Persistent Neurobehavioral Markers of Developmental Morphosyntax Errors in Adults

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Purpose: Child language acquisition is marked by an optional infinitive period (ages 2–4 years) during which children use nonfinite (infinitival) verb forms and finite verb forms interchangeably in grammatical contexts that require finite forms. In English, children’s errors include omissions of past tense /–ed/ and 3rd-person singular /–s/. This language acquisition period typically ends by the age of 4 years, but it persists in children with language impairments. It is unknown if adults still process optional infinitives differently than other kinds of morphosyntax errors. Method: We compared behavior and functional brain activation during grammaticality judgments across sentences with developmental optional infinitive tense/agreement errors ("Yesterday I play the song"), nondevelopmental agreement errors ("He am tall") that do not occur in typical child language acquisition, and grammatically correct sentences. Results: Adults (N = 25) were significantly slower and less accurate in judging sentences with developmental errors relative to other sentences. Sentences with developmental errors yielded greater activation in bilateral inferior frontal gyri relative to nondevelopmental error sentences in both auditory and visual modalities. Conclusions: These findings suggest that the heightened computational demands for finiteness extend well beyond early childhood and continue to exert their influence on grammatical mental and brain function in adulthood.

During the course of language acquisition, children go through periods when certain grammatical computations seem exceedingly complex, resulting in systematic errors in child language production. While it is generally assumed that periods of language acquisition might depend on the child’s learning experiences, cognitive abilities, and brain maturation (Newport, 1990; Wexler, 2003, 2011), little is known about the neural bases of these developmental periods and whether they leave a lasting impact on adult language processing. Child language acquisition in many languages, including English, Dutch, German, French, and others, is marked by an optional infinitive period (ages 2–4 years) during which children use nonfinite (infinitival) verb forms and finite (marked for tense) verb forms interchangeably in grammatical contexts that require finite forms (Schütze & Wexler, 1996; Wexler, 1994, 1998, 2003). In the English sentence, “Yesterday we baked cookies,” the finite verb form baked is used appropriately, whereas in the sentence, “Yesterday we bake cookies,” the nonfinite form bake is used erroneously. During the OI period of development, children interchangeably use both the correct finite form and the ungrammatical nonfinite form in sentences where a finite form is required. Here, we asked whether the additional processing demands of OI forms that underlie their protracted acquisition in children also leave an enduring mark on mature language processing and its brain bases in adults.

The OI syntactic immaturity has been of great theoretical interest due to the relatively widespread, cross-linguistic presence of this language acquisition period (e.g., Caprin & Guasti, 2009; Gavarró, Torrens, & Wexler, 2010; Guasti, 1993; Tsakali & Wexler, 2004; Varlokosta, 2002). Errors of finiteness are thought to reflect specific maturational demands on syntactic processing (Wexler, 2011).
because they rarely occur after the age of 4 years and because many other possible syntactic errors, including errors of subject–verb agreement, do not occur so frequently in children before this age. Children with specific language impairment (SLI) systematically make infinitival errors beyond the age of 4 years, giving rise to the “extended” OI hypothesis of SLI (Rice, Hoffman, & Wexler, 2009; Rice & Wexler, 1996; Wexler, 2003). This grammatical deficit might also have a specific genetic basis (Bishop, Adams, & Norbury, 2006). Importantly, errors of finiteness occur both in production and comprehension, as has been documented in children ages 3 years and older, in children with and without developmental disorders of language acquisition (SLI) and autism (Grinstead et al., 2013; Rice et al., 2009; Rice, Wexler, & Redmond, 1999; Wexler, 2011). Thus, errors of finiteness are thought to reflect a core competence level in language proficiency rather than a production-specific or comprehension-specific deficit (Grinstead et al., 2013; Wexler, 2011). Proficient speakers must simultaneously complete two competing computations for each verb, checking for tense (e.g., present tense: “Today we bake a cake”; past tense: “Yesterday we baked a cake”) and checking for agreement (e.g., agreement in present tense: “Today we bake a cake” vs. “Today we bakes a cake”).

Evidence for the OI period in typical development and its extension in SLI and autism is well established (Wexler, 2011), and related difficulties can be observed well into adolescents (e.g., Aram, Ekelman, & Nation, 1984; Bishop & Adams, 1990). Leonard, Miller, and Finneran (2009) found that typically developing adolescents and adolescents with SLI and nonspecific language impairment showed slower response times (RTs) when monitoring sentences with grammatical errors, indicating participants’ correct detection of the ungrammatical forms. However, adolescents with SLI and nonspecific language impairment showed different response patterns when the sentence involved omission of a tense/agreement inflection, suggesting continued difficulty with tense/agreement morphology that persists into adolescence.

Little to nothing is known about the neuro-anatomical bases of processing inflectional morphology marking tense and agreement, nor whether such processing remains differentiated in adults. A recent study on monolingual and bilingual typically developing children (ages 6–12 years) demonstrated lower behavioral accuracy and greater neural activation in the left inferior frontal gyrus (IFG) for English sentences with violations in later acquired (simultaneous tense/agreement) structures than earlier acquired elements of morphosyntax (–ing and to be errors; Arredondo, Hu, Seifert, Satterfield, & Kovelman, 2019). Typically developing children may show adultlike accuracy on judgments of finiteness and tense/agreement around the age of 6 years (Rice, Wexler, & Cleave, 1995), yet the automaticity of these processes and the cortical organization for language continues to develop into adolescence and possibly beyond (Friederici, 2011; Skeide & Friederici, 2016). Findings on adult aphasia show that finiteness is impaired in individuals with left IFG injury (Friedmann & Grodzinsky, 1997; tree pruning hypothesis). Here, we ask if a developmentally protracted processing of grammatical errors might leave traces in the neurobiology of mature language processing in healthy adults.

In this study, we report a novel investigation into the behavioral and neuro-anatomical correlates of processing developmental morphosyntax errors in adults with mature, intact language abilities. Proficient adult speakers may have diverse experiences with grammatical forms and errors in everyday speech (e.g., frequency of errors in second-language learners, social media, adults with neurological conditions). Furthermore, omissions of past tense, third person, or copular be are common and accepted grammatical forms across many dialects of English (Oetting, Lee, & Porter, 2013), and individuals may produce utterances containing more than one type of appropriate grammatical form under certain sociolinguistic contexts (Oetting & Pruitt, 2005; Roy, Oetting, & Moland, 2013; Wolfram & Schilling, 2015). To measure the neurocognitive bases of these grammatical forms in proficient adult speakers of standard/mainstream American English, we employed a grammaticality judgment task that was modeled after a sensitive developmental measure of grammatical competence and SLI diagnosis (the Test of Early Grammatical Impairment [TEGI]; Rice & Wexler, 2001). Similar to this developmental assessment, we included the contrasting errors of finiteness (developmental errors) and errors of agreement (nondevelopmental errors).

Different predictions could be made with regard to how adults would process developmental relative to nondevelopmental errors. On the one hand, it might be easier for adults to recognize developmental errors because these contain two (tense and agreement) rather than just one (agreement) violation. On the other hand, the developmental errors of finiteness might incur a more laborious analytical process (and thus greater RT and/or greater intensity or extent of brain activation) because a greater number of possible outcomes could be evaluated when both tense and agreement information are missing (e.g., it would be unclear whether, “He go home,” is meant to convey, “He goes/ was going/has gone/etc. home”). In contrast, in the nondevelopmental condition, agreement is missing but tense is present, and thus, the possible range of correct alternatives is limited (“He was go home,” reflects only, “He was going home”). The difference in magnitude of resulting neural activation between these two error types should thus reveal the brain mechanisms underlying the simultaneous search for both tense and agreement information—the very process that frequently fails in young children during the OI period.

Our first aim was to identify whether morphosyntax errors that occur developmentally in spontaneous speech and grammaticality judgments in young children remain more challenging relative to similar morphosyntactic errors that do not occur developmentally. Our second aim was to ascertain whether individual variation—even among adults—in performance on developmental errors would relate to performance on demanding measures of syntactic processing and other measures of cognition. The study’s primary focus is on the neural bases of auditory sentence processing,
given its developmental and ecological link to early and later acquired morphosyntactic features. Furthermore, because the brain regions activated for syntactic analysis (i.e., judging if a sentence is grammatical or not) may vary depending on whether participants listen or read sentences (Friederici & Kotz, 2003; cf. Scott, Gallée, & Fedorenko, 2017), we also explore these processes in the visual modality to investigate the amodal underpinnings of finiteness.

Material and Method

Participants

Twenty-five adults (13 men, 12 women; age range: 18–36 years, average age = 25 years) met eligibility criteria and participated in the study. Participants were healthy, were right-handed (assessed using the Edinburgh Inventory; Oldfield, 1971), were not taking any medication affecting the nervous system, and had normal hearing (self-reported). Participants were recruited from a student population within a university town and were native speakers of standard (mainstream) American English with no history of any language or reading impairments. Participants had average or above average verbal and nonverbal IQ (Kaufman Brief Intelligence Test–Second Edition [KBIT-2]; Kaufman & Kaufman, 1990, verbal standard score > 90). All 25 participants completed the task in the auditory modality (i.e., they listened to sentences during scanning). Of these 25 participants, 10 (six men, four women; average age = 25 years) also completed the task in the visual modality (i.e., they read sentences on the screen during scanning) as validation rather than a comparison approach. The institutional review board at the Massachusetts Institute of Technology approved this study. Participants provided written, informed consent forms and received monetary compensation for participating.

Behavioral Measures

Verbal and Nonverbal IQ

Participants completed standardized and experimental measures of language and cognition. The standardized assessment included the KBIT-2 (Kaufman Brief Intelligence Test–Second Edition [KBIT-2]; Kaufman & Kaufman, 1990, which includes a test of Receptive Vocabulary and Matrix Reasoning subtests to assess verbal and nonverbal IQ. Participants’ mean (± SD) verbal IQ was 115 (± 7.5), and mean nonverbal IQ was 111 (± 6.7).

Complex Syntax

In order to assess participants’ syntactic competence, we used a sentence plausibility judgment task with subject- and object-extracted relative clauses, as developed by David Caplan (e.g., “The juice that the child spilled stained the rug”; see Caplan, Alpert, & Waters, 1998; Caplan, Chen, & Waters, 2008, for more details on the stimuli). Whereas OI tasks are often used with very young children (e.g., the TEGI; Rice & Wexler, 2001), complex word order tasks are more sensitive to variation in sentence-processing capabilities among adults. These syntactic structures incur complex word order computations, emerge relatively late in development, are frequently impaired in individuals with aggrammatism following lesions, and are known to incur greater activation in the left IFG relative to control conditions (Caplan et al., 2008).

Participants read 20 sentences, one at a time, and were instructed to indicate with a button press as quickly and as accurately as possible whether the sentence was plausible or not (half the sentences were plausible, and half were implausible; implausible sentences contained animacy violations as in: “The waiter that the meal recommended discussed the child”). Each sentence was displayed visually for 6 s using E-Prime (Psychology Software Tools, Inc.). Participants’ mean accuracy was 83% (± 9.6%), with a mean RT of 3,077 ms (± 502 ms).

Brain Imaging Task

While in the scanner, participants completed a morphosyntax grammaticality judgment task consisting of three sentence conditions: developmental errors, nondevelopmental errors, and correct sentences (see Table 1 for sample sentences). This task was modeled after the comprehension portion of the TEGI Grammaticality Judgment task (Rice & Wexler, 2001; see also Rice, Wexler, & Redmond, 1999). The present task included 108 sentences, equally divided among the three conditions described below.

Developmental Errors

Sentences in this condition contained errors of omitted tense marking that are routinely made by young children during the OI period of development and by older children with SLI (Wexler, 2011). We employed three error types:

- Past tense –ed omissions
- Present tense –s omissions
- Copular (is/are/am) omissions
- -ing omissions
- to be agreement error
- Correct

Table 1. Example stimuli sentences.

<table>
<thead>
<tr>
<th>Developmental errors</th>
<th>Nondevelopmental errors</th>
</tr>
</thead>
<tbody>
<tr>
<td>Past tense –ed omissions</td>
<td>Last night, the baby cry.</td>
</tr>
<tr>
<td>Present tense –s omissions</td>
<td>Yesterday, he go off alone.</td>
</tr>
<tr>
<td>Copular (is/are/am) omissions</td>
<td>Last year, Bob play football.</td>
</tr>
<tr>
<td>Nondevelopmental errors</td>
<td>He is kick the ball.</td>
</tr>
<tr>
<td>--ing omissions</td>
<td>They are make some lunch.</td>
</tr>
<tr>
<td>to be agreement error</td>
<td>I am enjoy the book.</td>
</tr>
<tr>
<td>Correct</td>
<td>We are seeing a movie.</td>
</tr>
</tbody>
</table>

...
types: past tense omissions (half regular and half irregular verbs, e.g., “Yesterday he try to win,” “Last night she eat supper”), present tense third-person singular omissions (“She always copy her brother”), and copular omissions, both with adjectival (“We very wet and cold”) and prepositional phrase (“She behind the yellow door”) predicates. For past and present tense omissions, we always included a temporal adverb to make the omission of tense unambiguous. For third-person singular omissions, only verbs were used whose third-person singular form ends with the voiced consonant “/l/” (e.g., “hurry”/“hurries” rather than “sit”/“sits”) to facilitate the salience of this omission in the magnetic resonance imaging scanner. The omission of a third-person singular marker, likewise, never preceded a word with a sibilant (/s/, /z/, /ʃ/) onset.

There was a total of 36 sentences for this condition, with the three error types equally represented among them. Developmental error sentences with –ed and –s omissions contained a temporal adverb to provide the temporal context for the sentence and assist the participant in identifying that the tense morpheme was missing.

Nondevelopmental Errors

These ungrammatical sentences contained errors that are produced neither by typically developing children nor by children with SLI and which children in the OI period tend to successfully judge as ungrammatical (Rice et al., 1999). Half of the nondevelopmental error sentences contained a verb suffix omission, specifically, omission of the participle –ing (–ing omission; “He is the food”; this also constitutes a verb–verb agreement violation, since the presence of a form of be requires –ing on the main verb). Note that this type of sentence actually has a morpheme omission, so in that way, it is parallel to the missing morpheme in the OI sentences, yet research suggests that preschoolers show robust behavioral and neural error recognition responses when they encounter omission of –ing (Silva-Pereyra, Rivera-Gaxiola, & Kuhl, 2005). The other half of the sentences included a subject–verb agreement error (to be errors), including errors involving is/are (“Dad are washing the car”) and am (“Kate am playing the piano”).

Correct Sentences

Correct sentences paralleled the structure of the ungrammatical sentences, with the key difference that they were grammatically intact. Half of the correct sentences were similar to those in the developmental error condition, with the three subtypes again equally represented: correct past tense (“Last week I saw Dad”), correct third-person singular (“She always copy my answers”), and correct copular (“We are outside the tent”). The remaining half of the sentences were similar to the nondevelopmental error condition, with half containing proper use of –ing (“He is helping his brother”), and the other half containing the proper use of agreement (“Dad is washing the car”).

Stimuli Parameters

Stimuli consisted of five-word sentences matched across conditions for verb and noun age of acquisition, written frequency, concreteness, imageability, and familiarity (data from MRC Psycholinguistic database; one-way analysis of variance [ANOVA], ps > .05 within each condition; ad hoc t tests comparing the conditions were also nonsignificant, ps > .05). The 216 sentences were divided into two runs of 108 sentences. Each run lasted 14 min and included 36 trials per condition. The order of sentences was randomized using Optseq software, which optimizes the order of trials for an event-related design (Dale, 1999). Pilot results (n = 3) demonstrated that participants had similar accuracy and RT outside the scanner environment as compared to the in-scanner environment (p > .05)—an observation that we attribute to the sparse/silent scanning procedure.

Auditory Condition

The auditory paradigm included one run of 108 sentences (36 sentences per condition). The sentences were all recorded by the same adult female native speaker of American English and were equalized for root-mean-square (RMS) amplitude using Praat (Boersma & Weenink, 2008). Average sentence duration was 1.61 s (± 0.16 s).

Visual Condition

The visual paradigm consisted of two rounds. The first of which included the same 108 sentences as the auditory paradigm (presented in a different randomized order). The second visual run included 108 unique sentences (36 sentences per condition).

Procedure

Participants first completed a short behavioral battery of IQ- and language-focused assessments. Participants were then familiarized with the experimental task outside the scanner using six items (distinct from those used during scanning). All 25 participants completed the task in the auditory modality first. Of these participants, 10 then completed the task in the visual modality, which involved seeing the sentences that had been heard previously and then novel sentences. Participants were instructed to respond as quickly as possible via button press, using the right-hand index finger if they thought the sentence was grammatical and the right-hand middle finger if they thought the sentence was ungrammatical.

During each trial in the auditory modality, a sentence was presented binaurally at a comfortable level via pneumatic headphones. Participants saw a white fixation cross on a black background on the mirror screen in front of them, while they listened to the sentence. We used a sparse/silent design (see the Image Acquisition section). In this design, the first 4 s of each 6-s trial were silent, and the last 2 s were noisy due to scanner data acquisition. The sentences were thus presented during the silent portion of the trial.
During each trial in the visual modality, sentences were presented in white font on a black background. Each sentence was presented for 2 s, followed by a 4-s fixation. Each run had a duration of 14.4 min. In the visual paradigm, we used a continuous scanning procedure (see the Image Acquisition section). All stimuli were presented via E-Prime (Psychology Software Tools, Inc.) and PsychToolbox (Brainard, 1997; Pelli, 1997) software.

Image Acquisition

Image acquisition was performed on a Siemens 3T MAGNETOM Trio, A Tim System (Siemens Healthcare) using a commercial 12-channel matrix head coil (Siemens Healthcare). Head immobilization was achieved using foam pads. An automatic slice prescription, based on alignment of localizer scans to a multisubject atlas, was used to achieve a consistent slice alignment and position across subjects. Blood oxygenation-level–dependent (BOLD) measurements were performed using a gradient-echo T2*-weighted EPI sequence. Thirty-two 4-mm-thick slices, with an interslice gap of 1.2 mm, were positioned parallel to the AC–PC line. The imaging parameters were as follows: TE = 30 ms, flip angle = 90°, bandwidth = 2,298, echo spacing = 0.50, FOV = 200 × 200, matrix size = 64 × 64. Prior to each scan, five images were acquired and discarded to allow longitudinal magnetization to reach equilibrium. We used sparse acquisition for auditory (Hall et al., 1999) and continuous acquisition for visual conditions. Slice prescription, duration of the runs, and all other imaging parameters (except for the number of TRs) were kept constant for the two conditions. For the auditory sparse/silent acquisition method, we used a 6-s TR, consisting of a 4-s delay (period of silence) and 2-s acquisition (accompanied by scanner noise), for a total of 146 TRs. Sparse-sampling functional magnetic resonance imaging (fMRI) has been used extensively to study auditory language processing (Eden, Joseph, Brown, Brown, & Zeffiro, 1999; Gaab, Gabrieli, & Glover, 2007; reviewed in Perrachione & Ghosh, 2013). During the visual condition, we used continuous 2-s TR scanning, 435 TRs per run—totaling 870 TRs for the two runs.

fMRI Data Analyses

Individual-Level Analyses

Statistical analysis was performed with SPM5 statistical parametric mapping software (Wellcome Department of Cognitive Neurology). Each subject’s data were realigned to the first functional volume after image reconstruction. Extensive artifact detection was then conducted (see below). Sessions were normalized using the mean functional volume and resampled to fit Montréal Neurological Institute stereotaxic space. Spatial smoothing was done with a Gaussian filter (4 mm, full width at half maximum). Each subject’s data were analyzed using a fixed-effects model. Data were visually inspected and reviewed for artifacts using custom software (http://web.mit.edu/swg/software.htm).

Group-Level Analyses

In order to explore the differences and similarities between the different sentence conditions, the following analytical steps were taken. First, we conducted one-sample t tests for the key comparison of interest: developmental errors versus nondevelopmental errors (voxel p < .001; for all subjects, the mean signal intensity for each individual volume and the average mean signal intensity for all volumes in a functional imaging run were calculated. Individual volumes with a mean signal intensity of ≥ 3 SDs from the overall mean signal intensity of the run were excluded from subsequent statistical analyses. Additionally, movement parameters calculated by SPM5 realignment were used to exclude volumes with potential artifacts on an individual participant level. The difference series between subsequent scans was calculated for both translational and rotational movement. Using the derivative of the motion parameters allowed for the identification of volumes in which subjects were moving their heads, resulting in artifact activations. Volumes were excluded if the norm of translational movement (RMS displacement in x, y, and z) exceeded 0.5 mm and/or if the norm of rotational movement (RMS displacement in pitch, roll, and yaw) exceeded 0.01 radians. Exclusion of identified artifact volumes was executed by entering these volumes as regressors in participants’ model estimation. The motion regressors also included the six motion parameters produced during realignment (reflecting movements for each scan with respect to the first scan). These procedures to model movement-related noise offer improved detection of neural activation of interest (Siegel et al., 2014).

For both auditory and visual conditions, we convolved the trials with a canonical hemodynamic response function. For the visual condition, this was done using SPM5, and for the auditory condition, this was done via in-house software (Perrachione & Ghosh, 2013) integrated with SPM. Specifically, for each sentence-type condition of interest in the study (developmental, nondevelopmental, correct), we created a time series representing the onsets of each event of interest. Since such events are most likely not impulse-like, we convolved each event with a boxcar whose length corresponded to the duration of that specific event. The resulting time series was then convolved with a canonical hemodynamic response function in order to generate a simulated BOLD response for that condition. This BOLD response was then sampled (without low-pass filtering) at the time points where the data were actually acquired. The sampled vector was then used as a regressor in the general linear model analysis in SPM5. Such regressors were created for each condition of interest. This approach offers a more sensitive detection of neurophysiological response in task-related contrasts than alternative approaches to modeling sparse fMRI data (see Perrachione & Ghosh, 2013). Finally, we estimated pairwise contrasts between each of the sentence conditions (correct, developmental errors, and nondevelopmental errors) for each participant and for each modality (visual and auditory).
correction for multiple comparisons was achieved by controlling cluster-level FDR at $p < .05$, extent threshold [ET] > 10 voxels. A conjunction analysis (Nichols, Brett, Andersson, Wager, & Poline, 2005) was performed to identify shared activation across visual and auditory modalities for the developmental > nondevelopmental errors contrast (voxel $p < .001$; FDR-corrected at cluster level $p < .05$, ET > 10 voxels). Furthermore, we used the SPM toolbox MarsBaR (http://marsbar.sourceforge.net; Brett, Anton, Valabregue, & Poline, 2002) to extract beta values for brain-behavior correlational analyses.

Results

Behavioral Results

Auditory Sentences

Percent accuracy and RTs on the auditory sentence task behavioral responses are reported in Table 2. A one-way ANOVA revealed significant accuracy, $F(2, 74) = 21.66$, $p < .001$, and RT, $F(2, 74) = 13.89$, $p < .001$, differences between the conditions. Post hoc comparisons (Bonferroni correction of $p < .05$) revealed that participants were significantly less accurate in judging sentences with developmental errors ($p < .001$) and correct sentences ($p < .001$). Participants were also slower at judging sentences with developmental errors as compared to nondevelopmental errors ($p < .001$) and correct sentences ($p < .001$). Participants were also slower at judging sentences with developmental errors as compared to both other trial types (nondevelopmental faster than correct sentences, $p = .001$, and developmental sentences, $p < .001$). Only RTs for trials in which participants responded correctly were analyzed for each participant.

Participant's responses differed within conditions such that participants were faster at judging to be than –ing nondevelopmental errors ($p < .001$), and participants were also faster on to be omissions than –sl–ed past tense omission developmental errors ($p < .001$). There were no differences between –s and –ed developmental errors ($p = .62$). Nevertheless, participants were faster at responding to the slowest nondevelopmental (–ing omission) than the fastest developmental (copular omission) subcondition errors ($p = .002$), thus suggesting that results averaged across the subconditions are consistent with the results for the conditions overall.

Visual Sentences

Percent accuracy and RTs on the visual sentence task behavioral responses are reported in Table 2. A one-way ANOVA revealed no significant differences in accuracy, $F(2, 29) = 0.074$, $p = .929$, or in RT, $F(2, 29) = 1.43$, $p = .257$, between the conditions. Participants completed two runs for the visual condition. There were no significant differences in RT or accuracy across experimental task conditions between the two sets of visually presented sentences (paired-samples $t$ tests $p > .05$).

Correlation Between Language and IQ Measures

To investigate the relation between participants’ sensitivity to finiteness errors and their other verbal abilities, we calculated Pearson correlations between participants’ RT difference for developmental minus nondevelopmental errors in the auditory condition (for all 25 participants) and their scores on the KBIT-2 verbal and nonverbal IQ measures and the Complex Syntax task. There were no significant correlations between the in-scanner RT difference and either KBIT-2 verbal or nonverbal IQ measures ($p$ ranged between .27 and .83 for both standard and raw IQ scores). Smaller RT differences between conditions correlated with greater accuracy on the Complex Syntax task, $r(22) = -.44$, $p = .041$. This correlation was related to the difference between the two conditions, as RT in neither condition alone correlated with performance on the Complex Syntax task ($p > .36$). Finally, there was no relationship between the Complex Syntax task and nonverbal IQ, but a trend suggesting that participants with better and faster performance on the Complex Syntax task also had better verbal IQ—as measured in standard scores, accuracy: $r(22) = .49$, $p = .02$; RT: $r(22) = -.43$, $p = .045$.

Table 2. Participants’ accuracy and reaction time, M (SD), during in-scanner performance on the sentence judgment task ($N = 25$).

<table>
<thead>
<tr>
<th>Condition</th>
<th>Accuracy (%)</th>
<th>Response time (ms)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Audiatory</td>
<td>Visual</td>
</tr>
<tr>
<td>Developmental errors</td>
<td>95.59 (.37)</td>
<td>97.78 (2.38)</td>
</tr>
<tr>
<td>Past tense –ed omission</td>
<td>94 (2.3)</td>
<td>98 (1.3)</td>
</tr>
<tr>
<td>Present tense –s omission</td>
<td>95 (2.1)</td>
<td>98 (1.3)</td>
</tr>
<tr>
<td>Copular (is/are/am) omission</td>
<td>98 (1.2)</td>
<td>97 (1.7)</td>
</tr>
<tr>
<td>Nondevelopmental errors</td>
<td>99.33 (1.45)</td>
<td>97.64 (1.86)</td>
</tr>
<tr>
<td>–ing omission</td>
<td>98 (1.2)</td>
<td>100 (0.5)</td>
</tr>
<tr>
<td>to be omission</td>
<td>99 (0.7)</td>
<td>96 (1.9)</td>
</tr>
<tr>
<td>Correct</td>
<td>99.22 (1.51)</td>
<td>98.06 (3.01)</td>
</tr>
</tbody>
</table>

Note. Sentence subtype accuracies and response times were computed for subset of the participants who completed the experimental tasks in both the visual and auditory modalities.


**Imaging Results**

**Brain Sensitivity to OI Processing**

During the auditory condition, participants showed greater activation for developmental errors relative to nondevelopmental errors in bilateral IFG (pars triangularis and pars opercularis) and the superior temporal gyrus (STG; see Table 3 and Figure 1A). There were no significant activations for the reverse contrast at either the corrected or uncorrected threshold levels (p < .001, ET > 10). During the visual condition, participants also showed greater activation for developmental errors relative to nondevelopmental errors in bilateral IFG (pars triangularis and pars opercularis), the posterior regions of the middle frontal gyrus, the left STG, the left supplementary motor area (SMA), and the left cerebellum, as well as in bilateral parietal and occipital regions (see Table 3 and Figure 1C). Similar to the auditory condition, there were no significant activations for the reverse contrast. Conjunction analyses for the developmental > nondevelopmental errors between the auditory and visual conditions revealed that participants showed activation in bilateral IFG (pars triangularis and pars opercularis on the left and pars opercularis on the right) across both versions of the task (see Table 3 and Figure 1E).

For the auditory condition, participants’ beta values were extracted for both right and left IFG regions (using a 10-mm sphere around the peaks of activation for the group-level developmental > nondevelopmental error contrast for each hemisphere, respectively) and correlated with behavioral measures of task RT (developmental error minus nondevelopmental error) and also verbal and nonverbal IQ. No significant correlations were found between IFG activations and any of the behavioral measures (p > .05), possibly because the child-friendly sentences of this experimental task were relatively easy for adults. The correlations were initially conducted only for the auditory condition, as it included twice as many participants as the visual condition and given that the primary goal was to investigate the neural bases of auditory sentence processing. Exploratory brain–behavioral correlations with the visual condition revealed no significant results.

Across both auditory and visual conditions, participants performed faster during the nondevelopmental error trials as compared to the developmental error trials. We ran our group-level t-test analyses as an analysis of covariance (ANCOVA), with RT as a covariate. The results of the initial contrast and the contrast in which RT was statistically controlled with an ANCOVA were similar: For the auditory condition, we continued to observe significant activations in bilateral IFG (left: t = 4.38, k = 13, x = −45, y = 12, z = 21; right: t = 5.49, k = 20, x = 54, y = 6, z = 36), STG (left: t = 9.51, k = 556, x = −42, y = −30, z = −12; right: t = 9.53, k = 520, x = 66, y = −27, z = 6), and SMA (t = 5.75, k = 86, x = 3, y = 24, z = 39). Similarly, for the visual condition, we continued to observe significant bilateral activations in IFG (left: t = 10.06, k = 428, x = −54, z = −3, y = 42; right: t = 12.40, k = 439, x = 51, y = 27, z = 9), parietal/cuneus (t = 13.26, k = 733, x = 12, y = −78, z = −6), and SMA (t = 9.35, k = 207, x = 0, y = 12, z = 60). By controlling for differences in RT between conditions, these ANCOVA results indicate that RT differences did not drive activations in the language areas of interest.

**Discussion**

In adult native speakers of mainstream American English, we compared processing of morphosyntactic errors

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<tr>
<th>Brain region</th>
<th>Left hemisphere</th>
<th>Right hemisphere</th>
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<td>Developmental &gt; nondevelopmental errors: auditory condition</td>
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<tr>
<td>Inferior frontal gyrus (pars opercularis)</td>
<td>−45</td>
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<td>Inferior frontal gyrus (pars triangularis)</td>
<td>−30</td>
<td>24</td>
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<td>Superior temporal gyrus/medial temporal gyrus</td>
<td>−57</td>
<td>−12</td>
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<td>Developmental &gt; nondevelopmental errors: visual condition</td>
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<td>Inferior frontal gyrus (pars triangularis)</td>
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<td>Inferior frontal gyrus (pars opercularis)</td>
<td>−54</td>
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<td>Superior temporal gyrus</td>
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<td>18</td>
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<td>Middle frontal gyrus</td>
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<td>Supplementary motor area</td>
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<td>Occipital</td>
<td>−42</td>
<td>−66</td>
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<td>Cerebellum</td>
<td>−30</td>
<td>−84</td>
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<td>Parietal</td>
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<td>Developmental &gt; nondevelopmental errors: conjunction between auditory and visual conditions</td>
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that occur in early childhood in typical development (developmental errors) to processing of morphosyntactic errors that do not occur in early childhood (nondevelopmental errors) and asked, (a) do typically developed adults process these two kinds of errors differently in behavior and (b) what neuro-anatomical regions reflect differential processing of these two kinds of errors? Behaviorally, adults were significantly slower and made more errors in making grammaticality judgments for developmental than nondevelopmental errors when listening to sentences.

Across both auditory and visual conditions, participants showed greater activation in bilateral IFG (pars triangularis and pars opercularis) when judging developmental as compared to nondevelopmental errors when listening to sentences. Across both auditory and visual conditions, participants showed greater activation in bilateral IFG (conjunction analyses, \( p < .001 \), cluster-corrected for multiple comparisons). R = right; L = left.

Across participants, superior RT (smaller) differences between the developmental and nondevelopmental conditions correlated with greater accuracy on the Complex Syntax task, a task designed to maximize individual differences in syntactic accuracy (Caplan et al., 2008). The RT difference did not correlate with participants’ IQ scores, a finding consistent with developmental studies reporting no relation between finiteness and vocabulary measures (which is an essential component of KBIT-2 verbal IQ.
measures) or nonverbal IQ (Duff, Hayiou-Thomas, & Hulme, 2012; Eigsti & Bennetto, 2009; Roberts, Rice, & Tager-Flusberg, 2004). RTs in either condition alone did not correlate with accuracy on the Complex Syntax task, which suggests that the two measures reflected specific and shared syntactic abilities and not simply speed of response. The two tasks did differ in performance demands of semantic versus syntactic judgments, and in the nature of the syntactic manipulations (e.g., relative subject–object clauses), however, our results suggest that both measures may reflect a shared linguistic sophistication, even among mature native speakers.

Developmental errors were processed less efficiently and less accurately and showed greater neural activation as compared to nondevelopmental errors. One possible explanation for this observation is the unique checking constraint account of the OI period that proposes that young children can check for only one feature at a time and cannot complete two competing computations simultaneously (a double-checking difficulty; Wexler, 1998). As a result, the child omits either tense or agreement, which, in English, results in the production of an infinitival bare stem form, as in “Today he go home,” while agreement-only errors rarely occur (e.g., “Today I is home”; Wexler & Harris, 1996; Poeppel & Wexler, 1993; Wexler, 2003). Adults have outgrown the unique checking constraint period and are able to successfully check tense and agreement features at the same time. Nevertheless, we suppose that the computational load of checking two features at the same time remains, leading to a greater probability that an adult will erroneously consider the possibility that the OI sentences missing one such feature is correct. Thus, when an adult is presented with an OI, that is, a sentence in which the required features are not present, it may take more time and be more difficult to compute that the interface features must be present. Therefore, adults largely judge the sentences as ungrammatical, but doing so takes additional computational resources as reflected in longer RTs and greater neural response in particular brain structures known to be involved in grammatical processing.

Central to this experiment was the validity of comparing the developmental and nondevelopmental sentences. The two kinds of syntactically erroneous sentences were matched on many dimensions, including verb and noun age of acquisition, written frequency, concreteness, imageability, and familiarity. Bilateral IFG activation differences between the two morphosyntactic conditions is consistent with prior imaging studies of syntactic processing (Brauer & Friederici, 2007; Friederici, 2002; Stromswold, Caplan, Alpert, & Rauch, 1996; Whitehouse & Bishop, 2008) and a more recent study on bilingual children’s processing of these errors in English (Arredondo et al., 2019). Grammaticality judgment studies in adults suggest that error detection and sentence judgment might include several steps. Following the initial process of phonological decoding, rapid structure analyses might yield automatic and almost immediate detection of morphosyntactic violations, a process found to activate left anterior STG and IFG (Friederici, 2011).

This is followed by sentence re-analyses and repair of sentences with morphosyntactic violations, a process found to activate the left IFG and posterior STG and yield a P600 event-related potential response (Friederici, 2011; Hagoort, 2003; Hagoort & Indefrey, 2014). Left IFG activation may thus relate to both the structure evaluation (whether it is correct/possible) with regard to the finiteness status of the verb and also the evaluation of possible alternatives and repair options. Future studies could examine whether structural or functional maturation of the IFG is related to children learning to avoid OI errors.

Right IFG activation may be related to sentence structure violations that distort both sentence structure and semantics, impeding one’s ability to process the overall meaning of the verbal message. Right-hemisphere activation is frequently found in studies that involve sentence- or text-level judgments (relative to studies of single-word comprehension or subslexical processing; Vigneau et al., 2011). It has been hypothesized that the right hemisphere is also critical for understanding the overall sentence context (or pragmatics), rather than morphosyntactic processing of sentence structure (Bookheimer, 2002). Greater right IFG activations during sentences with OI errors may thus reflect participants’ enhanced attention toward the global meaning of the sentences.

A potential alternative account for the differences in pattern of brain activity between the developmental and nondevelopmental error sentences may relate to the possibility that subject–verb sequences in the developmental sentences may nonetheless be grammatically embedded in other, longer contexts. That is, while the nonfinite form of cry in one of the present developmental stimuli (e.g., “Last night, the baby cry,”) is ungrammatical in this context, the highly similar strings of words found in interrogative subject–verb inversions (e.g., “Last night, did the baby cry?”) or in embedded clauses (e.g., “Last night we heard the baby cry,”) are nonetheless grammatical (similarly for the copular omissions, the sequence of words in the ungrammatical sentence, “He the tallest in town,” may appear in the same sequence in the grammatical sentence, “Is he the tallest in town?”). In contrast, the subject–verb sequences in the nondevelopmental error sentences are unlikely ever to be found in some other grammatical context. It may, therefore, be that the additional computational demands involved in determining the ungrammaticality of our developmental errors arose from the need to reject competing interpretations of the sentence where those sequences may have been grammatical. Indeed, there is some evidence that children with SLI will accept tense mismatches that are otherwise sequentially legal (e.g., the ungrammatical sentence, “He made the robot fell into the pool,”) is disproportionately judged as grammatical by children with SLI, perhaps because the sequence, “The robot fell” is itself grammatical; Redmond & Rice, 2001). However, we believe that there are reasons to disprefer the possibility that the increased neurocomputational demands of the developmental error stimuli are related to competition from memories for these or similar subject–verb strings in other grammatical
contexts. First, no stimuli in our corpus occurred in question form or with embedded clauses, reducing the likelihood that listeners would parse these stimuli in such a context (e.g., Pickering & Ferreira, 2008). Furthermore, we designed our stimuli with an initial temporal adverb to make the tense error salient, and temporal adverbs are extremely unlikely to intervene before such subject–verb sequences in sentences where they would have been grammatical (e.g., “Did last night the baby cry?” or “We heard last night the baby cry,” which are highly unusual).

One limitation of the current study is that participants were recruited from the student population of a university town with consistent exposure to standard academic English. However, we did not directly evaluate participants’ diverse language or dialect use or ask them for their history and/or exposure to dialects other than standard English. Participants’ everyday experiences with different forms of English grammar and frequency of errors encountered likely vary across linguistic settings (e.g., outside an academic work or school setting). Future studies should include a dialect survey that asks participants to report daily exposure to or use of diverse English dialects. Likewise, there is a need to extend this work to larger and different groups of adults to fully uncover the neurocognitive processes of developmental morphosyntax errors in adulthood.

The primary goal of the study was to examine the processing of sentences in the auditory modality while the visual was included for cross-modal validation. Modality differences between the auditory and visual conditions were observed and should be taken with caution given the small sample size. Nevertheless, inclusion of the exploratory visual group provides converging evidence for particular regions as underlying these syntactic operations identified independently of the modality of input (visual vs. auditory). These are interpretable by the differences between brain regions involved in processing spoken and written language. We found greater posterior STG activations for developmental relative to nondevelopmental errors during the auditory condition, which is consistent with other auditory neuroimaging studies of grammar (e.g., Kaan & Swaab, 2002). This suggests that posterior STG may be involved in conditions demanding greater attention to and rehearsal of spoken information (Friederici & Kotz, 2003). Conversely, visual sentence presentation incurred greater parietal and occipital activations for developmental errors, both of which are likely due to greater attention and rehearsal efforts dedicated to printed sentences containing violations of finiteness. STG and parietal activations revealed by developmental versus nondevelopmental error comparison may be predominantly related to modality-specific memory and attention processes, rather than the estimation of finiteness. Critically, conjunction analyses between auditory and visual modality revealed significant activation in bilateral IFG region, highlighting the key role of this region, within the language network, on the ongoing nature of processing syntactic structure in the developing brain (Friederici & Gierhan, 2013). Here, we replicate the auditory results through the visual group, which, through its size, suggest the robustness of the IFG result.

In summary, this study offers novel insight into the computational nature of morphosyntax errors in the adult brain, specifically that processing demands for finiteness extend well beyond early childhood and continue to play a role in language function, behaviorally and neurologically, in adulthood. These results might be of interest to the field of speech-language pathology, especially the clinical assessment or remediation of language disorders. Future studies on children may draw on the current data to show how neurophysiological changes in left IFG correspond to patterns of syntactic acquisition and the neural specialization for language, inducing the specific grammar deficits associated with SLI and autism spectrum disorder.

Conclusions

This study used fMRI to probe the neural bases of processing syntactic finiteness in adults. We explored this inquiry through the lens of the OI period of language acquisition. This period in language development reflects the ongoing acquisition of syntactic structure, and operations in typical development and its cross-linguistic counterparts appear to be a consistent marker of grammar deficits in SLI (Arosio et al., 2010; Bishop et al., 2006; Rice et al., 1995; Wexler, 2003). Our results suggest that even adults with mature, intact language systems evince selective sensitivity in both behavior and its neural substrates to developmental errors of finiteness compared to nondevelopmental errors of tense and agreement. Moreover, the speed with which adults could detect errors of finiteness correlated with other measures of their language ability, particularly complex word order comprehension. The left IFG appears to play a key role in evaluating the assignment of finiteness in the linguistically mature brain, and we therefore hypothesize that the development of this region may underlie children’s grammatical maturation during the OI period.

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