



Syntax gradually segregates from semantics in the developing brain



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ABSTRACT

An essential computational component of the human language faculty is syntax as it regulates how words are combined into sentences. Although its neuroanatomical basis is well-specified in adults, its emergence in the maturing brain is not yet understood. Using event-related functional magnetic resonance imaging (fMRI) in a cross-sectional design, we discovered, that in contrast to what is known about adults 3-to-4- and 6-to-7-year-old children do not process syntax independently from semantics at the neural level already before these two types of information are integrated for the interpretation of a sentence. It is not until the end of the 10th year of life that children show a neural selectivity for syntax, segregated and gradually independent from semantics, in the left inferior frontal cortex as in the adult brain. Our results indicate that it takes until early adolescence for the domain-specific selectivity of syntax within the language network to develop.

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Introduction

Although only the interplay of syntax and semantics guarantees language comprehension, both functions are represented in segregated neural networks in the adult brain. While the pars opercularis of the left inferior frontal gyrus (left IFGoper) and the posterior portion of the left superior temporal gyrus (left pSTG) support complex syntactic processes (Friederici, 2011; Kinno et al., 2008; Makuuchi et al., 2009; Santi and Grodzinsky, 2010), the pars triangularis and the pars orbitalis of the left inferior frontal gyrus (left IFGtri/left IFGorb), together with parts of the temporal cortex, subserve semantic processes (Binder et al., 2009; Bruffaerts et al., 2013; Newman et al., 2010). In addition, the anterior portion of the left superior temporal gyrus (left aSTG) has been discussed as being involved in syntactic processing at the phrase level (Humphries et al., 2005, 2006; Snijders et al., 2009), as well as in combinatorial semantics (Bonner and Price, 2013; Reilly and Peelle, 2008; Rogalsky and Hickok, 2009; Vandenberghe et al., 2002).

Adults process syntactic and semantic features separately before finally integrating these two types of information for the interpretation of a sentence (Jackendoff, 2007). Accordingly, both language functions are experimentally separable both at the behavioral and the neural level (Friederici, 2011). In children, however, it has been demonstrated behaviorally that the syntactic analysis of a sentence is directly modulated by semantic features (Bates et al., 1984; Deutsch et al., 1999; Friederici, 1983). Children up to the age of 11 years performed significantly less accurate and slower in an on-line word-monitoring task when a target sentence, in which a function word had to be recognized,

was preceded by a semantically unrelated context sentence compared to a semantically related context sentence. Adults, however, did not show such an interaction of syntactic and semantic processes (Friederici, 1983). In line with the observation that syntax and semantics have a less autonomous status in children than in adults, it has been difficult to disentangle the neural networks underlying syntactic processing from those underlying semantic processing during sentence comprehension in developmental samples (Brauer and Friederici, 2007; Nuñez et al., 2011).

The goal of the present study was to test whether the long-lasting behavioral interdependence of syntactic and semantic information during development has its basis in the functional neuroarchitectonics. To this end, we used event-related fMRI in order to compare syntax- and semantics-related hemodynamic cortical activity at the whole-brain level cross-sectionally in children aged 3–4 years, 6–7 years and 9–10 years. The selection of the two youngest age groups was based on behavioral milestones of syntax acquisition. Canonical word order patterns and simple inflectional paradigms are already mastered by 3-year-old children (Clark, 2003; Guasti, 2002; Hirsh-Pasek and Golinkoff, 1996; Höhle et al., 2006). However, complex syntactic structures like passive- and object-first sentences are only acquired between 4 and 7 years of age (Dittmar et al., 2008; Fox and Grodzinsky, 1998). The motivation for testing 9- to 10-year-old children was based on neuroanatomical evidence that the left IFGoper as the main region supporting complex syntactic computations reaches an adult-like cytoarchitectonic asymmetry toward the left hemisphere only at the age of 11 years (Amunts et al., 2003).

At the behavioral level, we predicted interaction effects between syntax and semantics based on the hypothesis that syntactically complex sentences are easier to process for children if they are semantically plausible compared to a condition in which plausibility cues are not

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available. This should at least hold for the younger two age groups. At the neural level, we also expected differences between the age groups. 9- to 10-year-old children should show an adult-like BOLD effect in response to syntactic complexity located in the left IFG as well as an effect of semantics in the left IFGtri/left IFGorb, and potentially a syntax–semantics–interaction effect either in the left IFG and/or the left pSTG. With respect to the younger children, we predicted syntax effects in the left perisylvian cortex involving IFG and temporal regions, and expected that syntax interacts with semantics either in inferior frontal or temporal regions. We hypothesized that these interactions would be less likely to occur with increasing age, giving way to a gradually independently operating syntactic module.

Materials and methods

Participants

60 datasets from 3 age groups were subjected to the final fMRI analysis: 20 children 3 to 4 years of age (12 girls, mean: 4;4, range: 3;9–4;11), 20 children 6 to 7 years of age (11 girls, mean: 7;5, range: 6;7–7;11) and 20 children 9 to 10 years of age (8 girls, mean: 10;3, range: 9;7–10;11). Initially, 89 children underwent IQ (Kaufman ABC) and language comprehension (TROG-D Test for Reception of Grammar) assessment as well as the Edinburgh handedness test adapted for children. All children underwent a training session in a mock scanner in order to familiarize them with the scanning situation. 29 children had to be excluded due to critical assessment results, weak right handedness or excessive head motion. All experimental procedures were approved by the University of Leipzig Ethical Review Board.

Stimuli and task

The factor syntax was realized as different levels of syntactic complexity and operationalized by two types of German relative clauses. We contrasted canonical subject relative clauses with more demanding non-canonical object relative clauses in which the object noun phrase precedes the subject phrase. The factor semantics was operationalized by semantic plausibility. Given that 3- to 4-year-old children already have a prototype-semantic concept (Clark, 1979; Rosch, 1975) of the natural sizes of animals and how they constrain the plausibility of certain simple actions they can perform, a semantically plausible proposition was established if a tall animal was the agent (subject noun phrase) performing a certain action on a small animal, which was the patient (object noun phrase) undergoing this action. An inversion of this argument structure resulted in a semantically implausible proposition (see Inline Supplementary Table S1 and Inline Supplementary Fig. S1 for details regarding stimulus design). We used a sentence-picture matching task in which participants were required to select, from two pictures, the one depicting the correct agent–patient relation (who does what to whom) from a sentence they just heard.

Inline Supplementary Table S1 and Fig. S1 can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2014.05.080>.

Behavioral data

While lying in the scanner, participants listened to the sentences in child-directed prosody via headphones and saw the pictures through an eyeglass display in order to prevent strong eye and head motion. The whole experiment comprised 96 jittered target trials (24 trials per condition) and 12 null event trials presented in a pseudo-randomized order. The total experiment time was about 15 min. Mannheim spoken corpora frequencies (<http://celex.mpi.nl/>) of all nouns and verbs were neither significantly related to response accuracy (nouns: $r = .38$, $p = .22$, verbs: $r = .09$, $p = .87$), nor to reaction times (nouns: $r = .32$, $p = .3$, verbs: $r = -.12$, $p = .82$). Kolmogorov–Smirnov and Shapiro–Wilk tests revealed that the

reaction times but not the response accuracy values were normally distributed in all groups and conditions (see Inline Supplementary Table S2). Additionally, Levene's tests of equality of error variances revealed significant results for the reaction times (OR plausible: [$F_{(2,57)} = 6.61$, $p = .003$], OR implausible: [$F_{(2,57)} = 4.32$, $p = .018$], SR plausible: [$F_{(2,57)} = 16.59$, $p < .001$], SR implausible: [$F_{(2,57)} = 6.35$, $p = .003$]) but not for the accuracy values (OR plausible: [$F_{(2,57)} = .4$, $p = .67$], OR implausible: [$F_{(2,57)} = 1.97$, $p = .015$], SR plausible: [$F_{(2,57)} = 2.64$, $p = .18$], SR implausible: [$F_{(2,57)} = 2.77$, $p = .17$]). Two 3 (age group–AGE) \times 2 (syntactic complexity–SYN) \times 2 (semantic implausibility–SEM) ANOVAs were computed, a non-parametric ANOVA on the ranked mean accuracy values and a parametric ANOVA on the mean reaction times. Post hoc, three 2 (SYN) \times 2 (SEM) ANOVAs were run for each group considering all $p < .0167$, which equals a Bonferroni corrected $p < .05$, significant.

Inline Supplementary Table S2 can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2014.05.080>.

fMRI data

The experiment was carried out on a 3.0-Tesla Siemens TIM Trio (Siemens AG) whole-body magnetic resonance scanner using a 12-radiofrequency-channel head coil. A T2*-weighted gradient-echo echo-planar imaging (EPI) sequence was applied to 26 slices with TR = 2 s, TE = 30 ms, FOV = 192 mm, matrix size = 64 \times 64 voxels and voxel size 3 \times 3 \times 3 mm³. In order to correct for geometric distortions in EPI caused by magnetic field inhomogeneity, a field map was obtained for each dataset. For anatomical localization, T1-weighted three-dimensional magnetization-prepared rapid-acquisition gradient echo (MPRAGE) pulse sequences with TR = 1.480 ms, TE = 3.46 ms, TI = 740 ms, FOV = 256 \times 240, matrix size = 256 \times 240 \times 128 and voxel size = 1 \times 1 \times 1.5 mm³ were acquired.

Functional images were preprocessed using SPM8 (<http://www.fil.ion.ucl.ac.uk/spm/software/spm8/>). First, cubic spline interpolation was applied to the voxel time series before resampling them (slice time correction). Second, the images were realigned to the first acquired image (motion correction). Third, all images were coregistered to the corresponding T1-weighted structural volume and subsequently normalized to a Montreal Neurological Institute (MNI) template covering the whole age range (spatial normalization) (Fonov et al., 2011). We ensured that the scaling did not affect the functional data by also normalizing them to MNI templates exactly matching the group-specific mean age and afterwards comparing both volumes against each other: This did not reveal any significant differences. Finally, data were spatially low-pass filtered using a 4 mm full width half-maximum (FWHM) Gaussian kernel and temporally high-pass filtered with a cut-off frequency of 1/120 Hz (spatial and temporal smoothing).

For the statistical analysis, functional whole-brain data were passed through a general linear model in order to run a least-squares parameter estimation (regression analysis), as implemented in SPM8. In order to control for head motion, the realignment parameters were included as regressors into the model. The first-level contrasts were: syntactic complexity (object relative clauses vs. subject relative clauses), semantic implausibility (implausible proposition vs. plausible proposition), and the interaction of both factors (contrasting the simple-syntax-plausible-semantics condition and the complex-syntax-plausible-semantics condition with the two remaining conditions) as well as a baseline contrast (all four conditions against null events). Initially, a 3 (AGE) \times 2 (SYN) \times 2 (SEM) ANOVA was calculated using gender as a covariate. We determined the probability of a false detection by dual thresholding of both type I error ($p < .01$) and cluster size ($p < .05$, $k > 17$); running 10,000 iterations of a Monte Carlo Simulation using AFNI AlphaSim (<http://afni.nimh.nih.gov/afni>). Post hoc, three 2 (SYN) \times 2 (SEM) ANOVAs were run for each group and the same procedure for multiple comparison correction was applied, however this time with a more restrictive Bonferroni

corrected threshold: (type I error $p < .0033$ which equals a Bonferroni corrected $p < .01$; cluster size $p < .05$, $k > 10$).

Instead of family-wise error (FWE) and false discovery rate (FDR) correction, the standard multiple comparison correction methods implemented in SPM, a less conservative dual thresholding approach as implemented in AFNI AlphaSim was used. FWE correction, i.e. dividing the voxel-wise alpha level by the number of tests conducted, has been criticized for loss of power to detect areas of true activation (e.g. Xiong et al., 1995). While FWE correction reduces the probability to detect single false-positive-voxels, FDR correction is less conservative as it reduces the probability to detect only a certain proportion of false-positive voxels. However, neither FWE nor FDR consider any spatial correlation in the data. The described dual thresholding approach overcomes these disadvantages.

Results

Behavioral results

Children at the age of 3 to 4 years and 6 to 7 years performed above chance in all conditions and children at the age of 9 to 10 years performed above 90% in all conditions (Fig. 1).

Two 3 (age group—AGE) \times 2 (syntactic complexity—SYN) \times 2 (semantic implausibility—SEM) ANOVAs, one on accuracy and one on reaction times, revealed a significant AGE \times SYN interaction for accuracy [$F_{(2,57)} = 4.07$, $p < .05$] and a significant AGE \times SEM interaction for reaction times [$F_{(2,57)} = 3.88$, $p < .05$]. Finally, we ran three separate 2 (SYN) \times 2 (SEM) ANOVAs within each group for each of the two measures. Differences in processing syntactic complexity and semantic implausibility were mainly driven by the 3- to 4-year olds (main effect SYN accuracy: [$F_{(1,19)} = 4.69$, $p < .05$]; main effect SEM reaction times: [$F_{(1,19)} = 8.29$, $p < .01$]) and 6- to 7-year olds (main effect SYN accuracy: [$F_{(1,19)} = 12.76$, $p < .005$]). No significant AGE \times SYN \times SEM interactions were detected both for accuracy [$F_{(2,57)} = .95$] and reaction times [$F_{(2,57)} = .33$].

fMRI results

Running a 3 (AGE) \times 2 (SYN) \times 2 (SEM) ANOVA using gender as a covariate, we observed an AGE \times SYN interaction ($p < .01$, corrected) in left inferior frontal and posterior temporal cortices and an AGE \times SEM interaction ($p < .01$, corrected) in the left temporal cortex (Fig. 2).

Post-hoc, we attempted to isolate the within-group effects driving these between-group interactions running 2 (SYN) \times 2 (SEM) ANOVAs separately for each age group (Fig. 3).

In the 3- to 4-year-old children we found no significant main effects of either SYN or SEM, but there was an interaction between both factors in the left temporal cortex, extending from the posterior to the mid portion of the left superior temporal gyrus (left mSTG/pSTG, $p < .01$, corrected).

In the 6- to 7-year-olds, we detected main effects of SYN and SEM, both in the temporal cortex: a main effect of SYN ($p < .01$, corrected) in the posterior portion of the left superior temporal gyrus and sulcus (left pSTG/STS) and a main effect of SEM ($p < .01$, corrected) covering the left mid portion of the STG/STS (mSTG/STS). Moreover, we also found an interaction of SYN and SEM ($p < .01$, corrected), located in the left mSTG/STS (see Fig. 4 for details of these interactions). The 9- to 10-year-old children demonstrated a significant main effect of SYN in the inferior frontal cortex, i.e. left IFGtri and the left IFGoper ($p < .01$, corrected) and a main effect of SEM extending from the left anterior STG to the left anterior STS (left aSTG/aSTS; $p < .01$, corrected). No interaction effect was found in the oldest age group (see Inline Supplementary Table S3 for a list of all activations comprising cluster sizes, MNI coordinates and z_{Max} scores).

Inline Supplementary Table S3 can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2014.05.080>.

Finally, we conducted another post hoc analysis in order to compare directly if the observed within-group effects differed significantly between groups. The interactions in the 3- to 4-year-old children were stronger compared to both older age groups. Similarly, the interactions in the 6- to 7-year-old children were stronger compared to the 9- to 10-year-old children. Finally, the syntax effects in the 9- to 10-year-old children were stronger compared to both younger age groups. The groups did not differ with respect to semantics (Inline Supplementary Fig. S2).

Inline Supplementary Fig. S2 can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2014.05.080>.

Discussion

The present study provides evidence for a gradual functional specification of the cortical regions supporting the processing of complex syntax. Our experiment goes beyond previous work reporting strongly overlapping activation for syntax and semantics in children (Brauer and Friederici, 2007; Nuñez et al., 2011) by providing direct statistical evidence that both domains are not processed independently from each other already before they are integrated at the final stage of sentence comprehension until the age of 9 to 10 years.

At the behavioral level, we detected main effects, but no interaction effects between syntax and semantics with respect to either response accuracy or reaction times. This is in line with previous studies suggesting that behaviorally both language functions are experimentally separable in children (Brauer and Friederici, 2007; Nuñez et al., 2011). As expected,

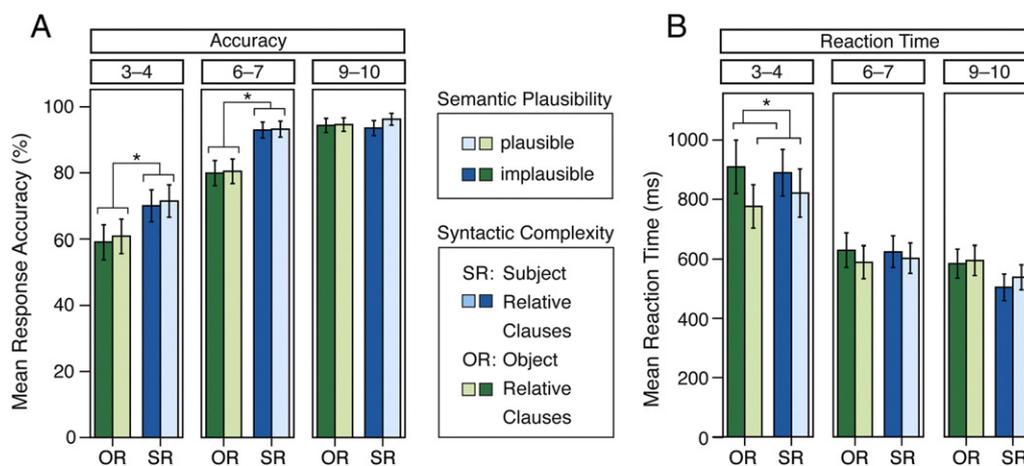


Fig. 1. Behavioral results. (A) Mean response accuracy (%) and (B) mean reaction times (ms) for the three age groups. Asterisks indicate significant differences between factors ($*p < .01$, Bonferroni corrected). Error bars indicate standard errors of the means (SEM).

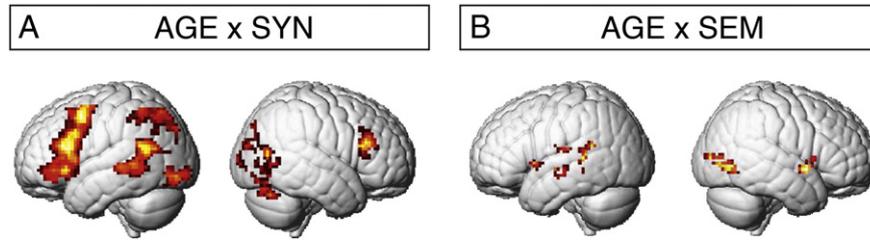


Fig. 2. Between-group BOLD interaction effects. Illustrated are (A) the AGE \times SYN interaction ($p < .01$) and (B) the AGE \times SEM interaction ($p < .01$) corrected at the cluster-size-level.

we found that syntactic complexity interacted with age indicating a better syntax performance the older the children are. Additionally, semantic plausibility interacted with age suggesting that children master the comprehension of syntactically complex sentences better and more efficiently once these sentences match their familiar prototype-semantic concepts and the resulting plausibility. This effect, driven by the two youngest age groups, provides evidence for semantic plausibility as a cue facilitating the processing of syntactically complex sentences during early childhood. Compatible behavioral effects of semantic cues on the comprehension of sentences in which word order and case marking cues are in conflict and therefore less reliable have been shown for animacy (Chan et al., 2009; Lindner, 2003). Our behavioral data indicate that the impact of semantic plausibility on syntax processing is stronger the younger the children are and no longer present at 9 to 10 years of age.

At the neural level, our fMRI results suggest interesting age-related differences with respect to the main effect of syntax and the syntax–semantics interaction, in particular for the two youngest groups. We will discuss these two groups first.

In the 3- to 4-year-old children we found a syntax–semantics interaction effect in the left pSTG/mSTG, but no separable main effects for either of the two factors. Interestingly, in the youngest age group all language-sensitive areas along the Sylvian fissure were activated in a way similar to older children and adults during sentence comprehension, but the cortical selectivities for syntax and semantics are not yet segregated from each other within this network at 3 to 4 years of age.

At age 6 to 7, however, children demonstrate distinct main effects for syntax and semantics in the temporal lobe in addition to an interaction effect. This finding is generally in line with electrophysiological event-related potential studies investigating the processing of object-first compared to subject-first German sentences. Testing children in different age groups between the age of 3 and 6 years it was found that only by the age of 6 years children process the case marked initial noun phrase similar to adults, but that their response to the second noun phrase is still not adult-like (Schipke et al., 2012).

The syntax–semantics interaction effects of the 3- to 4- and 6- to 7-year-old children were located in the left superior temporal cortex. An interaction between syntax and semantics in this region has already

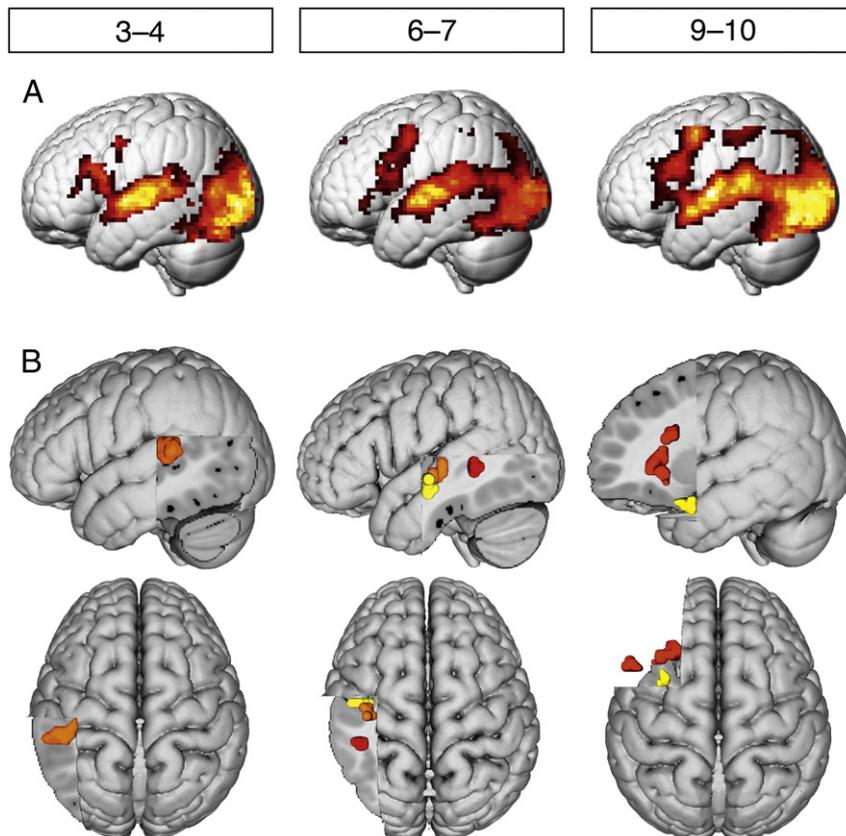


Fig. 3. Age-group-specific BOLD activations. (A) Baseline contrasts (all conditions vs. null events) thresholded at $p < .01$ (Bonferroni and cluster size corrected). (B) Main effects of syntactic complexity (red) and of semantic implausibility (yellow), as well as the interaction of both factors (orange) ($p < .01$, Bonferroni and cluster size corrected).

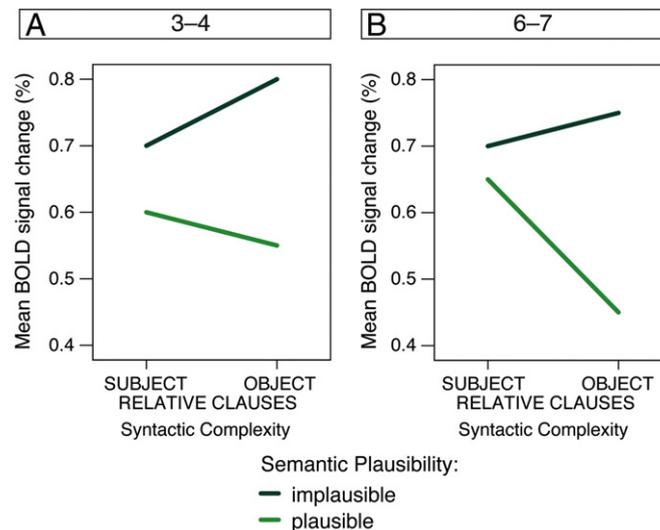


Fig. 4. Condition-wise BOLD percent signal change characterizing the ordinal interactions between syntactic complexity and semantic implausibility in the left mSTG/STS. Processing object relative clauses, in which word order and case marking conflict, is more resource-demanding than the processing of subject relative clauses in the two conditions with implausible semantics. However, when the plausibility cue is available, less cortical resources are needed in order to process the object relative clauses compared to the subject relative clauses.

been reported in a previous adult study (Bornkessel et al., 2005). Furthermore, the posterior part of the left superior temporal gyrus is known to crucially support the integration of syntactic and semantic information (Friederici, 2011).

The BOLD responses in the two younger child groups revealed that the processing of implausible object relative clauses consumes more cortical resources than the processing of implausible subject relative clauses. This result is in line with the mentioned finding that in object relative clauses word order and case marking conflict making these clauses more demanding to comprehend than subject relative clauses. Once the plausibility cue is available, less cortical resources are needed in order to process the object relative clauses compared to the subject relative clauses. Accordingly, the direction of the neural interaction effects suggests that semantic plausibility is a stronger cue than syntactic cues until the age of 6 to 7 years. Further neuroscientific studies are needed to support this result.

It is only in the 9- to 10-year-old children that syntax-specific responses in the left IFG were observed. In contrast to adults, however, the children at 9 to 10 years of age activated the entire IFG including both the IFGoper and the IFGtri. In adults there is increasing evidence that selectivity for complex syntax is most pronounced in the left IFGoper in the adult brain whereas semantics involves the left IFGtri and the left temporal cortex (Friederici, 2011; Newman et al., 2010). This developmental observation is in line with neuroanatomical findings indicating that the leftward asymmetry of the cell body volume fraction of the IFGoper is only apparent at the age of 11 years, whereas this cytoarchitectonic asymmetry of the IFGtri is present much earlier (Amunts et al., 2003). Thus, the left IFG at 9 and 10 years of age still seems to undergo anatomical maturation until the left IFGoper can serve as the primary processor for complex syntax in the adult brain. This view is supported by a study reporting a more confined syntax selectivity in the left IFGoper in older children at the age of 10 to 15 years (Nuñez et al., 2011).

All main effects of semantics were located in well-established candidate regions known from the adult literature, namely in the left temporal cortex, that is the left mSTG/STS (age 6 to 7) and in the left aSTG (age 9 to 10) (Bonner and Price, 2013; Reilly and Peelle, 2008; Rogalsky and Hickok, 2009; Vandenberghe et al., 2002). Since these clusters did not withstand the direct group comparisons it is likely that all age groups recruited large parts of the left temporal cortex for the processing of semantic plausibility information as it has been shown before for children aged 5 and 6 years (Brauer and Friederici, 2007). However, this

assumption needs additional support from future studies applying other semantic manipulations.

In conclusion, the present neuroimaging data indicate that syntax as a processing system gradually independent from semantics emerges during development by neural segregation and local specification of frontal and temporal cortices.

Conflict of interest

The authors declare no conflict of interest.

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