory & Cognition, 5*(1), 17–22.
- Lebel, C., Walker, L., Leemans, A., Phillips, L., & Beaulieu, C. (2008). Microstructural maturation of the human brain from childhood to adulthood. *NeuroImage, 40*(3), 1044–1055.
- Leff, A. P., Schofield, T. M., Crinion, J. T., Seghier, M. L., Grogan, A., Green, D. W., & Price, C. J. (2009). The left superior temporal gyrus is a shared substrate for auditory short-term memory and speech comprehension: Evidence from 210 patients with stroke. *Brain, 132*(12), 3401–3410.
- Leff, A. P., Schofield, T. M., Stephan, K. E., Crinion, J. T., Friston, K. J., & Price, C. J. (2008). The cortical dynamics of intelligible speech. *The Journal of Neuroscience, 28*(49), 13209–13215.
- Lehéricy, S., Ducros, M., Krainik, A., Francois, C., Moortele, P.-F. V. de, Ugurbil, K., & Kim, D.-S. (2004). 3-D diffusion tensor axonal tracking shows distinct SMA and Pre-SMA projections to the human striatum. *Cerebral Cortex, 14*(12), 1302–1309.
- Lenneberg, E. H. (1967). *Biological foundations of language*. New York: Wiley.
- Lenroot, R. K., & Giedd, J. N. (2006). Brain development in children and adolescents: Insights from anatomical magnetic resonance imaging. *Neuroscience & Biobehavioral Reviews, 30*(6), 718–729.
- Lewandowsky, S., Duncan, M., Brown, G. D. A., & Stephan. (2004). Time does not cause forgetting in short-term serial recall. *Psychonomic Bulletin & Review, 11*(5), 771–790.

- Leys, C., & Schumann, S. (2010). A nonparametric method to analyze interactions: The adjusted rank transform test. *Journal of Experimental Social Psychology*, 46(4), 684–688.
- Lidzba, K., Schwilling, E., Grodd, W., Krägeloh-Mann, I., & Wilke, M. (2011). Language comprehension vs. language production: Age effects on fMRI activation. *Brain and Language*, 119(1), 6–15.
- Lindner, K. (2003). The development of sentence interpretation strategies in monolingual German-learning children with and without language impairment. Special issue on specific language impairment. *Linguistics* 41, 213–254.
- Logothetis, N. K. (2008). What we can do and what we cannot do with fMRI. *Nature*, 453, 869–878.
- Logothetis, N. K., Pauls, J., Augath, M., Trinath, T., & Oeltermann, A. (2001). Neurophysiological investigation of the basis of the fMRI signal. *Nature*, 412, 150–157.
- Lu, L., Dapretto, M., O'Hare, E. D., Kan, E., McCourt, S. T., Thompson, P. M., ... Sowell, E. R. (2009). Relationships between brain activation and brain structure in normally developing children. *Cerebral Cortex*, 19(11), 2595–2604.
- Lu, L., Leonard, C., Thompson, P., Kan, E., Jolley, J., Welcome, S., ... Sowell, E. (2007). Normal developmental changes in inferior frontal gray matter are associated with improvement in phonological processing: A longitudinal MRI analysis. *Cerebral*, 17(5), 1092–1099.
- Makuuchi, M., Bahlmann, J., Anwender, A., & Friederici, A. D. (2009). Segregating the core computational faculty of human language from working memory. *Proceedings of the National Academy of Sciences of the United States of America*, 106(20), 8362–8367.

- Makuuchi, M., Bahlmann, J., & Friederici, A. D. (2012). An approach to separating the levels of hierarchical structure building in language and mathematics. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367, 2033–2045.
- Maldjian, J. A., Laurienti, P. J., Kraft, R. A., & Burdette, J. H. (2003). An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. *NeuroImage*, 19(3), 1233–1239.
- Marcus, M. (1980). *A theory of syntactic recognition for natural language*. Cambridge, MA: MIT Press.
- Marks, L. E. (1968). Scaling of grammaticalness of self-embedded English sentences. *Journal of Verbal Learning and Verbal Behavior*, 7(5), 965–967.
- McNealy, K., Mazziotta, J. C., & Dapretto, M. (2010). The neural basis of speech parsing in children and adults. *Developmental Science*, 13(2), 385–406.
- Mechelli, A., Price, C., Friston, K., & Ashburner, J. (2005). Voxel-based morphometry of the human brain: Methods and applications. *Current Medical Imaging Reviews*, 1(2), 105–113.
- Meyer, L., Cunitz, K., Obleser, J., & Friederici, A. D. (2014). Sentence processing and verbal working memory in a white-matter-disconnection patient. *Neuropsychologia*, 61, 190–196.
- Meyer, L., Obleser, J., Anwender, A., & Friederici, A. D. (2012). Linking ordering in Broca's area to storage in left temporo-parietal regions: The case of sentence processing. *NeuroImage*, 62(3), 1987–1998.
- Miller, G. A. (1956). The magical number seven plus or minus two: Some limits on our capacity for processing information. *Psychological Review*, 63(2), 81–97.

- Miller, G. A. (1962). Some psychological studies of grammar. *American Psychologist*, 17(11), 748–762.
- Miller, G. A., & Chomsky, N. (1963). Finitary models of language users. In R. D. Luce, R. Bush, and E. Galanter (Eds.), *Handbook of mathematical psychology* (pp. 419–492). New York: John Wiley & Sons.
- Miller, G. A., & Isard, S. (1964). Free recall of self-embedded English sentences. *Information and Control*, 7(3), 292–303.
- Montgomery, J. W., Magimairaj, B. M., & O'Malley, M. H. (2008). Role of working memory in typically developing children's complex sentence comprehension. *Journal of Psycholinguistic Research*, 37(5), 331–354.
- Mottier, G. (1951). Mottier-Test. Über Untersuchungen zur Sprache lesegestörter Kinder. *Folia Phoniatica et Logopaedica*, 3, 170–177.
- Murdoch, B. E. (2010). The cerebellum and language: Historical perspective and review. *Cortex*, 46(7), 858–868.
- Muzik, O., Chugani, D. C., Juhász, C., Shen, C., & Chugani, H. T. (2000). Statistical parametric mapping: Assessment of application in children. *NeuroImage*, 12(5), 538–549.
- Nairne, J. S. (2002). Remembering over the short-term: The case against the standard model. *Annual Review of Psychology*, 53(1), 53–81.
- Newman, S. D., Ikuta, T., & Burns, T. (2010). The effect of semantic relatedness on syntactic analysis: An fMRI study. *Brain and Language*, 113(2), 51–58.
- Novais-Santos, S., Gee, J., Shah, M., Troiani, V., Work, M., & Grossman, M. (2007). Resolving sentence ambiguity with planning and working memory resources: Evidence from fMRI. *NeuroImage*, 37(1), 361–378.

- Núñez, S. C., Dapretto, M., Katzir, T., Starr, A., Bramen, J., Kan, E., ... Sowell, E. R. (2011). fMRI of syntactic processing in typically developing children: Structural correlates in the inferior frontal gyrus. *Developmental Cognitive Neuroscience*, 1(3), 313–323.
- Oberauer, K., Kliegl, R., & Klaus. (2006). A formal model of capacity limits in working memory. *Journal of Memory and Language*, 55(4), 601–626.
- Ogawa, S., Lee, T. M., Kay, A. R., & Tank, D. W. (1990). Brain magnetic resonance imaging with contrast dependent on blood oxygenation. *Proceedings of the National Academy of Sciences of the United States of America*, 87(24), 9868–9872.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, 9(1), 97–113.
- Opitz, B., & Friederici, A. D. (2004). Brain correlates of language learning: The neuronal dissociation of rule-based versus similarity-based learning. *The Journal of Neuroscience*, 24(39), 8436–8440.
- Opitz, B., & Friederici, A. D. (2007). Neural basis of processing sequential and hierarchical syntactic structures. *Human Brain Mapping*, 28(7), 585–592.
- Papagno, C., Cecchetto, C., Reati, F., & Bello, L. (2007). Processing of syntactically complex sentences relies on verbal short-term memory: Evidence from a short-term memory patient. *Cognitive Neuropsychology*, 24(3), 292–311.
- Peelle, J. E., McMillan, C., Moore, P., Grossman, M., & Wingfield, A. (2004). Dissociable patterns of brain activity during comprehension of rapid and syntactically complex speech: Evidence from fMRI. *Brain and Language*, 91(3), 315–325.

- Perani, D., Saccuman, M. C., Scifo, P., Anwander, A., Spada, D., Baldoli, C., ... Friederici, A. D. (2011). Neural language networks at birth. *Proceedings of the National Academy of Sciences of the United States of America*, 108(38), 16056–16061.
- Petanjek, Z., Judas, M., Kostović, I., & Uylings, H. B. M. (2008). Lifespan alterations of basal dendritic trees of pyramidal neurons in the human prefrontal cortex: A layer-specific pattern. *Cerebral Cortex*, 18(4), 915–29.
- Peterson, L., & Peterson, M. (1959). Short-term retention of individual verbal items. *Journal of Experimental Psychology*, 58(3), 193–198.
- Picard, N., & Strick, P. L. (2001). Imaging the premotor areas. *Current Opinion in Neurobiology*, 11(6), 663–672.
- Portrat, S., Camos, V., & Barrouillet, P. (2009). Working memory in children: A time-constrained functioning similar to adults. *Journal of Experimental Child Psychology*, 102(3), 368–374.
- Rakic, P., Bourgeois, J. P., Eckenhoff, M. F., Zecevic, N., & Goldman-Rakic, P. S. (1986). Concurrent overproduction of synapses in diverse regions of the primate cerebral cortex. *Science*, 232, 232–235.
- Ravizza, S. M., Hazeltine, E., Ruiz, S., & Zhu, D. C. (2011). Left TPJ activity in verbal working memory: Implications for storage- and sensory-specific models of short term memory. *NeuroImage*, 55(4), 1836–1846.
- Reiss, A. L., Abrams, M. T., Singer, H. S., Ross, J. L., & Denckla, M. B. (1996). Brain development, gender and IQ in children. A volumetric imaging study. *Brain*, 119 (5), 1763–1774.

- Richardson, F. M., Thomas, M. S. C., Filippi, R., Harth, H., & Price, C. J. (2010). Contrasting effects of vocabulary knowledge on temporal and parietal brain structure across lifespan. *The Journal of Cognitive Neuroscience*, 22(5), 943–954.
- Roberts, L., Marinis, T., Felser, C., & Clahsen, H. (2007). Antecedent priming at trace positions in children's sentence processing. *Journal of Psycholinguistic Research*, 36(2), 175–188.
- Rodd, J. M., Davis, M. H., & Johnsrude, I. S. (2005). The neural mechanisms of speech comprehension: fMRI studies of semantic ambiguity. *Cerebral Cortex*, 15(8), 1261–1269.
- Röder, B., Stock, O., Neville, H., Bien, S., & Rösler, F. (2002). Brain activation modulated by the comprehension of normal and pseudo-word sentences of different processing demands: A functional magnetic resonance imaging study. *NeuroImage*, 15(4), 1003–1014.
- Rüschemeyer, S.-A., Fiebach, C. J., Kempe, V., & Friederici, A. D. (2005). Processing lexical semantic and syntactic information in first and second language: fMRI evidence from German and Russian. *Human Brain Mapping*, 25(2), 266–286.
- Santi, A., & Grodzinsky, Y. (2007). Working memory and syntax interact in Broca's area. *NeuroImage*, 37(1), 8–17.
- Santi, A., & Grodzinsky, Y. (2010). fMRI adaptation dissociates syntactic complexity dimensions. *NeuroImage*, 51(4), 1285–1293.
- Saur, D., Kreher, B. W., Schnell, S., Kümmerer, D., Kellmeyer, P., Vry, M.-S., ... Weiller, C. (2008). Ventral and dorsal pathways for language. *Proceedings of the National Academy of Sciences of the United States of America*, 105(46), 18035–18040.
- Scheerer, E. (1980). Wilhelm Wundt's psychology of memory. *Psychological Research*, 42(1-2), 135–155.

- Schipke, C. S., Knoll, L. J., Friederici, A. D., & Oberecker, R. (2012). Preschool children's interpretation of object-initial sentences: Neural correlates of their behavioral performance. *Developmental Science*, 15(6), 762–774.
- Schlaggar, B. L., Brown, T. T., Lugar, H. M., Visscher, K. M., Miezin, F. M., & Petersen, S. E. (2002). Functional neuroanatomical differences between adults and school-age children in the processing of single words. *Science*, 296, 1476–1479.
- Schmahmann, J. D. (1996). From movement to thought: Anatomic substrates of the cerebellar contribution to cognitive processing. *Human Brain Mapping*, 4(3), 174–198.
- Schmithorst, V. J., Holland, S. K., & Plante, E. (2006). Cognitive modules utilized for narrative comprehension in children: A functional magnetic resonance imaging study. *NeuroImage*, 29(1), 254–266.
- Schmithorst, V. J., Holland, S. K., & Plante, E. (2007). Object identification and lexical/semantic access in children: A functional magnetic resonance imaging study of word-picture matching. *Human Brain Mapping*, 28(10), 1060–1074.
- Schubotz, R. I. (2007). Prediction of external events with our motor system: Towards a new framework. *Trends in Cognitive Sciences*, 11(5), 211–218.
- Schwartz, M., Rothermich, K., & Kotz, S. A. (2012). Functional dissociation of pre-SMA and SMA-proper in temporal processing. *NeuroImage*, 60(1), 290–298.
- Shaw, P., Greenstein, D., Lerch, J., Clasen, L., Lenroot, R., Gogtay, N., ... Giedd, J. (2006). Intellectual ability and cortical development in children and adolescents. *Nature*, 440, 676–679.

- Sheldon, A. (1977). On strategies for processing relative clauses: A comparison of children and adults. *Journal of Psycholinguistic Research*, 6(4), 305–318.
- Simonds, R. J., & Scheibel, A. B. (1989). The postnatal development of the motor speech area: a preliminary study. *Brain and Language*, 37(1), 42–58.
- Skeide, M. A. (2012). *Syntax and semantics networks in the developing brain*. PhD Thesis, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig.
- Skeide, M. A., Brauer, J., & Friederici, A. D. (2014). Syntax gradually segregates from semantics in the developing brain. *NeuroImage*, 100, 106–111.
- Sowell, E. R., Peterson, B. S., Thompson, P. M., Welcome, S. E., Henkenius, A. L., & Toga, A. W. (2003). Mapping cortical change across the human life span. *Nature Neuroscience*, 6(3), 309–315.
- Sowell, E. R., Thompson, P. M., Leonard, C. M., Welcome, S. E., Kan, E., & Toga, A. W. (2004). Longitudinal mapping of cortical thickness and brain growth in normal children. *The Journal of Neuroscience*, 24(38), 8223–8231.
- Sowell, E. R., Thompson, P. M., & Toga, A. W. (2004). Mapping changes in the human cortex throughout the span of life. *The Neuroscientist*, 10(4), 372–392.
- Stabler, E. (1994). The finite connectivity of linguistic structure. In C. Clifton, L. Frazier, & K. Rayner (Eds.), *Perspectives on sentence processing* (pp.303–336). Mahwah, NJ: Lawrence Erlbaum Assoc Publ.
- Stiles, J., & Jernigan, T. L. (2010). The basics of brain development. *Neuropsychology Review*, 20(4), 327–348.

- Stromswold, K., Caplan, D., Alpert, N., & Rauch, S. (1996). Localization of syntactic comprehension by positron emission tomography. *Brain and Language*, 52(3), 452–473.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain: 3-dimensional proportional system: An approach to cerebral imaging*. Stuttgart: Thieme.
- Tanaka, C., Matsui, M., Uematsu, A., Noguchi, K., & Miyawaki, T. (2012). Developmental trajectories of the fronto-temporal lobes from infancy to early adulthood in healthy individuals. *Developmental Neuroscience*, 34(6), 477–487.
- Tavakolian, S. L. (1981). The conjoined-clause analysis of relative clauses. In S. L. Tavakolian, *Language acquisition and linguistic theory* (pp. 167–187). Cambridge, Mass: MIT Press.
- Tewes, U. (2003). *Intelligenzdiagnostik bei Kindern und Jugendlichen mit dem HAWIK-III*. Bern: Huber.
- Thomason, M. E., Race, E., Burrows, B., Whitfield-Gabrieli, S., Glover, G. H., & Gabrieli, J. D. E. (2009). Development of spatial and verbal working memory capacity in the human brain. *Journal of Cognitive Neuroscience*, 21(2), 316–332.
- Townsend, J. T., & Ashby, F. G. (1983). *The stochastic modeling of elementary psychological processes*. Cambridge, Mass.: Cambridge Univ. Press.
- Towse, J. N., & Hitch, G. J. (1995). Is there a relationship between task demand and storage space in tests of working memory capacity? *The Quarterly Journal of Experimental Psychology Section A*, 48(1), 108–124.
- Towse, J. N., Hitch, G. J., & Hutton, U. (1998). A reevaluation of working memory capacity in children. *Journal of Memory and Language*, 39(2), 195–217.

- Vannest, J. J., Karunanayaka, P. R., Altaye, M., Schmithorst, V. J., Plante, E. M., Eaton, K. J., ... Holland, S. K. (2009). Comparison of fMRI data from passive listening and active-response story processing tasks in children. *Journal of Magnetic Resonance Imaging*, 29(4), 971–976.
- Vasishth, S., Suckow, K., Lewis, R. L., & Kern, S. (2010). Short-term forgetting in sentence comprehension: Crosslinguistic evidence from verb-final structures. *Language and Cognitive Processes*, 25(4), 533–567.
- Vygotsky, L. S. (1986). *Thought and language* (Edition: Revised.). Cambridge, Mass: University Press Group Ltd.
- Vygotsky, L. S. (1962). *Thought and language*. Cambridge, MA: MIT Press.
- Wang, M. D. (1970). The role of syntactic complexity as a determiner of comprehensibility. *Journal of Verbal Learning & Verbal Behavior*, 9(4), 398–404.
- Wanner, E., & Maratsos, M. (1978). An ATN approach to comprehension. Linguistic theory and psychological reality. In M. Halle, J. Bresnan, & G. Miller, *Linguistic theory and psychological reality* (pp.119–161). Cambridge: Cambridge University Press.
- Waters, G. S., & Caplan, D. (2001). Age, working memory, and on-line syntactic processing in sentence comprehension. *Psychology and Aging*, 16(1), 128–144.
- Weighall, A. R., & Altmann, G. T. M. (2010). The role of working memory and contextual constraints in children's processing of relative clauses. *Journal of Child Language*, 38(03), 579–605.
- Wilke, M., Schmithorst, V. J., & Holland, S. K. (2002). Assessment of spatial normalization of whole-brain magnetic resonance images in children. *Human Brain Mapping*, 17(1), 48–60.

- Wilson, S. M., Galantucci, S., Tartaglia, M. C., Rising, K., Patterson, D. K., Henry, M. L., ... Gorno-Tempini, M. L. (2011). Syntactic processing depends on dorsal language tracts. *Neuron*, 72(2), 397–403.
- Woolrich, M. W., Ripley, B. D., Brady, M., & Smith, S. M. (2001). Temporal autocorrelation in univariate linear modeling of FMRI data. *NeuroImage*, 14(6), 1370–1386.
- Wundt, W. (1874). *Grundzüge der physiologischen Psychologie* (2nd edition). Leipzig: Engelmann.
- Yeatman, J. D., Ben-Shachar, M., Glover, G. H., & Feldman, H. M. (2010). Individual differences in auditory sentence comprehension in children: An exploratory event-related functional magnetic resonance imaging investigation. *Brain and Language*, 114(2), 72–79.
- Zetzsche, T., Meisenzahl, E. M., Preuss, U. W., Holder, J. J., Kathmann, N., Leinsinger, G., ... Möller, H. J. (2001). In-vivo analysis of the human planum temporale (PT): Does the definition of PT borders influence the results with regard to cerebral asymmetry and correlation with handedness? *Psychiatry Research*, 107(2), 99–115.
- Zevin, J. D., Datta, H., & Skipper, J. I. (2012). Sensitive periods for language and recovery from stroke: Conceptual and practical parallels. *Developmental Psychobiology*, 54(3), 332–342.

Appendix

Stimuli from the behavioral study

No. Embedding Subclause

1	no	first	Der Igel ist rot, er lacht und er malt den Hund.
	single	first	Der Igel, der rot ist und der den Hund malt, lacht.
	double	first	Der Igel, der den Hund, der rot ist, malt, lacht.
2	no	second	Der Käfer ist braun, er weint und er malt den Frosch.
	single	second	Der Käfer, der braun ist und der den Frosch malt, weint.
	double	second	Der Käfer, der den Frosch, der braun ist, malt, weint.
3	no	third	Der Tiger ist grün, er weint und er malt den Hund.
	single	third	Der Tiger, der grün ist und der den Hund malt, weint.
	double	third	Der Tiger, der den Hund, der grün ist, malt, weint.
4	no	first	Der Vogel ist grau, er lacht und er zieht den Frosch.
	single	first	Der Vogel, der grau ist und der den Frosch zieht, lacht.
	double	first	Der Vogel, der den Frosch, der grau ist, zieht, lacht.
5	no	second	Der Käfer ist blau, er lacht und er zieht den Hund.
	single	second	Der Käfer, der blau ist und der den Hund zieht, lacht.
	double	second	Der Käfer, der den Hund, der blau ist, zieht, lacht.
6	no	third	Der Tiger ist braun, er weint und er zieht den Frosch.
	single	third	Der Tiger, der braun ist und der den Frosch zieht, weint.
	double	third	Der Tiger, der den Frosch, der braun ist, zieht, weint.
7	no	first	Der Vogel ist blau, er weint und er schiebt den Hund.
	single	first	Der Vogel, der blau ist und der den Hund schiebt, weint.
	double	first	Der Vogel, der den Hund, der blau ist, schiebt, weint.
8	no	second	Der Igel ist blau, er lacht und er schiebt den Frosch.
	single	second	Der Igel, der blau ist und der den Frosch schiebt, lacht.
	double	second	Der Igel, der den Frosch, der blau ist, schiebt, lacht.
9	No	third	Der Tiger ist grün, er lacht und er schiebt den Hund.
	single	third	Der Tiger, der grün ist und der den Hund schiebt, lacht.
	double	third	Der Tiger, der den Hund, der grün ist, schiebt, lacht.

10	No	first	Der Vogel ist braun, er weint und er trägt den Frosch.
	Single	first	Der Vogel, der braun ist und der den Frosch trägt, weint.
	double	first	Der Vogel, der den Frosch, der braun ist, trägt, weint.
11	No	second	Der Igel ist grün, er weint und er trägt den Hund.
	single	second	Der Igel, der grün ist und der den Hund trägt, weint.
	double	second	Der Igel, der den Hund, der grün ist, trägt, weint.
12	No	third	Der Käfer ist gelb, er lacht und er trägt den Frosch.
	Single	third	Der Käfer, der gelb ist und der den Frosch trägt, lacht.
	double	third	Der Käfer, der den Frosch, der gelb ist trägt, lacht.
13	No	first	Der Vogel ist rot, er lacht und er wäscht den Hund.
	Single	first	Der Vogel, der rot ist und der den Hund wäscht, lacht.
	double	first	Der Vogel, der den Hund, der rot ist, wäscht, lacht.
14	No	second	Der Igel ist gelb, er weint und er wäscht den Frosch.
	single	second	Der Igel, der gelb ist und der den Frosch wäscht, weint.
	double	second	Der Igel, der den Frosch, der gelb ist, wäscht, weint.
15	No	third	Der Käfer ist grau, er weint und er wäscht den Hund.
	single	third	Der Käfer, der grau ist und der den Hund wäscht, weint.
	double	third	Der Käfer, der den Hund, der grau ist, wäscht, weint.
16	No	first	Der Tiger ist grau, er lacht und er kämmt den Frosch.
	Single	first	Der Tiger, der grau ist und der den Frosch kämmt, lacht.
	double	first	Der Tiger, der den Frosch, der grau ist ist, kämmt, lacht.
17	No	second	Der Igel ist gelb, er lacht und er kämmt den Hund.
	single	second	Der Igel, der gelb ist und der den Hund kämmt, lacht.
	double	second	Der Igel, der den Hund, der gelb ist, kämmt, lacht.
18	No	third	Der Käfer ist rot, er weint und er kämmt den Frosch.
	Single	third	Der Käfer, der rot ist und der den Frosch kämmt, weint.
	Double	third	Der Käfer, der den Frosch, der rot ist, kämmt, weint.

*Stimuli from the fMRI study***No. Condition**

- | | | |
|----|----------|--|
| 1 | Baseline | Der Vogel weint, er kämmt den Frosch und er ist blau. |
| | Single | Der Vogel, der weint und der den Frosch kämmt, ist blau. |
| | Double | Der Vogel, der den Frosch, der weint, kämmt, ist blau. |
| 2 | Baseline | Der Vogel lacht, er wäscht den Frosch und er ist braun. |
| | Single | Der Vogel, der lacht und der den Frosch wäscht, ist braun. |
| | Double | Der Vogel, der den Frosch, der lacht, wäscht, ist braun. |
| 3 | Baseline | Der Käfer ist lacht, er trägt den Frosch und er ist braun. |
| | Single | Der Käfer, der lacht und der den Frosch trägt, ist braun. |
| | Double | Der Käfer, der den Frosch, der lacht, trägt, ist braun. |
| 4 | Baseline | Der Tiger weint, er zieht den Frosch und er ist grau. |
| | Single | Der Tiger, der weint und der den Frosch zieht, ist grau. |
| | Double | Der Tiger, der den Frosch, der weint, zieht, ist grau. |
| 5 | Baseline | Der Käfer weint, er malt den Hund und er ist gelb. |
| | Single | Der Käfer, der weint und der den Hund malt, ist gelb. |
| | Double | Der Käfer, der den Hund, der weint, malt, ist gelb. |
| 6 | Baseline | Der Vogel lacht, er trägt den Hund und er ist grau. |
| | Single | Der Vogel, der lacht und der den Hund trägt, ist grau. |
| | Double | Der Vogel, der den Hund, der lacht, trägt, ist grau. |
| 7 | Baseline | Der Tiger weint, er wäscht den Hund und er ist grün. |
| | Single | Der Tiger, der weint und der den Hund wäscht, ist grün. |
| | Double | Der Tiger, der den Hund, der weint, wäscht, ist grün. |
| 8 | Baseline | Der Tiger lacht, er schiebt den Hund und er ist rot. |
| | Single | Der Tiger, der lacht und der den Hund schiebt, ist rot. |
| | Double | Der Tiger, der den Hund, der lacht, schiebt, ist rot. |
| 9 | Baseline | Der Igel ist gelb, er wäscht den Frosch und er weint. |
| | Single | Der Igel, der gelb ist und der den Frosch wäscht, weint. |
| | Double | Der Igel, der den Frosch, der gelb ist, wäscht, weint. |
| 10 | Baseline | Der Vogel ist grau, er malt den Frosch und er weint. |
| | Single | Der Vogel, der grau ist und der den Frosch malt, weint. |
| | Double | Der Vogel, der den Frosch, der grau ist, malt, weint. |

- | | | |
|----|----------|--|
| 11 | Baseline | Der Käfer ist rot, er zieht den Frosch und er lacht. |
| | Single | Der Käfer, der rot ist und der den Frosch zieht, lacht. |
| | Double | Der Käfer, der den Frosch, der rot ist, zieht, lacht. |
| 12 | Baseline | Der Igel ist rot, er schiebt den Frosch und er lacht. |
| | Single | Der Igel, der rot ist und der den Frosch schiebt, lacht. |
| | Double | Der Igel, der den Frosch, der rot ist, schiebt, lacht. |
| 13 | Baseline | Der Vogel ist blau, er schiebt den Hund und er weint. |
| | Single | Der Vogel, der blau ist und der den Hund schiebt, weint. |
| | Double | Der Vogel, der den Hund, der blau ist, schiebt, weint. |
| 14 | Baseline | Der Tiger ist blau, er malt den Hund und er lacht. |
| | Single | Der Tiger, der blau ist und der den Hund malt, lacht. |
| | Double | Der Tiger, der den Hund, der blau ist, malt, lacht. |
| 15 | Baseline | Der Igel ist gelb, er trägt den Hund und er weint. |
| | Single | Der Igel, der gelb ist und der den Hund trägt, weint. |
| | Double | Der Igel, der den Hund, der gelb ist, trägt, weint. |
| 16 | Baseline | Der Käfer ist grau, er wäscht den Hund und er lacht. |
| | Single | Der Käfer, der grau ist und der den Hund wäscht, lacht. |
| | Double | Der Käfer, der den Hund, der grau ist, wäscht, lacht. |

Filler

Subclause Condition

- | | | |
|-------|----------|--|
| First | Baseline | Der Tiger ist braun, er kämmt den Frosch und er lacht. |
| | Single | Der Tiger, der braun ist und der den Frosch kämmt, lacht. |
| | Double | Der Tiger, der den Frosch, der braun ist, kämmt, lacht. |
| First | Baseline | Der Vogel ist rot, er zieht den Hund und er weint. |
| | Single | Der Vogel, der rot ist und der den Hund zieht, weint. |
| | Double | Der Vogel, der den Hund, der rot ist, zieht, weint. |
| First | Baseline | Der Käfer weint, er schiebt den Frosch und er ist gelb. |
| | Single | Der Käfer, der weint und der den Frosch schiebt, ist gelb. |
| | Double | Der Käfer, der den Frosch, der weint, schiebt, ist gelb. |
| First | Baseline | Der Igel lacht, er kämmt den Hund und er ist grün. |
| | Single | Der Igel, der lacht und der den Hund kämmt, ist grün. |
| | Double | Der Igel, der den Hund, der lacht, kämmt, ist grün. |

Appendix

Second	Baseline	Der Igel lacht, er malt den Frosch und er ist blau.
	Single	Der Igel, der lacht und der den Frosch malt, ist blau.
	Double	Der Igel, der den Frosch, der lacht, malt, ist blau.
Second	Baseline	Der Käfer ist grün, er kämmt den Hund und er weint.
	Single	Der Käfer, der grün ist und der den Hund kämmt, weint.
	Double	Der Käfer, der den Hund, der grün ist, kämmt, weint.

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Abbreviations

ANOVA	analysis of variance
ART	adjusted rank transformation
BA	Brodmann area
BOLD	blood-oxygen-level dependent
DARTEL	diffeomorphic anatomical registration through exponentiated lie algebra
EEG	electroencephalography
EPI	echo planar imaging
FLASH	fast low angle shot
fMRI	functional magnetic resonance imaging
FOP	frontal operculum
FOV	field of view
FWHM	full width at half maximum
GLM	general linear model
GMP	gray matter probability
HDR	hemodynamic response
IES	inverse efficiency score
IFG	inferior frontal gyrus
IFS	inferior frontal sulcus
IPL	inferior parietal lobe
IPL/STG	inferior parietal lobe extending to eh superior temporal gyrus
ITG	inferior temporal gyrus
K-ABC	Kaufman Assessment Battery for Children
MNI	Montreal Neurological Institute

MP-RAGE	magnetization-prepared rapid gradient echo
MR	magnetic resonance
MRI	magnetic resonance imaging
MTG	middle temporal gyrus
PET	positron emission tomography
PO	pars opercularis
ROI	region of interest
SMA	supplementary motor area
SMG	supramarginal gyrus
SNR	signal-to-noise ratio
STG	superior temporal gyrus
STS	superior temporal sulcus
TE	echo time
TI	inversion time
TIV	total intracranial volume
TPM	tissue probability map
TR	repetition time
TROG-D	German version of the Test for the Reception of Grammar
VBM	voxel-based morphometry

Summary of the dissertation

The human brain is an impressive organ. During the course of evolution the brain's volume and with it its complexity increased. Especially the differentiation of the frontal lobe enables humans to highly specialized, cognitive processes like language processing. Brain development during ontogeny follows an innate, genetically determined development. Nonetheless, by its plasticity the human brain is also highly adaptive and open to lifelong learning processes. However, the plasticity of the brain decreases with age and with it learning in different cognitive domains changes from being effortless, unconscious, and implicit to being more effortful, conscious, and explicit. These changes in learning processes can be observed, in particular, during language acquisition. While infants and toddlers acquire new words and sentences extremely fast and without much effort, the learning of a foreign language can be quite challenging for adults. Especially the learning of grammatical aspects of a new language becomes more effortful with age.

Although the conjoint occurrence between brain-related changes, the decrease of plasticity, and changes in learning processes suggest a certain causality between these processes, concrete evidence for the relation between brain development, language processing, and language performance is rare. Therefore, the current dissertation investigates the tripartite relationship between behavior (in the form of language

performance and cognitive maturation as prerequisite for language processing), brain structure (in the form of gray matter maturation), and brain function (in the form of brain activation evoked by complex sentence processing).

In the first study, the processing of center-embedded sentences in 5- and 6-year-old children ($N = 22$), 7- and 8-year-old children ($N = 22$), and adults ($N = 20$) was tested. Center-embedded sentences were selected because they contain the recursive embedding of subclauses and the capacity to process this kind of recursion has been postulated to be the core of the human language faculty (Hauser, Chomsky, & Fitch, 2002). Moreover, the processing of center-embedded sentences requires sufficient verbal working memory capacity and, therefore, these sentences offer the possibility to test the relation between cognitive prerequisites and complex sentence processing. More specifically, if the verbal working memory capacity does not suffice, difficulties in processing center-embedded sentences are expected since the processing of these sentences requires the storage of multiple interrupted subclauses. Furthermore, long-distance dependencies in these sentences require the representation of the first noun phrase over a certain period of time until it can be integrated with its corresponding final verb phrase into the overall sentence meaning. To test the processing of embedded sentence structures, subjects were presented with non-embedded sentences such as 'Der Käfer ist blau, er lacht und er zieht den Hund.', single embedded

sentences such as 'Der Käfer, der blau ist und der den Hund zieht, lacht.' as well as double embedded sentences such as 'Der Käfer, der den Hund, der blau ist, zieht, lacht.' In parallel to the auditory presentation of these sentences, subjects saw two pictures: one matching the sentence and one not matching the sentence. Subjects were asked to pick the correct picture via button press as fast as possible. Minimal differences between these pictures (color differences, the opposite agent-patient relationship or the exchange of the depicted emotions) tested the comprehension of each subclause. After the experiment, verbal working memory capacity was determined by a digit span test.

Results of this study indicate that children between 5 and 8 years show difficulties in processing double embedded sentences. As hypothesized, the amount of correct responses for these type of sentences is positively correlated with their verbal working memory capacity. In 7- and 8-year-old children, it was found that especially the processing of long-distance dependencies between the initial phrase and its corresponding verb appears to be associated with the subject's verbal working memory capacity since only performance for this specific subclause and digit span correlated. These findings support proposals for cognitive changes of the task-switching account (Towse & Hitch, 1995) which postulates higher verbal working memory capacity to be related to a higher processing speed. Following this postulation, children with a higher digit span may show increased performance since they are able to

process all elements in the sentence before the onset of a time-based decay of the representation of the initial noun phrase. In contrast, children's performance in the younger age group did not correlate with digit span. However, previous behavioral studies show that German-speaking children of this age group cannot reliably process morphological information yet (Dittmar, Abbot-Smith, Lieven, & Tomasello, 2008; Schipke, Knoll, Friederici, & Oberecker, 2012). A positive correlation between their performance for double embedded sentences and their performance in a standardized sentence comprehension test, the German version of the Test for the Reception of Grammar (TROG-D; Fox, 2006), supports the hypothesis that processing difficulties in this age group may be mainly attributed to difficulties in processing case marking information.

However, it remains an open question to what extent different processing strategies influence complex sentence comprehension. While adults are able to maintain elements of a sentence over a longer period of time via subvocal rehearsal, children before 7 years of age do not spontaneously use this kind of strategy (e.g. Gathercole & Hitch, 1993; Gathercole, Pickering, Ambridge, & Wearing, 2004) which may facilitate complex sentence processing. Thus, although the first study of this dissertation provides evidence that sufficient verbal working memory capacity constitutes a necessary cognitive prerequisite for successful complex sentence comprehension, further investigations need to clarify qualitative processing differences in the different age groups. Functional

brain imaging provides the opportunity to measure these qualitative differences represented by differences in brain activity evoked by complex sentence processing. However, to allow for a substantiated interpretation of brain functional activity in different age groups, functional activity needs to be related to cortical maturation. Therefore, the second study addresses the maturational degree of the gray matter in language-relevant brain areas in children and whether different degrees of gray matter maturation can be related to differences in language performance.

While the brain volume rapidly increases until 6 years of age (Courchesne et al., 2000; Lenroot & Giedd, 2006; Reiss, Abrams, Singer, Ross, & Denckla, 1996), gray matter already starts to decrease during preadolescence (Giedd et al., 1999; Gogtay et al., 2004; Sowell, Thompson, & Toga, 2004). This loss of gray matter volume is region-specific (Lenroot & Giedd, 2006) following a functional maturation sequence whereas primary sensorimotor areas mature first and higher-order association areas last (Gogtay et al., 2004). Interestingly, the decrease of gray matter in frontal and parietal regions, which are assumed to subserve language processing, starts between 7 and 12 years of age (Giedd et al., 1999; Sowell et al., 2003). This period of time parallels the end of the sensitive phase for grammar acquisition (Johnson & Newport, 1989) which suggests a relation between the brain plasticity of these areas and language performance. In order to investigate whether the amount of gray matter in language-relevant brain areas is related to

children's grammatical skills, voxel-based morphometry (VBM) was applied to analyze structural brain images from 49 children (24 boys, 25 girls; mean age: 6;9 years, age range: 5;3 - 8;5 years). This technique allows for the determination of each brain voxel's probability to belong to either gray or white matter. In the subsequent statistical analysis, the computed gray matter probability was correlated to children's TROG-D scores. However, only values representing complex sentence processing were used. To disentangle different aspects of complex sentence processing, a principle component analysis on these values was applied. This analysis extracted two factors: one representing children's ability to assign thematic roles, the other representing verbal working memory-related performance for complex sentence processing.

Gray matter probabilities and factor scores representing thematic role assignment were positively correlated in the left inferior temporal cortex as well as in the left hippocampus. Functional imaging studies indicate the relevance of these regions for the processing of semantic-lexical aspects during sentence comprehension (Crinion, Lambon-Ralph, Warburton, Howard, & Wise, 2003; Hickok & Poeppel, 2004, 2007; Leff et al., 2008). Furthermore, since previous studies found that the left inferior frontal gyrus is activated whenever thematic role assignment is considerably more difficult because of a non-canonical word order in the sentence structure (Bornkessel, Zysset, Friederici, von Cramon, & Schleesewsky, 2005; Fiebach, Schleesewsky, Lohmann, von Cramon, &

Friederici, 2005; Friederici, Fiebach, Schlesewsky, Bornkessel, & Cramon, 2006; Grewe et al., 2005; Röder, Stock, Neville, Bien, & Rösler, 2002), the search volume of the VBM analysis was restricted to this region. A positive correlation between the first factor and the gray matter probability of the left inferior frontal gyrus confirms a relation between structural properties of this area and performance associated with thematic role assignment. Factor scores representing verbal working memory-related performance for complex sentence processing and gray matter probabilities were positively correlated in the left parietal operculum extending to the left posterior superior temporal gyrus. Functional data of previous studies show that this region is activated by increased storage demands of verbal material and therefore may support verbal working memory (Meyer, Obleser, Anwander, & Friederici, 2012; Novais-Santos et al., 2007). Thus, findings of the second study of the current dissertation confirm correlations between the amount of gray matter in language-relevant brain areas and children's language skills concerning complex sentence processing. Nonetheless, further research is needed to clarify if the increased gray matter probability in these regions comes as cortical prerequisite or if these different values represent different stages of cortical maturation.

The third study investigated the development of functional activation evoked by processing center-embedded sentence structures. Again 5- and 6-year-old (N = 18) and 7- and 8-year-old children (N = 20)

as well as adults ($N = 21$) were tested. During functional scanning, non-embedded sentences, single embedded sentences, and double embedded sentences were auditorily presented. As in the behavioral study, subjects saw two pictures and were asked to choose the correct one via button press. Since not all aspects of complex sentence processing can be implemented into a single, child-friendly fMRI design, the following restrictions were made: First, in order to focus the investigation on embedded sentence structures, the activation for non-embedded sentences was subtracted as complex baseline from the single and double embedded sentences. Second, the experimental condition focused on the comprehension of long-distance dependencies between the initial noun phrase and the final verb phrase. The restriction to this subclause was chosen since data of the behavioral study indicate a correlation between the processing of the long-distance dependencies in double embedded sentence and verbal working memory capacities. Thus, changes in activation patterns across age groups may clarify the effect of limited verbal working memory capacity on complex sentence processing. Other picture pairs testing the comprehension of the additional subclauses served as filler items.

The functional data revealed that adults and children activated a qualitatively comparable network of language-relevant brain regions while processing center-embedded sentences: the left pars opercularis, the left inferior parietal cortex extending to the left posterior superior temporal

gyrus, the supplementary motor area, and the cerebellum. However, only adults show a functional selectivity of these regions marked by an increase of activation parallel to the increase of sentence complexity. In contrast, children show comparable activation for single and double embedded sentences. In addition, the attunement towards an adult-like language development is reflected in the development of the relation between the different brain regions within the language network. While the activation in the left pars opercularis is predicted by the functional activation of the inferior parietal lobe extending to the left posterior superior temporal gyrus in adults, it is predicted by the functional activation of the supplementary motor area in the 5- and 6-year-olds. The older children represent an intermediate pattern with activation in both regions predicting the activation in the left pars opercularis.

A more detailed analysis of changes in brain activation across age groups for each specific sentence structure revealed that the functional selectivity in the left pars opercularis and in the supplementary motor areas develops by a decrease of activation for single embedded sentence structures, whereas the functional selectivity of the left inferior parietal lobe extending to the posterior superior temporal gyrus develops by an increase of activation for double embedded sentence structures. Functional selectivity of the cerebellum appears to depend on both increase and decrease of activation intensities for the respective condition. While the activation decrease for simple sentences in the left

pars opercularis is assumed to represent more efficient processing, the activation increase for complex sentences in the left inferior parietal lobe extending to the posterior superior temporal gyrus is suggested to represent the implementation of a verbal working memory-related strategy facilitating complex sentence processing. Increased cerebellar activity is proposed to reflect the application of timing and sequencing schemes provided by prosodic features to facilitate verbal working memory storage of embedded clauses.

To solve the question of the complex interplay between different maturational factors, the tripartite relation between cognitive, brain structural, and brain functional maturation was further investigated in the fourth study. To do this, multiple regression analyses were computed to test the predictive power of gray matter probability, verbal working memory capacity, and behavioral differences in performance for simple and complex sentence for the functional selectivity of each activated region. These analyses revealed that the establishment of the adult-like functional selectivity for complex sentences is predicted by a reduction of the left pars opercularis' gray matter probability across age groups. The same applies to the left inferior parietal lobe extending to the posterior superior temporal gyrus. Thus, gray matter maturation across age groups appears to have an important impact on the observed functional activation pattern in these regions. Furthermore, verbal working memory capacities are predictive for the functional activation pattern in the left inferior parietal

lobe extending to the posterior superior temporal gyrus and the cerebellum. Therefore, cognitive maturation appears to be associated with the development of the functional selectivity of those regions that may be engaged only by particular processing strategies.

Finally, the question rises whether higher functional selectivity is related to better performance. Indeed, correlative analyses confirm that the higher the functional selectivity of activation across brain regions, the better the performance for simple and complex sentences, while the latter correlation even remains independent of age.

Taken all findings together, the current dissertation provides evidence that complex sentence processing is related to cognitive (first study) and brain structural (second study) maturation. However, the data also indicate that these maturational processes are strongly associated with the development of brain functional activation in language-relevant brain areas and that the resulting functional selectivity of these regions is associated with more efficient sentence processing (third and fourth study). The fact that changes towards the adult-like performance and the adult-like activation pattern only emerge after 8 years of age suggests a relation of these changes to the closure of the specific time window for grammar acquisition.

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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List of publications

Articles

Fengler, A., & Friederici, A. D. (in prep.). Qualitative changes in children's complex sentence processing

Fengler, A., Meyer, L., & Friederici, A. D. (2015). Brain structural correlates of complex sentence comprehension in children. *Developmental Cognitive Neuroscience, 15*, 48-57.

Fengler, A., Meyer, L., & Friederici, A.D. (under review). How the brain attunes to language processing: Relating behavior, structure, and function.

Antonenko, D., Brauer, J., Meinzer, M., **Fengler, A.,** Kerti, L., Friederici, A.D., & Flöel, A. (2013). Functional and structural syntax networks in aging. *NeuroImage, 83*, 513 – 523.

Katsos, N., Ezeizabarrena, M.-J., Gavarró, A., Kuvac Kraljevic, J., Hrzica, G., Grohmann, K., Skordi, A., Jensen de López, K., Sundahl, L., van Hout, A., Hollebrandse, B., Overweg, J., Faber, M., van Koert, M., Cummins, C., Smith, N., Vija, M., Parm, S., Kunnari, S., Morisseau, T., Rusieshvili, M., Yatsushiro, K., **Hubert, A.,** Varlokosta, S., Konstantzou, K., Farby, S., Guasti, M. T., Vernice, M., Balciuniene, I., Ruzaitė, J., Grech, H., Gatt, D., Asbjørnsen, A., von Koss Torkildsen, J., Haman, E., Miekisz, A., Gagarina, N., Puzanova, J., Andjelkovic, D., Savic, M., Jošić, S., Slancová, D., Kapalková, S., Barberán Recalde, T., Özge, D., Hassan, S., van der Lely, H., Sauerland, U., & Noveck, I. (2012). The acquisition of quantification across languages: Some predictions. In A. K. Biller (Ed.), *Proceedings of the 36th Annual Boston University Conference on Language Development: Vol. 1* (pp. 258-268). Somerville, MA: Cascadilla Press.

Kamandulyte, L., Fürst, B., **Hubert, A.**, Sauerland U. & Dressler, W.U. On The Acquisition of adjective gradation in Lithuanian and German. Paper presented at: *The Baltics as an Intersection of Civilizational Identities*. Conference on Baltic Studies; 2009, June, 17. Vytautas Magnus University, Kaunas, Lithuania.

Hubert, A. & U. Sauerland. (2009). Europäische Zusammenarbeit in der SLI-Forschung. Die Projekte COST A33 und CLAD. In J. Heide, S. Hanne, O-C.Brandt, T. Fritzsche & M. Wahl (Eds.), *Spektrum Patholinguistik (Band 2) - Schwerpunktthema: Ein Kopf – Zwei Sprachen: Mehrsprachigkeit in Forschung und Therapie*, 135-144. Potsdam: Universitätsverlag.

Talks

Hubert, A., Meyer, L., & Friederici, A. D. (2012). *Aktivierungen im Sprachnetzwerk des kindlichen Gehirns: Ein Zusammenspiel aus grammatischen Fähigkeiten, Arbeitsgedächtnisleistungen und neuroanatomischen Voraussetzungen*. Talk presented at Tagung der Gesellschaft für interdisziplinäre Spracherwerbsforschung und kindliche Sprachstörungen im deutschsprachigen Raum e.V. Leipzig, Germany.

Poster

Hubert, A., Meyer, L., & Friederici, A. D. (2013). *How Broca's area attunes to syntactic processing*. Poster presented at *19th Annual Meeting of the Organization for Human Brain Mapping (OHBM)*, Seattle, WA, USA.

Hubert, A., Meyer, L., Skeide, M. A., & Friederici, A. D. (2011). Children's language comprehension abilities correlate with gray matter density in the left inferior parietal lobe. Poster presented at *17th Annual Meeting of the Organization for Human Brain Mapping (OHBM)*, Quebec City, QC, Canada.

Hubert, A., & Friederici, A. D. (2011). Die Rolle der Arbeitsgedächtnisleistung 5- und 6-jähriger Kinder beim Verständnis rekursiver Satzstrukturen. Poster presented at *Tagung experimentell arbeitender Psychologen*, Halle, Germany.

van der Lely, H., Arosio, F., Avram, L., Dabasinskiene, I., Dressler, W. U., Fürst, B., Guasti, T., **Hubert, A.**, Ruzaitė, J., Sauerland, U., Yatsushiro, K. (2010). Cross-linguistic adaptation of the grammar and phonology screening (GAPS) test. Poster session presented at: *Let the children speak: Learning of critical language skills across 25 languages*. Final conference of the COST Action A33, London, UK.

Hubert, A. (2009). The acquisition of ellipsis and the recursive structure of the noun phrase. Poster presented at: *Recursion: Structural Complexity in Language and Cognition*, University of Massachusetts, Amherst, USA.

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