Exploring the spatiotemporal dynamics of on-line sentence comprehension in 5-year-olds: The role of semantic context in syntactic processing and behavioral correlates of MEG-recorded brain activity

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A dissertation

Submitted in partial fulfillment of the

Requirements for the degree of

Doctor of Philosophy

University of Washington

2020

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Program Authorized to Offer Degree:

Speech and Hearing Sciences

University of Washington

Abstract

Exploring the spatiotemporal dynamics of on-line sentence comprehension in 5-year-olds: The role of semantic context in syntactic processing and behavioral correlates of MEG-recorded brain activity

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Despite evidence that the neural mechanisms underlying syntactic and semantic operations develop early in life, these processes are believed to remain functionally interdependent until much later in childhood. However, the nature of the dynamic interplay between syntax and semantics during on-line language comprehension in children is not well understood. While language and brain development are ongoing, children may rely on the availability of lexical-semantic information for syntactic processing and vice versa. Furthermore, the processing strategies children use to understand complex linguistic input may vary with their language skills. This study aims to advance the current knowledge of sentence processing in the developing brain, and to investigate relationships between children's language proficiency and sentence processing ability at kindergarten onset.

Magnetoencephalography (MEG) was used to record typically developing 5-year-olds' brain responses to syntactic manipulations in meaningful and semantically impoverished sentences. Correlations were performed between MEG-recorded brain activity in each condition and prospective and concurrent behavioral language measures. Results showed that the neural signatures of on-line sentence processing in 5-year-olds are indeed modulated by the availability of lexical-semantic information for grammatical parsing: phrase structure violations in meaningful sentences elicited a syntactic processing effect in the left hemisphere, whereas intact phrase structure in meaningless sentences elicited an attentional effect in the right hemisphere.

These qualitative differences in cortical activation to manipulations of syntax and semantics support the hypothesis that there is a protracted developmental period in which these processes remain functionally interdependent. Enhanced attention to grammatically congruent meaningless sentences may signify an important language learning mechanism and index of processing efficiency, associated with language skill; indeed, children with higher scores on behavioral measures of language development and proficiency attended more strongly to the salient structural features of language when lexical-semantic information was absent. These findings provide novel information about the dynamics of on-line sentence comprehension during development, and contribute to our understanding of processing strategies children may use to navigate complex linguistic environments.

TABLE OF CONTENTS

CHAPTER 1: INTRODUCTION

CHAPTER 2: METHODS

CHAPTER 3: RESULTS

CHAPTER 4: DISCUSSION

ACKNOWLEDGEMENTS

First and foremost, I would like to express my deepest appreciation to my academic advisor and committee chair, Dr. Patricia K. Kuhl. I thank Dr. Kuhl for her steadfast confidence in me, her willingness to let me explore my research interests to the fullest extent, and her trust in my vision for this project. I also thank her for encouraging my nonacademic career pursuits, and for her help in turning my long-term dreams into a tangible reality. I have grown immeasurably both professionally and personally under Dr. Kuhl's mentorship, and for that I am eternally grateful.

I would also like to extend my gratitude to the acting members of my Supervisory and Reading Committees, Drs. Julia Herschensohn and Adrian KC Lee, as well as former member Dr. Lee Osterhout. I thank my committee members for challenging me intellectually, and for their continued guidance throughout every stage of this process. I am appreciative to have had the opportunity to engage with each of them in various capacities throughout the years, and to draw inspiration from such a passionate, devoted, and insightful group of scientists. It has truly been an honor.

It has been an immense privilege to work with my colleagues and friends at I-LABS, whose procedural, technical, intellectual, and moral support made this work possible. In particular, I would like to acknowledge Dr. Eric Larson, Maggie Clarke, and Myles Reilly for their extensive contributions to the MEG portion of this project. I owe a debt of gratitude to Denise Padden for graciously offering me her professional assistance and wisdom throughout this process. Special thanks to my work wife, Julia Mizrahi, who has been on this journey with me from day one, and with whom I have grown in so many ways. I cannot imagine a better

group of individuals to collaborate with on a daily basis, and I thank each and every one of them for making my experience at I-LABS and so rewarding.

Words fail to express the extent of my appreciation for my friends and family, who have been my greatest source of strength and unwavering support since the beginning of this long endeavor. They have stood by me through every trial and tribulation, believed in me when I struggled to believe in myself, and reminded me to enjoy the thrill of the ride. Thanks in particular to my wonderful parents Jon and Jeanette Fish and partner Anthony for everything they have done and continue to do for me—I would not have made it to the finish line without them. To say this was a team effort would be a gross understatement, and I acknowledge all the hard work they put in to reach this incredible milestone by my side. We did it! And thank you to my precious fur babies, Pepper, Brimmy, and Kaida, for always brightening my day and bringing a smile to my face.

I would like to recognize each of the funding sources that have supported my graduate work during my tenure as a PhD student: The Ready Mind Project, I-LABS Outreach and Education, The UW Speech & Hearing Sciences Training Grant (T32 DC000033), and The Society for Research in Child Development (SRCD) Pre-Doctoral Policy Fellowship in Early Learning.

Finally, I extend my sincere thanks to the children and families who participated in this study. Their willingness to partake in research makes our work possible, and their enthusiasm for doing so makes it a pleasure.

CHAPTER 1: INTRODUCTION

1.1 General Introduction

Language is both uniquely human and universal across cultures, making it one of our species' most defining characteristics. It is set apart from other communication systems by its hierarchical structure, and critically depends on the cognitive ability to process structural hierarchies in real time (Friederici, 2020). At the sentence level, this involves implementing a set of rules that govern the mapping of form (syntax) onto meaning (semantics). The knowledge of syntactic rules, which dictate how linguistic units can be combined to form complex structures, is the foundation upon which a language is built. The ability to interpret the meaning of a sentence critically involves retrieval of the lexical-semantic information encoded in each word, to ensure its integration into the prior context. Therefore, it is the dynamic interaction of semantics and syntax that facilitates successful language comprehension. Despite the complexity of this cognitive task, all typically developing children accomplish it spontaneously, with apparent ease, and at a very early stage of development.

Behavioral research has demonstrated that children understand the basic structural elements of their first language by age three (e.g., Berko, 1958; Brown, 1973; Gleitman & Newport, 1995; Markman, Wasow, & Hansen, 2003), and more recent brain-based studies have detected the neural signatures of semantic and syntactic processing even earlier (e.g., Brusini, Dehaene-Lambertz, Dutat, Goffinet, & Christophe, 2016; Oberecker & Friederici, 2006). While the mechanisms underlying sentence-level linguistic operations appear to establish early, they remain functionally interdependent until late childhood (Skeide, Brauer, & Friederici, 2014, 2016). Functional specification of language-sensitive cortical areas for syntactic processes independent from semantic processes may emerge on the same developmental timeline (Brauer

& Friederici, 2007; Nuñez et al., 2011), co-occuring with growing language proficiency and brain maturation (Skeide et al., 2016). How semantic and syntactic processing strategies mature over time, the changing nature of their interaction during on-line language comprehension, and involvement of associated language-sensitive brain regions remain open lines of inquiry in the field of developmental neuroscience. Addressing these questions will be critical to developing a more robust understanding of the neurobiological basis of language, and forming a comprehensive model of language in the developing brain.

The following review centers on characterizing the neural signatures of sentence-level lexical-semantic and syntactic processing in children, using noninvasive neurophysiological and functional neuroimaging methods. Relevant adult literature is described in more detail where there is a paucity of developmental accounts. Consideration is given to functional and structural interactions between these processes and how they may gradually segregate from one another over the course of development. Finally, this review explores the relationships between language proficiency and sentence processing ability, as well as early predictors of later language and learning outcomes.

1.2 Neural Signatures of Semantic and Syntactic Processing

Historically, invasive methods, such as post-mortem lesion studies (Broca, 1865; Lichtheim, 1885; Wernicke, 1874) and intracranial recordings in pre-surgical epilepsy patients (e.g., Halgren et al., 1994a, b; McCarthy, Nobre, Bentin, & Spencer, 1995), were the only means of localizing language processes to specific brain regions. While these studies were foundational to subsequent research on the neural underpinnings of language, they could provide only limited information about typical language processes. As neuroimaging technology has advanced in recent years, a variety of noninvasive methods have been employed to characterize the temporal and spatial dynamics of language in healthy participants—some of which have been successfully adapted for use with infants and young children. A growing number of studies have used these methods to examine the properties of semantic and syntactic operations during language processing, and sought to understand the contributions of language-sensitive brain regions to these processes. The following sections review literature from three methods that have been employed for these purposes: electroencephalography (EEG), magnetoencephalography (MEG), and functional magnetic resonance imaging (fMRI).

1.2.1 The temporal domain: Evidence from event-related potentials

One established neurophysiological approach to investigating the characteristics of the language processing system during development is electroencephalography (EEG), which measures the electrical activity from the synchronous firing of pyramidal cells in the cerebral cortex via conductive electrodes placed on the scalp (see Luck, 2005). Amplitude, latency, and distribution of EEG waveforms, time-locked to the presentation of a stimulus, can be averaged to reveal event-related potential (ERP) components associated with various cognitive processes. Spatial resolution is poor because electrical signals are significantly distorted as they pass through the brain and skull, precluding the possibility of accurate source reconstruction. However, the precise temporal resolution of EEG, on the order of milliseconds, lends this technology to studies of on-line sentence comprehension. Furthermore, the lack of overt task requirements in detecting event-related neural activity makes it well suited to studies with infants and young children. Semantic and syntactic manipulations reliably elicit two distinct ERP components in adults. Violations of semantic expectation elicit a negative-going wave that occurs ~250–500 ms post–critical word onset, peaks at ~400 ms, and is usually greatest over centro-parietal electrodes, referred to as the N400 (e.g., Kutas & Hillyard, 1980, 1983, 1984; Osterhout & Nicol, 1999). Morphosyntactic and phrase structure violations typically trigger a positive deflection in the waveform that often begins ~500 ms post–critical word onset, persists for several hundred milliseconds, and is maximal over centro-parietal or frontal electrode sites, known as the P600[1] (Friederici, Hahne, & Mecklinger, 1996; Kaan & Swaab, 2003; Osterhout & Holcomb, 1992; Osterhout & Mobley, 1995). This component has been attributed to processes of structural integration (e.g., Hagoort & Brown, 2000), ambiguity resolution (e.g., Osterhout & Holcomb, 1992) or reanalysis/repair when a syntactic violation is detected (e.g., Friederici et al., 1996; Osterhout & Holcomb, 1993).

ERP components analogous to those described in the adult literature have been observed in children, though with longer peak latencies, greater amplitudes, and broader scalp distributions that become more adult-like with age (Hahne, Eckstein, & Friederici, 2004; Holcomb, Coffey, & Neville, 1992; Oberecker, Friedrich, & Friederici, 2005). Children as young as 14 months show N400-like effects to semantically incongruent words in a picture context (Friedrich & Friederici, 2005a), and 19- and 24-month-olds show N400-like responses to semantic anomalies in a sentential context (Friedrich & Friederici, 2005b). Children as young as 24 months show a P600-like effect to phrase structure violations (Brusini et al., 2016; Oberecker & Friederici, 2006) and by 30 months, children show different ERP responses to semantic versus syntactic anomalies, qualitatively similar to the adult N400 and P600 (Harris, 2000; Silva-Pereyra, Klarman, Lin, & Kuhl, 2005a, Silva-Pereyra, Rivera-Gaxiola, & Kuhl, 2005b). By age

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[1] Many studies have also reported two left-distributed anterior negativities associated with syntactic processing, which are thought to reflect more automatic phases of initial structure building, known as the ELAN (150–250 ms post-stimulus) and the LAN (300–500 ms post-stimulus) (e.g., Friederici, Pfeifer, & Hahne, 1993; Hahne & Friederici, 1999, 2002). These effects are not described in more detail here, but see Discussion.

three, children may show a P600 effect with adult-like latency, as demonstrated by Silva-Pereyra, Conboy, Klarman, and Kuhl (2007), who noted an increased positivity to phrase structure violations 500–750 ms post-stimulus in children at this age, over left frontal, temporal, and posterior temporal electrode sites.

These studies provide strong evidence that the neural mechanisms underlying semantic and syntactic operations may appear early in development and begin to approximate adult-like responses during the second year of life. Localizing the sources of these ERP components—or at least identifying sources of neural activity associated with comparable linguistic manipulations—is necessary to gain further insight into the nature of these processes, and requires methods with higher spatial resolution. MEG and fMRI studies have sought to specify brain regions involved in semantic and syntactic processing in adults, and to a lesser extent in children.

1.2.2 The spatial domain: Evidence from magnetoencephalography and functional magnetic resonance imaging

Qualitative and quantitative differences in ERP components suggest nonidentical neural generators of semantic versus syntactic processing, but the technology's lack of spatial resolution severely limits further specification of the underlying sources of recorded electrical activity. For this reason, MEG and fMRI have been used to localize the neural substrates of semantic and syntactic processes. Similar to EEG, MEG detects electromagnetic fields produced by brain activity at the scalp level (though through a sensor array inside a helmet positioned above the participant's head, rather than through electrodes placed directly on the scalp). While EEG measures electrical signals, MEG measures the orthogonal magnetic fields (Démonet, Thierry, & Cardebat, 2005). Analogous to ERP, MEG data allow measures of response amplitude and latency (but not polarity[2]) at the sensor level; likewise, the magnetic equivalent of ERPs, event-related magnetic fields (ERFs), can also be used to characterize various aspects of linguistic processing. In addition to the temporally accurate sensor-level information, MEG can use source models to provide reliable information about the neural correlates of a given response. While the electrical signal picked up by EEG is significantly distorted as it passes through the brain and skull, the magnetic signal measured with MEG is less impeded by these tissues, allowing for more accurate source reconstruction. MEG has the combined advantage of high temporal and spatial acuity and is increasingly used to investigate on-line language processing. It can now be readily adapted to infants and children, due to technological advances in the ability track and later correct for head motion (Taulu, Kajola, & Simola, 2004; Taulu & Simola, 2006).

While MEG is particularly well suited to studying on-line language comprehension in developmental populations, it has not been used extensively for this purpose. Functional magnetic resonance imaging (fMRI) has been used more widely to investigate the neural underpinnings of language functions in adults and older children. fMRI is a method of indirectly measuring brain activity through associated changes in blood oxygenation (i.e., the blood-oxygen-level dependence (BOLD) response), based on the assumption that neuronal activation and cerebral blood flow are coupled. This method provides high spatial resolution throughout the entire brain volume, but the slow hemodynamic response poses challenges to localizing activation triggered by rapid real-time cognitive processes, such as language comprehension.

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[2] Electromagnetic signals generated by neurons are modeled as dipoles, which consist of a pair of positive and negative charges. The electrical signal follows the main direction of the dipole, whereas the magnetic field is oriented perpendicularly (i.e., on the side of the dipole). Therefore, ERP signals reflect an increase in dipole activity in the positive or negative direction while event-related fields (ERFs) do not. This represents an important distinction between the two technologies, and precludes the ability to equate ERF and ERP components that share a latency.

Furthermore, its overt task requirements and sensitivity to motion curtail its adaptation for use with infants and young children.

Both MEG and fMRI have been used to identify sources of brain activity associated with semantic and syntactic processes. Determining the underlying neural generators of these processes is complicated by methodological limitations as well as the effects of different experimental designs and paradigms (e.g., different working memory load or task demands). However, several lines of research have corroborated ERP findings and converged to form a general picture of the structural correlates of language processing in the adult brain.

The magnetic equivalent of the N400 ERP component (N400m) has been identified with MEG. Studies of semantic processing in adults have generally reported N400m activity peaking at ~400 ms post–stimulus onset in left-dominant bilateral temporal sources in superior and middle temporal areas (e.g., Halgren et al., 2002; Helenius et al., 2002; Kwon et al., 2005; Maess, Herrmann, Hahne, Nakamura, & Friederici, 2006; Marinkovic et al., 2003; Service, Helenius, Maury, & Salmelin, 2007). Brain regions implicated in semantic processing with fMRI have been varied, though are generally consistent with those identified with MEG. Event-related fMRI studies[3] have found activation in the left (or bilateral) superior temporal gyrus (STG) (Copland et al., 2003; Friederici, Rüschemeyer, Hahne, & Fiebach, 2003; Kotz, Cappa, von Cramon, & Friederici, 2002; Kuperberg et al., 2003; Matsumoto, Iidaka, Haneda, Okada, & Sadato, 2005; Ni et al., 2000; Rissman, Eliassen, & Blumstein, 2003); fewer studies have reported activation in the left middle temporal gyrus (MTG) (Baumgaertner, Weiller, & Büchel, 2002), and some have reported no temporal activity (Kiel, Laurens, & Liddle, 2002; Rossell,

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[3] Compared to traditional blocked designs used in fMRI, event-related designs allow randomization of stimuli conditions (i.e., experimental vs. control), reducing the potential for habituation effects associated with presenting different stimulus conditions in separate blocks.

Price, & Nobre, 2003). Most of these studies also noted significant contributions by the left frontal regions, which some suggest may reflect task-related activity rather than semantic processing per se (e.g., Copland et al., 2003; Kotz et al. 2002; see Gan, Büchel, & Isel, 2013 for an alternative view).

At the time of this review, only two adult studies have attempted to localize the magnetic equivalent of the P600 (P600m)[4] using MEG. Kwon et al. (2005) identified increased left hemisphere activation in the middle temporal cortex to morphosyntactic violations in the P600 time window. Service and colleagues (2007) reported strong bilateral temporal activation in response to morphosyntactic and phrase structure violations, localized to the posterior superior and middle temporal areas. In fMRI, various syntactic manipulations have elicited activation in medial and lateral parietal regions bilaterally (Kuperberg et al., 2003) and several left hemisphere regions: the anterior STG/STS (Friederici, Meyer, & von Cramon, 2000; Humphries, Binder, Medler, & Liebenthal, 2006; Humphries, Willard, Buchsbaum, & Hickok, 2001), angular gyrus (AG) (Humphries et al., 2006), and inferior frontal gyrus (IFG) (Friederici et al., 2003; Friederici, Kotz, Scott, & Obleser, 2010; Lee & Newman, 2010; Makuuchi, Bahlmann, Anwander, & Friederici, 2009; Ni et al., 2000). As with frontal activation observed in response to semantic manipulations, activation in the IFG and surrounding areas during syntactic processing may not be syntax specific, but rather reflective of task demands or memory related syntactic operations (Kaan & Swaab, 2002; see Friederici, 2006, 2011 for an alternative interpretation). It is also important to note that fMRI studies of syntactic processing are unable to differentiate between initial stages of structure building and later processes of integration or

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[4] There is a growing body of literature that uses MEG to investigate neural oscillations—rather than event-related fields (ERFs)—associated with sentence-level linguistic operations in the brain, including syntax (e.g., Ding, Melloni, Zhang, Tian, & Poeppel, 2015). The literature will not be reviewed here, as the methodology is beyond the scope of this report.

revision/repair due to the time-insensitive nature of the BOLD response (however, see Friederici 2006, 2011).

Overall, MEG and fMRI studies have localized semantic and syntactic processes to a largely overlapping, generally left-lateralized temporofrontal network of regions in the mature brain. The neural correlates of sentence-level semantic and syntactic processing in young children, however, have not been well specified. One study used MEG to investigate the N400m in 12- and 18-month-olds at the word level, which reported increased cortical activation to semantically anomalous versus non-anomalous words in left temporofrontal cortices and weaker activation in right hemisphere homologues, akin to activation noted in adults in the same study (Travis et al., 2011). These findings suggest ontogenetic consistency of the neural mechanisms underlying semantic processing beginning in infancy, in keeping with many electrophysiological accounts that argue that the cortical language network develops early (Friedrich & Friederici, 2005a, b).

Due to methodological limitations, fMRI studies have focused primarily on the developmental pattern of language lateralization in school-age children, and have not attempted to differentiate among levels of linguistic representation (e.g., Ahmad, Balsamo, Sachs, Xu, & Gaillard, 2003; Balsamo, Xu, & Gaillard, 2006; Nuñez et al., 2011; Wilke et al., 2005). However, one study by Brauer and Friederici (2007) used event-related fMRI to investigate the neural resources recruited for sentence-level semantic and syntactic processing in 5- and 6-year-olds. Results showed broad and overlapping patterns of activation in both violation conditions as compared to the correct sentence condition, including in the IFC and supramarginal gyrus (SMG) of the left hemisphere and the STG bilaterally. While adults in the same study demonstrated functional specificity of the anterior, mid, and posterior STG for semantic and syntactic processes, children did not. The authors offer the interpretation that cortical areas involved in semantic and syntactic processing are not yet fully specialized by age 6 (Brauer & Friederici, 2007). In light of Travis et al.'s (2011) claim that the basic neural mechanisms used to encode semantic information are established in infancy and remain consistent through adulthood, it may be understood that it is the syntactic processing mechanisms that mature on a longer developmental timeline.

From the studies reviewed thus far, it is impossible to infer how the brain regions involved in different levels of linguistic computation interact in time or how this dynamic might change over the course of development. A limited number of investigations have sought to characterize the interplay between these processes during on-line language processing, as well as document changes in functional specificity of the language network over time.

1.3 The Syntax-Semantics Interface in the Developing Brain

Semantic and syntactic manipulations reliably elicit distinct ERP components in children beginning in their second year of life, indicating that the brain mechanisms underlying these processes may develop early (e.g. Brusini et al., 2016; Friedrich & Friederici, 2005a, b; Silva-Pereyra et al., 2005a, b). However, these processes seem to remain functionally interdependent well after children master the ability to detect semantic or syntactic violations in isolation. Preliminary MEG and fMRI findings have corroborated these claims in source space: a language-sensitive network of brain regions, comparable to the one identified in adults, has also been identified in young children, but specificity of areas within this network for different linguistic functions may not emerge until much later (Brauer & Friederici, 2007; Skeide et al., 2014). While language development is ongoing, children may comprehend the structural elements of language not only through syntax-related processing strategies, but also through semantic and other available linguistic cues (Conboy, Rivera-Gaxiola, Silva-Pereyra, & Kuhl, 2008). Until now, children's reliance on semantic cues for syntactic processing during on-line language comprehension has only been addressed in a small number of ERP studies and no MEG studies. Though methodological limitations preclude fMRI from addressing this question directly, it has recently begun to shed light on the emergence of functional specificity within the language network over the course of development.

1.3.1 "Jabberwocky" sentence processing

ERP studies using so-called "Jabberwocky" sentence paradigms have been employed to better understand the role of lexical-semantic information in syntactic processing. Jabberwocky sentences, which reference Lewis Carroll's nonsense poem by the same name (Carroll & Tenniel, 1871), are sentences that replace open-class content words with phonotactically legal pseudowords, but retain closed-class function words and inflectional morphemes (e.g., *My macle platched a flovie about my garily*). Unlike meaningful sentence processing, Jabberwocky sentence processing precludes an initial stage of semantic integration. Jabberwocky paradigms are therefore ideal for testing the extent to which listeners rely on lexical-semantic information to build expectations about sentence structure in real time (Silva-Pereyra et al., 2007).

Silva-Pereyra and colleagues (2007) used a Jabberwocky sentence paradigm to address whether preschool-age children show a syntax-related ERP component that is similar to or different from those observed in adults (i.e., the P600) under conditions of greatly reduced lexical-semantic content. The authors recorded ERPs in 36-month-olds to phrase structure violations Jabberwocky sentences, and reported two late negativities, from 750–900 ms and 950–

1050 ms post–critical word onset, in syntactically incongruent versus congruent Jabberwocky sentences (see also Harris, 2000). The first of these negativities had a left hemisphere distribution, while the second had a broad bilateral distribution. Importantly, these effects differed from the P600-like positivities elicited by phrase structure violations in meaningful English sentences in the same set of participants. These negativities may reflect an attempt at meaning extraction, rather than structural repair, when semantic information is not available (Silva-Pereyra et al., 2007). The absence of a P600 in response to anomalous Jabberwocky sentences in these children is in line with the attenuated P600 observed in some adults under similar experimental conditions (Canseco-Gonzalez, 2000; Münte, Matzke, & Johannes, 1997; Yamada & Neville, 2007). In contrast, a more recent study with 6- and 7-year-olds revealed a P600 effect in response to syntactically anomalous Jabberwocky sentences comparable to the effect elicited by the English sentences, indicating that the lack of semantic context did not affect phrase structure processing in slightly older children (Usler & Weber-Fox, 2015; see Hahne and Jescheniak, 2001 for an adult study with similar results). Together, these findings lend credence to the idea that young children may rely heavily on the availability of semantic information for structural analysis in the interpretation of sentences. How these processes interact in the developing brain, and how this interaction changes over the course of development, remain open questions that necessitate further investigation.

1.3.2 Development of functional specificity within the language network

Sentence-level MEG and fMRI studies have identified a primarily left-lateralized temporofrontal network of brain activation for both semantic and syntactic processing in adults; though few comparable studies have been conducted with young children, there is some evidence for the involvement of a similar—albeit broader, less left-lateralized, and perhaps less regionally specific—network of brain regions involved in sentence processing during development. Some accounts of sentence processing in adults suggest functional segregation of regions within language-sensitive brain areas for semantic versus syntactic processes (Friederici et al., 2003; Newman, Toshikazu, & Burns, 2010; see Friederici, 2011, 2012 for a proposed model of language in the brain including functional specificity within the identified network). However, it has proven challenging to disentangle the neural generators of syntactic operations from those of semantic operations during sentence processing in children (Brauer & Friederici, 2007; Nuñez et al., 2011). Those challenges could be attributed to the methodological limitations of fMRI and/or to the assumption that neural mechanisms involved with language processing develop early, but specialize for different linguistic functions gradually throughout childhood.

Recently, Skeide and colleagues (2014) used fMRI to dissociate syntax- and semantics-related hemodynamic activity in children aged 3-4, 6-7, and 9-10 years, using manipulations of semantic plausibility and syntactic complexity. The results revealed age-related differences with respect to the interaction of semantic and syntactic processing. The youngest age group showed activation in all language-sensitive areas along the Sylvian fissure, similar to older children and adults, but did not yet show functional specificity within this network for semantic versus syntactic processes (Skeide et al., 2014). The 6- to 7-year-olds, however, showed distinct main effects of semantics and syntax in the temporal lobe in addition to an interaction effect in the left superior temporal cortex. Only the oldest group of children exhibited neural selectivity for syntax independent from semantics (Skeide et al., 2014). All age groups recruited a broad area of the left temporal cortex for the processing of semantic information, in line with previous findings with 5- and 6-year-olds (Brauer & Friederici, 2007). Therefore, a strong functional interdependence may exist between semantic and syntactic representations in young children, with cortical selectivity for each linguistic representation gradually emerging in late childhood (Skeide et al., 2014). From these preliminary findings, it is difficult to fully characterize the nature of on-line semantic and syntactic processing in the developing brain. Additional research, taking into account potentially relevant considerations of language development and proficiency, is needed.

1.4 Brain and Behavior in Language Development

Research suggests that the neural substrates of language become increasingly specialized as higher linguistic competency is attained (Mills, Coffey-Corina, & Neville, 1993, 1997; Neville, Mills, & Lawson, 1992; Weber-Fox & Neville, 1996); moreover, language proficiency, independent of age, may affect brain activation during language processing in children (e.g., Hampton Wray & Weber-Fox, 2013; Harris, 2000; Mills et al., 1993, 1997; Nuñez et al., 2011; Usler & Weber-Fox, 2015) for similar assertions about adult native language processing, see Newman, Tremblay, Nichols, Neville, & Ullman, 2012; Pakulak & Neville, 2010; Weber-Fox, Davis, & Cuadrado, 2003). For instance, more mature neural indices of syntactic and semantic processing have been associated with higher language comprehension in toddlers (Harris, 2000), as well as with verbal working memory in school-age children (Hampton Wray & Weber-Fox, 2013). In 7- to 15-year-olds, level of syntactic proficiency has been shown to impact hemodynamic activity in the IFG during syntactic processing (Nuñez et al., 2011). Specifically, better syntactic skills were associated with increased activation in the left IFG and decreased activation in the right IFG, suggesting that hemispheric specialization for language functions may co-occur with language proficiency (Nuñez et al., 2011). Recent work has demonstrated that not only neural activation within temporofrontal language areas, but also structural brain maturation, is associated with grammatical processing skills in children between the ages of 3 and 10 (Skeide et al., 2016). The findings suggest that syntactically complex sentence processing ability is dependent upon functional selectivity of frontal and temporal regions in conjunction with the maturational status of the white matter pathway connecting these regions (Skeide et al., 2016). It is therefore important to take into consideration factors related to language proficiency in the interpretation of brain-based language processing effects in children.

In addition to notable associations between concurrent language skills and brain activity related to sentence-level language processing, it is possible to track infants' language learning trajectories from phonemic category discrimination in infants, to word- and sentence-level processing in preschoolers, to pre-literacy and later reading and other learning outcomes in school-age children (Kuhl, 2011; Kuhl & Rivera-Gaxiola, 2008). Speech perception in infants has been correlated with language skills through age two (Kuhl et al., 2008; Kuhl, Conboy, Padden, Nelson, & Pruitt, 2005; Tsao, Liu, & Kuhl, 2004), as well as with aspects of language and preliteracy skills through age five (Cardillo, 2010). Likewise, measures of speech processing efficiency have been shown to predict lexical and grammatical development in toddlers (Fernald, Perfors, & Marchman, 2006; see also Bosseler et al., 2013; Rivera-Gaxiola, Klarman, Garcia-Sierra, & Kuhl, 2005); these early measures in turn predicted linguistic and cognitive skills in the same cohort of children at age 8 (Marchman & Fernald, 2008). Oral vocabulary in 2-year-olds has also been associated with improved reading, math, and behavioral skills at kindergarten entry (Morgan, Farkas, Hillemeier, Hammer, & Maczuga, 2015). Forming a robust understanding of language development in the brain will critically involve drilling down into the relationship between emergent language in the earliest stages of acquisition, later language proficiency, and associated functional and structural brain changes associated with language processing. This may also have important clinical and educational implications.

1.5 The Present Study

Semantic and syntactic manipulations elicit distinct modulations of electrical brain activity in typically developing children as young as two years of age (Bernal, Dehaene-Lambertz, Millotte, & Christophe, 2010; Harris, 2000; Silva-Pereyra et al., 2005a, b); however, these levels of linguistic processing may remain functionally interdependent until much later in development. While 3-year-olds have demonstrated N400-like responses to syntactic violations in Jabberwocky sentences (Silva-Pereyra et al., 2007), 6- and 7-year-olds have shown activity resembling the P600 in a similar context (Usler & Weber-Fox, 2015). Likewise, fMRI has revealed largely overlapping areas of hemodynamic activity related to semantic and syntactic processing in children between the ages of three and seven, with some evidence of emerging—though not yet complete—functional specificity within this network in 6- and 7-year-olds (Brauer & Friederici, 2007; Nuñez et al., 2011; see Skeide & Friederici, 2016 for review). The present study sought to contribute to this nascent literature base by using a Jabberwocky sentence paradigm to investigate the syntax-semantics interface in 5-year-olds. This age was carefully chosen to assess children between the time that on-line syntactic analysis is mastered and the ability to perform grammatical parsing independent of meaning may be achieved.

As discussed above, MEG is well suited to the study of language processing in young children, given its high temporal and spatial resolutions, as well as its adaptability to developmental studies. Child-adapted MEG has begun to make substantial contributions to the field of developmental neurolinguistics, from phonetic-level processing in infants (Bosseler et al., 2013; Ferjan Ramirez, Ramírez, Clarke, Taulu, & Kuhl, 2017; Kuhl, Ramírez, Bosseler, Lin, & Imada, 2014) to word-level processing in toddlers (Bosseler et al., in preparation). While MEG has been used to investigate sentence-level semantic and syntactic processing in adults, the present study is, to our knowledge, the first to do so with children. As the neural characterization of sentence-level language processing may be closely tied to language proficiency (Hampton Wray & Weber-Fox, 2013; Harris, 2000; Mills et al., 1993, 1997; Nuñez et al., 2011; Usler & Weber-Fox, 2015), behavioral language measures were included to test whether children's sentence processing ability was related to earlier and/or concurrent grammatical and other linguistic skills.

1.5.1 Research questions and hypotheses

The present study aimed to advance the current knowledge of the spatiotemporal dynamics of sentence processing in the developing brain, and to investigate relationships between children's language proficiency and sentence processing ability at kindergarten onset. The study focused specifically on the processing of syntactic violations in meaningful and semantically impoverished contexts, and associations between longitudinal and concurrent language development measures and MEG-recorded brain activity. The three main questions driving this research were as follows:

1. To what extent do the combined spatiotemporal properties of on-line syntax processing in children resemble previous temporal and spatial characterizations of this process?
2. Do children show comparable spatiotemporal properties of syntactic processing in a semantically impoverished context as in a semantically intact context, or do they rely on the availability of lexical-semantic cues for on-line syntactic analysis?

3. Is cortical activation modulated by syntactic processing under these conditions (i.e., the presence and absence of semantic context) related to children's early or concurrent language proficiency?

To investigate these questions, a cohort of 5-year-old children, whose language development had been tracked between 18 and 30 months via parental report, returned to the lab to complete a battery of behavioral language assessments and an MEG recording of brain activity as they processed phrase structure violations in English and Jabberwocky sentences.

Expectations regarding the spatiotemporal dynamics of English syntax processing were strongly motivated by empirical evidence: we expected phrase structure violations to elicit an increased contribution of cortical activation in left-dominant frontal, temporal, and/or parietal areas within a time window resembling that of the P600 (Brauer & Friederici, 2007; Kwon et al., 2005; Service et al., 2007; Skeide et al., 2014). We explored correlations between brain and behavior using a data-driven approach, but expected associations between some measures of language proficiency and syntactic processing effects, in light of the previous research introduced above.

Expectations related to the spatiotemporal characterization of syntactic processing in Jabberwocky were highly speculative, and different potential outcomes were considered. If 5-year-olds are able to perform syntactic analysis in the absence of lexical-semantic context, we might expect the characteristics of the response to closely resemble those of English in time and space, i.e. a cortical response to incongruent sentences in frontotemporal language areas at a P600-like latency. If 5-year-olds rely on the availability of semantic cues for syntactic processing, however, we might observe different response latencies, spatial distributions, and/or extent of cortical activation associated with Jabberwocky processing. This second possibility was favorable given the current literature, but we made no further predictions about the nature of the experimental effect. As with English, brain-behavior correlations were data-driven, to better understand the potential role of language proficiency in children's ability to process complex sentences.

CHAPTER 2: METHODS

2.1 Participants

Participants were children between the ages of 5;2 and 5;4 (*N* = 32, 13 boys). These children were recruited from a list of subjects who met the following baseline criteria: 1) they had participated in research at the University of Washington's Institute for Learning & Brain Sciences (I-LABS) as infants and had completed the MacArthur-Bates Communicative Development Inventory (CDI) of Words and Sentences (Fenson et al., 1993, 2007) between the ages of 18 and 30 months, and 2) their families had consented to be re-contacted for future I-LABS research. Participants were originally recruited through the University of Washington Infant Communication Studies Participant Pool, a Human Subjects–approved database of people in the Seattle Metropolitan area who have volunteered to be contacted for research (https://studies.uw.edu/about). The present study re-recruited these families around the time their children turned five years old, either before or within three months of starting kindergarten (i.e., during the summer before kindergarten or in early fall shortly after the start of kindergarten). This timeframe was chosen to minimize the potential for confounding variables related to formal education experience. Furthermore, all participants were required to have birthdays within two months of each other, to prevent the possibility of confounds related to brain maturation. The age range 5;2–5;4 was chosen to maximize the number of children who were eligible to participate in the desired timeframe for data collection.

All participants were monolingual English speakers with no history of serious illness or developmental difficulties (including speech, language, or hearing problems), uncorrected vision impairments, or more than three months of kindergarten attendance at the time of data collection. Children's handedness was assessed using the Edinburgh Handedness Inventory; children were required to be right handed as defined by a Laterality Quotient score (see Section 2.2.1) between 61–100 to be considered for analysis (*N* = 21). A small number of eligible subjects (*n* = 4) were excluded due to their inability to complete all study procedures, excessive movement during the MEG session, or MEG equipment failure. Data from the remaining 17 subjects (7 boys) are included in the current report.

2.2 Materials and Procedures

Participants were scheduled for two visits to I-LABS within a 21-day timeframe. In general, these visits were conducted on separate days: the first visit included tabletop behavioral testing and a tour of the MEG center to familiarize the child with the testing environment, and the second visit included the MEG recording session. In a limited number of cases in which scheduling two lab visits within 21 days was not possible, all study procedures were conducted in one visit. Informed written consent was obtained from caregivers prior to participation in the study; oral assent was obtained from the children at the beginning of each visit and again before each experimental procedure. Parents were compensated for each visit and children received a small toy at the end of the study. All study procedures were approved by the University of Washington Institutional Review Board.

2.2.1 Behavioral measures and caregiver reports

MacArthur-Bates Communicative Development Inventories. Longitudinal data on children’s receptive and expressive language were collected via the MacArthur-Bates Communicative Development Inventories (CDI) of Words and Sentences (Fenson et al., 1993, 2007). The CDI: Words and Sentences form is a standardized parental report that assesses children’s developing abilities in several domains of early language, including vocabulary production, understanding of word forms, and complexity of multi-word utterances. Research assistants prepared CDI reports for each subject at five time points between the ages of 18 and 30 months (i.e., 18, 21, 24, 27, and 30 months). These reports were submitted online through electronic versions of the forms created by I-LABS, with permission from the MacArthur-Bates CDI Advisory Board and Brookes publishing company.

Measures of expressive vocabulary size and sentence complexity were selected as predictors of behavioral test performance and cortical activation modulated by sentence processing at five years of age. These specific measures were chosen for their well-documented ability to predict children’s later language outcomes (see Cardillo, 2010). For the productive vocabulary measure, parents were asked to indicate the words their child says from a 680-word checklist from 22 semantic categories (Fenson et al., 2007). The sentence complexity measure includes 37 phrase/sentence pairs in which the second member of the pair is the more advanced form (Fenson et al., 2007). Parents were asked to choose which member of each pair most closely resembled their child’s phrase/sentence construction.

Edinburgh Handedness Questionnaire. An adapted version of the Edinburgh Handedness Inventory (Oldfield, 1971) was used to determine children’s handedness. Children were asked to perform a series of 11 tasks, three to four times each, and the researcher recorded the hand that the child used for each (on a five-point scale from Exclusively Left to Exclusively Right). Each item was assigned a score as follows: Exclusively Left = -100; Usually Left = -50; Equally Used = 0; Usually Right = 50; Exclusively Right = 100. The Laterality Quotient (Oldfield, 1971) was calculated by adding the scores for all test items and dividing it by the number of test items. Children with Laterality Quotient scores ranging from -100 to -61 are classified as left handed, those with scores between -60 and 60 are considered mixed handed, and those with scores in the 61 to 100 range are considered right handed. Only children classified as right handed are included in the reported analyses.

Structured Photographic Expressive Language Test, Third Edition (SPELT-3). The SPELT-3 was used to measure children's morphological and syntactic (morphosyntactic) skills (Dawson, Stout, & Eyer, 2003), and to test associations between children's syntactic proficiency and cortical responses during sentence processing. This factor has been shown to affect brain activity associated with syntactic processing (Harris, 2000; Pakulak & Neville, 2010). Structured visual and auditory stimuli were used in the test to target children's ability to generate specific morphological and syntactic structures. Visual stimuli include 53 full color photographs of everyday situations or activities, which depict children, adults, and animals engaged in activities commonly understood by children of diverse backgrounds (SPELT-3 Manual). The researcher used verbal prompts in the form of short statements or questions as the accompanying photograph was shown, e.g. *"The boy is up in the tree, how did he get there?"* The visual and auditory stimuli established the context necessary to elicit the desired response from the child (e.g. the past tense marker *-ed*:*"He climbed."*). The child's responses were recorded onto the Response Form, with a total raw score out of 53 based on number of responses that adhered to the target structure. Raw scores were converted to standard scores for analysis (see SPELT-3 Manual).

Comprehensive Test of Phonological Processing. The version of the Comprehensive Test of Phonological Processing (CTOPP) developed for 5- and 6-year-olds (Wagner, Torgesen, & Rashotte, 1999) was used to assess children's phonological awareness (PA) and phonological memory (PM). The core subtests of PA and PM were included in the behavioral test battery of this study to test for a potential role of phonological skills and/or working memory in language-related brain functions. PA was selected as a measure of concurrent language proficiency, for its robust associations with both early language skills and later literacy; PM was included as a proxy for working memory, as working memory capacity has been shown to play a critical role in sentence processing ability in both adults (Alatorre-Cruz et al., 2018; Caplan, 2016; Caplan & Waters, 1999; Daneman & Merikle, 1996) and children (Hampton Wray & Weber-Fox, 2013).

The PA composite includes three subtests: Elision, Blending Words, and Sound Matching. Elision measures children's ability to segment spoken words into smaller parts. Children were asked to say a word, then to repeat it without a specific sound (e.g. "Say *toothbrush.*" The correct response is "toothbrush". *"*Now say *toothbrush* without saying *tooth*." The correct response is "brush"). Blending Words requires children to blend individually presented segments into whole words. Participants listened to a series of recorded sounds and was then asked to combine them (e.g. "What words do these sounds make? *ham er*?" The correct response is "hammer"). Sound Matching requires children to match words on the basis of initial and final sounds. The researcher would say a word, pause, then say three other words while pointing to drawings that represent each word. Children were instructed to point to the image that corresponds to the word that starts with or ends with the same sound as the first word that the researcher said (e.g. "Which word starts with the same sounds as *pan*? *Pig, hat, or cone*?" The correct response is "pig").

The PM composite includes two subtests: Memory for Digits and Nonword Repetition. Memory for Digits measures children's ability to repeat a series of digit spans ranging in length from two to eight digits. Subjects listened to the series of numbers and were asked to repeat them in the same order in which they were heard. Nonword Repetition measures children's ability to repeat nonwords ranging in length from 3 to 15 sounds. Participants listened to a series of pronounceable nonwords and were then asked to repeat them exactly as they were heard.

Children's responses for all test items were recorded in the Examiner Record Booklet. Raw scores were calculated for each subtest and converted into standard scores; standard scores for each subtest were then combined into PA and PM composite scores for analysis.

Parental questionnaire. This questionnaire was developed to collect demographic information about each family, including parental education, occupation, and marital status. This information was used to generate a socioeconomic status (SES) score based on the widely used Hollingshead scale (Hollingshead, 1975). SES was considered as a possible control variable in subsequent correlations between behavioral and brain measures (see Hackman & Farah, 2009; Raizada & Kishiyama, 2010 for reviews pertaining to associations between SES and language/brain development).

Behavioral test procedures. Behavioral assessments completed with the child and researcher seated at a table in a sound-attenuated booth, with the caregiver seated in an adjacent control room. A monitor and headphones were set up to allow the caregiver to observe and listen to the session. Caregivers were asked to fill out the demographic questionnaire during this time. The tests were administered in the same order for all participants, beginning with the Edinburgh Handedness Questionnaire, followed by SPELT-3, and concluding with CTOPP. The behavioral test session was typically completed within one hour. Snacks and breaks were provided to children during testing as needed. Behavioral assessments were scored in real time by the researcher and recorded onto a DVD for reference and additional offline scoring, when necessary.

2.2.2 Magnetoencephalography

Stimuli. Auditory stimuli were developed for a prior study at I-LABS, and adapted for use in the present study with author permission (Silva-Pereyra et al., 2007). Stimuli included two sets of 66 sentences[5]: one set of real English sentences (33 syntactically congruent sentences and 33 incongruent sentences) and one set of corresponding Jabberwocky sentences (33 syntactically congruent sentences and 33 incongruent sentences). Jabberwocky sentences are defined as sentences that retain grammatical elements (i.e. closed-class function words and morphological endings) but lack meaning (i.e. open-class content words). For this paradigm, Jabberwocky sentences were created by replacing all open-class words in each English sentence with phonotactically legal pseudowords, matched in syllable number and final consonant to their English counterparts. All closed-class words and regular past tense verb markers (i.e., *-ed*) were retained (e.g., *My grandma baked a muffin in the oven / My brondma leked a taffin in the baven*).

All English and Jabberwocky sentences were seven to eight words in length and contained a regular past tense transitive verb and a prepositional phrase. Sentences were paired such that each syntactically congruent English or Jabberwocky sentence had an incongruent counterpart, in which the order of the preposition and preceding noun phrase was reversed (e.g., My grandma baked a muffin *in the oven /* My grandma baked *in a muffin* the oven; My brondma leked a taffin in *the baven /* My brondma leked in a taffin *the baven*). In English, the critical word that rendered the sentence congruent or incongruent was the onset of the preposition; in Jabberwocky, the violation point was the onset of the final noun phrase (see Silva-Pereyra et al., 2007 for further justification of differing violation points in each condition). To verify the

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[5] Silva-Pereyra et al. (2007) included 80 sentences (40 congruent and 40 incongruent) in each (English and Jabberwocky) condition. The present study includes fewer sentence pairs because some of the original recordings were not located.

syntactic violation point in the incongruent Jabberwocky sentences, Silva-Pereyra et al. (2007) conducted pilot behavioral testing with five native English-speaking adults; only sentences in which the adults were in 100% agreement regarding the violation point were included in the final stimulus set (see Appendix for a complete list of experimental sentences). Twenty filler sentences of varied length and violation type were also included in each experimental condition.

All sentences were spoken by a female native English speaker and recorded with a digital-audio system. The recordings were originally sampled at 44,100 Hz with 16-bit resolution in stereo, and then resampled at 24,414 Hz for the present study. In order to ensure precise time-locking of the event-related potential (ERP) to the onset of each critical word in the sentences in the original study, Silva-Pereyra et al. (2007) inspected the waveforms and spectrograms of the critical words to verify their onset times. For the current study, the timing of critical word onset was verified using Praat software (Boersma, 2001), and the same values were used for time-locking with the magnetic event-related fields (ERFs). The mean duration from the onset of syntactically congruent English sentences to the critical word (i.e., the preposition) was 1346.58 ms (*SD* = 153.88 ms); the mean duration from the onset of incongruent English sentences to the preposition was 906.30 ms (*SD* = 102.36 ms). For syntactically congruent Jabberwocky sentences, the mean duration from the onset of the sentence to the critical word (i.e., the final noun phrase) was 1832.12 ms (*SD* = 237.21 ms); for incongruent Jabberwocky sentences, the mean duration from the onset of the sentence to the final noun phrase was 1879.30 (*SD* = 255.23).

Stimulus presentation. The pre-recorded sentences were presented via loudspeaker, calibrated at 65 dB SPL prior to each recording session. Stimuli were presented to participants in two blocks: one containing English sentences with and without phrase structure violations, and the other containing Jabberwocky sentences with and without phrase structure violations. The order of presentation of the blocks was counterbalanced across participants to rule out the possibility of sequence effects. The sentences were played in a preset pseudo-randomized order within each block at interstimulus intervals of 2000 ms. A Python-based routine using an auditory multiprocessor (RZ6, Tucker Davis Technologies, Alachua, FL) was used for stimulus presentation.

MEG preparation and recording. Magnetoencephalography (MEG) data were recorded at the University of Washington's Institute for Learning & Brain Sciences MEG Center, with an Elekta-Neuromag Vectorview whole-head MEG system (Helsinki, Finland). This MEG system has 306 superconducting quantum interference device sensors (SQUIDS), including 204 planar gradiometers and 102 axial magnetometers. To reduce external magnetic interference, the MEG is housed in a two-layer magnetically shielded room (MSR) with active compensation. Data were recorded at a sampling frequency of 1000 Hz with a low-pass filter of 330 Hz, a high-pass filter of 0.1 Hz, and a notch filter at 60 Hz to suppress line noise.

At the beginning of the MEG appointment, the subject was seated in the preparation area. A technician fit a stretchy nylon cap on the child's head and positioned five continuous head position indicator (cHPI) coils on the cap to track head movement and orientation with respect to the sensor array inside the MEG helmet. Two electrooculograph (EOG) electrodes were attached above and below the left eye to record eye blinks and other facial muscle movement, two electrocardiogram (ECG) electrodes were attached to the inner upper arms to record heartbeat, and one ground electrode was positioned on the left collarbone. The skin at each electrode site was prepared with an exfoliant; electrodes were secured to the skin with soft medical tape and filled with conductive saline gel. The MEG technician then used a Polhemus Fastrak 3D stylus digitizer (Polhemus, Colchester, VT) to establish the head coordinate system, including the locations of the cHPI coils, nasion, right and left pre-auricular points, and at least 100 points across the head to determine individual head shape for later data analysis.

When preparation was complete, a research assistant accompanied the child into the MSR. The assistant remained in the MSR to monitor the child and remind them to remain as still as possible throughout data collection. Typically, caregivers watched the session via a TV monitor from the control room. In the MSR, specially designed cushions were placed on the MEG chair to ensure the child's comfort and appropriate positioning under the helmet. The child was provided with a movie of their choosing, played silently, as a form of distraction during the session. Data collection was terminated when all trials had been presented (approximately 14 minutes in total) or when the child indicated to the research assistant that they did not wish to continue.

Data preprocessing. MEG data underwent a series of standardized preprocessing procedures to improve signal-to-noise ratio (SNR) and reduce signal distortions caused by movement. These procedures included Temporal Signal Space Separation (tSSS) (Taulu et al., 2004; Taulu & Simola, 2006) to remove external artifacts, and head movement compensation (Medvedovsky, Taulu, Bikmullina, & Peatau, 2007) transformed to the time-weighted average of each child's head position in the helmet. tSSS was performed using MNE Python (Gramfort et al., 2013) and head position estimation was performed using Maxfilter 2.2 (Elekta-Oy). Principal Component Analysis (PCA) was used to identify blink and cardiac artifacts from the EOG and ECG electrodes; Signal Space Projection (SSP) (Uusitalo & Ilmoniemi, 1997) was used to remove identified artifact components from the data. All data were downsampled to 500 Hz and low-pass filtered at 80 Hz.

Event-related fields (ERFs) were computed from the MEG recordings using 1300 ms epochs for each subject in each experimental condition. Epochs include 100 ms preceding and 1200 ms following the onset of the critical word in each sentence to obtain the ERFs time-locked to the syntactic violation point for each subject and condition. Epochs were rejected if child's head position or orientation with respect to the sensor array was unsatisfactory, or if the peak-to-peak amplitude exceeded 3 pT/cm (gradiometers) or 4 pT (magnetometers). Subjects with fewer than 15 epochs per condition were excluded from analysis. Noise-covariance was computed from the baseline period preceding each sentence onset (-100–0 ms)[6] to estimate noise in the data and improve the signal-to-noise ratio.

2.3. Analyses

2.3.1 Source estimation

Source localization was performed to estimate the sources of the measured magnetic fields. As expected given the nature of fluent speech processing, MEG grand average sensor data revealed signals with multiple peaks and complex topographies in each experimental manipulation (congruent and incongruent) within each language condition (English and Jabberwocky). Due to the widespread distribution of the signals, all quantitative analyses were performed in source space in order to best represent the data.

Anatomical and forward modeling. Ideally, individual magnetic resonance imaging (MRI) scans would be obtained for co-registration with each subject's MEG data to most accurately refine the spatial localization of recorded brain activity; however, it was not feasible

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[6] The original intention was to use the pre-word baseline (-100–0 ms) to compute the noise covariance matrix; however, because stimuli are presented as fluent speech, using a pre-sentence baseline provided a more accurate measure of baseline noise.

nor practical to obtain individual scans from 5-year-olds. Instead, a template source space and conductor model was constructed in FreeSurfer (Dale, Fischl, & Sereno, 1999; Fischl, Sereno, Tootell, & Dale, 1999) using an individual 5-year-old's structural MRI performed at the University of Washington Medical Center (Philips 3T Achieva, T1-weighted MPRAGE sequence, TR/TE/TI=2500/4.2/1300 ms, flip angle 8 degrees, FOV 220x220x160 mm, voxel size 1x1x1 mm, water fat shift 2.272 pixels or 191.2 Hz/pixel, sense factor of 2.6). The source space consisted of 4098 dipoles per hemisphere placed along the gray/white matter boundary on a decimated version of the cortical surface computed using FreeSurfer. The MRI was aligned and warped to optimally fit each subject's digitized head points, and the resulting affine transformation was applied to the template source space and inner skull surface. A boundary element method (BEM) was used for forward modeling, i.e. to calculate the expected signal at each sensor, for each dipole location.

Distributed source modeling. Cortical activation modulated by the experimental manipulations was expected to be widespread; thus, a distributed source model was chosen for source-level analyses. While equivalent current dipole methods model an observed signal using a small number of discrete sources (dipoles), thereby obscuring the spatial extent of an active area (Van Petten & Luka, 2006), distributed source approaches estimate the contribution of all cortical locations. To calculate spatiotemporal source distribution, the present study employed dynamic statistical parametric mapping (dSPM), a noise-normalized, anatomically constrained linear inverse technique (Dale et al., 2000) that creates statistical maps estimating dipole strength at each voxel and time point in 5 ms increments. Grand average dSPMs of the subtraction of estimated activation between manipulations (congruent minus incongruent) in each language condition across subjects were visualized as movies across the whole time window (-100–1200 ms) post-critical word onset. The dSPM movies were used to identify the effect of the syntactic congruency manipulation in the presence and absence of semantic context and to inform subsequent analyses.

Regions of interest. Functional ROIs were jointly defined using the anatomical cortical parcellation proposed by Glasser and colleagues (2016) and the grand-average activation differences across all subjects. Areas on the cortical surface were selected based on the criteria that they: 1) showed likely differences between manipulations (i.e. congruent minus incongruent) within each language condition by visual inspection of the difference dSPM movies, 2) appeared in frontal, temporal, and/or parietal areas of the left and/or right hemisphere, and 3) were sustained for at least 200 ms[7]. To define the ROIs, labels from the low-resolution atlas (Glasser et al., 2016, Supplemental Material 3) that contained the visually identified areas of activation were used to select a peak activation difference after averaging across the time window of observed activation. Vertices contiguously connected (along the cortical surface) to the peak activation and within 50% of the peak value were chosen to define the ROI. Values corresponding to average activation across a time interval and within vertices defining each ROI were then used to extract ROI activations for each experimental manipulation. This procedure resulted in one spatiotemporal ROI per hemisphere per congruency manipulation and per language condition. ROI values for congruent and incongruent manipulations were subtracted, revealing the effect of the syntactic manipulation in each language condition for each spatiotemporal ROI. The resulting values were correlated with longitudinal and concurrent behavioral measures of language proficiency, as described in Section 2.3.3.

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[7] In the English condition, a response to syntactic violations was expected to occur in a broad post-stimulus time window, ~400–900 ms; in Jabberwocky, there were no *a priori* assumptions about the temporal properties of the cortical response. Difference dSPMs for both conditions were inspected without pre-defined time constraints.

2.3.2 Conjunction/partial conjunction analyses

Due to the developmental age of participants, high inter-subject variability within areas of activation was likely, particularly in the Jabberwocky condition. Conjunction analyses (Benjamini & Heller, 2008) were performed on dSPM source estimates in each experimental condition to quantify this inter-subject variability in the vicinity of the functional ROIs. These analyses were chosen for their ability to determine the number of subjects driving the effects observed in the dSPM, and to reveal areas of greatest consistency across subjects (Benjamini & Heller, 2008; Friston, Holmes, Price, Buchel, & Worsley, 1999; Heller, Golland, Malach, & Benjamini, 2007; Nichols, Brett, Anderson, Wager, & Poline, 2005; Price & Friston, 1997; see Meltzoff et al., 2018).

Conjunction analysis protocols follow those described in Meltzoff et al. (2018). First, a multivariate Hotelling's T^2 test (Hotelling, 1931) pooling the current estimates for each source orientation (X, Y, Z) for each cortical location across trials was conducted on individual dSPMs, yielding *p*-values at each voxel and time point for each subject. To characterize the consistency of *p*-values across subjects, group-level subject consistency maps were created. These maps are uncorrected heuristics showing, for each cortical location, the number of subjects surpassing an activation threshold of $p < 10^{-8}$ at each latency. The post-stimulus time window of 500–850 ms was first used to create the consistency maps, as a syntactic incongruency effect was expected to peak within this window. Partial conjunction group analyses (Benjamini & Heller, 2008; Heller et al., 2007) were then used to formally correct for multiple comparisons across temporal and spatial dimensions, using spatiotemporal subject partial conjunction (st-sPC) mapping (Meltzoff et al., 2018). This method was adapted from the spatial partial conjunction test developed for fMRI analysis (Benjamini & Heller, 2008; Heller et al., 2007) to take into account the temporal dimension of MEG (Meltzoff et al., 2018). st-sPC analyses identify both significant effects at the group level and the number of individual subjects that show these effects, by determining the minimum number of subjects with an effect at each voxel and time point, under false discovery rate (FDR) control. The post-stimulus time window for the st-sPC analysis was expanded to 350–1040 ms, to encompass the observed activation of interest across both language conditions.

2.3.3 Brain and behavior

The final set of analyses pertained to linking brain and behavior. Specifically, this involved elucidating the relationship between language development measures (i.e., longitudinal and concurrent measures of language proficiency) and brain activity modulated by syntactic processing (i.e., measures of the syntactic manipulation effects within each functional ROI identified for English and Jabberwocky). To this end, Spearman rank-order correlations were performed between these categories of measures.

Correlations. All of the following statistical procedures were performed using the SPSS Statistics 19 software package (IBM Corp., Armonk, NY, United States). First, effects of SES and gender were investigated to determine whether these variables should be controlled for in subsequent analyses. Though SES has been linked to aspects of language development (Hackman & Farah, 2009; Raizada & Kishiyama, 2010), no significant correlations were found between Hollingshead SES scores and CDI measures of vocabulary size or sentence complexity; likewise, no significant correlations were found between SES and SPELT-3, CTOPP PA, or CTOPP PM. Independent samples *t*-tests revealed no significant gender differences in performance on measures of vocabulary size, sentence complexity, or tabletop behavioral tests

(SPELT-3, CTOPP PA, and CTOPP PM). Thus, SES and gender were not controlled for in the remaining correlations.

To determine whether the experimental effects of English and Jabberwocky sentence processing were related to children's language proficiency, bivariate Spearman rank-order correlations were performed between longitudinal and concurrent behavioral language development measures and cortical activation modulated by syntactic processing. Due to the data-driven nature of these analyses, and with the consideration that CDI scores at each data collection time point within subjects were highly correlated and inherently not independent measures, no formal corrections for multiple comparisons were made.

A series of bivariate Spearman rank-order correlations were conducted to determine if relationships exist between subjects' CDI scores between the ages of 18 and 30 months and tabletop behavioral test scores at age five years. While it was not a primary aim of this study to determine whether early measures of language development predict later performance on behavioral assessments of expressive language skills, this was an important step in confirming the validity of the CDI and behavioral test scores, to justify using them as predictors of brain activity associated with syntactic processing. Correlations were performed with the average of CDI scores across all time points as an omnibus test, then with scores at each individual time point to assess whether any significant overall correlation was persistent across time.

Strong and consistent positive correlations between CDIs and tabletop behavioral tests were found, providing justification for further investigating associations between these behavioral measures and cortical responses to syntactic manipulations. To this end, a series of bivariate Spearman correlations were conducted to determine the nature of the relationships between subjects' CDI scores and tabletop behavioral test scores and spatiotemporal ROIs derived from MEG-recorded cortical activation in English and Jabberwocky language conditions (refer to Section 2.3.1 for the method of calculating ROI values for these correlations).

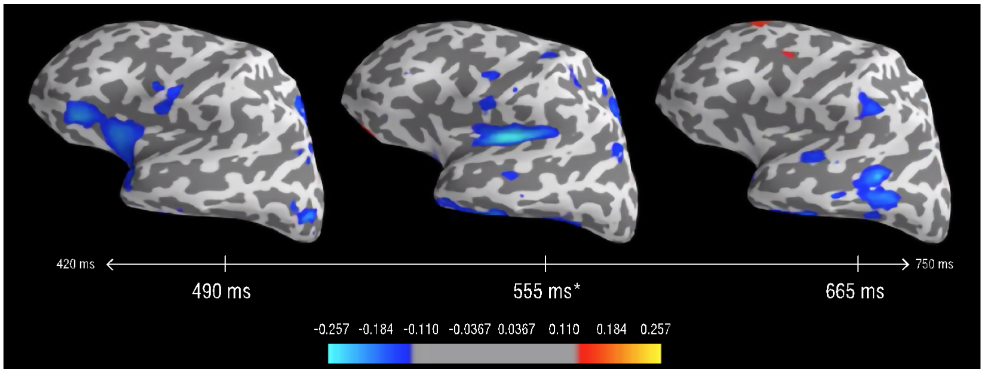
CHAPTER 3: RESULTS

3.1 Cortical Activation in English Sentence Processing

3.1.1 Source estimation

As anticipated, dSPMs for the difference in estimated activation between syntactically congruent and incongruent manipulations in the English condition revealed a pattern of brain activity that was temporally consistent with the P600 ERP component and concentrated in language-sensitive cortical areas. Specifically, the analyses found a sustained increase in activity in the incongruent versus congruent manipulation ~420–750 ms in left frontal, temporal, and parietal regions, referred to here as the syntactic incongruency effect. This activation began in insular and frontal opercular cortices and the anterior temporal lobe (ATL), gradually moving into areas within and surrounding the Sylvian fissure, superior and middle temporal gyri (STG/MTG), and the temporal-parietal junction (TPJ)/inferior parietal cortex (IPC). By visual inspection, the incongruency effect appeared to peak ~555 ms post–critical word onset in the Sylvian fissure (see Figure 1a). A similar pattern of activity was observed in right hemisphere homologues ~355–650 ms, and with more pronounced frontal involvement, peaking in the vicinity of the STG/MTG ~440 ms (see Figure 1b). These locations are generally consistent with those implicated in fMRI studies of syntactic processing in adults and children (see Sections 1.2.2 and 1.3.2, respectively). Corresponding ROIs in the Sylvian fissure and STG/MTG are shown in Figure 2 for the left (2a) and right (2b) hemispheres, respectively.

1a.



1b.

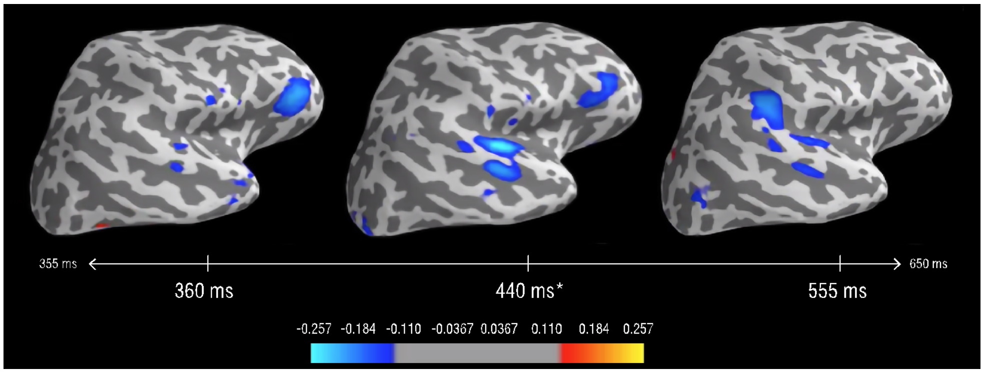
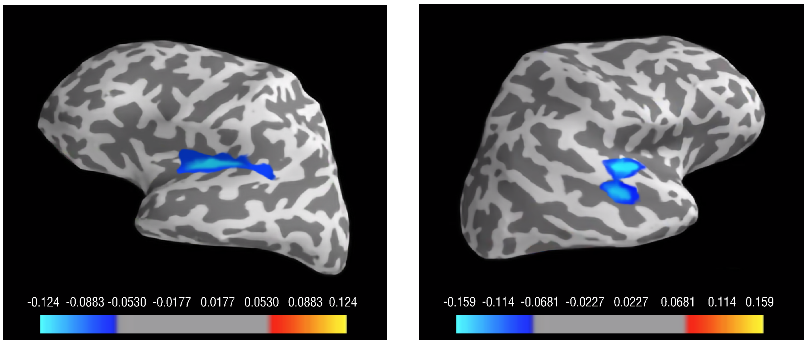


Figure 1. Estimated activity of the syntactic incongruency effect in English sentence comprehension, at three representative latencies within the time windows of interest for each hemisphere (420–750 ms for left; 355–650 ms for right), as determined by observed activation in the difference dSPM (congruent minus incongruent), and visualized on an inflated cortical surface. Color indicates the magnitude of the difference between experimental manipulations, with light blue representing areas where activation to incongruent words is greatest with respect to congruent words. Time points representing the peak difference in activation in each hemisphere are indicated by *.



2a.

2b.

Figure 2. Average cortical activity in English congruent minus incongruent experimental manipulations for the left (a) and right (b) hemispheres, within the post-stimulus time windows of 420–750 ms and 355–650 ms, respectively.

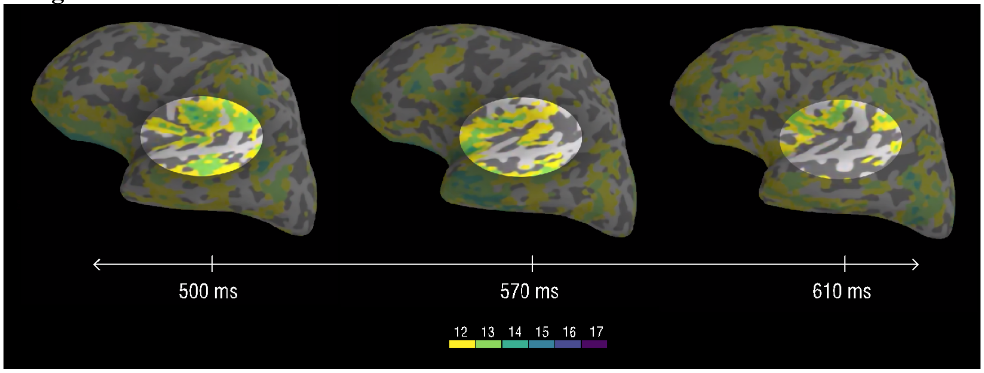
Paired samples *t*-tests were conducted to compare activity in the functionally defined ROIs between congruent and incongruent manipulations in the English condition. There was a significant difference in activity within the left hemisphere ROI between congruent (M = 0.32, SD = 0.07) and incongruent (M = 0.41, SD = 0.12) manipulations; $t(16) = -2.26$, $p = .038$. There was also a significant difference in activity within the right hemisphere ROI between congruent (M = 0.32, SD = 0.10) and incongruent manipulations (M = 0.43, SD = 0.17); $t(16) = -2.33$, $p = .033$. These results suggest that the syntactic manipulation had an effect on brain activity within the ROIs; specifically, children showed significantly more activation within both left and right hemisphere ROIs when presented with syntactically incongruent English sentences than when presented with syntactically congruent English sentences. To confirm that these effects were not driven by a small subset of subjects, conjunction analyses were performed to evaluate the consistency across participants of the observed activation in each experimental manipulation.

3.1.2 Conjunction/partial conjunction analyses

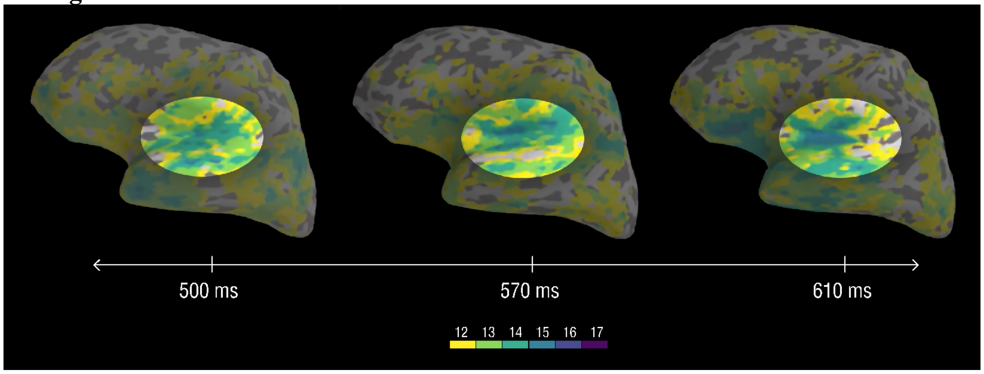
Consistency maps from uncorrected conjunctions provided heuristics of the single-subject statistics across the post-stimulus time window of 500–850 ms. Further group analyses using spatiotemporal partial conjunction (st-sPC) were performed, resulting in st-sPC maps of English congruent and incongruent manipulations across a broader time window, 350–1040 ms. In the left hemisphere, the syntactic incongruency effect peaked at ~555 ms in the Sylvian fissure; in the right hemisphere, activation peaked at ~420 ms in the STG/MTG. Partial conjunction maps surrounding these peak latencies were examined for each congruency manipulation[8], to reveal the number of subjects showing significant activation in the vicinity of the each functional ROI (see Figure 3).

3a.

Congruent



Incongruent



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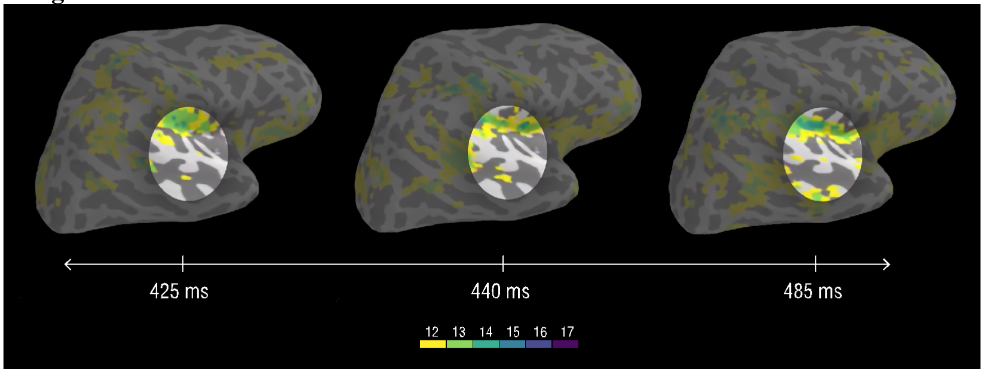
[8] Please be advised that the conjunction maps for each manipulation (i.e., congruent and incongruent) are shown separately, rather than combined as one map representing the difference between manipulations, as this would pose challenges to interpretation. These results must be interpreted within the context of those described in Section 3.1.1 with regard to strength of cortical activation and the effect of the syntactic manipulation (i.e. the difference in activation strength between congruent and incongruent manipulations).

3b.

Congruent



Incongruent

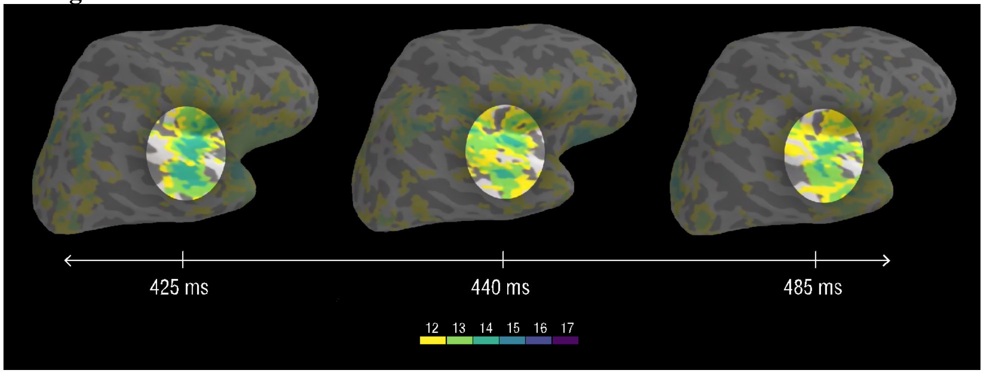


Figure 3. st-sPC maps showing the number of subjects (*N* = 17) meeting a threshold of $p < 10^{-8}$ surrounding peak latencies within the 350–1040 ms time window in syntactically congruent and incongruent manipulations in the English language condition for the left (a) and right (b) hemispheres, displayed on inflated cortical surfaces. Areas of the cortex encompassing the spatiotemporal ROIs shown in Figures 2a and 2b are highlighted here in 3a and 3b, respectively. Colors represent the number of subjects with activation in a given area; maps are visualized with a lower bound of 12 subjects.

Partial conjunction maps revealed that 12–13 subjects showed significant activation in the vicinity of the peak syntactic effect in the left hemisphere (Sylvian fissure) in the congruent manipulation, whereas at 14–16 subjects had significant activation in this area in the incongruent manipulation (Figure 3a). Fewer than 12 subjects had significant activation in the vicinity of the peak syntactic effect in the right hemisphere (STG/MTG) in the congruent manipulation, whereas up to 14 subjects had significant activation in these areas in the incongruent manipulation (Figure 3b). Due to the robust multiple comparison correction in the partial conjunction analyses, it can be validly inferred that at least 12 individuals showed significant cortical activity in these areas at a given time point when they encountered syntactically incongruent English sentences. Therefore, not only was cortical activation stronger in incongruent than congruent manipulations, but this effect was highly consistent across participants, particularly in the left hemisphere.

3.1.3 Summary

A robust syntactic incongruency effect was observed during English sentence processing, in which children showed greater cortical responses to incongruent than congruent sentences in perisylvian language areas of the left hemisphere. Right hemisphere homologue activity was noted in an overlapping, though slightly earlier, time window ~355–650 ms. This effect was highly consistent across participants, particularly in the left hemisphere, providing supporting evidence for the notion that the ability to process syntactic violations during on-line sentence comprehension is well established by five years of age.

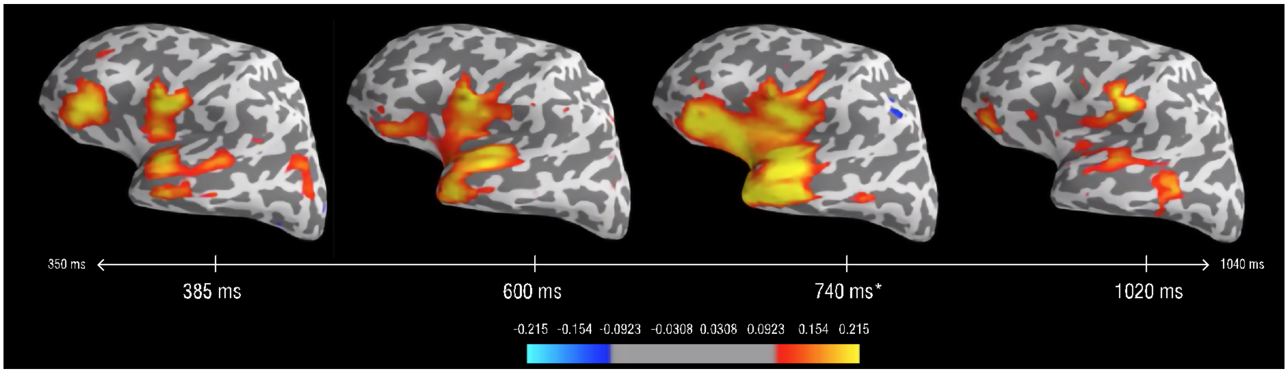
3.2 Cortical Activation in Jabberwocky Sentence Processing

3.2.1 Source estimation

Unlike in the English condition described above, the dSPM representing the difference in estimated cortical activation between syntactically congruent and incongruent Jabberwocky sentences did not show an incongruency effect, though notable differences between manipulations were observed, as projected. Unexpectedly, and in contrast to the pattern of activity observed in English, the Jabberwocky dSPM revealed stronger activation in the congruent versus incongruent condition; hence, it is referred to as a syntactic *congruency* effect.

In the left hemisphere, activity was sustained longer and peaked later than in the English condition, appearing ~350–1040 ms post-stimulus, and reaching its maximal effect ~740 ms (see Figure 4a). While Jabberwocky activation spanned similar frontal, temporal, and parietal areas as English, it was more anteriorly distributed and greater in magnitude in the IFC, insular cortex, and ATL. Right hemisphere involvement was noted in a more constrained time window post-stimulus, ~510–920 ms, peaking at ~770 ms, in regions posterior to those active in the left hemisphere, including the posterior STG, SMG, and TPJ (see Figure 4b). Corresponding ROIs in the vicinity of the insular cortex/ATL and SMG are shown in Figure 5 for the left (5a) and right (5b) hemispheres.

4a.



4b.

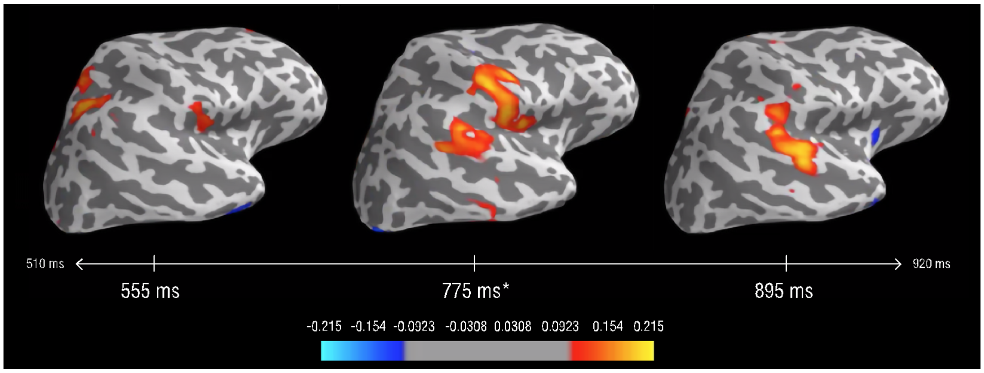


Figure 4. Estimated activity of the Jabberwocky syntactic congruency effect, at four representative latencies within the time window of interest for the left hemisphere (350–1040 ms) and three representative latencies for the right hemisphere (510–920 ms), as determined by observed activation in the difference dSPM (congruent minus incongruent), and visualized on an inflated cortical surface. Color indicates the magnitude of the difference between experimental manipulations, with yellow representing areas where activation to congruent words is greatest with respect to incongruent words. Time points representing the peak activation difference in each hemisphere are indicated by *.

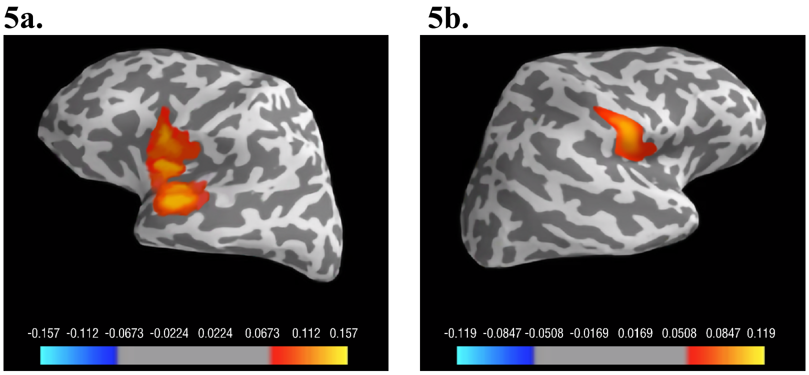


Figure 5. Average activity in Jabberwocky congruent minus incongruent experimental manipulations for the left (a) and right (b) hemispheres within the post-stimulus time windows of 350–1040 ms and 510–920 ms, respectively.

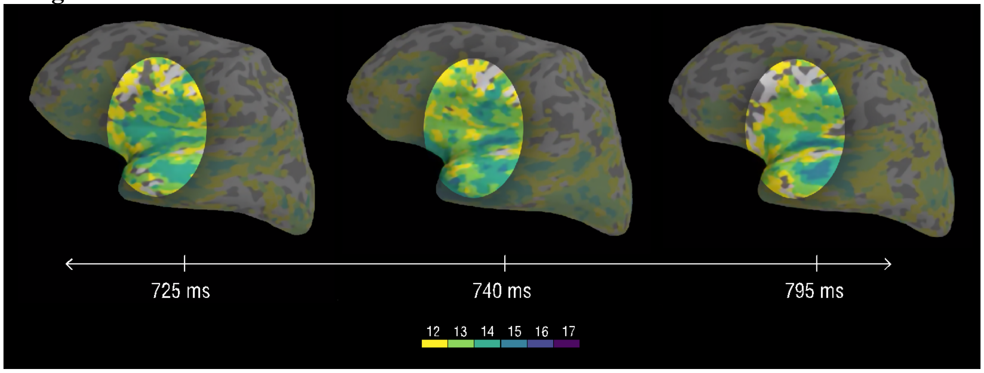
Paired samples t-tests were conducted to compare activity in the ROIs between experimental manipulations in the Jabberwocky condition. There was a significant difference in activity within the left hemisphere ROI between congruent ($M = 0.40$, $SD = 0.09$) and incongruent ($M = 0.30$, $SD = 0.04$) manipulations; $t(16) = 4.97$, $p < .001$. There was also a significant difference in activity within the right hemisphere ROI between congruent ($M = 0.41$, $SD = 0.14$) and incongruent manipulations ($M = 0.33$, $SD = 0.08$); $t(16) = 2.94$, $p = .010$. These results indicated a syntactic congruency effect within the spatiotemporal ROIs in the Jabberwocky condition; specifically, children showed significantly more activation within both left and right hemisphere ROIs when presented with syntactically congruent Jabberwocky sentences than when presented with syntactically incongruent Jabberwocky sentences. As with English, conjunction analyses were performed to determine whether these findings represented consistency of activation across subjects or if they were driven by a small number of subjects.

3.2.2 Conjunction/partial conjunction analyses

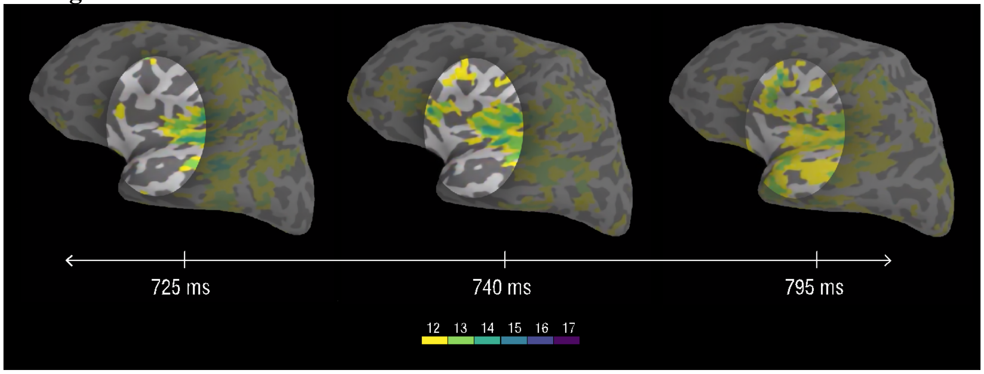
Consistency maps without formal correction were created to provide heuristics of the single-subject statistics across the *a priori* time window of 500–850 ms. Group-level st-sPC analysis was then performed, resulting in partial conjunction maps of maps of Jabberwocky congruent and incongruent manipulations between 350–1040 ms post-stimulus. In the left hemisphere, the cortical response following the syntactic manipulation peaked at ~740 ms in the vicinity of the insular cortex and ATL; in the right hemisphere, activation peaked at ~770 ms in the SMG. Partial conjunction maps surrounding these peak latencies were examined for each congruency manipulation[9], to reveal the number of subjects showing significant activation in the vicinity of each ROI (see Figure 6).

6a.

Congruent



Incongruent



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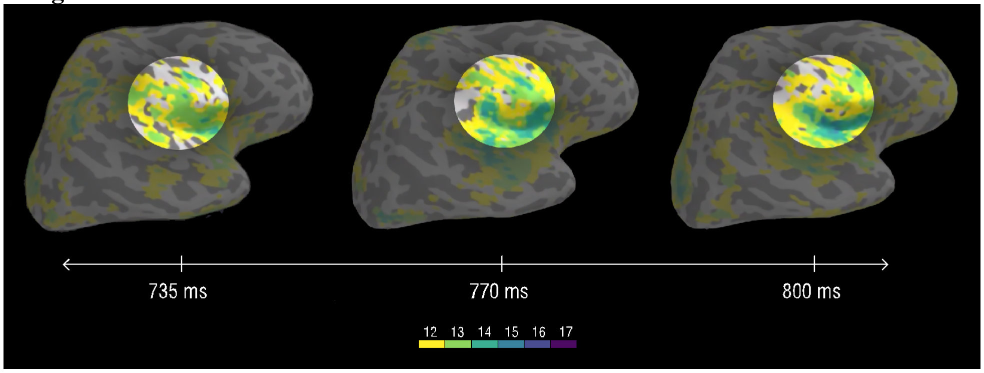
[9] Again, the reader is advised that the results of the partial conjunction analysis must be interpreted within the context of those described in Section 3.2.1 with regard to strength of cortical activation and the effect of the syntactic manipulation (i.e. the difference in activation strength between congruent and incongruent manipulations).

6b.

Congruent



Incongruent

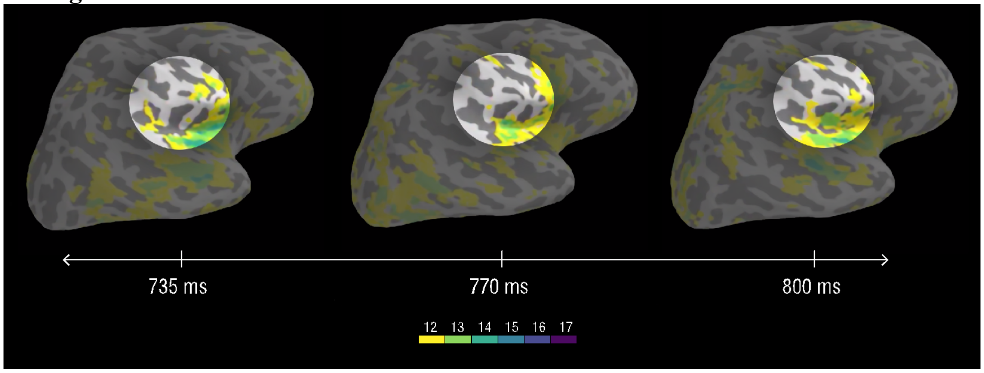


Figure 6. st-sPC maps showing the number of subjects (*N* = 17) meeting a threshold of $p < 10^{-8}$ surrounding peak latencies within the 350–1040 ms time window in syntactically congruent and incongruent manipulations in the Jabberwocky language condition for the left (a) and right (b) hemispheres, displayed on inflated cortical surfaces. Areas of the cortex encompassing the spatiotemporal ROIs shown in Figures 5a and 5b are highlighted here in 6a and 6b, respectively. Colors represent the number of subjects with activation in a given area; maps are visualized with a lower bound of 12 subjects.

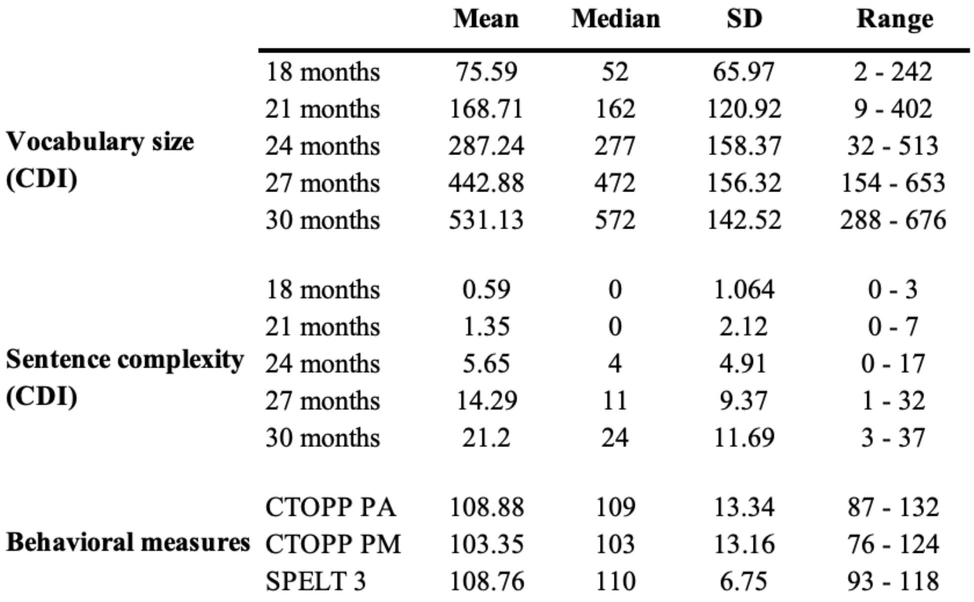
Contrary to the expectation that cortical activation during Jabberwocky sentence processing may not be consistent across subjects, some areas of high consistency were observed within areas of activation associated with the syntactic manipulation. Figure 6a shows that 12–16 subjects had significant activation in the area associated with the peak syntactic manipulation effect in the left hemisphere (insula/ATL) in the congruent manipulation, whereas consistency above 12 subjects was generally restricted to more focal areas within this ROI in the incongruent manipulation. Figure 6b illustrates that 12–15 subjects had significant activation in the vicinity of the peak syntactic effect in the right hemisphere (SMG/TPJ) in the congruent manipulation, while fewer than 12 subjects had significant activation in these areas in the incongruent manipulation. Due to the robust multiple comparison correction in the partial conjunction analyses, it can be validly inferred that at least 12 individuals showed significant cortical activity in these areas at a given time point when they encountered syntactically congruent Jabberwocky sentences. Therefore, the syntactic congruency effect in Jabberwocky was consistent across participants, particularly in the left hemisphere.

3.2.3 Summary

As tentatively predicted, different cortical responses were observed during Jabberwocky sentence processing than during English sentence processing, though the opposite directionality of these effects was unexpected: children showed syntactic congruency–rather than incongruency–effects, in which greater cortical activation was observed in response to syntactically congruent than incongruent sentences, in the absence of lexical-semantic context. Surprisingly, these effects showed some areas of consistency across participants in both left and right hemisphere ROIs, indicating that they may represent a common response among typically developing 5-year-olds, albeit a different response than that observed in English sentence processing.

3.3 Cortical Activation and Language Proficiency

The following section details analyses performed among subjects' MacArthur-Bates Communicative Development Inventory (CDI) scores, tabletop behavioral test scores, and strength of the syntactic manipulation effects within functional ROIs. See Table 1 for descriptive statistics of subjects' scores on CDI measures of expressive vocabulary size and sentence complexity at each of five data collection time points between 18 and 30 months and standardized scores on three tabletop behavioral measures, CTOPP PA, CTOPP PM, SPELT-3, collected at the time of the MEG recordings when subjects were five years old. See Table 2 for descriptive statistics of values representing the difference in activation between congruent and incongruent manipulations in English and Jabberwocky ROIs.



		Mean	**Median**	**SD**	**Range**
Vocabulary size (CDI)	18 months	75.59	52	65.97	2 - 242
	21 months	168.71	162	120.92	9 - 402
	24 months	287.24	277	158.37	32 - 513
	27 months	442.88	472	156.32	154 - 653
	30 months	531.13	572	142.52	288 - 676
Sentence complexity (CDI)	18 months	0.59	0	1.064	0 - 3
	21 months	1.35	0	2.12	0 - 7
	24 months	5.65	4	4.91	0 - 17
	27 months	14.29	11	9.37	1 - 32
	30 months	21.2	24	11.69	3 - 37
Behavioral measures	CTOPP PA	108.88	109	13.34	87 - 132
	CTOPP PM	103.35	103	13.16	76 - 124
	SPELT 3	108.76	110	6.75	93 - 118

Table 1. Descriptive statistics of subjects' scores on CDI measures of vocabulary size and sentence complexity between 18 and 30 months, and standardized scores on behavioral tests (CTOPP PA, CTOPP PM, SPELT-3) at five years ($N = 17$). It should be noted that two subjects are missing CDI scores at 30 months; $N = 15$ for this data collection time point.

		Mean	Median	SD	Range
English	LH (420-740 ms)	-0.083	-0.068	0.152	-0.452 - 0.122
	RH (355-650 ms)	-0.112	-0.094	0.199	-0.580 - 0.181
Jabberwocky	LH (350-1040 ms)	0.108	0.086	0.090	-0.035 - 0.289
	RH (510-920 ms)	0.080	0.063	0.112	-0.092 - 0.314

Table 2. Descriptive statistics of subjects' estimated cortical activation within spatiotemporal ROIs by hemisphere (LH/RH) and language condition (English and Jabberwocky), shown as values representing the difference between congruent and incongruent manipulations within each ROI.

3.3.1 Longitudinal and concurrent language measure correlations

Overall, early vocabulary size was highly predictive of scores on all three tabletop behavioral tests at the age of five years. A two-tailed test of significance indicated a positive relationship between CTOPP PA and average vocabulary size between 18 and 30 months $r_s(15) = .68$, $p = .003$. A pattern of significant positive relationships between CTOPP PA and vocabulary size was noted at 21 months $r_s(15) = .67$, $p = .003$; 24 months $r_s(15) = .75$, $p < .001$; 27 months $r_s(15) = .62$, $p = .009$; and 30 months $r_s(13) = .74$, $p = .002$. Similar correlations were found between CTOPP PM and vocabulary size. A significant positive relationship was noted between CTOPP PM scores and average vocabulary size $r_s(15) = .62$, $p = .009$, as well as a pattern of positive associations at four consecutive CDI time points: 21 months $r_s(15) = .56$, $p = .020$; 24 months $r_s(15) = .67$, $p = .004$; 27 months $r_s(15) = .53$, $p = .030$; and 30 months $r_s(13) = .56$, $p = .029$. Likewise, significant positive correlations were observed between SPELT-3 and average vocabulary size $r_s(15) = .61$, $p = .009$, vocabulary size at 24 months $r_s(15) = .61$, $p = .010$; 27 months $r_s(15) = .63$, $p = .007$; and 30 months $r_s(13) = .57$, $p = .026$ (see Table 3 for a summary of all correlations performed between standardized behavioral test scores and CDI measures of vocabulary size).

	Vocabulary size (CDI)					
	18 months	21 months	24 months	27 months	30 months	Avg
CTOPP PA	.356	**.671****	**.752*****	**.615****	**.736****	**.677****
CTOPP PM	.351	**.557***	**.665****	**.526***	**.563***	**.615****
SPELT-3	.295	.391	**.605***	**.627****	**.570***	**.614****

Table 3. Correlation coefficients (Spearman's *rho*) for correlations performed between tabletop behavioral tests at age five years (CTOPP PA, CTOPP PM, and SPELT-3) and CDI measures of vocabulary size at each of five time points between 18 and 30 months, and the average across these time points. Significant correlations are highlighted; * indicates significance at the $p < .05$ level; ** indicates significance at the $p < .01$ level; *** indicates significance at the $p < .001$ level.

CDI measures of sentence complexity were also predictive of behavioral test scores, though with less consistency than vocabulary size. A two-tailed test of significance indicated a significant positive relationship between CTOPP PA and average sentence complexity between 18 and 30 months $r_s(15) = .71$, $p = .001$. A pattern of significant positive relationships between CTOPP PA and sentence complexity was noted at 24 months $r_s(15) = .51$, $p = .037$; 27 months $r_s(15) = .60$, $p = .011$; and 30 months $r_s(13) = .65$, $p = .009$. A significant positive relationship was found between CTOPP PM and sentence complexity, though only for the average across time points $r_s(15) = .53$, $p = .028$ and at 24 months $r_s(15) = .58$, $p = .014$. Finally, one significant positive correlation was observed between SPELT-3 and sentence complexity at 21 months $r_s(15) = .50$, $p = .040$. Correlations between sentence complexity and CTOPP PM and SPELT-3 scores did not reveal patterns of associations across time, and should therefore be interpreted with caution (see Table 4 for a summary of all correlations performed between behavioral test scores and CDI measures of sentence complexity).

Sentence complexity

	18 months	21 months	24 months	27 months	30 months	Avg
CTOPP PA	.126	.411	**.509***	**.601***	**.651****	**.709****
CTOPP PM	.141	.180	**.583***	.442	.290	**.533***
SPELT-3	.052	**.502***	.420	.324	.315	.428

Table 4. Correlation coefficients (Spearman's *rho*) for correlations performed between tabletop behavioral tests at age five years (CTOPP PA, CTOPP PM, and SPELT-3) and CDI measures of sentence complexity at each of five time points between 18 and 30 months, and the average across these time points. Significant correlations are highlighted; * indicates significance at the $p < .05$ level; ** indicates significance at the $p < .01$ level.

Summary. Early measures of vocabulary size were found to be strong predictors of later performance on tabletop behavioral tests of phonological awareness, phonological memory, and morphosyntax. A relationship between vocabulary size and PA was to be expected, as there is a robust literature indicating the importance of early vocabulary on later PA (see, e.g., Cardillo, 2010). Though it is novel to observe a relationship between early vocabulary and later morphosyntax, this is not surprising given the interconnected nature of language learning across linguistic domains during early childhood[10] (see Kuhl, 2011; Kuhl & Rivera-Gaxiola, 2008 for review; refer to Section 1.4).

CDI measures of sentence complexity were also found to be strong predictors of performance on tabletop tests, though a pattern of correlations across time was noted only for the test of phonological awareness. This is at odds with the expectation that early sentence complexity would predict later expressive grammatical skills.

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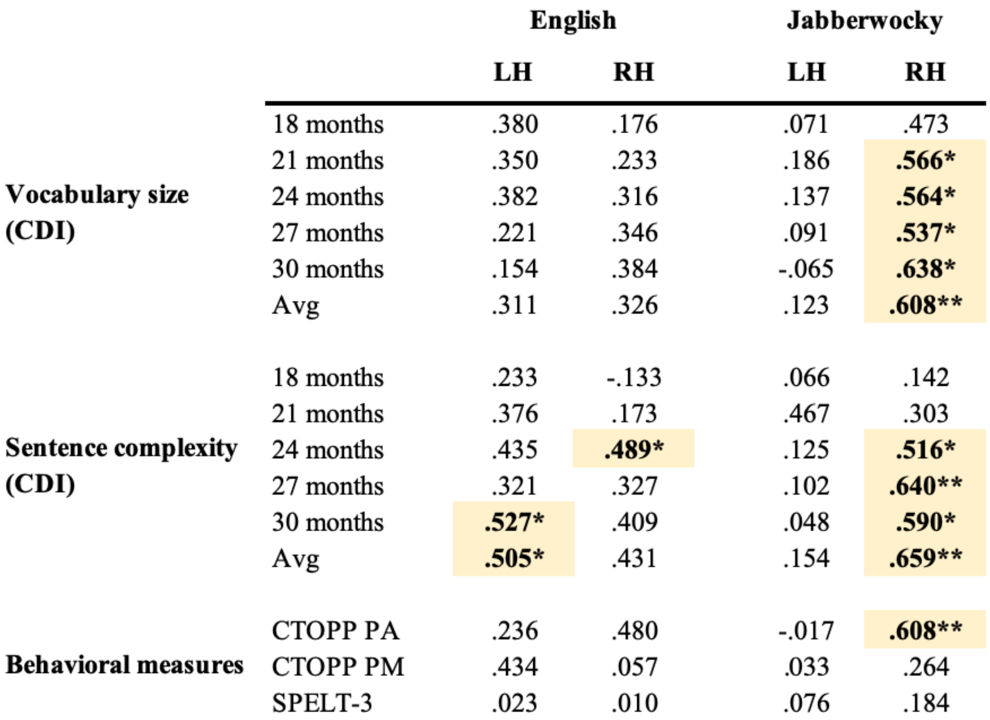
[10] The reader should be aware that, somewhat surprisingly, Spearman correlations yielded no significant associations among SPELT-3, CTOPP PA, and CTOPP WM scores.

3.3.2 Longitudinal/concurrent language measure and cortical activation correlations

No significant correlations were found between CDI scores for vocabulary size and activation in left or right hemisphere ROIs in the English language condition. Likewise, no significant correlations were found between tabletop behavioral test scores and activation in either English ROI. Significant positive associations were noted between sentence complexity and activation in the English left hemisphere ROI for the average of the five time points $r_s(15) = .51$, $p = .039$ and the 30 month time point $r_s(13) = .53$, $p = .043$. A significant positive association was also noted between sentence complexity at 24 months and activation in the English right hemisphere ROI $r_s(15) = .49$, $p = .046$. However, correlations between sentence complexity and cortical activation in English ROIs were not consistent across time. Persistent correlations between brain and behavior across CDI data collection time points were considered to be of greater theoretical importance than those at individual time points or across all time points, as they suggest continuity of an effect of early language proficiency on later sentence processing.

No significant correlations were found between any CDI scores or tabletop behavioral test scores and activation in the Jabberwocky left hemisphere ROI. Several interesting patterns of association were observed, however, between behavioral measures and activation in the Jabberwocky right hemisphere ROI. A two-tailed test of significance indicated a significant positive relationship between activation in the right hemisphere ROI and average vocabulary size between 18 and 30 months $r_s(15) = .61$, $p = .010$. A pattern of significant positive correlations between right hemisphere activation and vocabulary size was noted at 21 months $r_s(15) = .57$, $p = .018$; 24 months $r_s(15) = .56$, $p = .018$; 27 months $r_s(15) = .54$, $p = .010$; and 30 months $r_s(13) = .64$, $p = .010$.

A similar pattern was observed between activity in the right hemisphere ROI in Jabberwocky and sentence complexity. A significant positive relationship was noted for average sentence complexity scores $r_s(15) = .66$, $p = .004$, as well as positive associations at individual time points, including at 24 months $r_s(15) = .52$, $p = .034$; 27 months $r_s(15) = .64$, $p = .006$; and 30 months $r_s(13) = .59$, $p = .021$. Finally, a significant positive correlation was observed between right hemisphere ROI activity and CTOPP PA scores $r_s(15) = .61$, $p = .010$, (see Table 5 for a summary of all correlations performed between behavioral measures and cortical activation modulated by syntactic processing).



		English		**Jabberwocky**	
		LH	**RH**	**LH**	**RH**
Vocabulary size (CDI)	18 months	.380	.176	.071	.473
	21 months	.350	.233	.186	**.566***
	24 months	.382	.316	.137	**.564***
	27 months	.221	.346	.091	**.537***
	30 months	.154	.384	-.065	**.638***
	Avg	.311	.326	.123	**.608****
Sentence complexity (CDI)	18 months	.233	-.133	.066	.142
	21 months	.376	.173	.467	.303
	24 months	.435	**.489***	.125	**.516***
	27 months	.321	.327	.102	**.640****
	30 months	**.527***	.409	.048	**.590***
	Avg	**.505***	.431	.154	**.659****
Behavioral measures	CTOPP PA	.236	.480	-.017	**.608****
	CTOPP PM	.434	.057	.033	.264
	SPELT-3	.023	.010	.076	.184

Table 5. Correlation coefficients (Spearman's *rho*) for correlations performed between CDI measures of vocabulary size and sentence complexity, tabletop behavioral tests (CTOPP PA, CTOPP PM, and SPELT-3), and cortical activity in left and right hemisphere ROIs in the English and Jabberwocky language conditions. Significant correlations are highlighted; * indicates significance at the $p < .05$ level; ** indicates significance at the $p < .01$ level.

Summary. The brain-behavior correlations yielded several interesting findings. Neither CDI scores nor behavioral test scores reliably predicted neural activity modulated by syntactic incongruency in the English ROIs. Likewise, no significant correlations were found between CDI or behavioral test scores and strength of the syntactic congruency effect in the left hemisphere Jabberwocky ROI. However, both early vocabulary size and sentence complexity, as well as later PA, were shown to be strong predictors of the magnitude of the response to syntactic manipulations in the Jabberwocky right hemisphere ROI. In other words, children with larger vocabularies and higher sentence complexity scores as toddlers, and better phonological awareness at age five, exhibited stronger activation within this ROI during the processing of congruent versus incongruent Jabberwocky sentences.

3.4 Overall Summary of Findings

Visual inspection of cortical activation modulated by syntactic manipulations in English and Jabberwocky sentences revealed divergent patterns of activity within a broadly defined time window of interest (350–1040 ms post-stimulus). Participants showed increased activation in incongruent versus congruent manipulations during English sentence processing, with peak activation along the Sylvian fissure in the left hemisphere that was temporally compatible with the P600 ERP component and highly consistent across participants. On the other hand, participants showed increased activity in the congruent versus incongruent manipulations during Jabberwocky sentence processing, with peak activation in insular/anterior temporal areas of the left hemisphere and SMG in the right hemisphere. Somewhat surprisingly, the congruency effects associated with Jabberwocky sentence processing showed some areas of consistency across participants.

Further steps were taken to investigate the syntactic in/congruency effects in English and Jabberwocky sentence processing using a data-driven approach, to determine whether longitudinal and/or concurrent measures of language development would predict the strength of these effects. While no meaningful correlations were found between behavioral measures and brain activity in English, children with higher scores on early language development measures of vocabulary and sentence complexity, as well as higher PA, exhibited stronger syntactic congruency effects in well-formed Jabberwocky sentence processing in the right hemisphere.

CHAPTER 4: DISCUSSION

4.1 General Discussion

The primary goal of the present study was to improve upon the spatiotemporal characterization of on-line sentence processing in children. Specifically, it sought to determine 1) whether 5-year-olds show similar or different syntactic processing effects in the brain under conditions of intact versus greatly reduced semantic context, and 2) the role of language proficiency in sentence processing ability. To this end, this study examined MEG-recorded cortical activation associated with syntactic processing in typically developing 5-year-olds, in English and Jabberwocky sentences. Jabberwocky sentences, in which meaning was greatly reduced but structural elements were retained, were used to reveal whether children at this age rely on lexical-semantic information to process syntactic (phrase structure) violations in natural speech. We expected syntactic violations in the English sentence condition to elicit a response resembling the temporal characteristics of the P600 ERP component, characterized spatially by increased cortical activity in the incongruent versus congruent condition in left-dominant frontal, temporal, and/or parietal areas. In contrast, we expected syntactic violations in the Jabberwocky condition to elicit cortical activation with differing spatiotemporal characteristics than in English, suggesting reliance on the availability of lexical-semantic information to perform the syntactic parse. We used data-driven correlational analyses to examine the relationship between behavioral language development measures and cortical responses to syntactic manipulations in the presence and absence of semantic context, and to address whether children's early/concurrent language proficiency would predict brain activity under these experimental conditions.

The following discussion centers on the two primary findings of the present study: 1) the syntactic incongruency effect elicited by phrase structure violations in English sentences, and 2) syntactic congruency effects elicited by intact phrase structure in Jabberwocky sentences. The spatiotemporal properties of the English incongruency effect are discussed with respect to current temporal and spatial characterizations of syntactic processing in developmental and adult populations, and justifications for its interpretation as an index of syntactic processing are provided. Consideration is then given to the spatiotemporal properties of Jabberwocky congruency effects by hemisphere, as they relate to past accounts of the neural signatures of cognitively demanding processing tasks and children's preferential attendance to familiar over unfamiliar linguistic stimuli. Significant correlations between language proficiency and the right hemisphere Jabberwocky congruency effect are explored, and implications of an association between language skills and processing efficiency are discussed, as they pertain to language development. Finally, study limitations are addressed and future research directions are proposed, in light of the insights gained from this investigation.

4.2 The Syntactic Incongruency Effect in English Sentence Processing

The present study was the first to examine MEG-recorded brain responses in 5-year-olds to phrase structure violations in natural speech. The experimental manipulation of grammaticality within English sentences yielded a novel and theoretically meaningful finding, namely a syntactic incongruency effect that is temporally compatible with an adult-like P600, and spatially concentrated in perisylvian language-sensitive areas of the left hemisphere. We argue that this activation specifically reflects an effect of syntactic processing. Justifications for this interpretation are offered below.

4.2.1 Children show an effect of syntactic processing in the P600 time window

While all MEG analyses were performed in source space, it is important to first consider the temporal dynamics of the syntactic incongruency effect to justify its interpretation as a syntactic response. The results supported the hypothesis that children's brain activity would show an effect of syntactic processing in meaningful English sentences within a P600 time window: distributed source modeling estimated greater cortical activation for syntactically incongruent over congruent sentences ~420–750 ms after the onset of the phrase structure violation (i.e., the preposition) in the left hemisphere[11]. This is closely aligned with Silva-Pereyra and colleagues' (2007) finding with 36-month-olds using the same sentence paradigm: syntactically incongruent sentences elicited a larger positivity than congruent sentences 500–750 ms post-stimulus over frontal and temporal electrode sites. The authors considered this effect to reflect P600-like activity (Silva-Pereyra et al., 2007). While differences in the signal captured by MEG versus EEG preclude the ability to draw a direct comparison between the effects found in 3-year-olds in the previous study with 5-year-olds in the present study, the striking similarity in latency may indicate comparable processing events.

Importantly, it cannot be determined with certainty whether the incongruency effect found in the present study specifically reflects a process of syntactic reanalysis/repair, electrophysiologically indexed by the P600; hence, alternative explanations must be explored. The latency of the response is such that it could, in theory, reflect another linguistic process such as initial syntactic structure-building (E/LAN) or semantic integration (N400), or a general reaction to encountering an unexpected stimulus (P300). However, several considerations of this

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[11] Analyses examined activation in both hemispheres, but the temporal dynamics of the syntactic incongruency effect are discussed only with regard to left hemisphere activity, as right hemisphere activity is not presumed to reflect a separate processing event. The possible role of right hemisphere homologue activity is mentioned in Section 4.2.2.

investigation—including participant age, violation type, and experimental paradigm—lend considerable support to the original interpretation over these alternatives.

Anterior negativities (referred to collectively as E/LAN), are sometimes associated with detection of phrase structure (Hahne & Jescheniak, 2001) and morphosyntactic (Coulson, King, & Kutas, 1998; Gunter, Stowe, & Mulder, 1997) violations in adults. However, these effects are not reliably elicited in young children (Silva-Pereyra et al., 2005a, b; Silva-Pereyra et al., 2007), leading some to speculate that the automatic processing mechanisms underlying these effects do not emerge until later in development (Hahne et al., 2004; however, see Oberecker et al., 2005, 2006 for discrepant findings). The inconsistency of this response in adult studies (for review see Friederici & Weissenborn, 2007), as well as potential developmental factors, provide evidence against the designation of the observed syntactic effect as an E/LAN-type response. Interpreting the syntactic incongruency effect as N400-like versus P600-like activity is also unfavorable, in light of differences in polarity, latency, and scalp topography that exist between ERP effects elicited by semantic versus syntactic manipulations in preschool-age children (e.g., Silva-Pereyra et al., 2005 a, b). Distinct modulations of brain activity for each violation type have been recorded in children as young as 30 months; therefore, it is unlikely that phrase structure violations would trigger a response related to semantic versus syntactic integration in 5-year-olds. Finally, it is possible for the syntactic incongruency effect to reflect a general cognitive response associated with violation of expectancy, as opposed to a syntactic process per se, indexed by the P300 family of ERP components (Coulson et al., 1998). Indeed, Silva-Pereyra and colleagues (2005b) interpreted an early positivity to morphosyntactic violations in 3- and 4-year-olds as such. However, the P300 is typically observed when there is a low probability of encountering target items in the paradigm relative to the probability of encountering non-target items (i.e., the oddball paradigm). In the present study, the probability of encountering a target item (incongruent sentence) versus a non-target item (congruent sentence) was equal; thus, a P300-like response would be implausible. Future investigations seeking to corroborate the finding of P600-like activity to phrase structure violations using MEG should include additional manipulations with varying violation types and target item frequency, to better understand the extent to which the syntactic incongruency effect is specific to syntactic processing or to the experimental paradigm.

It is also necessary to consider the extent to which the latency of the effect observed in this study echoes those described in other developmental accounts of the P600. Discrepancies have been reported with regard to the P600 latency in children: some studies have found delayed P600 components in developmental populations, including in older children (Friederici & Hahne, 2001; Hahne & Friederici, 1999; Hahne et al., 2004; Usler & Weber-Fox, 2015), while others have observed more adult-like latencies in children of comparable ages (Atchley et al., 2006). Several studies with toddlers and preschoolers have found two temporally distinct ERP positivities associated with the processing of syntactic violations (Bernal et al., 2010; Schipke, Knoll, Friederici, & Oberecker, 2012; Silva-Pereyra et al., 2005a, 2005b, 2007). For instance, Silva-Pereyra and colleagues (2007) reported a very late positivity between 1050–1300 ms post-stimulus, in conjunction with the effect in the 500–750 ms time window[12]. The stimulus presentation in that (and the current) study poses challenges to interpretation of effects at such latencies. Sentences were presented as natural speech and critical words were sentence internal; therefore, it may be difficult to distinguish between late processing effects of the critical word and early processing effects of the following word. For this reason, we did not consider

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[12] However, this effect was only significant at one electrode site.

activation beyond ~1000 ms post–critical word onset in the present analyses. Future studies may wish to examine late activation associated with syntactic processing, using stimulus presentation that is better suited to this purpose, e.g., segmented as opposed to fluent speech.

4.2.2 Syntactic processing occurs in language-sensitive areas of the left hemisphere

Distributed source modeling (dSPM) was used to estimate the cortical locations of MEG-recorded magnetic field variations associated with syntactic processing, in the first attempt to localize cortical activation associated with syntactic processing in children. The results of this analysis supported the hypothesis that syntactic processing activity would be concentrated in language-sensitive areas of the left hemisphere, including frontal, temporal, and parietal sources. Within the ~420–750 ms time window post-stimulus onset, increased activation to incongruent over congruent manipulations was observed, beginning in the vicinity of insular and frontal opercular (FOP) cortices, spreading in a posterior direction into the Sylvian fissure, superior/middle temporal areas, and temporoparietal junction (TPJ). The effect of the experimental manipulation appeared to be maximal ~555 ms post–critical word onset within the Sylvian fissure.

The locations associated with the syntactic incongruency effect in the present study closely approximate those identified in brain-based investigations of syntax in adults (Friederici et al., 2000, 2003, 2010; Humphries et al., 2001, 2006; Kwon et al., 2005; Lee & Newman, 2010; Makuuchi et al., 2009; Ni et al., 2000; Service et al., 2011) and children (Brauer & Friederici, 2007; Skeide et al., 2014). The only two MEG studies to identify the neural generators of the P600 in adults have localized activation to temporal sources compatible with those implicated in the present study (Kwon et al., 2005; Service et al., 2007). The involvement of additional cortical areas for syntactic processing reported here may be attributed to the developmental age of participants, as children generally recruit broader areas for language processing than do adults (for a recent review, see Skeide & Friederici, 2016). Alternatively, these differences may be a by-product of the analysis techniques used in each. Whereas the present study employed a distributed source model to estimate the spatial contributions of this response, both Kwon et al. (2005) and Service et al. (2007) used equivalent current dipole modeling, which assumes focal activation localized to a small number of discrete dipole sources and may obscure the spatial extent of event-related activity (Van Petten & Luka, 2006). As so few studies have attempted to localize the magnetic equivalent of the P600, only tentative claims can be made about the specific cortical areas involved in on-line syntactic processing in children based on the results presented here.

Notably, the spatiotemporal characterization of the syntactic incongruency effect found in the current study is in keeping with Friederici's (2011, 2012; Skeide & Friederici, 2016) model of syntactic information transfer in the adult brain, and more tentatively in the developing brain (Skeide & Friederici, 2016). It is important to acknowledge that this model attempts to reconcile incomplete temporal and spatial characterizations of language and is therefore largely speculative in nature; hence, interpretations of the syntactic incongruency with respect to this model should be considered with caution. That said, consistency between the proposed neurocognitive model of syntactic processing and the findings of the current study warrant mention. The model assumes that syntactic information propagates from the inferior frontal cortex (IFC) to the posterior superior temporal gyrus/sulcus (STG/STS) (Skeide & Friederici, 2016). We noted similarities to this account in both location and directionality of cortical activation associated with syntactic processing, with activation generally propagating from frontal to posterior temporal/temporoparietal sources between ~420–750 ms post-stimulus. The model also suggests a role of sentence-level prosodic processing in the right STG and IFG between 300–500 ms post-stimulus, which might account for right hemisphere homologue activity of the syntactic incongruency effect, observed at a latency of ~355–650 ms after the onset of the phrase structure violation. See Figure 7 for a schematic of the language network proposed by Skeide and Friederici (2016).

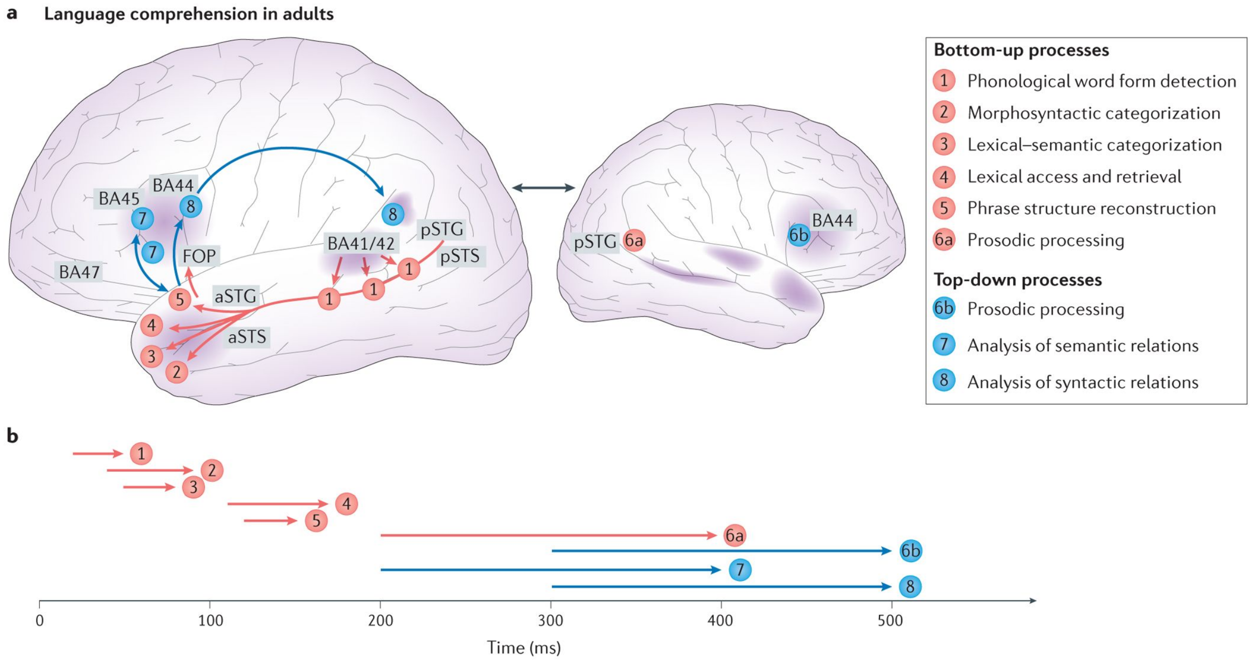

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Figure 7. Skeide and Friederici's (2016) characterization of the adult auditory language comprehension network, including linguistic processes from the level of phonological word form detection through high-level syntactic analysis. Cortical areas associated with each level of processing and the direction of information transfer between them is represented in 7a. The temporal characteristics of each process are shown in 7b. Of primary relevance to this discussion are sentence-level processes of semantics (7) and syntax (8) in the left hemisphere, as well as prosody in the right hemisphere (6b). Adapted from Skeide & Friederici, *Nature Reviews Neuroscience*, 2016.

While the temporal and spatial characteristics of the incongruency effect give credence to its interpretation as a syntax-related response, it cannot be presumed to reflect a process of pure syntactic analysis independent from semantics. ERP studies have arguably dissociated semantic and syntactic processing mechanisms in 30- to 48-month-olds, reflected by the N400 and P600 (Harris, 2000; Silva-Pereyra et al., 2005a, b); on the other hand, fMRI studies have found spatially indistinguishable areas of hemodynamic activity associated with both semantic and syntactic manipulations in children between the ages of three and seven (Brauer & Friederici, 2007; Nuñez et al., 2011), with evidence of functional specificity within the language network only in older children (Nuñez et al., 2011; Skeide & Friederici, 2014). Furthermore, it is possible that the activity captured in the ~420–750 ms time window does not reflect a single processing event, but rather two separate events with distinct spatial distributions and functions with respect to semantic and syntactic processes. Frontal activation in the earlier half of the window might reflect a phase of thematic role assignment including the parallel processing of semantic and syntactic information, while the temporal/temporoparietal activation in the second half of the window may reflect the phase of syntactic reanalysis/repair (see Friederici, 2011). Such an interpretation would be aligned with the previous findings of overlapping cortical contributions to semantic and syntactic manipulations between 300–500 ms post-stimulus (Kwon et al., 2005; Service et al., 2007). This study was not designed to address the interaction of semantic and syntactic processes during meaningful sentence comprehension; however, this will be an important next step in understanding the temporal and spatial relationship between these processes in the developing brain.

4.2.3 Syntactic processing may not be related to language proficiency

A series of bivariate correlations were performed between a variety of behavioral language measures and brain activity reflecting the effect of the syntactic manipulation within functionally defined regions of interest (ROIs). Correlations between longitudinal measures of language development (expressive vocabulary size and sentence complexity between 18–30 months) and the magnitude of the syntactic incongruency effect within left and right hemisphere ROIs yielded no theoretically meaningful significant results[13]. Correlations performed between concurrent language proficiency measures (phonological awareness (PA), phonological memory (PM), and morphosyntax) and response magnitude were also not significant. Though these analyses were data driven, previous literature would suggest a relationship between language proficiency and syntactic processing effects (Alattore-Cruz et al., 2018; Hampton Wray & Weber-Fox, 2013). There are a few potential explanations for these null findings, outside the possibility that syntactic processing is unrelated to language skill. For instance, these analyses took into account the syntactic manipulation effect in only one spatiotemporal ROI per hemisphere, representing the area in which the effect was greatest across subjects within the time window of activation. It is possible that contributions of other cortical areas not captured here would correlate with these behavioral indices of language proficiency. Alternatively, it could be that response characteristics other than magnitude, such as peak latency or duration, might be sensitive to differences in language abilities across individuals (for example, Harris, 2000). The present study was not designed to test these possibilities, though future research seeking to understand the brain-behavior relationship in language development should take them into consideration.

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[13] A small number of individual correlations are reported; however, only those that persisted across time were considered to be of theoretical importance.

4.2.4 Summary

We consider the syntactic incongruency effect observed in MEG-recorded brain activity to syntactic violations in English to reflect a process of on-line syntactic analysis, perhaps one of reanalysis/repair analogous to the P600 ERP component. The effect is spatially consistent with prior characterizations of syntactic processing in adults, which supports the idea that the cortical organization of language functions may be established early in life. Contrary to expectation, no correlations were found between longitudinal or concurrent measures of language development and the magnitude of the syntactic incongruency effect. Due to the limitations of this analysis, no definitive claims can be made regarding a potential association, or lack thereof, between language proficiency and syntactic processing ability in 5-year-olds.

4.3 Syntactic Congruency Effects in Jabberwocky Sentence Processing

The present study investigated the extent to which children rely on lexical-semantic information for syntactic processing. As the first to do so using MEG, it provided novel findings regarding the spatiotemporal properties of on-line syntactic processing in semantically impoverished (i.e., Jabberwocky) sentences. The experimental manipulation of grammaticality within the Jabberwocky condition yielded unexpected results, namely syntactic congruency effects, in which cortical activity was greater with respect to syntactically congruent versus incongruent sentences bilaterally. While the effect was characterized by left hemisphere dominant bilateral activation, we argue that activity in the left hemisphere reflects a general increase in processing effort, associated with the higher cognitive demand of attempting to making sense of nonsensical sentences. On the other hand, we offer the interpretation that right hemisphere activation reflects an attentional process elicited by the syntactic manipulation in this experimental condition.

4.3.1 Children do not perform syntactic analysis without lexical-semantic information

The effects of syntactic congruency, i.e. greater cortical responses to congruent than incongruent sentences, were unanticipated. However, the qualitatively different brain response to Jabberwocky sentences as compared to English sentences, in which a syntactic incongruency effect was reported, is aligned with the expectation of a distinct pattern of brain activity associated with sentence processing in the absence of lexical-semantic information. Moreover, this finding is consistent with the hypothesis that semantic and syntactic operations remain tightly coupled long after children master the ability to process each type of information during on-line language comprehension (see Skeide & Friederici, 2016). In the present study, distributed source modeling estimated greater cortical activation for syntactically congruent over incongruent sentences with different latencies and spatial distributions by hemisphere. Interpretations of syntactic congruency effects in each hemisphere are offered below.

Left hemisphere activity reflects increased processing effort. The congruency effect in the left hemisphere was strong and broadly distributed among frontal, insular, and anterior temporal areas, and was sustained ~340–1050 ms after the onset of the final noun phrase. The spatiotemporal properties of this response suggest that it may reflect continuous processing effort, rather than an effect of the syntactic manipulation per se. Unlike the left hemisphere activity elicited by syntactic incongruencies in the English condition[14], increased left hemisphere

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[14] It is important to note that the results of English and Jabberwocky cannot be compared directly, due to differing critical points that rendered sentences in each language condition grammatical or ungrammatical (see Section 2.2.2; Silva-Pereyra et al., 2007 for further justification of differing violation points across conditions).

involvement during the comprehension of structurally intact Jabberwocky sentences did not follow an anterior-to-posterior trajectory; instead, activation remained concentrated in the vicinity of the IFC, insular cortex, and ATL throughout the post-stimulus time window. Furthermore, a distinction between the effects of Jabberwocky and English sentence processing can be drawn in the extent of observed activation: more widespread activity was noted in the areas implicated in Jabberwocky sentence processing, while more focal activity was observed in areas associated with English sentence processing. Considering these factors, we posit that the left hemisphere activation to congruent Jabberwocky sentences reflects an overall increase in processing effort, characterized by the recruitment of additional neurocognitive resources over a sustained post-stimulus time window, to comprehend semantically impoverished sentences (Zhang et al., 2009). This interpretation is based upon the idea that more cognitively demanding tasks require increased allocation of information-processing resources (Shenhav et al., 2017; Trujillo, 2019). We assert that the increased processing demands imposed by Jabberwocky sentences, in which lexical-semantic information could not be leveraged for syntactic parsing, inhibited children's ability to perform on-line syntactic analysis when a violation of phrase structure was encountered. The cognitive processes underlying this activity are not specified in the present study, though some have suggested an association between increased processing effort and working memory (Chein, Moore, & Conway, 2011; Engström, Landtblom, & Karlsson, 2013; Jansma, Ramsey, de Zwart, van Gelderen, & Duyn, 2007). Additional research will be needed to better understand how processing effort interacts with language comprehension, and what specific cognitive strategies children may use to perform complex linguistic processing tasks.

Right hemisphere activity reflects increased attention. While left hemisphere cortical activation elicited by congruent Jabberwocky sentences may reflect increased processing effort, right hemisphere activation may reflect a more specific attentional response to the grammatical manipulation itself. The congruency effect in the right hemisphere was characterized by increased activation to congruent over incongruent Jabberwocky sentences ~510–920 ms post-stimulus, in superior temporal, supramarginal, and temporoparietal areas, and peaking in the vicinity of the supramarginal gyrus (SMG). As compared to left hemisphere activation, right hemisphere activity was more temporally and spatially constrained, lending support to its interpretation as a response to the experimental manipulation of syntactic congruency rather than a global processing effect. Furthermore, the spatial distribution of this effect is consistent with a body of adult neurophysiological research, which has implicated right hemisphere TPJ/SMG activity in processes of selective auditory attention (Bareham et al., 2017; Bushara et al., 1999; Kong et al., 2014; Pugh et al., 1996; Westerhausen et al., 2010; Wu, Weissman, Roberts, & Woldorff, 2007). Past studies of language processing in infants and young children at sentence level, as well as at the phonetic and single word level, also provide compelling evidence for this interpretation.

Notably, the temporal dynamics of the right hemisphere congruency effect were comparable to Silva-Pereyra and colleagues' (2007) findings, which showed a negative-going ERP wave 750–900 ms post-stimulus in the same experimental manipulation as the current study. While 5-year-olds in the present study showed increased cortical activation in response to congruent Jabberwocky sentences, 3-year-olds in Silva-Pereyra's (2007) study showed an increased ERP negativity to incongruent Jabberwocky sentences. It should be understood, however, that a positive or negative deflection in the ERP waveform associated with an experimental manipulation (e.g., a syntactic violation) does not necessarily indicate increased neural activity to that manipulation. Because ERP data depicts potentials relative to one another, without a true baseline, it is impossible to determine with certainty whether the congruent or incongruent manipulation is driving the effect. Therefore, we consider the possibility that the congruency effect found in the present study reflects a similar processing event as the late ERP negativity reported by Silva-Pereyra et al. (2007). The authors believed this effect "to reflect the use of greater attentional resources and integration processes as listeners try to extract semantic information from the nonsense sentences" (Silva-Pereyra et al., 2007, p. 1061), i.e., that Jabberwocky sentence processing might elicit a semantic rather than syntactic response in young children, more closely resembling an N400-like than a P600-like response. Given the syntactic congruency effect noted in the MEG source-space analyses of the present study, we offer a similar but slightly refined interpretation. We agree that the effect may indeed reflect increased attention, but that this attentional resource allocation is associated with syntactically well-formed sentence processing—rather than a reaction to ill-formed sentences—when lexical-semantic information is unavailable. Furthermore, we do not assume this effect to be a semantic response in the traditional sense.

The interpretation of the right hemisphere congruency effect as an attentional process is corroborated by studies of language comprehension at the levels of phonetic- and word-level processing in infants and toddlers. In an MEG study of oscillatory brain rhythms during phonetic processing, 12-month-olds showed higher activity in the theta band to native versus nonnative syllables (Bosseler et al., 2013). As oscillatory rhythms at this frequency have been associated with increased attentional processes in adults, the authors interpreted this finding as evidence that, while native language specialization is on-going, infants implicitly direct attentional resources to the processing of familiar over unfamiliar phonetic categories (see also Thierry, Vihman, & Roberts, 2003). Likewise, toddlers have been shown to preferentially attend to known versus unknown words both behaviorally (Hallé & Boysson-Bardies, 1994) and neurophysiologically (Bosseler et al., in preparation; Mills et al., 1993, 1997; Mills, Conboy, & Paton, 2005) during the developmental period of rapid vocabulary growth. For instance, Mills and colleagues (1997) reported a negative ERP effect to known versus unknown words in the 600–900 ms post-stimulus time window in 13- to 17-month-olds, which the authors attribute to the need for enhanced attention to familiar words while word-learning is underway (Mills et al., 2005).

Importantly, these attentional processes have been shown to undergo a qualitative shift as greater language proficiency is attained: older children and adults direct their attention to unfamiliar, rather than familiar, linguistic stimuli (Bosseler et al., 2013; Nora et al., 2017). It follows that children whose syntactic processing abilities have not yet reached adult-like status, characterized by independence of syntactic analysis from semantics, would show evidence of increased attention to more familiar (i.e., grammatical) sentences when meaningful information is removed. Furthermore, the right hemisphere is believed to play a critical role in language processing in infants and young children, while acquisition of their native language is still in progress (see Bosseler et al., in preparation for a detailed account of this theory). In the context of these findings, right hemisphere areas of the cortex implicated in attentional processing may be hypothesized to activate as children attempt to interpret complex sentences in real time. The data from the present study are consistent with this expectation. Thus, we characterize the right hemisphere syntactic congruency effect to Jabberwocky sentences as: 1) an effect of enhanced attention to the more salient, syntactically congruent manipulation, and 2) an index of immature syntactic processing ability in 5-year-olds.

While the spatiotemporal dynamics of the right hemisphere syntactic congruency effect support the hypothesis that this activation reflects increased attention to the more salient congruency manipulation, limitations to this interpretation must be acknowledged. Consistent accounts of increased attention to salient stimuli have been reported in developmental populations, but the temporal and spatial properties of these effects have varied. For instance, some studies have reported increased attentional responses in earlier time windows (e.g., Bosseler et al., in preparation; Bosseler et al., 2013; Mills et al., 1993, 1997; Thierry et al., 2003) instead of, or in addition to, a later time window. Likewise, different studies have noted left-lateralized (Silva-Pereyra et al., 2007), bilateral (Mills et al., 1993, 1997, 2005), or right hemisphere dominant (Bosseler et al., in preparation; Conboy & Mills, 2006) attentional processing effects. Some authors have suggested a gradual shift from right- to left-dominant patterns of brain activity as age and language proficiency increases (e.g., Mills et al., 1997; Mills, Plunkett, Prat, & Schafer, 2005); however, differences in methodology and level of linguistic analysis under investigation among these studies (i.e., phonetic versus word level) may also account for some of the temporal and spatial inconsistencies mentioned. Several adult studies have localized auditory attentional control processes to the right TPJ/SMG, but they can provide no insight into the temporal dynamics of these effects, how they may be leveraged during sentence-level processing, nor how their spatial distribution may change over the course of development. In light of these considerations, we do not offer further interpretations of the effect latency or spatial distribution reported in this study. Nevertheless, the discovery of a right hemisphere attentional processing effect in 5-year-olds, elicited by syntactically congruent

Jabberwocky sentences, provides a novel insight into the role of attention in language processing during development, and necessitates consideration in future research.

4.3.2 Attentional processing is related to language proficiency

As in the English language condition, bivariate Spearman rank order correlations were performed between longitudinal and concurrent behavioral language proficiency measures and cortical activation reflecting the effect of the syntactic manipulation in Jabberwocky sentences, within one functionally defined spatiotemporal ROI per hemisphere. No correlations were found between any behavioral language measure and the magnitude of the syntactic congruency effect within the left hemisphere ROI, identified in the vicinity of the insular cortex/ATL. Under the assumption that left hemisphere activity in this condition reflects a global processing effect, as opposed to a manipulation-dependent response, this null result is not surprising. It provides evidence that enhanced processing effort, associated with the cognitively challenging task of making sense of meaningless sentences, may not depend on children’s early or concurrent language proficiency.

Conversely, significant associations were found between both longitudinal language measures (expressive vocabulary size and sentence complexity), one concurrent language measure (phonological awareness (PA)), and strength of the attention-related syntactic congruency effect within the right hemisphere ROI, localized to the SMG. The longitudinal correlations were persistent across time: CDI scores of expressive vocabulary beginning at 21 months, and sentence complexity beginning at 24 months, predicted right hemisphere activity at five years. These findings are consistent with a recent MEG investigation of word processing in infants, which reported significant positive correlations between a right hemisphere attentional processing effect to known versus unknown words (albeit in an earlier time window than the effect reported here) and CDI scores of vocabulary size (Bosseler et al., in preparation). The authors discovered that response magnitudes to familiar words at 14 months predicted faster vocabulary growth at 18–30 months; the present study found that larger vocabulary size and greater sentence complexity in the second year of life predicted response magnitudes to familiar/congruent sentence constructions at five years. Taken together, the results of these studies provide convincing evidence for the continuity of language abilities between early and later stages of development, and across different levels of language processing.

The results of the present study lend tentative support to the claim that concurrent language proficiency, independent of age, may affect the neural signatures of linguistic processing in children. Analyses revealed a significant association between children's CTOPP PA scores and the syntactic congruency effect: children with higher PA showed greater response magnitudes in the right hemisphere SMG to congruent Jabberwocky sentences. It is somewhat surprising that PA–but not PM or morphosyntax–predicted the strength of children's brain responses to the syntactic congruency manipulation, as both working memory (e.g., Alatorre-Cruz et al., 2018; Hampton Wray & Weber-Fox, 2013) and syntactic skills (Nuñez et al., 2011; Skeide et al., 2016) have been associated with variations in the spatiotemporal properties of syntax processing. The most likely explanation for this finding is that activation in the functionally-defined right hemisphere ROI, i.e. the SMG, is not a syntactic response per se; indeed, we suggest that activity in this region reflects enhanced attention to structurally intact Jabberwocky sentences. While this response may be elicited by the syntactic manipulation[15], we

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[15] In other words, children preferentially attend to congruent over incongruent sentences, indexed by the right hemisphere syntactic congruency effect, when they encounter the critical word in the sentence that renders it grammatical versus ungrammatical.

do not assume it to reflect a syntax-specific, or even a language-specific, response. Therefore, response magnitude may not be sensitive to differing levels of PM or morphosyntactic proficiency. As with English, limitations of the correlational analyses must be considered: it is conceivable that different properties of the experimental effect (e.g., latency), or activation in other ROIs, would be found to vary with PM or morphosyntactic proficiency. Further analyses of this dataset and/or follow-up studies should be designed to test for these possibilities.

While not all concurrent language proficiency measures predicted magnitude of the right hemisphere response to Jabberwocky sentences, the association between PA and the syntactic congruency effect is noteworthy and, to the best of our knowledge, a unique contribution to the literature. PA has been linked to activation in left prefrontal cortex (Kovelman et al., 2011); likewise, selective attention to phonology has been reported to recruit left-lateralized posterior and temporal areas (Yoncheva, Maurer, Zevin, & McCandliss, 2014). Previous studies have not investigated associations between PA and right hemisphere activity in typically developing children, nor have they offered insight into the potential role of phonological skills on attentional processes during on-line language comprehension. Therefore, we take caution by drawing limited interpretations of the brain-behavior correlation reported here; further investigation is warranted to better understand the relationship between PA and attentional processing in children.

Overall, the associations found in the current study between children's longitudinal language development measures, concurrent language proficiency, and response magnitude to syntactically congruent Jabberwocky sentences are both novel and theoretically relevant. In light of these findings, we offer the interpretation that allotment of greater attentional resources to salient features in the processing stream—in this case, intact phrase structure in sentences that lack meaning—may reflect a critical processing strategy that children leverage while language development is on-going. Children with higher language proficiency, beginning in the second year of life, may rely more heavily on this attentional process to perform complex language processing tasks than those with lower language proficiency. Thus, we consider magnitude of the syntactic congruency effect in the right hemisphere to reflect processing efficiency in more proficient language learners. One important limitation to this interpretation cannot be overlooked: we did not include a behavioral measure to account for nonverbal cognition. Thus, it is unknown whether language proficiency independently contributes to the reported processing effect, or if cognitive ability might fully mediate these associations (however, see Durand, Loe, Yeatman, & Feldman, 2013 for an argument against this possibility). In addition to controlling for cognition in future studies, we make the case for extending this work to children at other stages of development, to better understand the role of the attentional effect in on-line language comprehension, how its spatiotemporal dynamics may change over time, and how it may interact with growing language skills.

4.3.3 Summary

The finding of bilateral syntactic congruency effects in MEG-recorded brain activity to structurally well-formed Jabberwocky sentences supports the hypothesis that 5-year-olds rely on lexical-semantic information for on-line syntactic analysis. We interpret the sustained and broadly distributed left hemisphere activation to this experimental manipulation as an index of increased processing effort, imposed by the cognitively demanding task of making sense of nonsensical sentences. On the other hand, we consider the temporally and spatially constrained right hemisphere effect to reflect increased attention to familiar (i.e., intact) sentence constructions. It is possible that children do in fact detect syntactic incongruencies when meaningful context is absent, but do not expend mental energy to attempt to process them. Therefore, the effect may be considered to reflect an efficient processing strategy, leveraged to a greater extent by children with higher language proficiency. Positive correlations between longitudinal/concurrent language measures and strength of the syntactic congruency/attentional processing effect lend considerable support to this interpretation.

4.4 Study Limitations

There are limitations of the present study that should be recognized and taken into consideration in future research. One such limitation is the small sample size. With a larger cohort of children, subsequent studies could provide deeper insights into the relationship between language proficiency and processing ability. For example, participants could be grouped by language proficiency, allowing for differences in syntactic processing effects between high- and low-proficiency groups to be examined. It is possible that this type of study design would reveal qualitative or quantitative differences in the spatiotemporal properties of syntactic processing effects between groups that are obscured in the present study. A second limitation of this study is the lack of an adult comparison group. As this was among the first investigations to examine the spatiotemporal properties of on-line syntax processing, the extent to which the syntactic manipulation effects reported in 5-year-olds may resemble those of adults cannot be determined. A replication of this study with adults, as well as with children at different stages of development, will be necessary to improve upon our understanding of the trajectory toward mature sentence processing in the brain. Finally, the experimental paradigm did not include a pure semantic manipulation. It will be important to compare the spatiotemporal dynamics of brain activity associated with syntactic manipulations to those of semantic manipulations, to more thoroughly characterize differential brain activity associated with each linguistic process. Despite these limitations, as well as those discussed in the sections above, we believe that this study provides meaningful contributions to the study of language in the developing brain.

4.5 Conclusions

This study has shown that the neural signatures of on-line sentence processing in 5-year-olds are modulated by the availability of lexical-semantic information for grammatical parsing. Syntactically ill-formed yet meaningful sentences elicit a syntactic processing response in the left hemisphere, whereas syntactically well-formed but meaningless sentences elicit an attentional response in the right hemisphere. The qualitative differences in cortical activation to manipulations of syntax and semantics confirm the hypothesis that there is a protracted developmental period in which these processes remain functionally interdependent. We propose that enhanced attention to congruent Jabberwocky sentences signifies an important language learning mechanism and index of processing efficiency, which may vary with linguistic skill; indeed, children with higher language proficiency attend more strongly to salient structural features of language when lexical-semantic information is absent, likely in an attempt to construct meaning from meaningless sentences.

These findings have far reaching implications for developmental cognitive neuroscience. They provide novel information about the dynamics of on-line sentence comprehension in children, and contribute meaningfully to the current knowledge of processing strategies children use to navigate aspects of language they have not yet mastered. The results of this study also raise new questions about the nature of the interaction between syntactic and semantic processing in developmental populations, which will pave the way for many future lines of inquiry.

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APPENDIX: EXPERIMENTAL SENTENCES

	English Sentences	**Jabberwocky Sentences**
1	My sister opened the present from my uncle. *My sister opened from the present my uncle.	My bacter drepened the chosent from my macle. *My bacter drepened from the chosent my macle.
2	The nurse knocked my knees with the hammer. *The nurse knocked with my knees the hammer.	The berse chacked my clees with the treemer. *The berse chacked with my clees the treemer.
3	My aunt spilled some juice on my bed. *My aunt spilled on some juice my bed.	My dant plalled some birce on my lod. *My dant plalled on some birce my lod.
4	The child wanted a pancake from that store. *The child wanted from a pancake that store.	The frild clonted a brongake from that spere. *The frild clonted from a brongake that spere.
5	My brother wanted his teddybear on the bed. *My brother wanted on his teddybear the bed.	My cother clonted his gaddyler on the lod. *My clother clonted on his gaddyler the lod.
6	My teacher played the song about Santa Claus. *My teacher played about the song Santa Claus.	My bacher chayed the teng about Danta Praus. *My bacher chayed about the teng Danta Praus.
7	My grandma kissed my daddy on the cheek. *My grandma kissed on my daddy the cheek.	My brondma gissed my chidy on the preck. *My brondma gassed my chidy on the preck.
8	The man dumped the garbage in the trash. *The man dumped in the garbage the trash.	The gan dremped the birbage in the presh. *The gan dremped in the birbage the presh.
9	My uncle closed the door with his hand. *My uncle closed with the door his hand.	My macle clised the chor with his shond. *My macle clised with the chor his shond.
10	My mommy kissed my daddy in the kitchen. *My mommy kissed in my daddy the kitchen.	My bammy gissed my chiddy in the skachen. *My bammy gissed in my chiddy the skachen.
11	My daddy wiped his hands with a napkin. *My daddy wiped with his hands a napkin.	My chiddy juped his shonds with a garkin. *My chiddy juped with his shonds a garkin.
12	The baby smashed the table with her toy. *The baby smashed with the table her toy.	The giby steshed the beable with her tay. *The giby steshed with the beable her tay.
13	The cowboy loved his bread with butter. *The cowboy loved with his bread butter.	The bawbroy juved his cread with satter. *The bawbroy juved with his cread satter.
14	The mailman climbed the tree with his bag. *The mailman climbed with the tree his bag.	The bailgan plambed the gree with his jeg. *The bailgan plambed with the gree his jeg.
15	My dolly touched the cat with her hand. *My dolly touched with the cat her hand.	My cholly daunched the glat with her shond. *My cholly daunched with the glat her shond.
16	The nurse poured some water into the pitcher. *The nurse poured into some water the pitcher.	The berse dured some gluter into the betcher. *The berse dured into some gluter the betcher.
17	My teacher shared her yogurt with my brother. *My teacher shared with her yogurt my brother.	My bacher clored her pregurt with my cother. *My bacher clored with her pregurt my clother.

18	My grandma baked a muffin in the oven. *My grandma baked in a muffin the oven.	My brondma leked a taffin in the baven. *My brondma leked in a taffin the baven.
19	The man fixed my tricycle with glue. *The man fixed with my tricycle glue.	The gan daxed my brafycle with clo. *The gan daxed with my braficle clo.
20	The boys loved the stories about Christmas. *The boys loved about the stories Christmas.	The broys juved the chories about grastmas. *The broys juved about the chories grastmas.
21	My uncle pulled the dog with his rope. *My uncle pulled with the dog his rope.	My macle cloled the wog with his drep. *My macle cloled with the wog his drep.
22	My aunt hugged my bear with her arms. *My aunt hugged with my bear her arms.	My dant cleagged my ler with her berms. *My dant cleagged with my ler her berms.
23	That man bumped my truck with his foot. *That man bumped with my truck his foot.	That gan lomped my morck with his tet. *That gan lomped with my morck his tet.
24	My uncle watched a movie about my family. *My uncle watched about a movie my family.	My macle platched a flovie about my garily. *My macle platched about a flovie my garily.
25	My brother kicked the ball in the garden. *My brother kicked in the ball the garden.	My cother finked the mool in the farden. *My cother finked in the mool the farden.
26	The policeman chased the zebra in the zoo. *The policeman chased in the zebra the zoo.	The brolicegan cosed the pabra in the foo. *The brolicegan cosed in the pabra the foo.
27	My sister dressed her doll on the table. *My sister dressed on her doll the table.	My bacter grissed her choll on the beable. *My bacter gissed on her choll the beable.
28	The monkey touched the bananas in that tree. *The monkey touched in the bananas that tree.	The nurkey daunched the buranas in that gree. *The nurkey daunched in the buranas that gree.
29	My aunt watched television in my bedroom. *My aunt watched in television my bedroom.	My dant plached selegosion in my lodram. *My dant plached in selegosian my lodram.
30	My mommy poured some water in my glass. *My mommy poured in some water my glass.	My bammy dured some gluter in my bress. *My bammy dured in some gluter my bress.
31	The doctor checked my body with his camera. *The doctor checked with my body his camera.	The broctor gicked my daby with his pamera. *The broctor gicked with my daby his pamera.
32	The boys carried the books inside their bags. *The boys carried inside their books their bags.	The broys dorried their gaks inside their jegs. *The broys dorried inside their gaks their jegs.
33	The nurse liked the movies about animals. *The nurse liked about the movies animals.	The berse huked the flovies about polimals. *The berse huked about the flovies polimals.