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How the brain attunes to sentence processing: Relating behavior, structure, and function

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ABSTRACT

Unlike other aspects of language comprehension, the ability to process complex sentences develops rather late in life. Brain maturation as well as verbal working memory (vWM) expansion have been discussed as possible reasons. To determine the factors contributing to this functional development, we assessed three aspects in different age-groups (5–6 years, 7–8 years, and adults): first, functional brain activity during the processing of increasingly complex sentences; second, brain structure in language-related ROIs; and third, the behavioral comprehension performance on complex sentences and the performance on an independent vWM test. At the whole-brain level, brain functional data revealed a qualitatively similar neural network in children and adults including the left pars opercularis (PO), the left inferior parietal lobe together with the posterior superior temporal gyrus (IPL/pSTG), the supplementary motor area, and the cerebellum. While functional activation of the language-related ROIs PO and IPL/pSTG predicted sentence comprehension performance for all age-groups, only adults showed a functional selectivity in these brain regions with increased activation for more complex sentences. The attunement of both the PO and IPL/pSTG toward a functional selectivity for complex sentences is predicted by region-specific gray matter reduction while that of the IPL/pSTG is additionally predicted by vWM span. Thus, both structural brain maturation and vWM expansion provide the basis for the emergence of functional selectivity in language-related brain regions leading to more efficient sentence processing during development.

Introduction

Language acquisition rests on coherent developmental trajectories on cognitive behavioral, brain structural, and brain functional levels. Children typically acquire their native language spontaneously and without conscious effort. Newborns are equipped with amazing implicit mechanisms to acquire each language they are exposed to, but their ability to discriminate non-native sound contrasts (Werker and Tees, 2002) or to automatically extract rules from the auditory input (Mueller et al., 2012) is dramatically reduced as the underlying brain systems mature (Citron et al., 2011). For languages learned after childhood, high proficiency can only be achieved via more explicit learning mechanisms (for a review, see Zevin et al., 2012), suggesting that native language acquisition is confined to a certain period (Lenneberg, 1967). Within this period, acquisition of native phonetic and prosodic processing skills take place during the first year of life (for a review, see Kuhl and Rivera-Gaxiola, 2008; Kuhl, 2004), whereas grammar acquisition, although starting before the age of 3 years (Hamburger and Crain, 1982; Weissenborn, 1994), extends until the age of 7 years (Dittmar et al., 2008; Johnson and Newport, 1989; Meisel, 2011; Zevin et al., 2012).

The observed developmental 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 structural brain maturation and language development found that receptive and productive phonological skills of children between 5 and 11 years correlate with measurements of gray matter probability (GMP) in the left inferior frontal gyrus (IFG; Lu et al., 2007), and that gray matter of the left supramarginal gyrus and left posterior temporal regions correlate with vocabulary knowledge in teenagers between 12 and 17 years of age (Richardson et al., 2010). In general, gray matter density decreases along development, with higher-order association regions decreasing later than lower-order sensorimotor regions (Brain Development Cooperative Group, 2012; Gogtay et al., 2004). Specifically, gray matter in those frontal and parietal brain regions that are involved in sentence processing in adults (for a review, see Friederici, 2011) only appears to decrease between 7 and 12 years (Giedd et al., 1999; Sowell et al., 2003), and recent structural imaging data have shown that the structural integrity of these regions correlates with the crucial cognitive abilities underlying complex sentence comprehension (Fengler et al., 2015).

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However, it is unclear whether the maturation of cortical gray matter constrains the functional attunement of language-relevant brain areas to sentence processing. In the fully matured adult brain, a functional dissociation of syntactic and semantic processing has been shown within the IFG (Goucha and Friederici, 2015; Newman et al., 2010), with the left PO being involved in syntactic processing, and semantic processes involving more anterior parts of the IFG (Friederici, 2011). Children, around the age of 6 years, however, do not yet show a similar functional segregation in the IFG (Brauer and Friederici, 2007; Skeide et al., 2014). Moreover, in adults, the left PO has been found to increase its activation with the complexity of sentences (Friederici, 2011; Kinno et al., 2008; Makuuchi et al., 2009; Newman et al., 2010; Röder et al., 2002), whereas a functional selectivity for sentence complexity in this region only emerges around the age of 6 years (Knoll et al., 2012). In adults, the processing of complex sentences, however, is not supported by the IFG alone, but rather by a frontotemporal network (Friederici, 2011). This network also includes the pSTG, which is thought to subserve the integration of syntactic and semantic information; in addition, the network involves the IPL, which is proposed to subserve verbal working memory (vWM) during sentence comprehension (Meyer et al., 2012). In children, the pSTG and the IPL are also part of the network active during sentence processing—at least in 6-years-olds (Brauer and Friederici, 2007; Knoll et al., 2012). Thus, there are indications that the functional language network develops toward an adult-like system around the age of 6 years. While developmental trajectories from children-like to adult-like functional activation patterns within this network have been described with respect to both brain functional changes and brain structural changes of the gray matter, descriptions of the tripartite relationship between brain structure, brain function, and behavioral performance are rare. From the two studies investigating the tripartite relationship at school age, one used orthographic naming (Lu et al., 2009) and the other a sentence comparison paradigm (Nuñez et al., 2011).

Here, we investigate three age-groups: children aged 5–6 years, aged 7–8 years and adults. We hypothesized that gray matter maturation of the language-relevant brain regions in the left hemisphere across age-groups may lead to adult-like brain activation patterns for complex sentence processing, and that more mature activation patterns are associated with better performance. In addition, a hypothesis concerning the vWM was formulated, based on the findings that the processing of complex sentences is memory-demanding (Felser et al., 2003a), and vWM expansion has been proposed as a crucial predictor of children's sentence processing skills between 6 and 8 years of age (Felser et al., 2003b; Montgomery et al., 2008; Weighall and Altmann, 2011). We hypothesized that the activation pattern for complex sentence processing may partially be predicted by activation in the IPL; in turn, the activation of the IPL should correlate with an increase of vWM span. To test these hypotheses, a number of different analyses were performed. First, to assess functional brain activation, we conducted functional magnetic resonance imaging (fMRI) during the processing of syntactically complex as compared to simple sentences in all three age-groups. Sentence complexity was operationalized by varying the number of embedded relative clauses with increasing levels of hierarchy systematically leading to more complex sentence structures (see Fig. 1). Previous studies attributed children's difficulties in processing relative clauses to limitations in the cognitive capacities such as vWM (e.g., Kidd and Bavin, 2002; Kidd et al., 2007), which result in a non-adult-like processing strategy (Felser et al., 2003b; Sheldon, 1977; Tavakolian, 1981). Behavioral performance on these sentences was assessed during fMRI scanning for each participant using a sentence–picture-matching paradigm (see Fig. 1 and Method Section). In addition to these sentence comprehension tests, the vWM capacity of each participant was measured by a standardized Digit Span test (Tewes, 1994). Second, to evaluate whether brain structural maturation underlies brain functional maturation, we conducted a voxel-based morphometry (VBM) analysis extracting the GMP for those regions of interests (ROIs) that are reported in the literature to support sentence processing (Friederici, 2011) and which in the present data showed increased functional activation during sentence processing in the whole-brain functional analysis. Based on prior studies, we expected functional activation in PO and STG as core parts of the language network and in IPL as a region supporting vWM during the processing of complex sentences. Third, to investigate which age-related

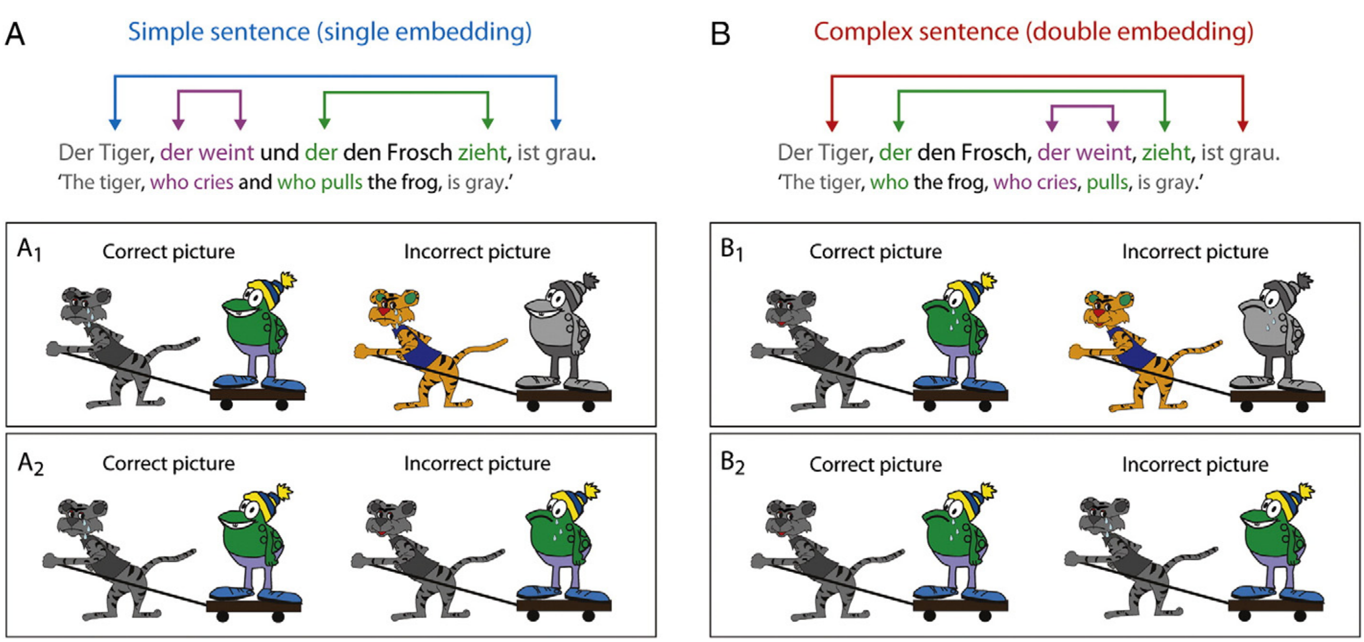

Fig. 1. Exemplary sentence materials and picture sets. Sentence complexity was manipulated by the number of embeddings. (A) Simple sentences contained a single relative clause and (B) complex sentences contained two relative clauses. In parallel to the auditory presentation of the simple and complex sentences, participants were presented with two pictures, one matching the stimulus sentence and one not matching the stimulus sentence. Picture set A_1 and B_1 illustrate stimuli of the experimental condition which tested the comprehension of the long-distance dependencies, picture set A_2 and B_2 are filler items which were included in order to prevent the application of processing strategies. Via button press participants indicated which of these pictures was the correct one.