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Functional organization of the language network in three- and six-year-old children

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ABSTRACT

The organization of the language network undergoes continuous changes during development as children learn to understand sentences. In the present study, functional magnetic resonance imaging and behavioral measures were utilized to investigate functional activation and functional connectivity (FC) in three-year-old (3yo) and six-year-old (6yo) children during sentence comprehension. Transitive German sentences varying the word order (subject-initial and object-initial) with case marking were presented auditorily. We selected children who were capable of processing the subject-initial sentences above chance level accuracy from each age group to ensure that we were tapping real comprehension. Both age groups showed a main effect of word order in the left posterior superior temporal gyrus (pSTG), with greater activation for object-initial compared to subject-initial sentences. However, age differences were observed in the FC between left pSTG and the left inferior frontal gyrus (IFG). The 6yo group showed stronger FC between the left pSTG and Brodmann area (BA) 44 of the left IFG compared to the 3yo group. For the 3yo group, in turn, the FC between left pSTG and left BA 45 was stronger than with left BA 44. Our study demonstrates that while task-related activation was comparable, the small behavioral differences between age groups were reflected in the underlying functional organization revealing the ongoing development of the neural language network.

1. Introduction

When children acquire language, they are confronted with the challenge to decode the relationship between the entities of an utterance, which requires identification of the specific grammatical and thematic roles each entity plays. To do so, they have to detect the linguistic cues and regularities that the particular language provides. In a transitive sentence, for instance, they have to identify the action and discriminate the actor from the patient of the action. Several cues are available to decode the relationship between noun phrases in a sentence (e.g., case marking, word order, animacy hierarchy). The weighting of these cues varies across language. A popular framework used to explore the acquisition of linguistic cues, the Competition Model (Bates, 1982; MacWhinney et al., 1984), proposes that consistency and frequency of a cue in a given language determine how early it will be learned. In a German transitive sentence like (1a), the word order indicates the first argument as the agent and the second as the patient, which coincides with the case marking cue expressed at the determiners of the noun phrases. The determiner *der* in German marks the nominative (NOM) singular (SING) case and assigns the agent role to the first noun, whereas the accusative (ACC) marking *den* on the second noun phrase indicates the patient role. In sentence (1b) that conveys the same semantic information, however, word order and case marking cues would suggest competing interpretations, in which case the latter is the reliable solution.

(1a) Der Fuchs trägt den Wolf.
The [NOM.SING] fox carries the [ACC.SING] wolf.
"The fox carries the wolf".
(1b) Den Wolf trägt der Fuchs.
The [ACC.SING] wolf carries the [NOM.SING] fox.
"The fox carries the wolf".

Assumptions of the Competition Model about the consecutive acquisition of such cues are supported by several behavioral observations. Dittmar et al. (2008) showed that two-year-old German children were capable of interpreting prototypical transitive sentences above chance level when word order and case marking cues were consistent. Moreover, Chan et al. (2009) extended this finding by demonstrating the transition of cue reliance towards word order in three age groups (2;6, 3;6 and 4;6) with the highest use of word order in the oldest group while the youngest still relied on a combination of two cues (word order

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and animacy). From the age of five, case marking becomes more pivotal for sentence interpretation than word order (Lindner, 2003; Schanerwolles, 1989), and children could rely on case marking over word order when the two cues conflicted only by the age of seven (Dittmar et al., 2008). These behavioral findings highlight two critical periods for the transition of cue acquisition: sentence comprehension relies more on word order at the ages of two to four and case marking becomes more prominent at the ages of five to seven.

In the context of syntactic cue processing, two brain regions have been consistently observed in the adult brain: the posterior part of the left superior temporal gyrus/sulcus (pSTG/pSTS) and a subdivision of the left inferior frontal gyrus (IFG), Brodmann area (BA) 44 (pars opercularis). These regions have been reported repeatedly in language studies dealing with the need to process syntactic relationships, such as reading sentences containing syntactic movement operations (Ben-Shachar et al., 2004), reading sentences opposed to word lists (Humphries et al., 2005; Snijders et al., 2009), or reading sentences with different levels of syntactic complexity (Friederici, 2011; Friederici et al., 2009; Santi and Grodzinsky, 2010). The left pSTG has been suggested to fulfill an integrative role in verb-argument-dependent information (i.e., lexico-semantic features of a verb which determine the predictability of an argument) in natural language processing (Friederici, 2011, 2012) and is often reported together with activation of the left IFG in experimental paradigms varying the degree of syntactic complexity (e.g., the number of embedded structures). The left IFG is an important region involved in complex syntactic processing and has been shown to be involved in processing of recursion (i.e., the ability of linguistic structure to contain itself) (Friederici et al., 2009). In another study, Friederici et al. (2006b) also demonstrated BA 44 as being sensitive to the degree of syntactic manipulation in grammatical sentences but insensitive to ungrammatical sentences that involved violations of phrase structure. This is concordant with findings on artificial grammar learning, in which BA 44 repeatedly showed activation for syntactic operations in expressions without lexical content (Bahlmann et al., 2006, 2007, 2008; Friederici et al., 2006a). Whereas activation of the left BA 44 is mostly found for syntactic processes, the more anterior part of the left IFG, namely BA 45 (pars triangularis), is thought to subserve semantic processing (Friederici, 2002, 2011; Newman et al., 2003, 2010; Wu et al., 2016). For instance, it has been interpreted as being involved in processing thematic aspects of verb semantics in a study by Newman et al. (2003), in which the presence of an extra verb elicited activation in BA 45 whereas activation for agreement violations was found in BA 44.

Recent studies have focused more on the functional interplay of the language network. A functional relationship between the left IFG and pSTG in the adult brain was shown earlier in resting state functional connectivity (FC) studies (Cordes et al., 2000; Kelly et al., 2010; Muller and Meyer, 2014; Zhu et al., 2014). Another study examined the low-frequency components of task activation residuals and showed connectivity between the left pSTG and BA 44 in language over non-language experiments (Lohmann et al., 2010). As indicated in studies on functional localization (e.g., Ben-Shachar et al., 2004; Friederici et al., 2006a), there is established knowledge of a general functional relationship between these two regions but only few studies investigated how FC is modulated by task requirements. Yue et al. (2013) found that FC between the left BA 44 and pSTG was higher in a sentence comprehension task requiring active responses compared to passive listening. In another study, FC between the left BA 45 and pSTG was found to be higher for intelligible compared to unintelligible speech processing (Ge et al., 2015). The functional relation between frontal and temporal regions of the language network has been described as a top-down relationship (Skeide and Friederici, 2016). One aspect of top-down processing may be that it focuses on task relevant components of the input and is thought to increase as development advances (Bitan et al., 2006, 2009). These latter findings indicate task responsiveness of the mature language network, although its particular role and possible modulations regarding syntactic processing remain to be further investigated.

Accounts have been made to track the development of the language network with age and to link them to behavioral changes. As demonstrated in a study on syntactic and semantic interaction in three- to ten-year-old children (Skeide et al., 2014), the specialization of the language network is gradually established as development progresses. The authors investigated sentence comprehension in children from three age groups (ages of three to four, six to seven, and nine to ten) using a picture matching task in which syntactic complexity and semantic plausibility of relative clauses were varied. An interaction of syntax and semantics was observed in the left mid to posterior STG for the youngest group of three- to four-year-olds. In addition to an interaction, the group of six- to seven-year-olds also showed a main effect of syntax in the left pSTG, whereas only the older children (nine- to ten-year-olds) showed an adult-like main effect of syntax in the left IFG (including BAs 44/45). Moreover, several developmental studies on language processing have shown that the neural organization undergoes several changes accompanied by behavioral changes. Nunez et al. (2011) found a correlation between syntactic proficiency and activation in the left BA 44 for the processing of complex syntax in children aged between seven and fifteen, with those who performed better in a standardized language task showing more prominent activation. Knoll et al. (2012) observed that activation of the left BA 44 was dependent on the grammatical capabilities of the children, and only the more proficient group of children showed adult-like activation for object-initial compared to subject-initial sentences. Wu et al. (2016) also reported a positive correlation between syntactic capability and brain activation in the left BA 44 and left pSTG/pSTS for processing non-canonical object-initial sentences in five-year-old children. These studies all showed that the correlation between behavioral proficiency and activation in the left fronto-temporal regions was independent of age.

While the development of the language network has gained increasing attention over the past ten years, research on its functional interplay especially in the context of syntactic processing remains sparse. Few studies investigating resting state functional connectivity in children reported a functional relationship between the left IFG and pSTS. Xiao et al. (2016a) found FC between the left BA44 and pSTS in five-year-old children associated with their understanding of object-initial transitive sentences assessed by an offline picture selection task and that this functional network develops with increasing syntactic abilities over one year from age 5 to age 6 (Xiao et al., 2016b). In a causal connectivity analysis in six- to fifteen-year-old children, Wilke et al. (2009) reported that in a “beep” story passive listening task (in which keywords were replaced by sinus tones) the left inferior frontal region (including BA 44) and the left posterior region (including pSTG) induced the strongest effect on other regions. However, they differed in the amount of input they received: lowest in the frontal and highest in the posterior regions. In addition, the development of structural connections also allows us to draw inferences on the information flow in the language network during different developmental stages. In a diffusion-weighted imaging study, Skeide et al. (2015) showed that fractional anisotropy (FA) of the dorsal pathway (connecting the left BA 44 and the left pSTG via the arcuate fasciculus) was significantly higher in six- to seven-year-olds compared to three- to four-year-olds, whereas the ventral route (connecting the left BA 45 and the left pSTG via the inferior fronto-occipital fasciculus) showed no difference in FA values between these age groups. Another series of studies also reported relatively late maturation of the arcuate fasciculus. Perani et al. (2011) demonstrated that in newborns the ventral pathway was already present, whereas the connection of the left BA 44 to the left pSTG was only detectable in seven-year-old children (Brauer et al., 2011, 2013). These findings suggest that the dorsal route from BA44 to pSTG needs a certain maturation status in order to be fully employed