Phonological and Semantic Influences on Auditory Word Perception in Children with and without Reading Impairments using Magnetoencephalography (MEG) and Electroencephalography (EEG)

by

Daniel T. Wehner

Submitted to the Harvard-MIT Division of Health Sciences and Technology
in partial fulfillment of the requirements for the degree of

Doctor of Philosophy in Speech and Hearing Biosciences and Technology

at the

MASSACHUSETTS INSTITUTE OF TECHNOLOGY

June 2007

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Abstract

Children with dyslexia struggle with learning to read despite adequate intelligence, motivation, and schooling. Over the years, there has been a growing consensus about the role of phonological processing in reading disability. Poor readers typically do worse than their normal reading peers on tasks that require phonological processing which has been linked, directly or indirectly, to their speech perception abilities. The work in this thesis combined behavioral, MEG, and EEG methods to examine how normal and reading-impaired children, 7-13 years of age, perceive speech under varying degrees of phonological contrast (1 vs. 3 phonetic features).

In a series of auditory word perception experiments, good and poor readers were found to do worse in accuracy and/or reaction times in phonologically similar (i.e., 1-feature contrast) than phonologically dissimilar (i.e., 2 or 3-feature contrast) conditions. Despite the similar behavioral performance and EEG responses for the two groups, a region of interest (ROI) based MEG approach revealed differences in the brain activation of the two groups in superior temporal regions at 140 to 300 ms. In the auditory word discrimination task, differences in activation were found in good readers but not poor readers, as a function of the degree of phonological contrast, reflecting poor readers' lack of sensitivity to the phonological characteristics of the word stimuli. In the sentence plausibility judgment task, the impaired phonological processing abilities of the poor readers may have led them to rely more on top-down sentence context to perceptually disambiguate phonologically confusing terminal words, thereby deceiving them into accepting the phonologically similar incongruent sentences as being congruent. This may account for the poor reader group's reduced brain activation in the phonologically demanding condition in the sentence task.

The results of the experiments are consistent with a phonological view of reading disability according to which children with reading impairments have poorly defined phonological representations.

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Acknowledgments

A fortuitous decision six years ago to spurn medical school in the midwest and travel to the east coast for the good seafood and a top notch education at Harvard and MIT has led me down an exciting path of personal and professional discovery. It has been a long interesting journey and I would not have been able to make it through without the support of many people over the years including my family, friends, and coworkers.

First I would like to thank my research supervisor, Maria Mody. I could not have made it this far without your patience, as the engineer in me tried to understand this strange new world of cognitive psychology and reading impairment.

I would also like to thank my thesis committee for their support of me over the last few years. I have enjoyed many lively conversations with Seppo Ahlfors discussing the finer points of MEG physics and Finnish politics. I am inspired by the unbridled enthusiasm of Stefanie Shattuck-Hufnagel who has always been there to lend an ear and ask insightful questions that push my thinking forward. I am grateful for Charles Perfetti's willingness to serve on the committee despite our oft technical difficulties with setting up conference calls. His knowledge, accumulated over several decades of being a reading researcher, has been invaluable to me. Finally, I would like to thank my committee chair, Ken Stevens, whose passion for research, and life in general, always shines through and encourages me.

The contributions of my fellow labmates and coworkers at the Martinos Center have been particularly valuable. I especially want to thank Sue Mosher, Surina Basho, and Cherif Sahyoun for their insight and support in the lab over the years. I would also like to thank Matti Hämåläinen who has been an invaluable resource for all questions relating to MEG. Deirdre von Pechmann and Dan Wakeman have also helped out tremendously in assisting with the MEG recordings.

I am also grateful to the wonderful staff at HST and the Athinoula A. Martinos Center for Biomedical Imaging for evening out the bumps in the inevitable bureaucracy that exists with large institutions, to make my life run much smoother over the years.

To my family back home: Leo, Judy, Peter, Jaime, and Jennifer, thank you for encouraging me to follow my dreams and for supporting me in all of my endeavors here in Boston.

To my family in Massachusetts: Ken, Lucille, Travis, Jen, and Evan, thank you for welcoming me into your family and supporting me over the past six years. It has truly meant a lot to me. Relaxation through aggressive canoeing!

And that brings me to Asa Masaki. The journey is so much easier when you have a compassionate partner to share it with. Words can't express what you mean to me. I wake up every day and am just so thankful that you are in my life.

Finally, I would like to thank all the children and parents for their willingness to participate in the studies in this thesis.

This work has been supported in part by several grants from the NIH (DC00159, HD056355), the National Center for Research Resources (P41RR14075), and the Mental Illness and Neuroscience Discovery (MIND) Institute. Additional funding was from an NIH Training Grant (DC00038) and an NIH Neuroimaging Training Program Fellowship (5T32EB001680; PI: Bruce Rosen).

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Chapter 1: Thesis Overview

1.1 Introduction

Development of skilled reading is essential for educational success. Unfortunately, many children with developmental dyslexia struggle to learn to read despite adequate intelligence, motivation, and schooling. Although reading disability has been studied for more than a century, there appears to be a lack of consensus about its origins. Failure to develop a unifying theory to describe reading disability may be due to several factors. First, dyslexia appears to be characterized by a large amount of heterogeneity, such that some children with reading difficulties show deficits on certain perceptual and cognitive tasks, whereas other children, also classified as reading disabled, do not show these deficits. Second, difficulty in interpreting the intermediary processes encapsulated within behavioral measures such as reaction time and accuracy has also created challenges in understanding differences between good and poor readers. Despite these difficulties, some behavioral measures have come to be incorporated into clinical practice. For example, performance on phonological awareness tasks has been suggested to be the best predictor of later reading difficulties (for a review, see Mody, 2003).

Although an extensive amount of research has led to improved reading interventions, a neurobiological explanation for the behavioral deficits characterizing reading impairment has remained elusive. Functional neuroimaging methods with high time resolution, such as electroencephalography (EEG) and magnetoencephalography (MEG), has provided a conduit for examining processes such as speech perception, which unfold rapidly in time. The work in this thesis combined behavioral, EEG, and MEG methods to build upon our current understanding of the language basis of speech perception deficits believed to characterize impaired readers. More specifically, we examined auditory word perception in children with and without reading disability, using words that varied in the degree of phonological contrast. Using these methods, we aimed to examine the brain networks that are engaged by poor readers under phonologically demanding conditions with and without sentence context. The thesis thus provides insight into how poor readers may compensate for their subtle speech perception deficits by relying on top-down semantic information provided by sentence context.

1.2 Thesis layout

The outline of the thesis is as follows. In Chapter 2, we describe the phonological theory of dyslexia and discuss empirical results that lend support for or against other competing theories. It is concluded that children with reading disorders can be best characterized as having difficulties in phonological processing, which may be a consequence of poorly defined phonological representations in long-term memory. We then examine how phonological representations may develop differently in normal and reading-impaired children. Poor readers' deficits in three primary areas involving phonological processing: phonological awareness, short-term memory, and speech processing (production and perception) are then discussed. The neurobiological correlates of normal and impaired language processing are discussed along with relevant electroencephalographic (EEG) and magnetoencephalographic (MEG) evoked-response components. We end Chapter 2 by discussing the potential role of semantic context in good and poor readers' perception of written and spoken words.

In Chapter 3, the theoretical motivation for investigating speech perception abilities in reading-impaired children is provided. An MEG/EEG experiment in which children, who were good or poor readers, discriminated auditory words with varying degrees of phonological contrast is described. Despite similar behavioral task performance of the two groups, poor readers showed deviant patterns of brain activation for the more demanding phonological condition, suggestive of their phonological processing difficulties.

In Chapter 4, we extend these results with two more experiments that examine good and poor readers' auditory perception of words with and without sentence context. In the first of these experiments, subjects listened to word pairs and decided if consecutive pairs were the same or different. The words in the first pair varied in the degree of phonological contrast, thereby making it easier or difficult to encode words in phonological working memory. In the next experiment, the terminal words in sentences were the same words used in the previous experiment, and were selected to be phonologically similar or dissimilar to the congruent target word using a sentence plausibility judgment task. Again, we observed similar behavioral performance for the two groups, but different patterns of brain activation for the poor readers in the more demanding phonological condition. A comparison of the results from the two experiments showed that both good and poor readers appear to use top-down semantic information provided by sentence context during auditory word perception, although in different ways.

In Chapter 5, we discuss the combined the results from the experiments in Chapters 3 and 4. First we discuss the similarities and differences between good and poor readers on the three tasks. Then we discuss how semantic information provided by sentence context differentially affected good and poor readers, thereby providing further insight into poor readers' phonological processing deficits. Lastly, we discuss the implications that our results may have on the phonological theory of dyslexia.

Finally, Chapter 6 summarizes our work and suggests future studies. This thesis contributes to our understanding of the neural basis of speech perception in normal and reading-impaired children. Although the neural basis of auditory word perception has been extensively studied in normal adults (Scott & Johnsrude, 2003), relatively few studies have involved children with and without reading impairments. It has been suggested that 40% of children with reading difficulties may also have deficits in speech perception (McGuinness, 2005), although this statistic might be higher under phonologically demanding conditions. The series of three experiments presented in this thesis used auditory words varying in their degree of phonological contrast to provide further insight into the phonological basis of reading disability in children.

Chapter 2: The phonological basis of reading disability

In this chapter, we discuss previous literature suggesting that impaired readers' difficulties with grapheme to phoneme conversion during reading result from poorly defined phonological representations. First, we provide a brief overview of the main theories of dyslexia. Then, we explore the developmental nature of phonological representations in good and poor readers. The impact of degraded phonological representations as revealed through behavioral and neuroimaging studies of word reading and speech perception are then discussed. Finally, since poor readers may rely on semantic information from sentence context during speech perception due to their phonological processing difficulties, we present studies that have investigated the effects of sentence context on visual and auditory word recognition.

2.1 Theories of dyslexia

Over the past few decades, numerous research studies have attempted to investigate the underlying cause of dyslexia (for recent reviews see Ramus et al., 2003; Vellutino, Fletcher, Snowling, & Scanlon, 2004). Although it is beyond the scope of this thesis to exhaustively detail the history of this research, the following sections briefly review the major theories and discuss select studies that support or challenge these theories.

2.1.1 Visual Deficits

For most of the twentieth century, it was thought that dyslexia was primarily caused by deficiencies in visual perception, although the popularity of this view has declined since the advent of linguistic theories in the 1970's (Stanovich, 1992; Vellutino et al., 2004). The majority of these visual deficit theories met their demise when studies were carefully constructed to control for visual memory, spatial orientation, and visual learning (Hulme, 1988; Morrison, Giordani, & Nagy, 1977; Vellutino, 1979). Thus, visual deficits are no longer considered to be a major cause of reading disability (Stanovich, 1982; Vellutino, 1979; Vellutino et al., 2004).

2.1.2 Rapid Naming and Automatization Deficits

More recent research has suggested that poor readers may show deficits on tasks that require rapid access to verbal labels for visually presented stimuli (Bowers & Swanson, 1991; Catts, Gillispie, Leonard, Kail, & Miller, 2002; Walker, 2002; Wolf, Bowers, & Biddle, 2000). Furthermore, as fluent reading requires rapid sequential access to verbal labels for visually presented items (letters, words), it has been proposed that the deficits in Rapid Automatized Naming (RAN), evident with pictures, may also explain reading difficulties (Savage et al., 2005; Wolf & Bowers, 1999). Nicolson and Fawcett broadened these claims to suggest that poor readers may have difficulty automatizing any over-learned process (e.g., balancing on one foot) (Fawcett & Nicolson, 1992, 1994; Nicolson & Fawcett, 1990; Nicolson, Fawcett, & Dean, 2001). In these studies, children with and without reading impairments carried out primary motor tasks such as balancing on one or two feet, while performing a secondary task such as counting backwords. Children with dyslexia performed more poorly than the good readers under the dual task condition, but not when only a single task had to be performed. Although subsequent research has provided further behavioral (Fawcett & Nicolson, 1999; Nicolson & Fawcett, 1996; Nicolson et al., 2001) and neurobiological (Brown et al., 2001; Fawcett & Nicolson, 1999; Leonard et al., 2001) evidence for concurrent balance and cerebellar deficits in poor readers, these studies have been criticized for their methodological confounds (Savage, 2004). Furthermore, other studies have not found motor problems in dyslexic subjects (Kronbichler, Hutzler, & Wimmer, 2002; van Daal & van der Leij, 1999) or only a subset of dyslexic subjects (Yap & van der Leij, 1994).

2.1.3 Auditory deficits

Another theory of dyslexia that has gained much attention relates to difficulties with processing rapid auditory stimuli (Farmer & Klein, 1995; Tallal, 1980). This theory was based on research that Tallal and her colleagues conducted showing that poor readers had greater difficulty making temporal order judgments (TOJ) of tones that were presented with a short (50 ms) interstimulus interval (ISI), whereas both good and poor readers performed similarly when the ISI was increased to 400 ms. This was taken as evidence that poor readers suffered from a non-linguistic deficit in processing rapidly changing auditory stimuli, thereby also impairing speech perception, which relies on the perception of rapidly changing formant transitions. A study that included a well-defined dyslexic group and carefully controlled verbal and non-verbal stimuli challenged this interpretation (Mody, Studdert-Kennedy, & Brady, 1997). Mody and colleagues showed that poor readers' difficulties on Tallal's /ba/-/da/ TOJ task appeared to stem from deficits in speech discrimination rather than in temporal order judgment of the speech sounds. Various other attempts to replicate the results of Tallal's earlier studies have also failed (Bishop, Carlyon, Deeks, & Bishop, 1999; Bradlow et al., 1999; McAnally, Hansen, Cornelissen, & Stein, 1997; Nittrouer, 1999). However, as a definitive test of the theory appears unattainable, the possibility remains that differences in rapid perception of auditory stimuli may contribute to the observed reading deficits in some children with dyslexia.

2.1.4 The magnocellular theory

A neurobiological account for the observed visual deficits in dyslexia was based on the idea that poor readers may have abnormal magnocellular pathways in the brain (Livingstone, Rosen, Drislane, & Galaburda, 1991). Post-mortem analysis of several poor readers' brains revealed magnocellular abnormalities within the geniculate nuclei of the thalamus, providing support for the magnocellular theory (Galaburda, Menard, & Rosen, 1994; Livingstone et al., 1991). The magnocellular system is believed to process transient stimuli such as visual motion or formant transitions in speech perception (Renvall & Hari, 2002). Therefore, this theory was extended beyond the visual domain to encompass poor readers' deficits in auditory processing, rapid naming, and motor-related processing (Stein & Walsh, 1997). Although the magnocellular theory attempts to account for a variety of behavioral manifestations in dyslexia, it has come under fire in recent years (Ramus, 2001; Ramus et al., 2003; Skoyles & Skottun, 2004). A major drawback appears to be that magnocellular deficits, either auditory, visual, or cerebellar, are not observed in the majority of dyslexics (Adlard & Hazan, 1998; Johannes, Kussmaul, Munte, & Mangun, 1996; Manis et al., 1997; Reed, 1989; Victor, Conte, Burton, & Nass, 1993).

2.1.5 Language-based deficits

As reading is primarily an acquired linguistic skill, it has been speculated that the basis of reading disability may have a linguistic deficit at its core (Vellutino et al., 2004). In fact, there is evidence that vocabulary knowledge is a good predictor of early and later reading achievement (Snowling, Gallagher, & Frith, 2003) and is necessary for the acquisition of essential phonological skills for reading (Goswami, 2000; Walley, Metsala, & Garlock, 2003). However, tasks that require semantic and syntactic processing do not differentiate the reading abilities of beginning readers (Shankweiler et al., 1999; Vellutino et al., 2004). Therefore, deficits in semantic and syntactic processing appear to be a consequence rather than a cause of reading disability.

In contrast to the above findings, a vast amount of research supports the premise that a fundamental deficit in the phonological component of language may be primarily responsible for reading impairments in children (Fletcher et al., 1994; Liberman, Shankweiler, Liberman, Fowler, & Fischer, 1977; Shankweiler et al., 1999; Stanovich & Siegel, 1994; Wagner & Torgesen, 1987; Wagner, Torgesen, & Rashotte, 1994). Poor readers routinely perform worse than their normal reading peers on a variety of phonological processing tasks (Goswami & Bryant, 1990; Perfetti, 1985). In fact, there appears to be near consensus that while subgroups of poor readers may show perceptual deficits (e.g., auditory, visual), poor readers as a whole can be best characterized by difficulties in phonological processing (Shaywitz & Shaywitz, 2005). These difficulties in phonological coding are thought to arise from a subtle deficit in speech perception (Brady, Shankweiler, & Mann, 1983; Mody et al., 1997) due to poorly defined phonological representations. Results from several behavioral and neuroimaging studies have provided evidence consistent with this view, and they are discussed more in detail below (for a review see Mody, 2003).

2.1.6 The double-deficit hypothesis

As we have just reviewed, phonological processing appears to be a core deficit in developmental dyslexia. However, since some poor readers also show deficits in rapid naming, these deficits may be attributed to an independent core deficit, leading to the so-called double-deficit hypothesis (Wolf & Bowers, 1999). The double-deficit hypothesis aims to categorize poor readers according to whether they have primarily phonological processing deficits, naming speed deficits, or both types of deficits. Unfortunately, the underlying skills necessary for rapid naming tasks are not well understood (Wolf & Bowers, 1999). It has been suggested that naming speed may best be conceptualized as a multi-componential construct that involves many different skills under timed conditions (Vukovic & Siegel, 2006). Furthermore, since empirical support for the double-deficit hypothesis is limited (McCardle, Scarborough, & Catts, 2001; Vukovic & Siegel, 2006), more research and intervention studies are necessary before the double-deficit hypothesis can be validated.

In summary, there is close consensus that phonological processing is a core deficit in dyslexia, this will be the underlying theory throughout the thesis. In the next section, we will further examine the phonological processing deficits in poor readers by describing the specification of phonological representations in good and poor readers.

2.2 Phonological representations

Phonological representations are mental representations of the spoken units (e.g., words) of a language that are stored in long-term memory (Elbro & Jensen, 2005). Although there is much debate with regards to the primary cause of phonological processing deficits in poor readers, a prominent hypothesis is that their phonological representations of lexical items in long-term memory are underspecified[1] (Elbro, 1998; Elbro, Borstrøm, & Petersen, 1998; Elbro & Jensen, 2005; Fowler & Swainson, 2004;

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[1] In the thesis we use the term "underspecified" to represent the concept of an ill-defined phonological representation of a lexical entry. This is in contrast to the usage of the term "underspecified" in linguistic theory, where underspecified refers to sound segments that have missing phonological features (e.g., Lahiri & Marslen-Wilson, 1991).

Foy & Mann, 2001; Goswami, 2000; Griffiths & Snowling, 2002; Hulme & Snowling, 1992; Metsala & Walley, 1998; Snowling, 2000; Swan & Goswami, 1997). In theory, an underspecified phonological representation must only contain an incomplete rendering of the phonological material in the lexical entry. According to the distinctness hypothesis (e.g., Elbro et al., 1998), poor readers have less 'distinct' phonological representations (e.g., *sub* vs. *submarine*) that share overlapping phonological segments with many neighbors in the lexicon (i.e., *substitute, subway*). Distinctness might also be characterized as the extent to which phonological representations are well specified in terms of their distinctive features (Chomsky & Halle, 1968; Halle, 1990; Jakobson, Fant, & Halle, 1952; Stevens, 1998). This hypothesis might explain why poor readers' deficits in speech perception and speech production are often described as "subtle", even though poor readers struggle with phonological awareness tasks. This is because phonological awareness tasks draw on one's explicit knowledge of the sound patterns of a language and the rules governing their combination. The question then arises as to how poorly defined phonological representations come to exist in the lexicons of impaired readers. A developmental view might conceptualize phonological representations in the guise of the lexical restructuring hypothesis (Metsala & Walley, 1998; Walley, 1993). In this hypothesis, phonological representations begin as holistic "whole-word" representations that cannot be segmented into smaller constituents (e.g., syllables, onset-rimes, phonemes), until it is necessary to restructure their phonological content to make for better separability and thus avoid ambiguity in the lexicon. Presumably phonological representations that remain fuzzy are those that have not been broken down into their phonemic content. Hence, in this conceptualization, the phonological representations of all words undergo gradual phonological differentiation over the course of development.

2.2.1 Development of phonological representations

Before we delve into how phonological representations might be weak in children who are poor readers, we must first understand how phonological representations might develop in normal readers. The following sections discuss the development of phonological representations in normal infants and in reading-impaired children.

2.2.1.1 Phonological representations in infants

Both early (Edwards, 1974; Garnica, 1973; Shvachkin, 1973) and more recent studies (e.g., Halle & de Boysson-Bardies, 1996; Stager & Werker, 1997) have been used to support the idea that infants' representation of lexical forms lacks phonetic detail (Charles-Luce & Luce, 1990). They have also been taken as evidence that words are stored as holistic patterns of sound, with only a few salient phonetic features (Walley, 1993), for an opposing view, c.f., Swingley, 2003). Hence, it can be hypothesized that holistic or global representations lack phonetic or featural specifications necessary to differentiate minimal pairs of words. However, this hypothesis is challenged from experimental evidence which shows that infants are able to perceptually differentiate minimal pairs (Jusczyk & Aslin, 1995). These holistic representations are thought to gradually transform into more segmental phonological (adult-like) representations through the process of increasing vocabulary size. As children learn more phonetic neighbors, words lose their holistic character and become specified as discrete segments, such as syllables and phonemes. Thus, the development of phonological representations is argued to go hand in hand with the acquisition of new phonetic neighbors. If this were the case, then languages that have many phonetic neighbors among the earliest words children learn, should provide an easier route to word learning compared with a language that does not have this feature. In addition, children with larger receptive vocabularies should also have more detailed adult-like representations of words. Below, we examine some of the studies providing evidence for this view.

Early studies examining the perceptual word-learning abilities of infants, typically showed that they did not reliably perceive single phoneme differences when they were taught novel words (e.g. *bak* vs. *mak*). Shvachkin (1973) reported that 18 month-old Russian children could correctly distinguish *bak* from *zub* or *mak* from *zub*, but not *bak* from *mak*. The children were taught novel word pairs that differed in the degree to which the first phoneme was phonologically similar, and the nonsense words were associated with a particular toy. The child's task was to pick out the appropriate toy from an array of different toys after hearing the word. Shvachkin found that children could not consistently pick out the correct toy for the phonetically similar word pairs, but they could for the phonetically dissimilar pairs, suggesting that children's lexical representations at this age are not well differentiated in terms of their degree of phonological contrast. Other researchers have carried out investigations using infants who were slightly older, and have found similar results (17-22 month-olds: (Garnica, 1973) ; 3 year-olds: (Edwards, 1974). One potential confound in these studies may have been task difficulty. If the toy selection and pointing tasks were too difficult for infants, then task difficulty alone may have led to the findings that young children did not attend to phonetic detail. To address this confound, more recent studies have used easier tasks, and have shown that infants appear to be insensitive to changes in voicing or manner of articulation in initial consonants of pseudowords (Halle & de Boysson-Bardies, 1996; Stager & Werker, 1997). Although it may be unclear how these results fit with the preexisting literature showing that 7-8 month old infants could already distinguish minimal pairs (Jusczyk & Aslin, 1995), further experiments suggested that the discrepancy may have been related to attention to a particular task (Stager & Werker, 1997) or possible developmental shifts from speech perception to meaning-based word learning (Halle & de Boysson-Bardies, 1996). If younger infants, such as those in Jusczyk and Aslin (1995), were not trying to recognize words, but instead were focusing on segmenting and analyzing the phonemes in the words, they may have been able to detect the voicing contrast. It is thought that infants first start to recognize the sounds of the language (phonology), then combinations of those sounds into meaningful units (morphology), then later, words and sentences. The driving force that produces the change from early perceptual to more phonologically underspecified representations may be the emergence of meaning, thought to occur between 8 and 14 months. This is consistent with Stager and Werker's (1997) study which showed differences between 8 month-old and 14 month-old groups, and with Hallé and de Boysson-Bardies's (1996) study which showed differences between 11 month-old infants and the 7-8 month old infants of Jusczyk and Aslin's (1995) study.

As mentioned earlier, the lexical restructuring hypothesis (Metsala & Walley, 1998) provides one potential explanation for the development of phonological representations from infancy to early childhood. The lexical restructuring hypothesis posits that spoken vocabulary growth and item-based phonological relations are the major driving forces during the pre-lexical restructuring phase. In terms of the phonological relations between words in the lexicon, recent studies have shown that neighborhood density and age of acquisition may play a larger role in restructuring, than word frequency (Garlock, Walley, & Metsala, 2001). Storkel (2002) discusses how lexical restructuring can be driven by phonologically similar neighborhoods. She suggests that children initially may be able to uniquely differentiate words with poorly defined phonological representations, but as the child's vocabulary and neighborhood density increases, these representations become more contrastive. Hence, she concludes that the mental representations of words gradually changes due to the acquisition of new words, and the restructuring of known words. Although Storkel (2002) investigated lexical restructuring in good readers, an important consideration in this thesis is to consider how lexical restructuring may differ in poor readers.

2.2.1.2 Phonological representations in poor readers

The segmentation hypothesis, a prominent theory for how poor readers fail to develop adult-like phonological representations (Bird & Bishop, 1992; Boada & Pennington, 2006; Fowler, 1991), centers on the view that lexical restructuring for poor readers occurs more slowly or deviates from normal development. Recent evidence has shown support for this hypothesis since the developing lexicons of good and poor reading children are shaped by the same factors, albeit significantly slower for poor readers (Thomson, Richardson, & Goswami, 2005). To our knowledge, since the development of phonological representations in children who become poor readers have not been examined, longitudinal studies may be necessary to directly investigate when deviation from normal lexical restructuring occurs in most poor readers. Although these longitudinal studies have not been forthcoming, 6-month old infants with a familial risk for dyslexia were shown to already exhibit speech categorization difficulties (Leppänen et al., 2002). Other studies using older children have also provided support for the idea that poor readers' phonological representations are not as well defined as their normal reading peers (Boada & Pennington, 2006; Metsala, 1997).

Using a lexical gating paradigm (Grosjean, 1980), it was found that unlike age-matched good readers, poor readers required as much input to recognize words from sparse neighborhoods as dense neighborhoods (Metsala, 1997). Thus, good readers are able to discriminate words with few phonetic neighbors, unlike poor readers who cannot, perhaps due their weak representations. Boada and colleagues (2006) replicated and extended these results by showing that poor readers performed worse than both chronological age-matched controls (as in Metsala, 1997) and reading age-matched controls, suggesting that the phonological representations of poor readers were less mature than those for younger children who were matched on reading ability. This suggests that lexical restructuring does not completely account for differences in phonological representations between good and poor readers. Studies using a variety of speech perception tasks have found consistent differences between groups of good and poor readers, however, speech perception deficits at the individual subject level have been less consistent (Adlard & Hazan, 1998; Mody et al., 1997), perhaps due to a lack of statistical power. Recent studies, discussed below, using both behavioral and neuroimaging measures provide evidence that despite similar performance on behavioral measures of speech perception, brain activity elicited by speech perception tasks may differ between good and poor readers (e.g., Bradlow et al., 1999).

Factors such as reading and spelling experience are also thought to affect the post-lexical phase of restructuring in normal-reading children (Goswami, 2000). According to the lexical restructuring hypothesis, reading acquisition should cause phonological representations to become more differentiated, since consistent grapheme to phoneme correspondences allow segmental information to be represented at the phoneme level. If this were the case, poor readers who learn to read in a language with transparent orthographies, i.e., consistent grapheme to phoneme correspondences (e.g., Finnish), should have fewer phonological deficits compared to children who learn to read a language with a non-transparent orthography (e.g., English). In Dutch, a language with a high degree of grapheme-phoneme consistency, 11-year old poor readers performed similarly to reading- and age-matched controls on phonological awareness tasks at the syllable and rime levels (de Gelder & Vroomen, 1991). Furthermore, although phonemic awareness did differ between the good and poor reading groups in Dutch, this deficit did not persist into adulthood. In contrast, phonemic awareness have been shown to persist into adulthood for poor readers who speak English (Bruck, 1992; Flowers, 1995;

Gallagher, Laxon, Armstrong, & Frith, 1996). Poor readers' difficulties in using post-lexical information for lexical restructuring may be compounded by the fact that that they often read less than good readers (Stanovich, 1986) which may be exacerbated by their difficulties with phonological processing (Goswami, 2000). In this section, we have summarized evidence for the persistence of poorly defined phonological representations in reading-impaired children. Next, we will discuss some of the difficulties poor readers encounter due to their underdeveloped phonological representations.

2.3 Behavioral implications of poorly defined phonological representations

It is now widely accepted that poor readers show weaknesses in at least three areas related to phonological processing: phonological awareness, phonological short-term memory, and speech perception (Mody, 2003; Thomson et al., 2005). Below we present evidence for poor readers' deficits in each area.

2.3.1 Phonological awareness

Phonological awareness is a measure of one's ability to detect or manipulate the sound structure of spoken words (Thomson et al., 2005). Tasks of phonological awareness include tapping out the number of sounds in a word, reversing the order of sounds in a word, or combining sounds in isolation to form a word (Wagner & Torgesen, 1987). Phonological awareness is believed to be the single best predictor of later alphabetic reading skill (Liberman, 1973; Wagner & Torgesen, 1987). Accordingly, interventions that stress phonological awareness have been shown to result in improved reading outcomes (Bradley & Bryant, 1983; Hurford & Sanders, 1990). However, development of phonological awareness can be quite challenging, as there are few cues in the speech stream to alert the listener to the segmental nature of words (e.g., syllables, phonemes). Despite this, most children without reading impairments develop phonological awareness without explicit instruction. There is some disagreement as to the cause of poor readers' difficulties on phonological awareness tasks, with most recent research favoring a language-specific explanation (for a review, see Chiappe, Chiappe, &

Siegel, 2001). If poor readers are unable to discover the segmental elements of spoken words due to poorly defined phonological representations, phonological awareness may not develop as rapidly as in good readers (Fowler, 1991; McBride-Chang, 1995; Morais, 2003; Swan & Goswami, 1997).

2.3.2 Phonological short-term memory

Several studies have shown that reading-disabled children also have impaired phonological short-term memory (Brady, Mann, & Schmidt, 1987; Hansen & Bowey, 1994; Jorm, 1983; McDougall, Hulme, Ellis, & Monk, 1994; Roodenrys & Stokes, 2001; Siegel & Ryan, 1988; Thomson et al., 2005), specific to verbal rather than visual short-term memory. For example, poor readers compared to good readers show deficits in memory for digits and letters (Katz, Healy, & Shankweiler, 1983), words (Mark, Shankweiler, Liberman, & Fowler, 1977), and sentences (Mann, Liberman, & Shankweiler, 1980), but not for abstract shapes or nonsense drawings (Katz, Shankweiler, & Liberman, 1981; McDougall et al., 1994). This is an important distinction, as it shows that poor readers do not suffer from a general deficit in working memory.

Several studies suggest that poor readers' difficulties in working memory have a phonological basis. For example, recall of phonologically similar items in working memory is more difficult for good readers than poor readers (Brady et al., 1983; Liberman et al., 1977; Mark et al., 1977). According to these arguments, good readers superior phonological coding abilities appear to penalize their recall performance on phonologically similar, i.e., confusable, words than on phonologically dissimilar words. On the other hand, poor readers' overall difficulties in phonological coding are evident in their equally poor performance on recall regardless of the degree of phonological contrast. Thus, although both good and poor readers use phonological codes, poor readers do so less efficiently (Katz, 1986). Good and poor readers' use of phonological coding strategies is evident in studies that examine the types of errors made by good and poor readers on recall tasks. For example, the majority of poor readers' errors involve recombination of phonemes in either the word to be recalled or in the preceding word (Byrne & Shea, 1979). Such errors would be expected to be less prevalent if poor readers were not using a phonological coding strategy.

2.3.3 Speech processing

Speech processing tasks require accurate coding and retrieval of phonological representations, and there is accumulating evidence suggesting that poor readers show subtle yet persistent deficits in speech processing. In this section, we review several speech processing studies that have been influential in supporting the premise that impaired phonological representations lie at the heart of poor readers' difficulties on a variety of speech perception and speech production tasks (Fig. 2.1).

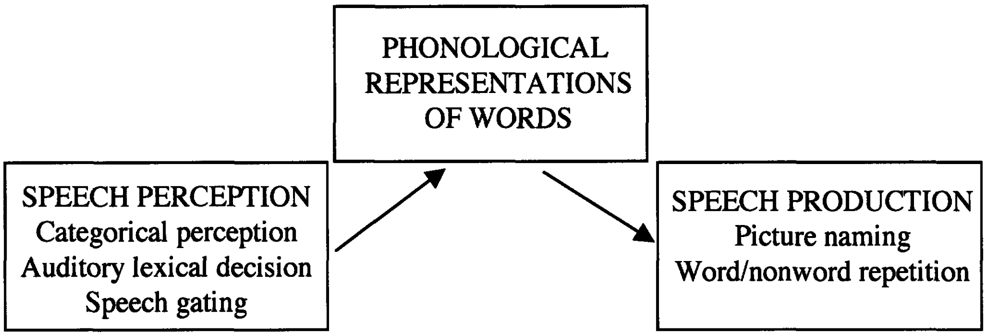

Figure 2.1: Speech processing tasks used to understand the nature of phonological representations in poor readers [Adapted from Goswami, 2000].

2.3.3.1 Speech production

Studies investigating speech production in good versus poor readers have found subtle deficits in some poor readers (Catts, 1989; Snowling, 1981). These deficits are most apparent during production of complex phonological sequences (Blalock, 1982; Miles, 1974) or when rapid access to and production of verbal labels are required, e.g., rapid naming (Ackerman & Dykman, 1993; Bowers, Sunseth, & Golden, 1999; Catts et al., 2002; de Jong & Olson, 2004; Fawcett & Nicolson, 1994; Wolf et al., 2000). Examination of errors in speech production under these demanding conditions suggests that most of poor readers' errors can be characterized as "context-conditioned slips of the tongue" (Catts, 1989), thought to arise during the planning stage of speech production (Dell, 1986). Poor readers may have difficulties selecting and ordering phonological segments during speech production, possibly resulting from their poorly defined phonological representations. Alternatively, the poor performance of reading-impaired children in rapid naming may be interpreted as difficulties in retrieving phonological codes from long-term memory (e.g., Ellis, 1981). Although difficulties with rapid naming may represent a separate core deficit in dyslexia (Wolf & Bowers, 1999), they may be characteristic of only a subset of poor readers (Wolf et al., 2000).

Poor readers also have more difficulties than good readers in nonword repetition tasks (for a review, see Rack, Snowling, & Olson, 1992). Nonwords are utterances that satisfy phonotactic constraints, yet lack meaning. Therefore, repeating nonwords necessarily requires accurate encoding, storage, and retrieval of phonological forms in verbal working memory. Impaired performance on nonword repetition could have its locus in one of many foci. On the one hand, nonwords might not be coded with sufficient phonetic detail in verbal working memory. Alternatively, poor readers' phonological representations may be poorly defined, leading to decreased performance on nonword repetition tasks. Although to date, it remains an empirical question as to which processing stage poor readers have the most difficulty with, degraded phonological representations may explain poor readers' difficulties with both nonword repetition and speech production.

2.3.3.2 Speech perception

Compared to the limited number of studies examining speech production deficits in poor readers, there is a vast amount of evidence that speech perception, particularly under demanding conditions, is deficient in poor readers compared to good readers (for a review see McBride-Chang, 1995). For example, Brady and colleagues showed that poor readers compared to good readers had more difficulty repeating monosyllabic words embedded in noise (Brady et al., 1983). However, when the words were presented without noise, or when the stimuli were non-speech environmental sounds (with and without noise), both groups performed equally well. This could be due to the fact that poor readers' degraded phonological representations may be more vulnerable to disruption by noise. Brady and colleagues also showed that the perception of speech, but not non-speech, was affected by noise in poor readers but not good readers, suggesting that good readers, but not poor readers, may be able to take advantage of better phonological coding to correctly perceive words in noise. Although other studies have attempted to replicate these results (Pennington, Van Orden, Smith, Green, & Haith, 1990; Snowling, Goulandris, Bowlby, & Howell, 1986), and their failure could be related to the different subject populations studied. Whereas the poor readers in Brady et al. (1983) were 3rd grade children, the poor readers in Snowling et al. (1986) were slightly older (9-12 year old) children, and Pennington and colleagues studied adult dyslexics (Pennington et al., 1990). According to the lexical restructuring hypothesis, phonological representations become increasingly segmented over the course of development. Therefore, the younger poor readers in Brady's study could have had phonological representations that were not as developed as their normal reading peers. However, as the poor readers became older (Pennington et al., 1990; Snowling et al., 1986), their phonological representations, although still poorly defined relative to good readers, were developed enough to preclude group differences in the speech in noise experiments.

Another area of speech perception research that has shown differences between good and poor readers is the identification or discrimination of speech segments. For example, on tasks of categorical perception, poor readers compared to good readers are typically less accurate at discriminating between stimuli that cross a phoneme boundary, whereas they tend not to be impaired on within-category discrimination (Boada & Pennington, 2006; Chiappe, Chiappe, & Gottardo, 2004; Godfrey, Syrdal-Lasky, Millay, & Knox, 1981; Reed, 1989; Serniclaes, Sprenger-Charolles, Carre, & Demonet, 2001). This difficulty of discriminating phonetically similar stimuli that are phonologically contrastive has been taken as evidence of poor readers' phonological problems. Godfrey and colleagues (1981) showed that poor readers were less skilled than good readers in both phoneme identification and in discriminating pairs of phonemes. Interestingly, they showed that poor readers had more difficulty discriminating between /da-ga/ compared to /ba-da/, where the critical difference was that /da/ and /ga/ only differed in the transition of the third formant, whereas /ba/ and /da/ differed in both the second and third formant transitions. Thus, poor readers were impaired on the contrast that was perceptually more difficult, i.e., had fewer differing cues. A reexamination of data from an earlier study by Brandt & Rosen (1980) also showed that poor readers had difficulties discriminating /da-ga/ compared to /ba-da/, supporting the idea that the phonological representations of poor readers are poorly defined (Godfrey et al., 1981; Werker & Tees, 1987).

Here we have reviewed several studies showing subtle, yet pervasive and persistent deficits in speech production and perception in poor readers. The phonological deficits hypothesis discussed earlier posits that all of these results may be accounted for by poorly defined phonological representations in poor readers compared to good readers. Despite the strong evidence for a phonological core deficit, many children with dyslexia appear to develop normal spoken language and adequate reading comprehension. An examination of the role of higher-level processes (e.g., meaning) on phonological processing in good and poor readers may provide further insight into the language basis of reading disability.

2.4 Context effects in good versus poor readers

In a large study of beginning readers, Shankweiler and colleagues (Shankweiler et al., 1999) found that differences in reading comprehension are strongly correlated with skills such as phonological decoding, that enable the child to recognize individual words. However, in many children, reading comprehension may be achieved through a greater reliance on word and/or sentence level semantic context cues. A large body of behavioral research supports the idea that context provided by other words (West & Stanovich, 1978) or sentences (Chiappe et al., 2004; Perfetti, Goldman, & Hogaboam, 1979; Stanovich & West, 1981) helps word recognition skills in poor readers. In this thesis, we further explore the role of sentence context in auditory word perception for good and poor readers by comparing subjects' behavioral and brain responses to words presented with and without semantic context.

2.4.1 Visual word perception

The majority of studies investigating the contribution of semantic context to word identification in good and poor readers have been conducted using visual stimuli. Early proponents of top-down whole-word models of word recognition suggested that skilled readers, but not poor readers, used contextual information to enhance visual word recognition abilities (e.g., Goodman, 1976; Smith, 1971). It was believed that as readers became more fluent, they actively engaged in hypothesis testing during reading to aid word recognition. However, subsequent research questioned this theory by indicating that fluent readers do not use hypothesis testing (Stanovich & West, 1979), as it is too slow to facilitate word recognition. In fact, later behavioral studies measuring reaction times for reading words in isolation versus embedded in sentences, have suggested that children who are poor readers use contextual information to aid in word recognition more than children who are good readers (Perfetti et al., 1979; Perfetti & Roth, 1981; Stanovich, 1980; Stanovich & West, 1981). A common explanation for these findings is that skilled readers are too quick to identify words; thereby semantic context does not have time to influence the word recognition process. In contrast, poor readers' impaired phonological decoding skills cause them to be slower at word recognition, thus enabling context to aid in this process (Perfetti, 1995). Collectively, these results may be best accounted for by an interactive-compensatory model of word recognition (Stanovich, 1980), which allows for the integration of bottom-up (decoding) and top-down (context) processes. Furthermore, in a previous study, we showed that children and adults who were good readers activated both semantic and phonological codes during a visual homophone judgment task with semantic foils, causing them to respond slower to the semantically-related words (Wehner, Ahlfors, & Mody, in press). The findings suggested that phonological and semantic information interact during visual word perception.

2.4.2 Speech perception

Semantic priming studies have provided evidence that semantic context can both facilitate and inhibit the recognition of phonologically ambiguous words in normal readers (Gaskell & Marslen-Wilson, 2002; Zwitserlood, 1989). However, there have only been a few studies investigating sentence context effects during speech perception comparing good versus poor readers, although both groups appear to benefit from semantic context (Cole & Perfetti, 1980). In a recent MEG study, adults who were either good or poor readers listened to sentences in which the final word was semantically congruent or incongruent with the preceding context (Helenius, Salmelin, Service et al., 2002). Additionally, half of the incongruent sentences ended with words that were phonologically similar to the expected congruent word. Compared to good readers, poor readers showed abnormal brain responses between 100-300 ms, but normal responses within the time window associated with semantic processing (300-500 ms). Similarly, another study with normal and reading-impaired children showed evidence for abnormal brain responses in the N1 (acoustic) and N2 (phonological) time ranges, but not in the later N4 (semantic) time range (Bonte & Blomert, 2004). Results from both of these studies can be interpreted in light of the phonological deficit hypothesis, such that the poor readers showed abnormal brain activity during the time range associated with phonological processing (N2), but not during the time range associated with semantic processing (N4). To our knowledge, there have been no previous studies comparing auditory perception of words with and without sentence context in normal versus reading-impaired children.

Insight into how poor readers with degraded phonological representations might use sentence context to compensate for poor phonological processing during speech perception can be obtained from studies that examine context effects on 'phonemic restoration' in normal adults (Samuel, 2001; Sivonen, Maess, & Friederici, 2006; Sivonen, Maess, Lattner, & Friederici, 2006; Warren, 1970). For example, Warren showed that when a short noise burst was substituted for the initial phoneme of a word embedded in a sentence, the difference was not perceptible (Warren, 1970). This suggests that similar to reading connected text, listeners also use top-down semantic information provided by sentence context during speech perception. Another study investigating the phonemic restoration effect using behavioral responses and ERPs had subjects listen to sentences where the terminal word was either semantically congruent or incongruent to the preceding context (Sivonen, Maess, Lattner et al., 2006). Additionally, half of the terminal words had their first phonemes replaced by noise. In the behavioral experiment, subjects were instructed to repeat the last word of the sentence, whereas for the ERP experiment, subjects passively listened to the sentences. It was found that congruent words were repeated faster than incongruent words irrespective of onset manipulation, suggesting that semantic context aided word recognition. The ERP responses for normal adults, in the study by Sivonen and colleagues (2006), were similar to the results for poor readers in the MEG studies reviewed earlier (Bonte & Blomert, 2004; Helenius, Salmelin, Service et al., 2002); that is N1 and N2 responses were abnormally large for words with modified onsets, but the amplitude of the N4 responses did not differ as a function of onset modification. Therefore, it appears that when phonemic input is degraded, normal adults use a combination of top-down semantic information provided by the sentence context and bottom-up phonological information from the remaining word fragment during word recognition. In the present thesis, we further investigate whether poor readers rely extensively on context during phonologically demanding conditions, as a consequence of poorly defined phonological representations.

In the next section, we review neuroimaging studies that have begun to examine the neurobiological basis of impaired phonological processing in poor readers.

2.5 Neurobiological correlates of language processing

A considerable amount of evidence has accumulated over the past twenty years showing differing brain activation patterns between good and poor readers during phonological processing tasks. The neuroimaging literature can be classified into two factions: studies primarily interested in comparing the location and magnitude of brain responses between groups using hemodynamic measures such as functional magnetic resonance imaging (fMRI) and positron emission tomography (PET), and studies that investigate subtle differences in the timing of brain activity between groups using electroencephalography (EEG) and magnetoencephalography (MEG). First, we briefly review neuroimaging studies that examine differences in phonological processing abilities between good and poor readers. Then, given the focus of the present thesis, a review discussing the neurobiological underpinnings of speech perception differences between good and poor readers is provided.

2.5.1 Neuroimaging studies of phonological processing

One of the earliest studies examining poor readers' brain activation patterns during phonological processing was conducted by Rumsey and colleagues using PET (Rumsey et al., 1992). Adults who were classified as good or poor readers listened to pairs of words and judged whether or not they rhymed. It was found that poor readers showed less left temporoparietal activation and increased right middle temporal activation compared to good readers (Rumsey et al., 1992). A subsequent PET study suggested a disconnection between posterior (temporal and parietal) and anterior (inferior frontal) regions in adults who were poor readers (Paulesu et al., 1996). This is shown by converging results from fMRI, PET and MEG studies which suggest that reading words and pseudowords activates two distinct posterior (ventral and dorsal) and one anterior reading circuitry in the left hemisphere (Fig. 2.2).

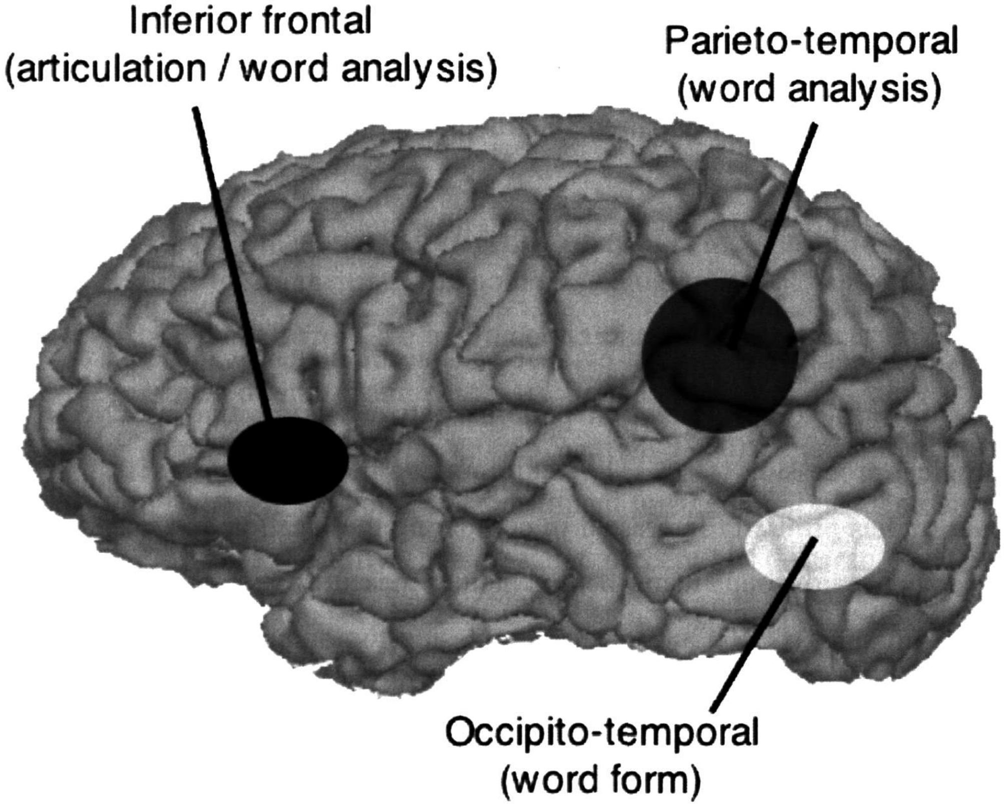

Figure 2.2: Left hemisphere brain regions typically implicated in reading studies [Adapted from Shaywitz et al., 2006].

The ventral posterior circuit, including lateral extrastriate and occipitotemporal areas, appears to be most active during word recognition. Occipitotemporal areas have been consistently activated more for words in neuroimaging studies which contrast word and nonword reading (Buchel, Price, & Friston, 1998; Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999). This area is often referred to as the Visual Word Form area, although it appears to be activated in other tasks as well (Price & Devlin, 2004). In addition, it has been hypothesized that fluent readers are able to rely extensively on an occipitotemporal neural network to be able to read words quickly with few errors (Pugh et al., 2000). This area also plays an increasingly important role in word identification for beginning readers (Salmelin, Service, Kiesila, Uutela, & Salonen, 1996; Shaywitz et al., 2002).

The dorsal posterior circuit appears to support phonological analysis and includes inferior parietal areas, such as the supramarginal gyrus and angular gyrus, as well as the posterior aspect of the superior temporal gyrus. The areas in this dorsal circuit, particularly angular gyrus, have been considered to be regions critically involved in orthographic to phonological conversion during reading (Geschwind, 1965) and have shown abnormal activation in reading-disabled subjects during reading tasks under phonologically demanding conditions such as nonword decoding (Pugh et al., 2000; Shaywitz et al., 1998; Simos, Breier, Fletcher, Foorman et al., 2000).

The anterior circuit is comprised of areas in the inferior frontal gyrus (IFG) and appears to support sequencing and execution of articulatory recoding during reading. Studies with reading-impaired children have shown increased activation in the IFG, presumably to compensate for deficient development of the left hemisphere posterior reading circuits (Pugh et al., 2000; Salmelin et al., 1996; Shaywitz et al., 1998).

2.5.2 Neuroimaging studies of speech perception

Since speech perception abilities serve as a scaffold for the development of word reading, there is a fair amount of overlap between brain regions activated during word reading (Fig. 2.2) and speech perception (Fig. 2.3).

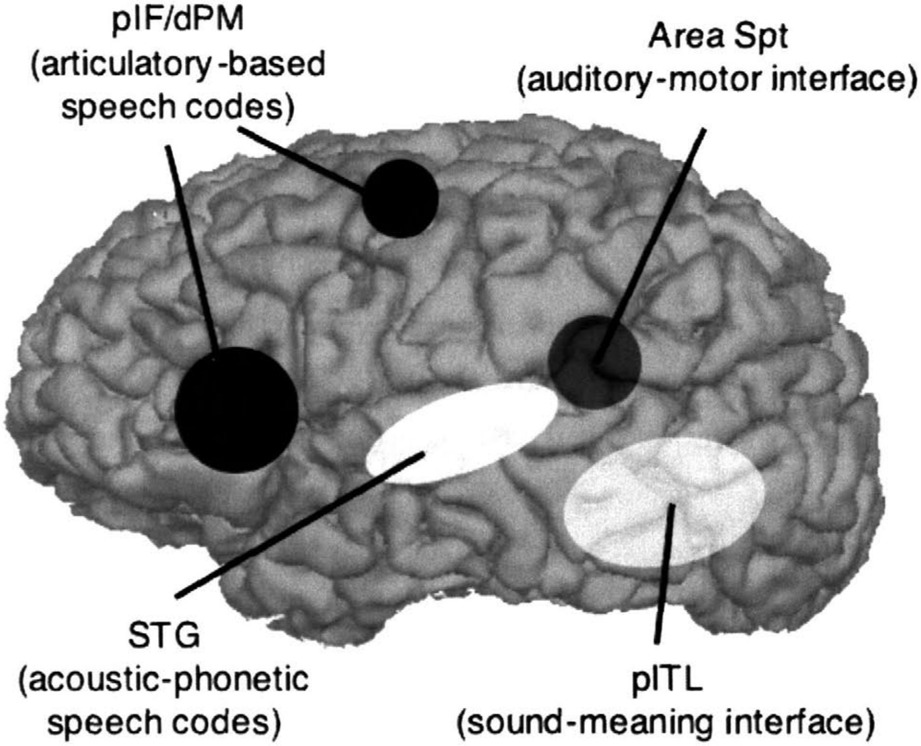

Figure 2.3: Brain regions often implicated in speech perception tasks. Regions: posterior inferior frontal (pIF), dorsal premotor (dPM), superior temporal gyrus (STG), posterior inferior temporal lobe (pITL), Sylvian fissure temporo-parietal (Spt) [Adapted from Hickok & Poeppel, 2004].

The degree to which each of these regions is activated during speech perception is dependent on the tasks and stimuli used. Acoustic information arrives at the auditory cortex (Heschl's gyrus) within 10-15 ms after stimulus onset (Celesia, 1976; Liegeois-Chauvel, Musolino, Badier, Marquis, & Chauvel, 1994). Time-structured signals (e.g., speech and pure tones) compared to unstructured signals (e.g., noise), show activation along the dorsal aspect of the superior temporal plane, whereas speech compared to nonspeech (e.g., tones) activates the ventral part of the left superior temporal gyrus (STG) extending into the superior temporal sulcus (STS) (Binder et al., 2000; Scott, Blank, Rosen, & Wise, 2000; Zatorre, Evans, Meyer, & Gjedde, 1992). Increasing levels of task complexity by involving lexical-semantic manipulations show additional activation in ventral areas, such as the left middle temporal gyrus (MTG) (Binder et al., 2000; Castillo et al., 2001). For the purposes of the present thesis, it is notable that speech perception tasks emphasizing phonological processing elicit brain responses in the left auditory association cortex along the superior temporal plane (e.g., Breier et al., 2003; Simos, Breier, Zouridakis, & Papanicolaou, 1998). In addition, several studies have shown that poor readers activate left STG less than good readers during speech perception (Breier et al., 2003; Corina et al., 2001; Rumsey et al., 1992). Furthermore, when active phonological coding is required, good and poor readers also often show increased activation in left inferior frontal cortex (Pugh et al., 2001).

Since speech perception is a dynamic process, methods with fine time resolution, such as EEG and MEG, might help identify subtle differences in the relations between language processes in the brain, even though the cortical regions underlying the interactions between these processes may not be fully resolved (Mody, 2004). In the next section, we review a series of EEG and MEG studies that have identified early and late event-related potential/field (ERP/ERF) components either related to or modulated by linguistic factors such as semantic incongruity and phonological anomalies.

2.5.3 EEG/MEG components in language processing

From the first discovery that electrical activity from the brain could be measured using electrodes placed on the scalp (Berger, 1929) to the more recent discovery that small magnetic fields arising from neural populations in the brain could be measured with superconducting devices (Cohen, 1972), the use of EEG and MEG methods have become an indispensable tool to noninvasively investigate language processes with millisecond time resolution. Although there are many ways to examine electrical and magnetic activity in both the temporal and spectral domains, here we focus on evoked brain activity that is averaged over many trials and time-locked to the presentation of some stimulus. The latencies and amplitudes of peaks (components) in the evoked waveforms are thought to represent specific cognitive processes. Whereas many components have been defined over the years, only those relevant to this thesis are discussed below.

2.5.3.1 N100

The N100 (or N1) is an obligatory component, typically observed between 70-120 ms, thought to reflect the basic encoding of acoustic information (Hari, 1990; Näätänen & Picton, 1987). Neural sources contributing to the N1 have been consistently localized to the auditory cortex (Heim, Eulitz, & Elbert, 2003; Helenius, Salmelin, Service, & Connolly, 1998; Kuriki, Okita, & Hirata, 1995; Nagarajan et al., 1999) or the planum temporale (Liegeois-Chauvel et al., 1994; Lutkenhoner & Steinstrater, 1998). The N1 has also been shown to be modulated by cognitive influences, such that binaurally presented speech stimuli (e.g., syllables, phonemes) preferentially activate the left auditory cortex during the N1 time range whereas tones typically elicit bilateral responses (Kuriki & Murase, 1989; Poeppel et al., 1996). Studies investigating the differences in N1 amplitude or latency between good and poor readers in response to speech or tones have been mixed, with some studies finding an increased N1 amplitude in poor compared to good readers (Helenius, Salmelin, Richardson, Leinonen, & Lyytinen, 2002), and others finding a decreased N1 amplitude in poor readers (Nagarajan et al., 1999; Neville, Coffey, Holcomb, & Tallal, 1993). It appears that task conditions such as the choice of interstimulus interval plays a major role in these discrepancies (Helenius, Salmelin, Richardson et al., 2002).

2.5.3.2 N200/PMN

Oddball paradigms involving occasional 'deviants' among repeated 'standard' stimuli have been commonly used in EEG and MEG studies of speech perception. One such measure, the N200 (or N2) response is thought to reflect stimulus contrast and is generally observed between 200-350 ms. It is viewed as an index of attention, stimulus classification and discrimination (Näätänen & Picton, 1986; Ritter, Simpson, Vaughan, & Friedman, 1979). When an N2 response is elicited during auditory tasks requiring phonological processing, it is sometimes referred to as a phonological mismatch negativity (PMN) (Connolly & Phillips, 1994; Connolly, Phillips, Stewart, & Brake, 1992; Connolly, Stewart, & Phillips, 1990; Diaz & Swaab, 2006; Kujala, Alho, Service, Ilmoniemi, & Connolly, 2004; Newman, Connolly, Service, & McIvor, 2003; Phillips, Klein, Mercier, & de Boysson, 2006; van den Brink, Brown, & Hagoort, 2001).

Although the functional significance of the PMN is still debated, it is thought to reflect integration of phonological expectations with incoming acoustic information, as it is typically elicited when there is a phonological mismatch between a word that is anticipated from context and the word that is heard. Interestingly, the degree of mismatch between the anticipated and the heard input does not appear to modulate the amplitude or latency of PMN, suggesting that the PMN reflects an "all-or-none" process (Newman et al., 2003). Others have suggested that this component reflects early lexical and semantic influences on word recognition (Diaz & Swaab, 2006; Hagoort & Brown, 2000; van den Brink et al., 2001). This account is based on the idea that in spoken word recognition, word-initial sounds activate a cohort of possible lexical candidates (Marslen-Wilson & Tyler, 1980). As word recognition proceeds, top-down contextual information further constrains the number of possible candidates leading to the actual word that is perceived. If the phonological representations of lexical entries are not well defined for poor readers, there is a higher probability that the initial cohort of activated words will erroneously contain words that will lead the poor reader down the wrong path. As a consequence, poor readers may rely more extensively on contextual information than good readers during speech perception.

Recent studies using word priming paradigms have localized neural sources contributing to the PMN in the left anterior auditory (Kujala et al., 2004) and/or left inferior frontal cortices (Connolly, Service, D'Arcy, Kujala, & Alho, 2001; D'Arcy, Connolly, Service, Hawco, & Houlihan, 2004) in normal adults. A recent ERP study examining the PMN elicited by word priming and sentence context violations suggests that these two types of contexts may have differential effects on speech processing (Diaz & Swaab, 2006). They found that the PMN was elicited only when phonological processes were maximally engaged as in their alliteration word priming task, but not when the primary focus was on semantic integration, as in their conceptual word priming and sentence context tasks. This finding is further supported by an MEG study using an auditory sentence paradigm with normal and reading-impaired adults (Helenius, Salmelin, Service et al., 2002) that did not reveal a distinct PMN component.

To our knowledge, there have been no previous reports of PMN effects in children, although some ERP studies have reported a childhood N250 with a fronto-central distribution (Ceponiene, Rinne, & Näätänen, 2002). A recent MEG study with children has localized sources contributing to the N250 in the superior temporal plane (Takeshita et al., 2002). The N250 has been implicated as a marker for the development of auditory and language abilities (Tonnquist-Uhlen, 1996), and may reflect subtle abnormalities in basic aspects of pre-lexical speech processing (Bonte & Blomert, 2004) or increased processing effort during translation of acoustic input into phonological representations (Newman et al., 2003) in poor readers.

2.5.3.3 N400

In contrast to the role of phonological processing in the PMN, the N400 (or N4) is thought to index semantic expectancy or ease of lexical integration and is elicited by all word-like stimuli (Halgren et al., 2002; Helenius, Salmelin, Service et al., 2002; Holcomb, 1993; Kutas & Hillyard, 1980; Kutas, Neville, & Holcomb, 1987). In their seminal study, Kutas and Hillyard (1980) showed that the amplitude of the N4 elicited by reading the terminal word of a sentence was modulated by the word's semantic expectancy from the preceding sentence context (Kutas & Hillyard, 1980). In particular, it was shown that the amplitude of the N4 was increased for semantically anomalous stimuli relative to semantically congruent stimuli, referred to as the N4 effect. More recent studies using primed lexical decision have shown the N4 has contributions from both automatic (Deacon, Hewitt, Yang, & Nagata, 2000) and controlled (Brown, Hagoort, & Chwilla, 2000; Hill, Strube, Roesch-Ely, & Weisbrod, 2002; Rossell, Price, & Nobre, 2003) processes. While the cognitive basis of the N4 is still debated, there are two main hypotheses concerning its generation. The lexical hypothesis suggests that the N4 reflects activation of a lexical and/or semantic representation of a word (Van Petten & Kutas, 1987), whereas the nonlexical hypothesis proposes that the N4 reflects postlexical integration of a word into an existing context (Holcomb, 1993; Neville, Nicol, Brass, Forster, & Garrett, 1991).

ERP studies using auditory paradigms with children often show a widespread source distribution related to the generation of the N4 (Holcomb, Ackerman, & Dykman, 1985; Juottonen, Revonsuo, & Lang, 1996) often peaking maximally for anterior scalp locations (Coch & Holcomb, 2003; Holcomb, Coffey, & Neville, 1992). This is in contrast to the classic centro-parietal source distribution of the N4 often observed in adults and for visual tasks (Kutas & Hillyard, 1980). Given the widespread scalp distribution of the N4, there have been efforts to localize neural generators of the N4 using intracranial methods and MEG studies. Intracranial studies have suggested that generators of the N4 might be located in the medial temporal cortex (McCarthy, Nobre, Bentin, & Spencer, 1995; Nobre & McCarthy, 1995; Smith, Stapleton, & Halgren, 1986), while recent MEG studies have localized sources contributing to the N4 in left hemisphere anterior temporal (Halgren et al., 2002; Marinkovic et al., 2003), and superior temporal regions near the auditory cortex (Helenius et al., 1998; Makela, Makinen, Nikkila, Ilmoniemi, & Tiitinen, 2001; Simos, Basile, & Papanicolaou, 1997). The differences between the results obtained using intracranial and MEG methods likely result from the sensitivity of each method. Whereas intracranial measurements with depth electrodes can record local field potentials in deep brain structures, MEG is generally insensitive to deep sources (Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993).

Results of the few studies that have examined N4 modulation in children (Coch, Grossi, Coffey-Corina, Holcomb, & Neville, 2002; Coch & Holcomb, 2003; Coch, Maron, Wolf, & Holcomb, 2002; Helenius, Salmelin, Service, & Connolly, 1999; Holcomb et al., 1992) have suggested that children may be more sensitive to context than adults. Furthermore, it has been shown that the amplitude and latency of the N4 decreases over the course of normal reading development as lower-level reading processes such as phonological decoding become more automatic (Coch & Holcomb, 2003; Hahne, Eckstein, & Friederici, 2004; Holcomb et al., 1992). Differences in the N4 effect between good and poor readers appears to depend on the task used. Although N4 modulation in poor readers is still not well understood, tasks that explicitly tap phonological processing (e.g., McPherson, Ackerman, Holcomb, & Dykman, 1998) tend to report decreases in the N4 effect for poor readers compared to good readers, while tasks that don't emphasize phonological processing (Bonte & Blomert, 2004; Sabisch, Hahne, Glass, von Suchodoletz, & Friederici, 2006) tend to show little or no differences in N4 modulation between good and poor readers. Other authors have suggested that abnormal N4 responses in poor readers may simply be a reflection of earlier phonological processing difficulties as evidenced by increased N1 (Helenius, Salmelin, Service et al., 2002) or N1/N2 (Bonte & Blomert, 2004) amplitudes.

Historically, the definition of different ERP components has been very useful to allow comparisons of perceptual and cognitive brain responses between normal and impaired populations. In recent years, the advent of more advanced methods and analysis techniques, such as high-resolution EEG, MEG, and fMRI-constrained MEG/EEG solutions, have provided researchers with better spatiotemporal resolution for source analysis. In the present thesis, we chose to examine brain activation within time ranges associated with auditory, phonological, and/or semantic processing, using a region of interest (ROI) approach, which took advantage of the localization capabilities of MEG.

2.6 Subjects

Two groups of children participated: fifteen good readers (11 females; 7 to 13 years old, mean = 9.7), and fifteen poor readers (8 females; 8-13 years old, mean 10.4). Although the participants in the poor readers group were slightly older, the difference in age between the two groups was not significant (*t*-test, $p > 0.1$). Written informed assent/consent was obtained from all subjects/parents in accordance with the Human Subjects Committee at Massachusetts General Hospital. All children had English as their primary language and had normal or corrected-to-normal vision, with no history of neurological, psychological or hearing problems. Additionally, all children passed a standard hearing screening at 20 dB for 500 to 4000 Hz, (ANSI, 1989) and were screened for implanted metal devices. Most of the subjects were right-handed, with the exception of three children in each group who were left-handed (Annett, 1970).

Good and poor reader groups were selected on the basis of their performance on the subtests of the Woodcock Reading Mastery Tests-Revised (Woodcock, 1987). Poor readers scored below the 25th percentile on the Word Attack and/or Word Identification subtest of the Woodcock Reading Mastery Tests-Revised. Children in the good reader group were reading above the 39th percentile on both Woodcock subtests to allow for clear separability between the two groups. Additionally, children in the poor reader group were identified by the school system as reading below grade level, and they were receiving reading remediation. Both groups had scores in the normal range (85-120) on verbal and nonverbal IQ. Nonverbal IQ was assessed using the Test of Nonverbal Intelligence (TONI-3) (Brown, Sherbenou, & Johnsen, 1997); verbal IQ was estimated from the Peabody Picture Vocabulary Test (PPVT-3) (Dunn & Dunn, 1997), a measure of receptive vocabulary that correlates closely with verbal IQ. All children were also tested on rapid naming performance (color naming and object naming subtests) and phonological memory (nonword repetition and memory for digits subtests) of the Comprehensive Test of Phonological Processing (CTOPP) (Wagner, Torgesen, & Rashotte, 1999). Children with a diagnosis of attention deficit hyperactivity disorder (ADHD) were excluded from the study. A summary of the standardized testing scores for the two groups is shown in Table 2.1. Planned *t*-tests revealed that the groups did not differ significantly on any standardized testing measure other than reading standard score (SS).

Children's Reading Scores

	PPVT	TONI	Reading SS	PM	RN
Good Readers	105 (9.7)	104 (9.6)	114 (9.7)	99 (7.4)	89 (9.7)
Poor Readers	101 (10.4)	98 (9.3)	87 (6.7)	94 (9.3)	91 (9.7)

Table 2.1: Reading scores for both groups for the Peabody Picture Vocabulary Test (PPVT-3), the Test of Nonverbal Intelligence (TONI-3), Reading Standard Score (Word ID/Word Attack subtests of Woodcock), and Phonological Memory (PM) and Rapid Naming (RN) subtests of the Comprehensive Test of Phonological Proficiency (CTOPP). Group means and standard deviations (in parentheses) are provided.

Chapter 3: Auditory word discrimination in good and poor readers

Effects of phonological contrast on auditory word discrimination in children with and without reading disability: A magnetoencephalography (MEG) study

Submitted to Neuropsychologia

3.1 Abstract

Poor readers perform worse than their normal reading peers on a variety of speech perception tasks, which may be linked to their phonological processing abilities. The purpose of the study was to compare the brain activation patterns of normal and impaired readers on speech perception to better understand the phonological basis in reading disability. Whole-head magnetoencephalography (MEG) was recorded as good and poor readers, 7-13 years of age, performed an auditory word discrimination task. We used an auditory oddball paradigm in which the 'deviant' stimuli (/bat/, /kat/, /rat/) differed in the degree of phonological contrast (1 vs. 3 features) from a repeated standard word (/pat/). Both good and poor readers responded more slowly to deviants that were phonologically similar compared to deviants that were phonologically dissimilar to the standard word. Source analysis of the MEG data using Minimum Norm Estimation (MNE) showed that compared to good readers, poor readers had reduced left-hemisphere activation to the most demanding phonological condition reflecting their difficulties with phonological processing. Furthermore, unlike good readers, poor readers did not show differences in activation as a function of the degree of phonological contrast. These results are consistent with a phonological account of reading disability.

3.2 Introduction

Poor readers' performance on a variety of tasks such as phoneme identification (Chiappe et al., 2001; Mody et al., 1997), categorical speech perception (Godfrey et al., 1981; Watson & Miller, 1993; Werker & Tees, 1987), nonword repetition (Brady et al., 1983; Snowling, 1981; Snowling et al., 1986), rapid naming (Bowers & Swanson, 1991; Wolf et al., 2000), and perception of speech in noise (Brady et al., 1983) has been found to be inferior to that of their normal reading peers. There is mounting evidence in favor of a phonological core deficit as a basis of these observed difficulties, that is children with reading disabilities appear to have deficient phonological representations (for a review see Boada & Pennington, 2006), which would account for their grapheme to phoneme correspondence problems. Insofar as the perception of speech requires accurate coding and retrieval of phonological representations, we used a speech perception task to compare the brain activation patterns between normal and impaired readers to better understand the phonological basis in reading disability.

Poor readers' difficulties with speech perception are known to be subtle, typically exacerbated under phonologically demanding conditions (Bonte, Poelmans, & Blomert, 2007; Brady et al., 1983; Godfrey et al., 1981; Mody et al., 1997; van der Leij & van Daal, 1999; Yap & van der Leij, 1993). For example, on categorical perception tasks, poor readers compared to good readers have been found to be less accurate in discriminating between stimuli that cross a phoneme boundary, whereas they tend not to be impaired on within-category discrimination (Boada & Pennington, 2006; Chiappe et al., 2004; Godfrey et al., 1981; Reed, 1989; Serniclaes et al., 2001). This difficulty with discriminating phonetically similar stimuli that are phonologically contrastive has been taken as evidence of poor readers' phonological problems. Studies involving speech discrimination of minimal pairs have also revealed impaired performance in poor readers (Adlard & Hazan, 1998). Children with reading impairments were less accurate than unimpaired readers in discriminating words with a small degree of phonological contrast (initial phoneme differing in one feature) that were also acoustically similar. In the present study, we used words differing in their initial phoneme by one versus three phonetic features, in order to examine the effect of degree of phonological contrast on speech perception in good and poor readers.

Neuroimaging studies have shown that good and poor readers exhibit different neural response patterns during speech perception (Breier et al., 2003; Corina et al., 2001; Ruff, Marie, Celsis, Cardebat, & Demonet, 2003). In a categorical perception task using magnetoencephalography (MEG), Breier and colleagues (2003) found that good readers primarily activated left temporoparietal cortex during perception of speech stimuli along a synthetic /ga/-/ka/ voicing continuum, whereas poor readers showed initial right temporoparietal activation followed by later left temporoparietal activation. These results are consistent with the idea that poor readers may use right hemisphere ancillary systems to compensate for underdeveloped left hemisphere language systems (Shaywitz et al., 2002; Simos, Breier, Fletcher, Bergman, & Papanicolaou, 2000; Simos, Breier, Fletcher, Foorman et al., 2000). Studies using functional magnetic resonance imaging (fMRI) have similarly found differences in brain activation between good and poor readers in areas implicated in phonological processing, including left superior temporal and inferior frontal cortices (e.g., Corina et al., 2001; Georgiewa et al., 1999; Temple et al., 2001).

In the present study we used an oddball task. Oddball paradigms involving occasional 'deviants' among a repeated 'standard' stimulus have been commonly used in EEG and MEG studies of speech perception. Under passive listening conditions, deviant stimuli evoke a mismatch negativity (MMN) response (Näätänen, 1992). However, research on the use of the MMN to investigate speech perception in children with learning disabilities has yielded inconsistent results (Bradlow et al., 1999; Kraus et al., 1996; Lachmann, Berti, Kujala, & Schroger, 2005; Schulte-Korne, Deimel, Bartling, & Remschmidt, 1998). Although some of the conflicting results may partially be accounted for by methodological differences between studies (Boada & Pennington, 2006; Heim et al., 2000), it appears that MMN for speech stimuli may not be a clinically reliable measure (Kurtzberg, Vaughan, Kreuzer, & Fliegler, 1995).

An attended oddball task, however, which actively engages poor readers' phonological processing abilities, may in contrast help to capture the subtle differences between good and poor readers in speech perception. When using this design, two attention-dependent evoked components, the N2 (or N200) and the P3 (or P300), are typically observed in the EEG waveforms (Lawson & Gaillard, 1981; Näätänen & Picton, 1986; Ritter et al., 1979). The N2 is purported to reflect focused attention, stimulus classification and discrimination, whereas the P3 is generally held to reflect processes associated with dynamic update in working memory, cognitive resource allocation and task involvement (Breznitz & Meyler, 2003). In the present study, we focused on the time range of the N2 response (150-300 ms), given its association with phonological processing (Connolly et al., 2001; Kujala et al., 2004). Neural generators contributing to the N2 have been localized to the superior temporal gyrus or prefrontal cortices (Alho et al., 1998; Giard, Perrin, Pernier, & Bouchet, 1990; Opitz, Mecklinger, Von Cramon, & Kruggel, 1999; Paavilainen, Alho, Reinikainen, Sams, & Näätänen, 1991; Scherg, Vajsar, & Picton, 1989).

There have been a limited number of N2 studies comparing normal and reading-impaired children (Bernal et al., 2000; Bonte & Blomert, 2004; Taylor & Keenan, 1990). In an auditory lexical decision study with alliteration priming, children who were poor readers, showed significantly smaller N1 amplitudes in temporal electrodes, with larger N2 amplitudes in midline electrodes compared to good readers (Bonte & Blomert, 2004). The authors suggest that the smaller N1 responses for the poor readers may be a result of deviant source locations and/or diminished activation related to auditory processing. However, the abnormally large N2 responses for the poor readers compared to the good readers may represent subtle differences in prelexical speech processing between the two groups, reflecting poor readers' difficulties with accessing phonological representations.

The present study aimed at characterizing spatiotemporal differences in brain activation related to phonological processing between good and poor readers during auditory perception of deviant target words that differed in the degree of their phonological contrast (one vs. three feature difference) from a repeated standard word. We predicted that poor readers would show longer reaction times and more errors to phonologically similar than phonologically dissimilar target words when compared to the good reader group. Additionally, we hypothesized that poor readers compared to good readers would show decreased response amplitudes between 150-300 ms to phonologically similar than phonologically dissimilar deviants compared to the standard stimulus, in areas important for phonological processing.

3.3 Materials and Methods

Subjects: See section 2.6

3.3.1 Stimuli

A phonetically-trained native male speaker of American English recorded the standard token (*pat*) as well as three deviant tokens (*bat, cat, rat*) with neutral intonation in a sound treated room using a unidirectional microphone attached to a PC running the program WaveSurfer (Sjolander & Beskow, 2000) with a 22 kHz sampling rate. To control for acoustic differences between the stimuli, new deviants were constructed by extracting the formant contours (F1, F2, F3, F4) of the initial phonemes of the recorded deviants (i.e., /k/, /b/, /r/) using the sound-editing program XKL (Klatt, 1980). New instances of /k/, /b/, and /r/ were created using the Klatt synthesizer by mimicking the formant contours observed in the natural utterances. The synthesized consonants were appended to the rime of the standard stimulus (/at/), resulting in new deviant tokens (/bat/, /kat/, /rat/) that were controlled for acoustic differences. Care was taken to create smooth transitions between the formant contours of the synthesized consonants and the formant contours of the vowel /a/. As the synthesis of /r/ was more complex than for /b/ and /k/, it was found that the insertion of an additional pole-zero pair at 1750 Hz resulted in a more natural sounding /r/. Small sections of the initial phonemes were modified, so that the duration of each stimulus was maintained at a constant length of 420 ms. Spectrograms of the stimuli are shown in Figure 3.1

The stimuli were tested with adults and children to verify that all tokens sounded natural prior to use in the actual study. The stimuli were chosen, as they were all highly familiar words (word frequency: *pat*-35, *bat*-18, *cat*-23, *rat*-6) (Kucera & Francis, 1967). Two of the deviants differed in one phonetic feature (/kat/ in place of articulation, /bat/ in voicing) from the standard, while the other deviant (/rat/) differed in three phonetic features (voicing, place of articulation, and manner of articulation) from the standard. The deviants will be hereafter referred to as phonologically similar for /bat/ and /kat/, and phonologically dissimilar for /rat/.

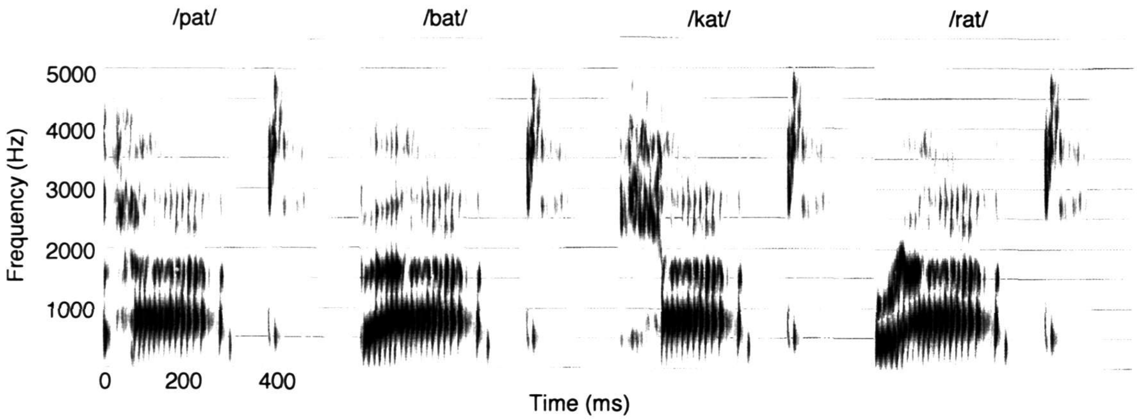

Figure 3.1: Spectrograms of the stimuli

3.3.2 Experimental procedure

During the experiment, subjects were presented with a train of standard (*pat*) stimuli embedded with occasional deviants (*bat, cat,* or *rat*) played at a comfortable listening level through headphones. Consecutive stimuli were separated by 300 ms of silence. Subjects were instructed to press a response button as soon as they heard one of the deviant words, to indicate that the deviant was detected. To ensure an adequate signal to noise ratio, each deviant was presented 100 times, and the standard was presented 1000 times for a total of 1300 trials, giving each of the deviants an 8% probability of occurrence. To help the subjects maintain focus, they were instructed to fixate on a cross that was projected on the middle of a screen in front of them. The stimuli were presented in five runs containing an equal number of stimuli (200 standards, and 20 of each deviant). Short five-second breaks after every twenty stimuli, and longer two-minute breaks between runs helped prevent subject fatigue. The order of the stimuli was identical for all subjects. It was pseudorandomized so that at least two but no more than five standards occurred between two deviants. In addition, deviants did not occur within the first five trials of each run or within the first three trials after a break, to allow subjects to build up a memory trace of the standard against which the deviant was to be compared. Subjects were instructed to respond as quickly and accurately as possible using the index finger of their dominant hand.

3.3.3 Behavioral Measures

Response time (RT) and accuracy measures for each deviant were calculated for each subject. RTs were measured from the onset of the deviant word. Trials with response times less than 200 ms or greater than 1500 ms were counted as incorrect. The choice of these cutoffs was justified given the range of mean RTs was 400-950 ms. The number of missed deviants (i.e., when the button was not pressed), as well as the number of false positives was calculated for each subject. Subjects were provided with 26 practice trials (20 standards, 2 each of the deviants) before beginning the actual experiment, to determine a comfortable listening level and to ensure a complete understanding of the task instructions. The total recording time was about 25 minutes. Pearson product-moment correlation coefficients were also calculated for comparisons of standardized testing measures and performance measures on the oddball task to determine if test scores predicted performance on the oddball task.

3.3.4 MEG recording

Simultaneous MEG and EEG were recorded using a 306-channel (204 first-order planar gradiometers, 102 magnetometers) VectorView MEG system (Elekta-Neuromag Ltd., Helsinki, Finland), with 19 electrodes of EEG in a cap arranged approximately according to the 10-20 system. The impedances of all EEG electrodes were kept below 5 kΩ. For the source analysis, only the MEG signals were used given the optimization of our analysis tools for this purpose. Horizontal and vertical EOG electrodes were used for detection and subsequent rejection of large eye movements and eye blinks, which cause artifacts in the MEG data. The locations of the electrodes were digitized with a Fastrak digitization device (Polhemus, Colchester, VT). Landmark anatomical features (nasion and preauricular points), along with additional points along the surface of the head were also digitized for the co-registration of the MEG data with the subject's MRI.

Subjects were seated in a comfortable chair facing a screen, with hands resting on a flat surface holding the response pad, and with their head placed under the helmet-shaped bottom of the dewar housing the MEG sensors. A microphone was used for communication with the subject, and all subjects were monitored during the experiment with a video camera inside the magnetically shielded room linked to a display outside of the room.

The MEG and EEG signals were recorded continuously during each of five runs, and sampled at 601 Hz after filtering from 0.03 to 200 Hz. At the beginning of each run, low-level current was fed to each of 4 HPI coils attached to the subject's head for calculation of the head position with reference to the MEG sensors. Stimulus presentations and corresponding brain responses were time locked to trigger pulses sent by the Presentation program and coded by the data acquisition computer. Event-related MEG and EEG responses related to each stimulus condition were averaged. The epoch window used for averaging was 900 ms (100 ms before to 800 ms after the onset of the stimulus). Trials containing eye movements, blinks, or other channel artifacts (peak-to-peak amplitude >150 μV in EOG, >500 fT/cm in gradiometers) were rejected. The good readers had on average 82 artifact-free epochs per condition, the poor readers 73. This difference was not significant (t-test, $p > 0.1$). The averaged epochs were low-pass filtered at 40 Hz, and the zero level in each channel was taken to be the mean value in the 100-ms baseline period before stimulus onset. Although the visualization of the MEG and EEG sensor data was important for validating the task design and comparison of our results with previous studies, differences between the groups were primarily assessed using MEG source analysis.

3.3.5 Structural Magnetic Resonance Imaging

High-resolution structural T1-weighted magnetic resonance images (MRIs) were acquired on a 3T Siemens Sonata or Allegra scanner (TR = 2530 ms, TE = 3.25 ms, flip angle = 7°, 128 sagittal slices, slice thickness = 1.3 mm, voxel size = 1.3 x 1.0 x 1.3 mm^3). A representation of the cortical surface was constructed from the individual structural MRIs with the Freesurfer software (Dale et al., 1999; Fischl, Sereno & Dale, 1999). Cortical white matter was segmented in the high-resolution MR images, and the estimated border between gray and white matter was tessellated, providing a triangular representation of the surface. The surface was also "inflated" to unfold cortical sulci, providing a convenient viewing of cortical activation patterns (Dale, Fischl, & Sereno, 1999; Fischl, Sereno, & Dale, 1999).

3.3.6 MEG source analysis

Cortical sources of the MEG signals were estimated using a distributed model, the Minimum Norm Estimate (MNE) (Hämäläinen & Ilmoniemi, 1994). The sources were assumed to lie on the cortical surface that was reconstructed from the structural MRI. To calculate the forward model which describes the signal pattern generated by a unit dipole at each allowed location on the surface, a single-compartment boundary element model (BEM) was used (Hämäläinen & Sarvas, 1989). For the BEM, the inner surface of the skull for each subject was determined from the T1-weighted MRI. To compensate for small head movements between runs, a forward solution was generated for each run, and the average was used in the analysis (Uutela, Taulu, & Hämäläinen, 2001). To compensate for the bias of MNE toward superficial sources, the inverse operator was constructed with depth weighting (Lin, Witzel et al., 2006). To avoid numerical instability a regularization parameter, $\lambda^2 = 0.33$ was used when computing the inverse operator (Hämäläinen & Ilmoniemi, 1994). Regularization reduces the sensitivity of MNE to noise and effectively results in a spatially smoothed solution. To allow flexibility of the model against small co-registration errors, the orientations of the dipole elements were not strictly constrained to be perpendicular to the cortical surface, and a "loose orientation constraint parameter" of 0.6 was used (Lin, Belliveau, Dale, & Hämäläinen, 2006). Using the MNE, the activation at each location on the cortical surface was estimated every 5 ms.

To examine differences in the pattern of brain activation between the two groups, noise-normalized MNE, called dynamic Statistical Parametric Map (dSPM) was also calculated (Dale et al., 2000). The dSPM converts the MNE into a statistical test variable that is essentially the signal-to-noise ratio (SNR) of the current estimate at each spatial location. Thus dSPM is useful for visualization of the data as it identifies locations where the MNE amplitudes are above the noise level. Average dSPM for the three deviant-standard subtraction conditions (*bat-pat, cat-pat, rat-pat*) was calculated in 50-ms time windows from 0 to 500 ms separately for the two groups.

We quantified the observed group differences in the dSPM by defining regions of interest (ROIs) (Wehner et al., in press). ROIs based on activated cortical regions in each hemisphere were manually drawn on the omnibus (all deviants combined) MNE solution averaged across all subjects. The locations of these ROIs on the individual subjects were determined using spherical morphing of the ROI cortical labels from one subject to another (Fischl et al., 1999). Two symmetrical 50-ms windows (65-115 ms, 190-240 ms) surrounding the peak latencies associated with the P1/N1 and N2 evoked brain responses were identified from the omnibus solution for the subtraction (i.e., *bat-pat, cat-pat, rat-pat*) conditions. Inclusion of an additional time window from 140-190 ms was warranted after observation of additional activation in the right hemisphere during this time range. Mean MNE values in these time bins were used for statistical comparisons between the two reading groups.

3.4 Results

3.4.1 Behavioral Data

The mean reaction times (RTs) and accuracy for the three deviant conditions are shown in Fig. 3.2 for the two groups of children. Only correct answers were used for the calculation of RTs. The RT and accuracy data were subjected to repeated-measures ANOVAs with condition as the within-subjects factor and group as the between-subjects factor. For accuracy, no main effects or a group x condition interaction were found (Fig. 3.2A). For the RTs, there was a main effect of condition, $F(2,28) = 42.6, p < 0.0001$, and a marginally significant effect of group, $F(1,28) = 3.1, p < 0.09$ (Fig. 3.2B). No group x condition interaction was observed. Post-hoc paired t-tests revealed that both groups had longer RTs for *bat* compared to *cat* and *rat* and also longer RTs for *cat* compared to *rat* (all p-values < 0.05). Since poor readers had slightly faster RTs compared to good readers, we wanted to determine if poor readers also had more false positive responses compared to good readers. To test this, we calculated d' values for each subject. A common metric in signal detection theory, d' is a measure relating percent correct responses to percent false positive responses. A false positive response was defined as pressing the button to the standard word, *pat*. No significant difference was observed in d' values between the two groups (mean d' - good readers: 2.46, poor readers: 2.45, 1-tailed t-test: $p > 0.1$).

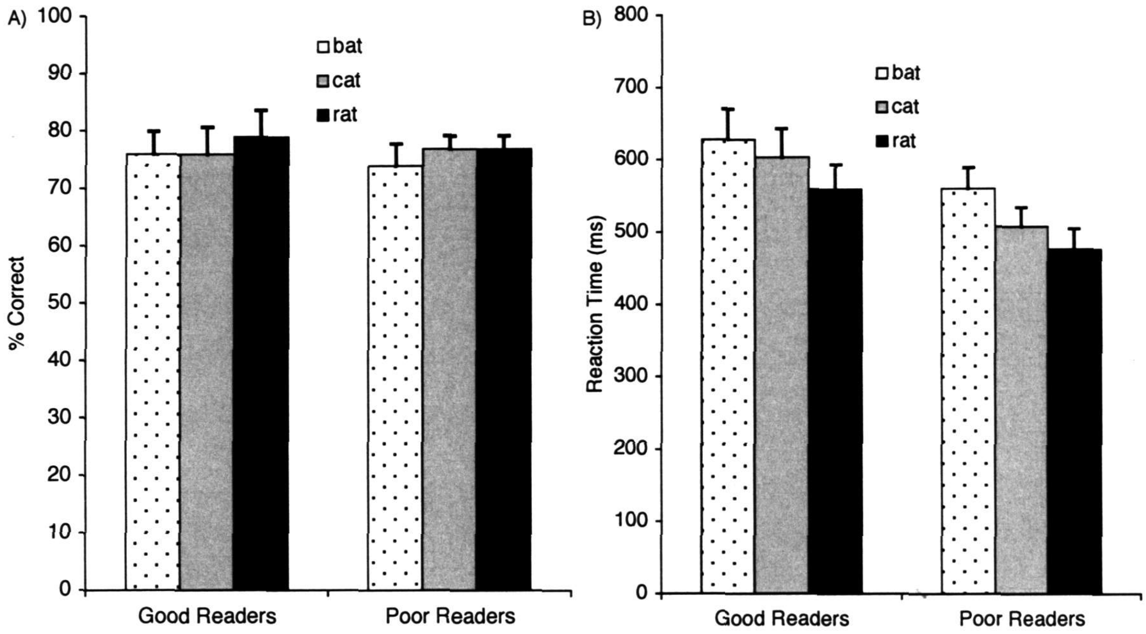

Figure 3.2: Behavioral results: mean accuracy (A) and reaction time (B) for the three deviant conditions for the two groups.

Differences in the number of missed deviants for the three deviant conditions were examined with *t*-tests for within (paired, 2-tailed), and between (unpaired, 1-tailed) group comparisons. One-tailed *t*-tests were used for between group comparisons, as we had the *a priori* hypothesis that poor readers would miss more deviants than good readers due to their impoverished phonological representations. Within group comparisons revealed that both groups missed more *bat* deviants compared to *rat* deviants (good readers: $p < 0.02$, poor readers: $p < 0.01$). No between-group comparisons were significant.

Correlations between standardized testing scores (PM, RN) and performance (RT and accuracy) on the oddball task were conducted to determine if children with poorer standardized scores also performed differently on the task. No correlations between standardized testing scores and task performance were significant. However, overall accuracy was correlated with overall RT for both groups (good readers: $r = 0.72$, $p < 0.01$, poor readers: $r = 0.81$, $p < 0.001$), indicating that children who responded quickly to the deviants also had lower accuracy on the task.

3.4.2 MEG data

Averaged MEG responses in two gradiometers for the three subtraction conditions for one child are shown in Fig 3.3A. Prominent responses can be seen in both hemispheres for all conditions at about 150-250 ms. This latency range coincides with the N2 response as seen in the grand-averaged EEG responses for a parietal midline electrode (Fig 3.3B).

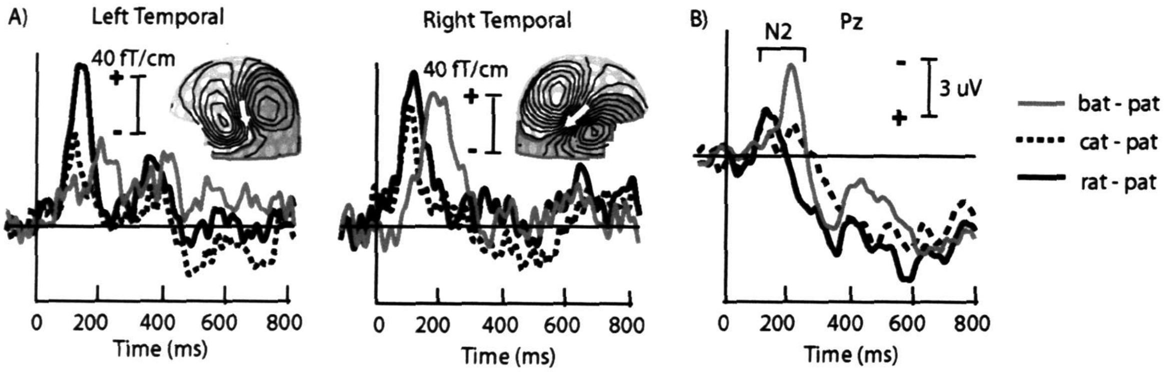

Figure 3.3: A) Event-related MEG waveforms for one child. Averaged responses for the three subtraction conditions are shown for one left temporal gradiometer and one right temporal gradiometer. Also shown are magnetic field patterns corresponding to the peak MEG responses between 150-300 ms for the *rat-pat* condition. The white arrows represent equivalent current dipoles indicating approximate locations of the underlying neural activity. B) Grand-average (n=30 subjects) EEG waveforms for the three subtraction conditions for the posterior midline Pz electrode. The time range associated with the N2 is indicated.

Differences in the spatiotemporal pattern of brain activation for the two groups were compared using consecutive averaged 50-ms time segments of the dSPM solution for the three subtraction contrasts (Fig. 3.4). Both groups showed activation in the superior temporal cortex typically beginning around 100-150 ms for all contrasts. However, some group differences were also observed. For poor readers, activation persisted throughout the recording epoch. In comparison, good readers showed a response for all conditions between 100-250 ms that diminished during the 250-350 ms time range, before the re-emergence of widespread activation after 400 ms. Brain activity after 400 ms may be partially attributed to reactivation of the auditory word form and the motor response associated with the button press to the deviants, as reaction times were on average 596 ms for the good readers and 514 ms for the poor readers. So as not to confound the later motor response-related activation with earlier activation related to the discrimination of the deviants, we have focused our source analysis on the earlier time range (before 400 ms).

In the phonologically similar *bat-pat* condition, good readers showed activation that began early in the left hemisphere (50-100 ms) and peaked bilaterally around 150-200 ms. In contrast, the poor readers showed bilateral activation that began later (150-200 ms) and was stronger in the right hemisphere. The right hemisphere activation peaked around 200-250 ms and was followed by left hemisphere activation that peaked between 250-300 ms. The other phonologically similar contrast (*cat-pat*) also showed bilateral activation that was stronger in the right hemisphere temporal cortex for the poor readers, whereas the good readers showed a weak bilateral response between 200-300 ms. As opposed to the different patterns of brain activation for the two groups to the phonologically similar contrasts, both groups showed an early (100-150 ms) bilateral response to the phonologically dissimilar (*rat-pat*) contrast. However, even for this seemingly easy contrast, the general pattern of persistent activation for the poor reader group versus a more transient then diminishing response for the good reader group was evident.

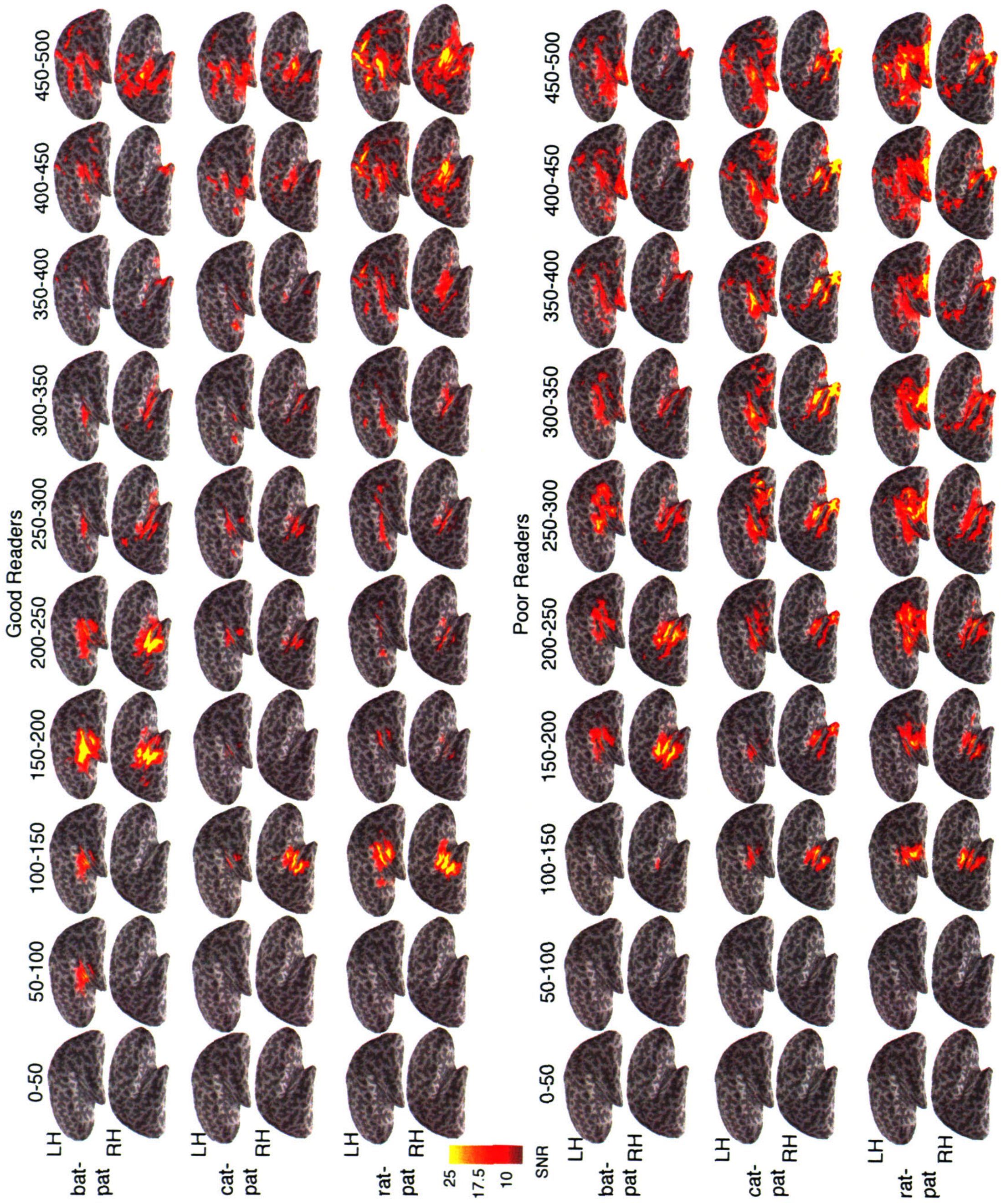

Figure 3.4: MEG source estimates. Dynamic statistical parametric maps (dSPM) averaged in sequential 50-ms time bins from 0-500 ms for the good reader group (top) and the poor reader group (bottom). The group-averaged dSPM for the three subtraction contrasts are shown on the reconstructed cortical surfaces of one child. The lateral surfaces have been inflated for better visualization of activation within the sulci (dark gray) as well as the gyri (light gray). Both left and right hemispheres are shown for all time points.

3.4.3 MEG ROI analysis

To quantify the observed differences between the two groups, brain activation was compared within three regions of interest (ROIs) for each hemisphere; superior temporal gyrus (STG), middle temporal gyrus (MTG) and inferior frontal gyrus (IFG), and three time windows (65-115 ms, 140-190 ms, and 190-240 ms) as determined from the MNE solution for the three deviant conditions (Fig. 3.5). The MNE time courses for the subtraction contrasts averaged across all subjects within a group for each ROI are shown in Fig. 3.6.

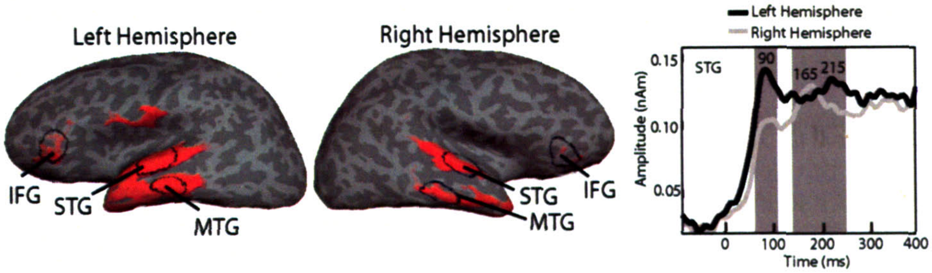

Figure 3.5: Regions of interest (ROIs) for the MEG analysis. Left: Minimum-norm estimates (MNE) for the combined deviant condition, averaged across all subjects (n=30) are displayed on inflated lateral views of the left and right hemisphere during the time range of interest (65-240 ms). The maps indicate locations where the maximum values of the MNE exceed the threshold value of 0.1 nAm. The group averaged-MNE data are shown on the reconstructed cortical surfaces of one child. The selected ROIs are outlined: superior temporal gyrus (STG), middle temporal gyrus (MTG), and inferior frontal gyrus (IFG). Right: MNE waveforms for left and right STG ROIs for the combined deviant condition. The latencies of the peaks (90 ms, 165 ms, 215 ms) are shown. Shading indicates the time windows of analysis (65-115 ms, 140-190 ms, 190-240 ms).

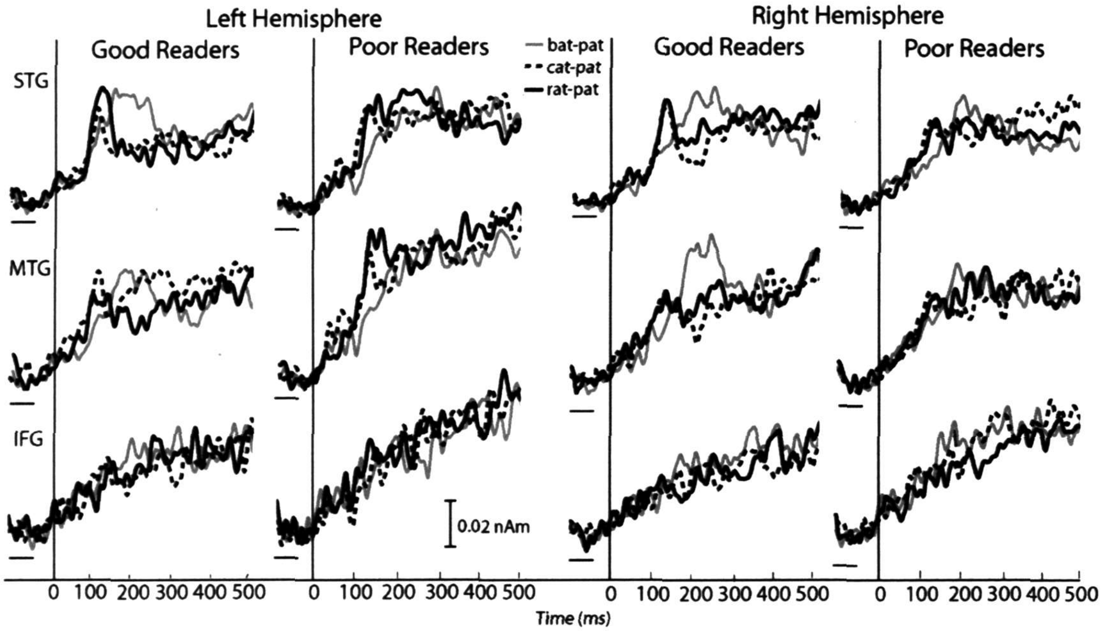

Figure 3.6: MEG source waveforms. The estimated source strength as a function of time, as obtained from minimum norm estimates (MNE), averaged across all subjects in the good and poor reader groups are shown for all ROIs: superior temporal gyrus (STG), middle temporal gyrus (MTG), and inferior frontal gyrus (IFG). The zero level for each curve is indicated by a horizontal line in the prestimulus period. The vertical lines indicate the onset of the stimulus.

To examine whether the amplitude or latency of the peak MEG response in the early (65-115 ms) time range differed between the two groups, repeated measures ANOVAs were conducted for the STG ROIs, with condition (*pat, bat, cat, rat*) as the repeated within subjects factor and group as the between subjects factor. The dependent measure was either the peak MNE value or the latency of the peak MNE value within the 65-115 ms time window. No main effects of group or group x condition interactions for the peak MNE value or peak latency were observed, suggesting that the groups did not process the acoustic properties of the stimuli differently. However, the peak MNE value in the left and right STG was significantly larger for the *bat* condition relative to the other conditions irrespective of reading group, evidenced as a main effect of condition (left: $F(3,84) = 7.2$, $p < 0.001$, right: $F(3,84) = 7.3$, $p < 0.001$).

To examine differences between the groups in the later time range, repeated-measures ANOVAs were conducted for each ROI and the two time bins (140-190 ms, 190-240 ms), with condition (*bat-pat, cat-pat, rat-pat*) as the within subjects factor and group as the between subjects factor. As activation during the later time bins did not show clear peaks, we used the mean rather than the peak MNE value within each ROI and time bin as the dependent measure in the ANOVAs. Two significant effects were observed in the left hemisphere STG (Fig. 3.7). First, a group x condition interaction, $F(2,56) = 5.2, p < 0.01$, was found during the 140-190 ms time range. Post-hoc *t*-tests ($p < 0.05$) revealed that good readers compared to poor readers showed more activation for the *bat-pat* contrast, whereas poor readers showed more activation than good readers for the *rat-pat* contrast. Good readers also showed more activation for *bat-pat* than to *cat-pat* and *rat-pat* during this time range, whereas the poor readers showed no differences between the conditions (Fig. 3.8). Second, a main effect of group, $F(1,28) = 5.7, p < 0.03$, and a group x condition interaction, $F(2,56) = 4.1, p < 0.03$, were observed within the 190-240 ms time range. Post-hoc *t*-tests ($p < 0.05$) revealed that poor readers showed more activation than good readers in this ROI and time bin, and had greater activation for the *rat-pat* contrast. No other significant differences were found for the left hemisphere ROIs.

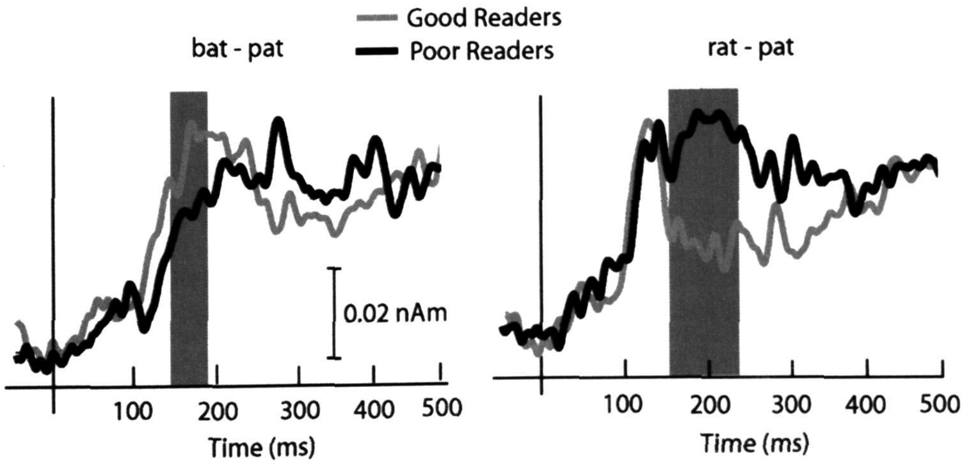

Figure 3.7: Group MNE activation in the left STG ROI for the *bat-pat* contrast (left) and the *rat-pat* contrast (right). The shading indicates the time windows that showed significant differences between the good readers (gray lines) and the poor readers (black lines).

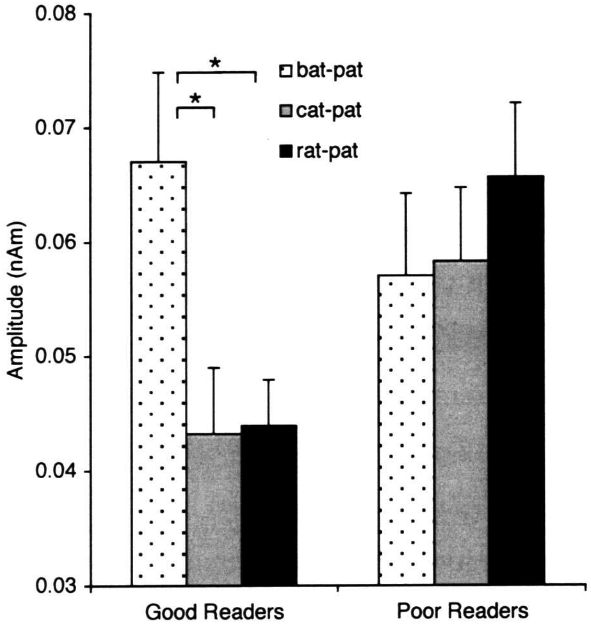

Figure 3.8: Group MNE activation in the left STG ROI (140-190 ms) for the three subtraction conditions. * $p < 0.05$.

Analysis of the right hemisphere ROIs revealed a main effect of condition for all three ROIs and both time bins except the right IFG during the 190-240 ms time bin. Post-hoc *t*-tests ($p < 0.05$) revealed that all main effects of condition could be explained as more activation for the *bat-pat* contrast relative to the other contrasts. No main effects of group or group x condition interactions were observed in any of the right hemisphere ROIs.

3.4.4 Brain-behavior relationships

To examine the relationship between standardized testing measures (PM, RN) and mean MNE activation within ROIs and time bins, Pearson product-moment correlations were calculated for all subjects combined, and for each group separately. To control for the potential increase in Type 1 errors arising from multiple comparisons (6 ROIs, 3 time bins), significant correlations were those with a corrected p-value $< 0.05/18 = 0.0028$. No across group or within group correlations between standardized testing measures and mean MNE activation were significant.

We also calculated correlations between behavioral performance (RT, accuracy) for each deviant and the mean MNE activation associated with discriminating each deviant (e.g., *bat-pat* for *bat* RT) within all ROIs and time bins. Two significant correlations were observed. First, for all subjects combined, accuracy on the *bat* condition negatively correlated ($r = -0.54, p < 0.002$) with mean MNE activation for the *bat-pat* contrast in right IFG for the 190-240 ms time range. Therefore, children who were less accurate at detecting phonologically similar stimuli showed more right hemisphere IFG activation during this time range. Second, a negative correlation was observed for the good readers between accuracy on the *bat* condition and mean MNE activation for the *bat-pat* contrast in left IFG during the 140-190 ms time range ($r = -0.77, p < 0.001$), and the right IFG during the 190-240 ms time range ($r = -0.78, p < 0.001$). A negative correlation ($r = -0.71, p < 0.01$) was also observed for the good readers between accuracy to *rat* and mean MNE activation for *rat-pat* within right IFG during the 140-190 ms time range. As such, it appears that lower accuracy on the task is generally associated with an increase in inferior frontal (particularly right IFG) activation. No within group correlations for the poor readers were significant. Additionally, no correlations between RT and MNE activation were significant.

3.5 Discussion

Differences in the discrimination of spoken words that varied in the degree of phonological contrast were examined in good and poor readers using an attended oddball task. Both groups had greater difficulty detecting the phonologically similar deviants compared to the phonologically dissimilar deviants, evidenced by longer reaction times, and a larger number of missed deviants for the phonologically similar items. Despite the similar behavioral performance, MEG source analysis revealed different patterns of brain activation for the two groups as a function of phonological contrast. Compared to the good readers, poor readers' delayed and reduced left-hemisphere activation to the most demanding phonological contrast (*bat-pat*), and the overall sustained bilateral activation may reflect their greater difficulty with phonological processing. Below we first discuss patterns of behavioral performance and brain activation that were similar in both groups, and then elaborate on the observed group differences.

3.5.1 Effects of varying degree of phonological contrast

Both good and poor readers took longer to respond to the phonologically similar deviants relative to the phonologically dissimilar deviant, indicating that phonological contrasts involving one feature were indeed harder to discriminate than those involving three features. Additionally, both groups had more difficulty discriminating a voicing contrast (*bat* vs. *pat*) than a place of articulation contrast (*cat* vs. *pat*), suggestive of disproportionate weightings of different acoustic cues by children (Nittrouer, 1992; Nittrouer & Studdert-Kennedy, 1987).

The good and poor readers also showed similar patterns of brain activation within the STG. In the early time range (65-115 ms), both groups showed larger peak MNE amplitudes to *bat* than to the other deviants, possibly due to the large difference in acoustic energy between the initial phoneme of this deviant (viz., /b/) and that of the standard (viz., /p/) (Fig. 1). Importantly, no group differences in peak MNE amplitude or latency were observed in this early time range, suggesting that both groups processed the acoustic properties of the stimuli similarly. In the later time ranges, good readers showed a more sustained response to the phonologically similar *bat-pat* condition relative to the phonologically dissimilar *rat-pat* condition. A similar sustained response was observed for the poor readers for all conditions, regardless of the contrast. That good and poor readers showed sustained activation during the *bat* condition may reflect both groups' struggle with this phonologically demanding discrimination. Furthermore, decreased accuracy on *bat* was associated with increased inferior frontal activation in the right hemisphere (all children) or bilaterally (good readers). Inferior frontal regions are known to be involved in phonological processing (Gold & Buckner, 2002; Poldrack et al., 1999). Processing of a phonologically demanding contrast (viz., *bat-pat*), thus appears to have drawn more on these areas (Pugh et al., 2001).

3.5.2 Differences between good and poor readers

Despite similar behavioral performance, good and poor readers showed different patterns of brain activation in the time range associated with phonological processing. Compared to good readers, the poor readers showed greater activation in the phonological dissimilar (and more contrastive) *rat-pat* condition but reduced activation in the phonologically similar (and less contrastive) *bat-pat* condition in left STG, an area implicated in phonological processing (Binder et al., 2000; Helenius, Salmelin, Richardson et al., 2002; Okada & Hickok, 2006; Poldrack et al., 2001). These results may reflect a difference in the processing of these conditions by the two groups as a function of their phonological abilities. More specifically, despite both good and poor readers taking longer to respond to *bat* than to *rat*, good readers showed a significant difference in brain activity between these two conditions, whereas poor readers did not. This suggests that good readers were able to take advantage of their superior coding abilities to respond differently to the phonologically similar vs. dissimilar stimulus pairs. Poor readers, in contrast, did not show this difference, perhaps due to their reduced sensitivity to the phonological characteristics of the stimuli (Brady et al., 1983; Liberman et al., 1977). It is worth noting that poor readers showed greater activation than good readers on the phonologically easier (i.e., more contrastive) *rat-pat* condition, which points to their use of phonological processing strategies as in normal readers; however, poor readers' weaker activation under demanding conditions, compared to good readers, suggests a deficiency in their phonological abilities. When discrimination was difficult, the poor readers in our study also showed a bilateral response that was initially larger on the right then peaked later on the left. This sequence of right hemisphere activation followed by activation in the left hemisphere is in line with previous findings in the literature on reading disability (Breier et al., 2003). We found no activation differences between the groups in the *cat-pat* condition, despite it having a one-feature contrast as in the *bat-pat* condition, suggesting that further investigation is needed. That both groups had more difficulty with the *bat-pat* contrast than the *cat-pat* contrast may partially explain these findings. In summary, the aberrant brain activation patterns observed in the poor readers appear to be consistent with a phonological account of reading disability.

The absence of group differences in reaction times or accuracy may be explained in terms of the degree to which the task stressed the phonological processing system. Although subjects had to attend to the stimuli to detect the deviant targets, they did not have to actively identify or label them. Previous research has shown that poor readers have difficulties with such labeling processes (e.g., Breier et al., 2001; Godfrey et al., 1981; Mody, 2003; Swan & Goswami, 1997). Given the subtle nature of the speech perception deficit in poor readers, perhaps a task that required active phonological coding of the stimuli would have shown more robust group differences.

3.6 Conclusion

Both good and poor readers had more difficulty discriminating phonologically similar than phonologically dissimilar spoken words. Whereas the two groups were able to detect the deviants, evident in their similar behavioral performance on the task, the pattern of brain activation was different for the good and poor readers under varying degrees of phonological contrast. Delayed and reduced left hemisphere activation for the poor readers compared to the good readers in the most demanding phonological contrast may reflect their greater difficulty with phonological processing. As such the results are consistent with a phonological core deficit in reading disability.

Appendix 3.A: Stimulus Characteristics

The duration of all stimuli was kept constant at 420 ms. The naturally recorded utterance /at/ that was common to all stimuli had the following characteristics: duration of vowel /a/ = 220 ms, mean formant values, F0: 105 Hz, F1: 785 Hz, F2: 1580 Hz, F3: 2650 Hz; duration of /t/ = 85 ms. The natural utterance /p/ had the following characteristics: voice onset time (VOT) = 55 ms, F1 transition 742-757 Hz, F2 transition 1555-1597 Hz, F3 transition 2572-2705 Hz. All synthesized formant transitions were approximately linear, and were based on the extracted formant contours for the natural utterances. For /b/, VOT: 10 ms, F1 transition 536-757 Hz, F2 transition: 1495-1597 Hz, F3 transition: 2440-2705 Hz. For /k/, VOT = 80 ms, F1 transition: 458-757 Hz, F2 transition: 1199-1597 Hz, F3 transition: 2431-2705 Hz. For /r/, VOT = 0 ms, F1 transition: 451-757 Hz, F2 transition: 1052-1597 Hz, F3 transition: 1500-2000 Hz.

Appendix 3.B: EEG results

Analysis of the EEG data was not included in the submitted paper, as our focus was on the MEG source analysis. We report and discuss the EEG results here for completeness.

3.B.1 EEG analysis method

Grand-averaged EEG waveforms for the two groups were constructed by averaging responses at each electrode location for all subjects (Fig. 3.B.1). All electrodes were referenced to an electrode placed on the nose. One subject in the good reader group was excluded due to poor quality of the EEG data. Individual electrodes with poor data quality were identified from the EEG responses for each subject, and were excluded from the grand average. Excluded electrodes were rare and accounted for only 2.5% of the data. For consistency with the MEG analysis, we used the same time windows (65-115 ms, 140-190 ms, 190-240 ms) for comparisons between the conditions and groups. The frontal (Fz) and parietal (Pz) midline electrodes were selected for statistical comparisons, based on the previous literature showing the largest EEG responses at these locations. For the early time range (65-115 ms), we determined the maximum value for each condition *(bat, cat, rat, pat)* and subject. For the later time ranges (140-190 ms, 190-240 ms), we calculated the mean value in the time window for each condition (*bat, cat, rat, pat*) and subject. These values were subjected to repeated-measures ANOVAs with condition as the repeated factor and group as the between subjects factor.

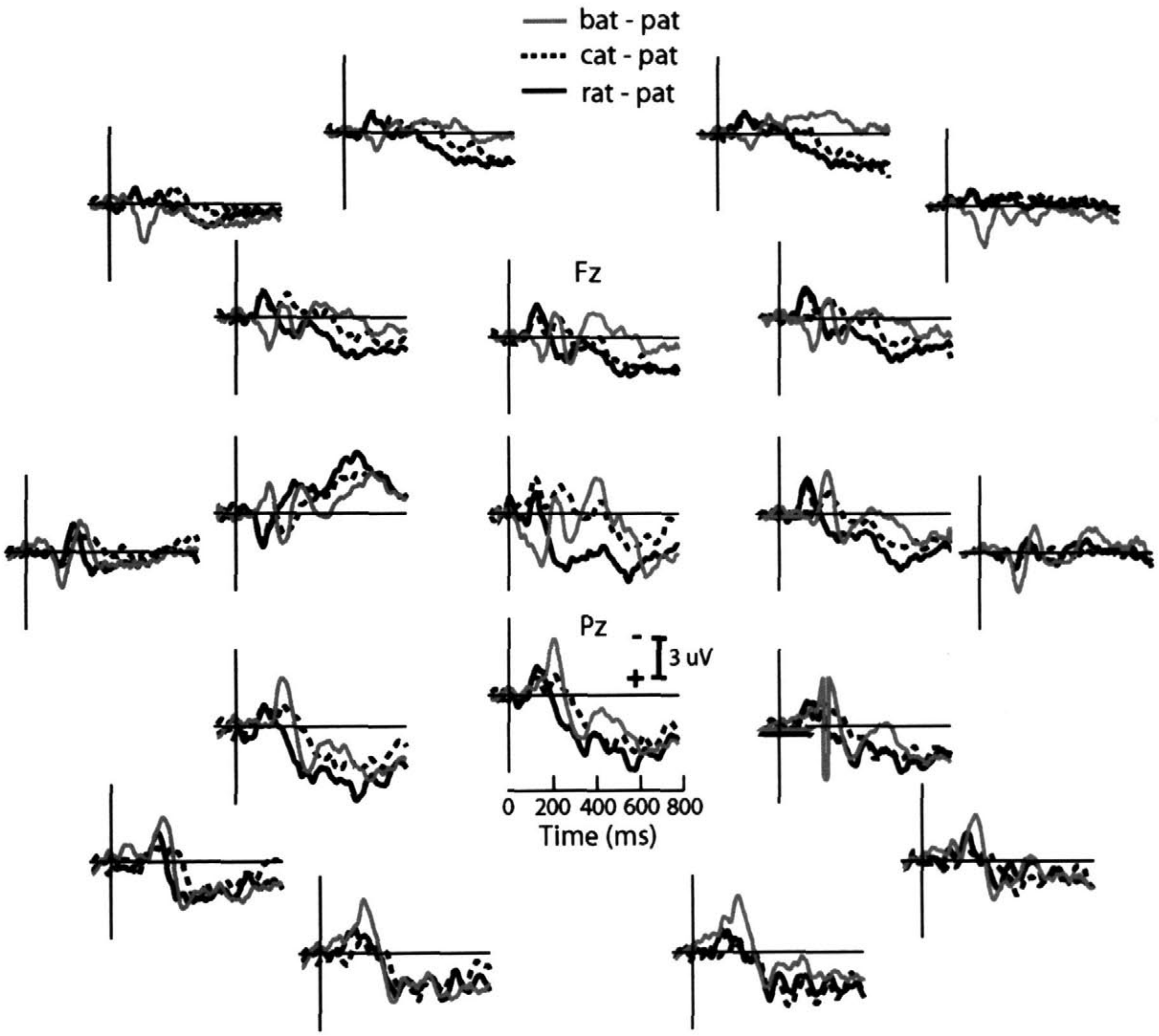

Figure 3.B.1: Grand-average EEG waveforms for the three subtraction conditions for all electrodes. Statistical comparisons between conditions and groups were performed on a frontal midline electrode (Fz) and a parietal midline electrode (Pz).

3.B.2 EEG results

No main effects or group x condition interactions were significant for either the Fz or Pz electrode in the early time range (65-115 ms). For the later time ranges, no main effects of group or group x condition interactions were significant. However, for Fz, there was a main effect of condition between 140-190 ms, $F(3,81) = 3.955$, $p < 0.03$. Post-hoc *t*-tests revealed that the response to rat was significantly smaller, i.e., less positive, than to bat ($p < 0.02$) and pat ($p < 0.03$). For Pz, there was a main effect of condition between 190-240 ms, $F(3.81) = 9.947$, $p < 0.0001$. Post-hoc *t*-tests revealed that the response to bat was larger, i.e., more negative, than to cat ($p < 0.03$), rat ($p < 0.0001$), and pat ($p < 0.001$), and the response to cat was larger than to rat ($p < 0.04$). These results are summarized in Fig. 3.B.2.

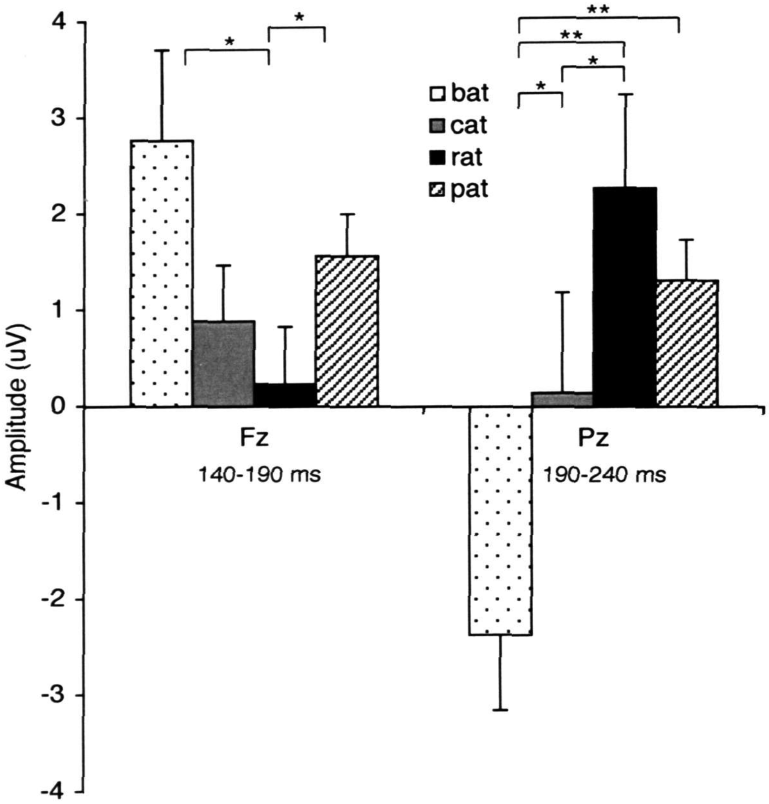

Figure 3.B.2: Mean EEG response for the three deviant conditions (*bat, cat, rat*) and the repeated standard condition (*pat*), for a frontal midline electrode between 140-190 ms, and a parietal midline electrode between 190-240 ms. Significant differences between the conditions are indicated. * $p < 0.05$, ** $p < 0.01$

3.B.3 Discussion

Both groups showed large responses in the time range of the N2 to all deviant stimuli. This response had a posterior distribution and was maximal at the posterior midline electrode Pz. Similar to the MEG data, it was found that the largest responses were to the *bat* condition relative to the *rat* condition for both anterior and posterior scalp locations, despite *bat-pat* being the most difficult phonological contrast. However, in contrast to the MEG data, we did not observe any group differences within any of the three time ranges. As such, EEG appears to be less sensitive than MEG at detecting the subtle differences in brain activation related to the phonological manipulation in this task. This may be related to the fewer number of EEG channels (19 electrodes) than MEG channels (306 channels) used in this study, or the fact that EEG and MEG provide different information about the underlying brain currents (for a discussion, see Appendix A).

Chapter 4: Context effects on auditory word perception

Effects of phonological contrast on auditory sentence comprehension in children with and without reading impairments: A magnetoencephalography study

Submitted to Brain Research

4.1 Abstract

Difficulties in reading may be traced to a phonological core deficit that appears to have its origin in poor speech perception abilities (Mody, 2003). In spite of this, many children with reading impairments have normal spoken language and adequate reading comprehension, suggesting that they may use contextual cues to compensate for their impaired phonological processing abilities. We investigated auditory word perception under varying degrees of phonological contrast with and without sentence context to better understand the phonological basis in reading disability. Good and poor readers, 7-13 years of age, were tested on an auditory word pair discrimination task, and an auditory sentence plausibility task. Additionally, whole-head magnetoencephalography (MEG) was recorded in the sentence task. Good and poor readers showed higher accuracy in the phonologically dissimilar than the phonologically similar condition in both tasks. The MEG source analysis of the sentence data revealed group differences as a function of phonological contrast. Poor readers showed reduced brain activation when phonological contrast was small (viz. phonologically similar condition) than when it was large (viz. phonologically dissimilar condition) in the left superior temporal gyrus between 200-300 ms; good readers did not show a difference. This difference in activation between the groups suggests that poor readers' difficulties with phonological processing may have led to a greater reliance on sentence context and consequent processing of the phonologically similar stimuli more like the congruent stimuli. These results are consistent with a phonological core deficit account of reading disability.

4.2 Introduction

Approximately 5-20% of children struggle with reading despite adequate intelligence, motivation, and schooling considered necessary for accurate and fluent reading (Shaywitz, 1998). While the underlying cause of dyslexia is still debated, one prominent hypothesis implicates a deficit in phonological processing, such that direct access to, and manipulation of phonemic language units retrieved from long-term memory is impaired (e.g., Goswami, 2003). Individuals with dyslexia have problems on tasks of phonological awareness, nonword repetition, rapid naming, and verbal memory, among others. These problems are believed to arise directly or indirectly from a deficit in speech perception rooted in poorly encoded phonological representations lacking in phonetic detail (Brady et al., 1983; Mody, 2003). However, in spite of this phonological core deficit, many children with reading disabilities appear to develop relatively normal spoken language abilities and adequate reading comprehension skills by adolescence or early adulthood (Frith & Snowling, 1983; Nation & Snowling, 1998; Shaywitz et al., 1999).

In a large study of beginning readers, Shankweiler and colleagues (Shankweiler et al., 1999) found that differences in reading comprehension are strongly correlated with skills such as phonological decoding that enable a child to recognize individual words, although other oral language factors such as listening comprehension, vocabulary, and semantic skills may be important as well (Muter, Hulme, Snowling, & Stevenson, 2004; Nation & Snowling, 2004). For many impaired readers, reading comprehension may be achieved through a reliance on sight word knowledge and/or sentence context cues to compensate for poor phonological decoding skills. Consequently, studies investigating reading disabilities have focused on reading words in isolation to avoid the effects of sentence context, so as to better understand printed word identification deficits that appear to be a hallmark of dyslexia.

Studies investigating higher-level cognitive influences on word recognition suggest that poor readers may take advantage of context provided by other words (West & Stanovich, 1978) or sentences (Chiappe et al., 2004; Perfetti et al., 1979; Stanovich & West, 1981) to facilitate word recognition. In fact, poor readers' use of top-down influences in auditory and visual word recognition may be expected, given their poorly encoded phonological representations (Brady et al., 1987; Godfrey et al., 1981; Mody et al., 1997; Yap & van der Leij, 1993). In the present study, we investigated auditory word perception under varying degrees of phonological contrast with and without sentence context in normal and impaired readers to better understand the phonological basis in reading disability. We examined speech perception abilities by comparing the behavioral and neurophysiological responses to phonetically-manipulated words presented with and without sentence context in good and poor readers.

Poor readers' deficits are particularly evident when phonological demands of a task are high as in nonword (Stone & Brady, 1995). One may also use a task that makes multiple demands on phonological processing abilities. In the present study, in Experiment 1, participants compared consecutive auditory word pairs where the initial pair was made to vary in the degree of phonological contrast. Success on this task required the participants to accurately encode, store, retrieve, and compare phonological forms across the consecutive stimulus pairs, thereby stressing phonological processing abilities know to be disrupted in poor readers (Brady et al., 1983; Godfrey et al., 1981). We expected poor readers to have greater difficulty with the task, particularly when the degree of phonological contrast between the words was small.

The majority of studies investigating the contribution of semantic context to word identification in good and poor readers have been conducted using visual stimuli. Early proponents of top-down models of word recognition suggest that skilled readers, but not poor readers, take advantage of contextual information, thereby making for faster visual word recognition (e.g., Goodman, 1976; Smith, 1971). However, later studies measuring reaction times to words read in isolation versus embedded in sentences, have suggested that children who are poor readers use contextual information to aid in word recognition more than children who are good readers (Perfetti et al., 1979; Perfetti & Roth, 1981; Stanovich, 1980; Stanovich & West, 1981). Skilled readers are quick to identify words; thereby semantic context effects have less time to influence word recognition. In contrast, poor readers' impaired phonological skills may cause them to be slower at word recognition, allowing context to aid in the process (Perfetti, 1995). This is not to say that skilled readers do not use context. Whereas poor readers may use context to supplement their poor phonological decoding skills, normal readers may use context, for example, to help disambiguate between competing meanings of homographic words (e.g., bank).

As mentioned earlier, top-down strategies may also be used in auditory comprehension. However, the relationship between bottom-up phonological and top-down semantic processing to facilitate speech perception in good and poor readers remains poorly understood. We used magnetoencephalography (MEG), which, like electroencephalography (EEG), has the millisecond time resolution to detect neural processes related to the effects of sentence context on phonological processing in speech perception.

Several EEG and MEG studies have investigated the effect of word or sentence context on speech perception in children and adults (Coch, Maron et al., 2002; Connolly & Phillips, 1994; Connolly et al., 1992; Diaz & Swaab, 2006; Friederici, Gunter, Hahne, & Mauth, 2004; Hagoort & Brown, 2000; Halgren et al., 2002; Helenius et al., 1998; Perrin & Garcia-Larrea, 2003; Praamstra, Meyer, & Levelt, 1994; Radeau, Besson, Fonteneau, & Castro, 1998; van den Brink et al., 2001; van den Brink & Hagoort, 2004; Van Petten, Coulson, Rubin, Plante, & Parks, 1999). These studies suggest that context has a rapid effect on spoken word processing, which is evident in two evoked response components related to phonological and semantic processing; the phonological mismatch negativity (PMN) and the N400, respectively.

The PMN is generally observed between 200-350 ms post-stimulus in auditory tasks that engage phonological processing, and is thought to reflect integration of phonological expectations with incoming acoustic information (Connolly & Phillips, 1994; Connolly et al., 1992; Phillips et al., 2006). The PMN is typically elicited when there is a phonological mismatch between a word that is anticipated from context and the word that is heard. Additionally, the degree of mismatch between the anticipated and the heard input does not appear to modulate the amplitude or latency of the PMN, suggesting that the PMN reflects an "all-or-none" process (Newman et al., 2003). Yet others have suggested that the PMN may represent early lexical and semantic influences on word recognition (Diaz & Swaab, 2006; Hagoort & Brown, 2000; van den Brink et al., 2001).

In contrast to the phonological processing related explanations for the PMN, the N400 is thought to index semantic expectancy or ease of lexical integration and is elicited by all word-like stimuli (Halgren et al., 2002; Helenius, Salmelin, Service et al., 2002; Holcomb, 1993; Kutas & Hillyard, 1980; Kutas et al., 1987). The amplitude of the N400 elicited by reading the terminal word of a contextually-constrained sentence is known to be modulated by the word's semantic expectancy (Kutas & Hillyard, 1980). In children, the amplitude and latency of the N400 has been found to decrease over the course of normal reading development as lower-level processes such as phonological decoding become more automatic (Coch & Holcomb, 2003; Hahne et al., 2004; Holcomb et al., 1992). Studies using auditory stimuli with children have shown a widespread scalp distribution related to the generation of the N400 (Holcomb et al., 1985; Juottonen et al., 1996), which is maximal at anterior locations (Coch & Holcomb, 2003; Holcomb et al., 1992) and contrasts with the centro-parietal distribution typically observed in adults and for visual tasks (Kutas & Hillyard, 1980).

MEG studies have localized sources contributing to the N400 in left hemisphere anterior temporal regions (Halgren et al., 2002; Marinkovic et al., 2003), superior temporal regions near the auditory cortex (Helenius et al., 1998; Makela et al., 2001; Simos et al., 1997). Sources contributing to the PMN have been localized in the left anterior superior temporal (Kujala et al., 2004) and/or left inferior frontal cortices (Connolly et al., 2001; D'Arcy et al., 2004) in normal adults. These studies have shown that sources contributing to the PMN are both temporally and spatially separate from later N400-like responses in the posterior superior temporal cortex. To our knowledge, there have been no previous reports of PMN effects in children, although some studies have reported a childhood N250 with a fronto-central distribution (Ceponiene et al., 2002). The N250 may represent activation related to phonological processing as it occurs in the same time range as the PMN. A recent MEG study with children has localized sources contributing to the N250m in the superior temporal plane (Takeshita et al., 2002).

Differences in the N400 between good and poor readers appear to depend on the task and stimuli used. Paradigms that emphasize explicit phonological processing have shown decreases in the N400 effect for poor readers compared to good readers (e.g., McPherson et al., 1998), whereas paradigms that do not emphasize phonological processing frequently show little or no differences between the two groups (Bonte & Blomert, 2004; Sabisch et al., 2006). In Experiment 2, we used a sentence plausibility task in which the phonological contrast between the congruent and the incongruent words was manipulated. Since the phonological manipulation was implicit, we expected no differences between the groups in the N400 time range. However, we predicted that good and poor readers would show differences in brain activation, as measured by MEG, in the time range associated with phonological processing (200-300 ms) under the different conditions of phonological contrast. Poor readers are likely to be deceived by semantically incongruent but phonologically similar words and treat them as congruent stimuli, which may result lower accuracy in this condition and reduced activation in this time range. In contrast, we predicted that good readers would be less affected by context with no difference in their responses to semantically incongruent words as a function of phonological contrast.

In summary, Experiment 1 was designed to provide an index of phonological processing abilities, whereas the results of Experiment 2 allowed us to examine the differential effects of sentence context on the perception of phonological contrasts to better understand the phonological basis in reading disability.

4.3 Materials and Methods

Subjects: See section 2.6

4.3.1 Experiment 1: Auditory discrimination task

4.3.1.1 Stimuli:

Word pairs were constructed so the two words in a pair were either phonologically similar (e.g., *ball-doll*), or phonologically dissimilar (e.g., *ball-hall*). The first phoneme of phonologically similar word pairs differed in one of the phonetic features; voicing or place of articulation, whereas the first phoneme of phonologically dissimilar word pairs differed in two or more of the features; voicing, place of articulation, and manner of articulation. The first word of a pair was heard twice: once with a phonologically similar word, and once with a phonologically dissimilar word, yielding a total of 100 phonologically similar and 100 phonologically dissimilar word pairs. The order of the stimuli was identical for all subjects and was pseudorandomized such that the same words were not heard within 20 trials of each other.

All words were of high frequency (Francis & Kucera, 1982) and familiar to children reading at a first or second grade level. The stimuli were recorded by a phonetically-trained native male speaker with neutral intonation in a sound treated room using a unidirectional microphone attached to a PC running the program WaveSurfer (Sjolander & Beskow, 2000) with a 22 kHz sampling rate. The output sound level for all words was normalized using speech-editing software. Words in the phonologically similar and phonologically dissimilar conditions were matched for word frequency (median: 23.5 occurrences/million), word length (median: 4 letters), and number of syllables (median: 1 syllable).

4.3.1.2 Experimental Procedure

Subjects heard two consecutive pairs of words played at a comfortable listening level. The first pair of words (e.g., *ball-doll*) was either identical (e.g., *ball-doll*) or not identical (e.g., *doll-ball, ball-ball, doll-doll*) to the second pair of words. The words in the first pair were always different, and were either *phonologically similar* or *phonologically dissimilar* to each other. To discourage subjects from listening to just the first or last word in a pair, trials requiring a 'different' answer were constructed in two ways: same words in both pairs, but order reversed (e.g., *ball-doll* then *doll-ball*) or word in second pair repeated (e.g., *ball-doll* then *ball-ball* or *doll-doll*). An equal proportion of 'reversed' and 'repeated' trials were used. The interstimulus interval (ISI) between the words in a pair was 50 ms, whereas the ISI between the two pairs in each trial was 800 ms. Consecutive trials were separated by 1000 ms of silence.

Subjects were required to press a button to make a 'same' vs. 'different' judgment. They were instructed to press one button if the word pairs matched exactly, and to press another button if the two pairs did not match exactly. Subjects were instructed to respond as quickly and accurately as possible using the index and middle finger of their dominant hand. Accuracy and mean reaction times (RTs), measured from the offset of the second word in the second word pair, for each condition were calculated for each subject. Accuracy and RT measures were also calculated separately for phonologically similar and phonologically dissimilar 'different' trials containing reversed vs. repeated stimuli to determine if subjects had more difficulty with ordering in memory or discrimination. Response times less than 200 ms or longer than 3000 ms were counted as errors. Only 6% of the data was rejected using these cutoff criteria. Breaks every 10 trials helped prevent subject fatigue. Before beginning the main part of the experiment, subjects were provided with 10 practice trials to ensure complete understanding of the task instructions. The total time for the experiment was about 15 minutes. To further examine the effect of working memory on task performance, we correlated accuracy and RT measures with the standardized measure of phonological working memory (nonword repetition and memory for digits).

4.3.2 Experiment 2: Auditory sentence task

4.3.2.1 Stimuli

Four hundred spoken sentences were constructed, consisting of a sentence stem and a critical word. Sentence stems, ranging from 5-10 words, were recorded with neutral intonation and a normal speech rate with the same parameters used for the recording of the words for Experiment 1. Most sentence stems were heard three times. The exception was 100 filler sentence stems that were added to balance the number of 'yes' and 'no' responses, which were heard only once. The 200 words from Experiment 1 were used as the critical words. When heard together, a sentence stem followed by the critical terminal word resulted in either a semantically appropriate sentence (e.g., "The boy rolled the *ball*"), or a semantically incongruent one (e.g., "The boy rolled the *hall*"). Each critical word was heard two times: once in a semantically congruent context, and once in a semantically incongruent context. Additionally, the critical words for the semantically incongruent trials were either phonologically similar to a congruent word, differing by one phonetic feature: voicing or place of articulation (e.g., "The boy rolled the *doll*": congruent word *ball*), or phonologically dissimilar to a congruent word, differing by two or three phonetic features: voicing, place of articulation, manner of articulation (e.g., "The boy rolled the *hall*": congruent word *ball*). Ten adults used a five-point scale to assess semantic plausibility of sentences in the incongruent conditions to ensure that there was no difference in semantic plausibility between test items in the phonologically similar and phonologically dissimilar incongruent conditions.

4.3.2.2 Experimental Procedure

During the experiment, subjects listened to sentences at a comfortable listening level, and they had to decide if a sentence made sense or not by pressing one of two buttons on a response pad. Immediately upon completion of the sentence, subjects saw a question mark appear on a screen, as a cue to make a response. Subjects were instructed to respond as quickly and accurately as possible. Accuracy and RT measures for each condition were calculated for each subject. RTs were measured from the onset of the question mark. Only correct responses were included in the reaction time measure. Response times less than 200 ms or longer than 3000 ms were counted as errors; these accounted for 8% of the data. The average presentation time for each sentence was 3500 ms. To reduce eye movements during recording, a fixation cross was visually presented on a screen, with subject instructions to look at the cross while listening to the sentences. The order of the sentences was identical for all subjects and was pseudorandomized such that at least twenty trials occurred between consecutive presentations of identical sentence stems. There were a total of eight runs per subject (50 sentences per run), with two-minute breaks between runs during which the subjects could rest. The total recording time for all runs was approximately 30 minutes. Pearson product-moment correlation coefficients were calculated for comparisons of standardized testing measures and accuracy and RT measures to determine if performance on the tests predicted performance on the sentence task.

4.3.2.3 MEG recording

Simultaneous MEG and EEG were recorded using a 306-channel (204 first-order planar gradiometers, 102 magnetometers) VectorView MEG system (Elekta-Neuromag Ltd., Helsinki, Finland), with 19 electrodes of EEG in a cap arranged approximately according to the 10-20 system. The impedances of all EEG electrodes were kept below 5 kΩ. For the source analysis, only the MEG signals were used given the optimization of our analysis tools for this purpose. Horizontal and vertical EOG electrodes were used for detection and subsequent rejection of large eye movements and eye blinks, which cause artifacts in the MEG data. The locations of the electrodes were digitized with a Fastrak digitization device (Polhemus, Colchester, VT). Landmark anatomical features (nasion and preauricular points), along with additional points along the surface of the head were also digitized for the co-registration of the MEG data with the subject's MRI.

Subjects were seated in a comfortable chair facing a screen, with hands resting on a flat surface holding the response pad, and with their head placed under the helmet-shaped bottom of the dewar housing the MEG sensors. A microphone was used for communication with the subject, and all subjects were monitored during the experiment with a video camera inside the magnetically shielded room linked to a display outside of the room.

The MEG and EEG signals were recorded continuously during each of five runs, and sampled at 601 Hz after filtering from 0.03 to 200 Hz. At the beginning of each run, low-level current was fed to each of 4 HPI coils attached to the subject's head for calculation of the head position with reference to the MEG sensors. Stimulus presentations and corresponding brain responses were time locked to trigger pulses sent by the Presentation program and coded by the data acquisition computer. Event-related MEG and EEG responses for each stimulus condition were averaged. The epoch window used for averaging was 900 ms (100 ms before to 800 ms after the onset of the stimulus). Trials containing eye movements, blinks, or other channel artifacts (peak-to-peak amplitude >150 μV in EOG, >500 fT/cm in gradiometers) were rejected. The good readers had on average 74 artifact-free epochs per condition, the poor readers 66. This difference was not significant (*t*-test, $p > 0.1$). The averaged epochs were low-pass filtered at 40 Hz, and the zero level in each channel was taken to be the mean value in the 100-ms baseline period before stimulus onset. Although the visualization of the MEG and EEG sensor data was important for validating the task design and comparison of our results with previous studies, differences between the groups were primarily assessed using MEG source analysis.

4.3.2.4 Structural Magnetic Resonance Imaging

High-resolution structural T1-weighted magnetic resonance images (MRIs) were acquired on a 3T Siemens Sonata or Allegra scanner (TR = 2530 ms, TE = 3.25 ms, flip angle = 7°, 128 sagittal slices, slice thickness = 1.3 mm, voxel size = 1.3 x 1.0 x 1.3 mm^3). A representation of the cortical surface was constructed from the individual structural MRIs with the Freesurfer software (Dale et al., 1999; Fischl, Sereno & Dale, 1999). Cortical white matter was segmented in the high-resolution MR images, and the estimated border between gray and white matter was tessellated, providing a triangular representation of the surface. The surface was also "inflated" to unfold cortical sulci, providing a convenient viewing of activation patterns (Dale et al., 1999; Fischl et al., 1999)

4.3.2.5 MEG source analysis

Cortical sources of the MEG signals were estimated using a distributed model, the Minimum Norm Estimate (MNE) (Hämäläinen & Ilmoniemi, 1994). The sources were assumed to lie on the cortical surface that was reconstructed from the structural MRI. To calculate the forward model which describes the signal pattern generated by a unit dipole at each allowed location on the surface, a single-compartment boundary element model (BEM) was used (Hämäläinen & Sarvas, 1989). For the BEM, the inner surface of the skull for each subject was determined from the T1-weighted MRI. To compensate for small head movements between runs, a forward solution was generated for each run, and the average was used in the analysis (Uutela et al., 2001). To compensate for the bias in MNE toward superficial sources, the inverse operator was constructed with depth weighting (Lin, Witzel et al., 2006). To avoid numerical instability a regularization parameter, $\lambda^2 = 0.33$ was used when computing the inverse operator (Hämäläinen & Ilmoniemi, 1994). Regularization reduces the sensitivity of MNE to noise and effectively results in a spatially smoothed solution. To allow flexibility of the model against small co-registration errors, the orientations of the dipole elements were not strictly constrained to be perpendicular to the cortical surface, and a "loose orientation constraint parameter" of 0.6 was used (Lin, Belliveau et al., 2006). Using the MNE, the activation at each location on the cortical surface was estimated every 5 ms.

To examine differences in the pattern of brain activation between the two groups, noise-normalized MNE, called dynamic Statistical Parametric Map (dSPM) was also calculated (Dale et al., 2000). The dSPM converts the MNE into a statistical test variable that is essentially the signal-to-noise ratio (SNR) of the current estimate at each spatial location. Thus dSPM is useful for visualization of the data as it identifies locations where the MNE amplitudes are above the noise level. Average dSPM for the two subtraction contrasts (*phonologically similar-congruent, phonologically dissimilar-congruent*) was calculated in 50-ms time windows from 0 to 500 ms separately for the two groups.

We quantified the observed group differences in the dSPM by defining regions of interest (ROIs) (Wehner et al., in press). ROIs based on activated cortical regions in each hemisphere were manually drawn on the omnibus (all deviants combined) MNE solution averaged across all subjects. The locations of these ROIs on the individual subjects were determined using spherical morphing of the ROI cortical labels from one subject to another (Fischl et al., 1999). As the MNE solution sometimes contains spurious activation because the noise estimate at each cortical location is not taken into account, the dSPM solution was also consulted when drawing the ROIs. Three time windows associated with acoustic (70-120 ms), phonological (200-300 ms) and semantic (300-500 ms) processing were used for statistical comparisons between the two reading groups. Insofar as the mean reaction times on the task were on average 830 ms, we included an additional time bin (500-700 ms) to capture later potentially task-related cognitive processes. For statistical comparisons between conditions and across the subjects, the MNE current amplitudes were used rather than the SNR values provided by the dSPM. The absolute value of the estimated current amplitude at each location was calculated. The mean MNE activation for sources located within each ROI was calculated and averaged within each time window.

4.3.3 Relationship between Experiment 1 and Experiment 2

As a primary motivation for this study was to use sentence context to understand the phonological processing difficulties in good and poor readers, additional analyses were carried out to investigate group differences in performance on the two speech perception experiments, one with limited context (Experiment 1) and one with sentence context (Experiment 2). First, we calculated the difference in RT and accuracy between the phonologically similar and phonologically dissimilar trials in Experiment 1. As Experiment 1 was intended to stress the phonological processing system the most, these difference scores provided us with a measure of phonological processing impairment for each subject. We wanted to answer the question: Would the subjects who were impaired the most on phonological processing rely the most on sentence context? To determine the amount of context facilitation for each subject, we plotted these difference scores from Experiment 1 against the same difference scores (*phonologically similar – phonologically dissimilar*) for RT and accuracy measures on Experiment 2. Additionally we correlated behavioral performance (RTs and accuracy) from Experiment 1 with behavioral performance on Experiment 2.

4.4 Results

4.4.1 Experiment 1: Auditory discrimination task

In the discrimination task, subjects were required to make a 'same' versus 'different' judgment about consecutive word pairs; the words in the first pair were either phonologically similar or phonologically dissimilar to each other. The accuracy and mean reaction times (RTs) for the two conditions (*phonologically similar, phonologically dissimilar*) are shown in Fig. 4.1 for the two groups of children. RTs are only reported for correct answers. The accuracy and RT data were subjected to repeated-measures ANOVAs with condition as the within-subjects factor and group as the between-subjects factor. For accuracy, there was a main effect of condition, $F(1,28) = 5.9$, $p < 0.03$, indicating that subjects were more accurate on the *phonologically dissimilar* condition relative to the *phonologically similar* condition. No other effects were significant. For the RTs, a group x condition interaction, $F(1,28) = 4.2$, $p < 0.05$ was found. Post-hoc *t*-tests revealed that good readers had longer RTs for the *phonologically dissimilar* stimuli than the *phonologically similar* stimuli ($p < 0.04$), whereas poor readers showed no difference between the conditions. Responses longer than 3000 ms were counted as incorrect; *t*-tests were conducted to examine group differences in the number of these "timeout" trials. No significant group differences were observed.

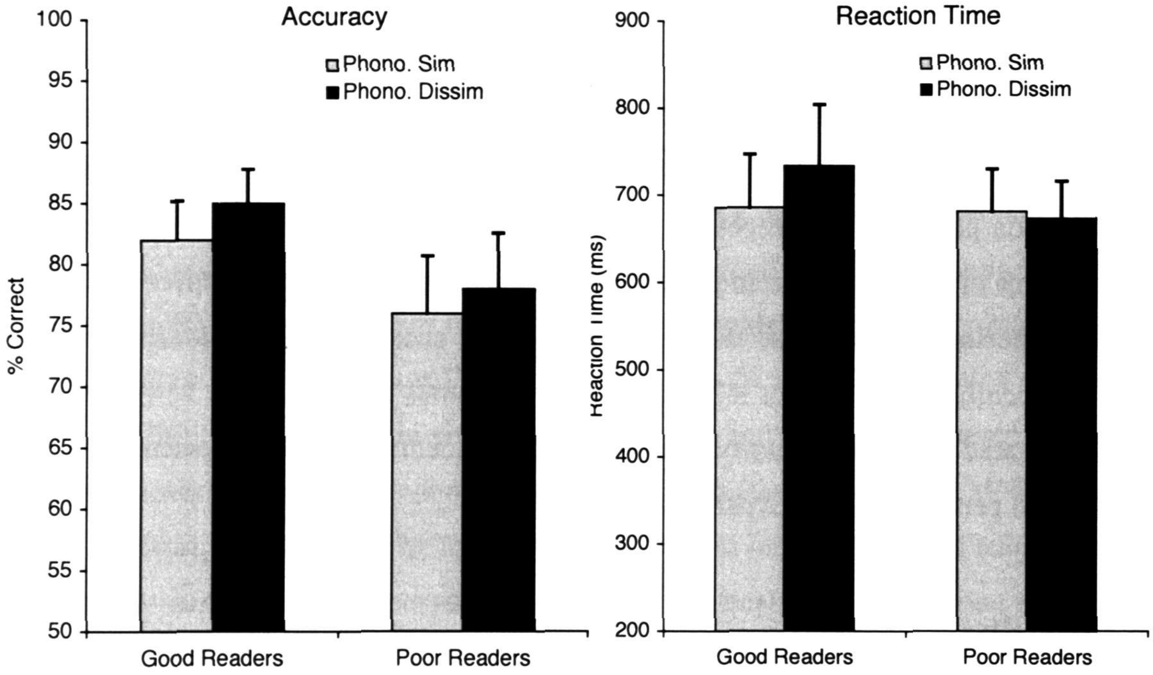

Figure 4.1: Experiment 1: Auditory discrimination task. Accuracy (left) and mean reaction times (RTs) (right) for the *phonologically similar* and *phonologically dissimilar* conditions.

Trials where the consecutive word pairs were 'different' fell into one of four categories in equal proportion: phonologically similar repeated, phonologically similar reversed, phonologically dissimilar repeated, and phonologically dissimilar reversed. We tested for group differences in accuracy within each of these subcategories using *t*-tests. Within each reading group, accuracy was similar across subcategories, and none of the group comparisons were significant, indicating the two groups did not differ in recall or discrimination. Pearson product-moment correlation coefficients were computed to examine the relationship between the standardized measure of phonological working memory and performance (RT and accuracy) on the discrimination task for the two groups. None of the correlations were significant.

4.4.2 Experiment 2: Auditory sentence task

In the auditory sentence task, subjects were required to make a plausibility judgment; the semantically incongruent terminal words of the sentences were either phonologically similar or phonologically dissimilar to a congruent word. Accuracy and reaction times (RTs) for the three conditions (*congruent, phonologically similar, phonologically dissimilar*) are shown in Fig. 4.2 for the two groups of children. RTs are only reported for correct answers. The accuracy and RT data were subjected to repeated-measures ANOVAs with condition as the within-subjects factor and group as the between-subjects factor. No main effects of group or group x condition interactions were found for either accuracy or RTs. For accuracy, a main effect of condition, $F(1,28) = 46.8$, $p < 0.001$ was observed. Post-hoc t-tests revealed that subjects were less accurate on the phonologically similar condition than the congruent condition ($p < 0.03$) and the phonologically dissimilar condition ($p < 0.0001$). For RTs, a main effect of condition, $F(2,56) = 15.1$, $p < 0.001$ was also observed. Post-hoc t-tests revealed that subjects responded faster to the congruent condition than the *phonologically dissimilar* condition ($p < 0.001$) and the *phonologically similar* condition ($p < 0.0001$). Responses longer than 3000 ms were considered incorrect; t-tests were conducted to examine group differences in the number of these "timeout" trials. No significant group differences were observed.

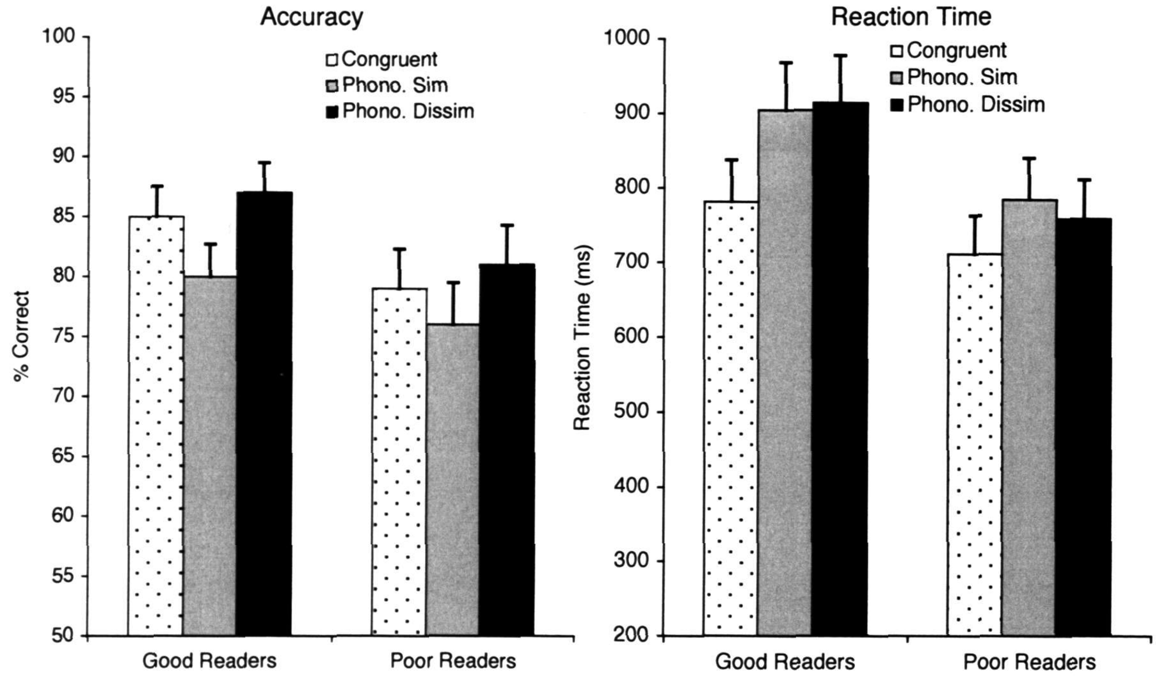

Figure 4.2: Experiment 2: Auditory sentence task. Accuracy (left) and mean reaction times (RTs) (right) for the semantically congruent condition, and the two semantically incongruent conditions (*phonologically similar* and *phonologically dissimilar*).

Correlations between standardized testing scores (PM, RN) and performance (accuracy and RT) on the sentence task were conducted to determine if children with poorer standardized scores also performed differently on the task. No significant correlations between standardized test scores and behavioral performance were observed. However, the poor readers showed negative correlations between RT and accuracy for the *phonologically dissimilar* condition ($r = -0.69$, $p < 0.01$) and the *phonologically similar* condition ($r = -0.63$, $p < 0.02$), indicating that poor readers who responded faster on the semantically incongruent conditions, were also less accurate.

Averaged MEG responses in two gradiometers for the subtraction contrasts for one child are shown in Fig 4.3A. Prominent responses can be seen in both hemispheres for both conditions at about 300-500 ms. This latency range coincides with the N400 response as seen in the grand-averaged EEG responses for a parietal midline electrode (Fig. 4.3B).

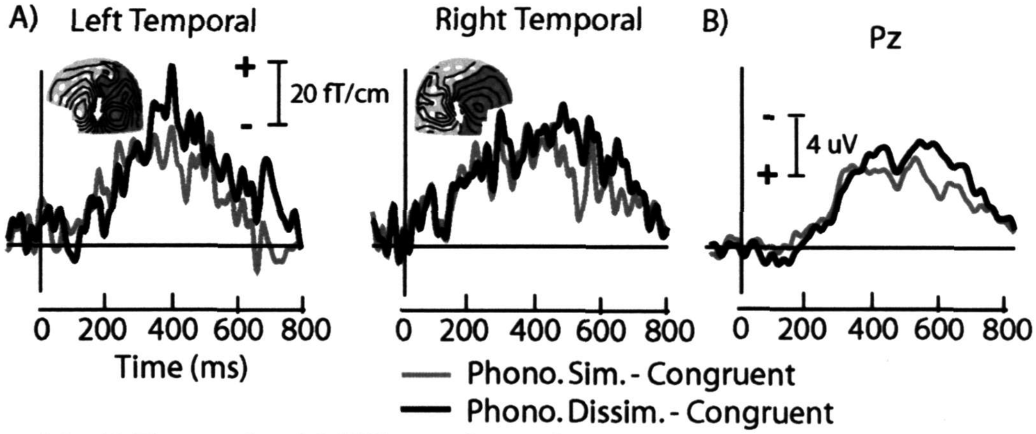

Figure 4.3: A) Event-related MEG waveforms for one child. Averaged responses for the two subtraction conditions are shown for one left temporal gradiometer and one right temporal gradiometer. The insets depict magnetic field patterns corresponding to the peak MEG responses in the time window associated with the N400 for the *phonologically dissimilar - congruent* condition. The white arrows represent equivalent current dipoles that approximate the location of the underlying neural activity. B) Grand-average (n=30 subjects) EEG waveforms for the two subtraction conditions for the posterior midline (Pz) electrode. Negative is plotted up.

The differences in spatiotemporal brain activation for the two groups were compared using consecutive averaged 50-ms time segments of the dSPM solution for the subtraction contrasts (Fig. 4.4). No activation for the any of the subtraction conditions was observed before 200 ms. The good readers showed a response for the *phonologically dissimilar* contrast, with bilateral activation in the superior temporal cortex beginning at 300-350 ms. After 450 ms, additional activation in the right inferior parietal cortex was observed. In contrast, the pattern of brain activation for the *phonologically similar* condition was weaker and began later (350-400 ms) in left temporal cortex, with additional right hemisphere activation in frontal cortex. The poor readers showed a similar but slightly earlier pattern of brain activation as the good readers in the left hemisphere to the *phonologically dissimilar* condition. Additional activation in the left IFG in the later time range was observed for the poor readers. In the right hemisphere, the poor readers showed a weak response in the superior and middle temporal cortices. For the *phonologically similar* contrast, both groups showed a weak response in the left hemisphere beginning around 300-350 ms. However, the poor readers also showed strong right hemisphere activation within the posterior temporal cortex as early as 250-300 ms.

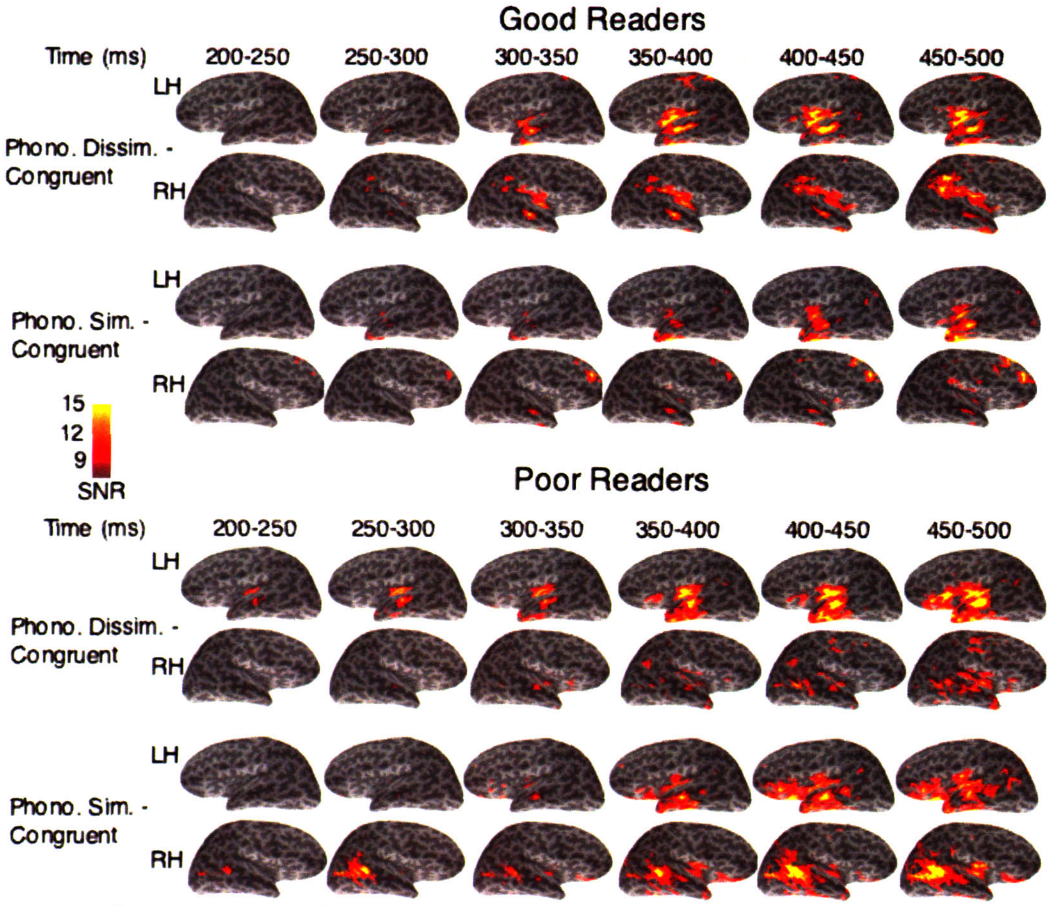

Figure 4.4: Dynamic statistical parametric maps (dSPM) averaged in sequential 50-ms time bins from 200-500 ms for the good reader group (top) and the poor reader group (bottom). The group-averaged dSPM for the two subtraction contrasts (*phonologically dissimilar – congruent*, *phonologically similar – congruent*) are shown on the reconstructed cortical surfaces of one child. The lateral surfaces have been inflated for better visualization of activation within the sulci (dark gray) as well as the gyri (light gray). Both left and right hemispheres are shown for all time points.

To quantify the differences in brain activation patterns between the groups we used a region of interest (ROI) approach. Based on the omnibus activation in the 200-500 ms time range (Fig. 4.5A: top), an ROI in the superior temporal gyrus (STG) was identified in each hemisphere. Spurious regions of activation sometimes appear in the MNE maps due to the inability of this method to take into account an estimate of the noise at each cortical location. Therefore, the dSPM solution averaged across all subjects was also consulted in drawing the ROIs (Fig. 4.5A: bottom). The waveforms representing the mean MNE values within each ROI for the three conditions (*congruent, phonologically dissimilar, phonologically similar*) averaged across all subjects within a group are shown in Fig. 4.5B.

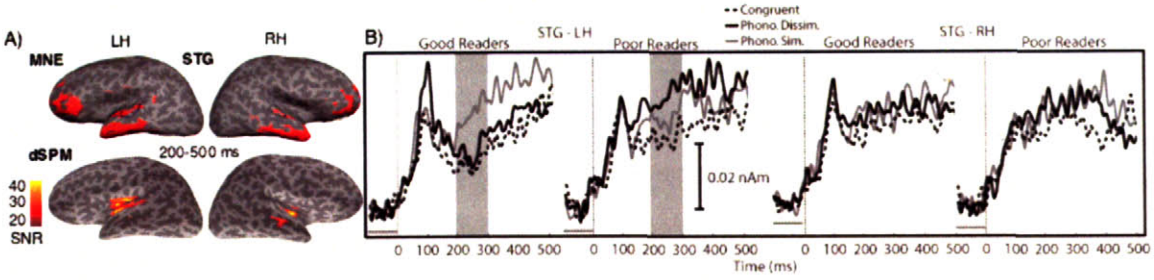

Figure 4.5: Region of interest (ROI) analysis of the MEG data. A) Minimum-norm estimates (MNE: top) and dynamic statistical parametric maps (dSPM: bottom) for the combined semantically incongruent conditions (*phonologically similar*, *phonologically dissimilar*), averaged across all subjects (n=30) between 200-500 ms are displayed on lateral views of the left hemisphere (LH) and right hemisphere (RH). The MNE maps indicate locations where the maximum values of the source estimates exceeded the threshold value of 0.6 nAm . The group averaged maps are shown on the reconstructed cortical surfaces of one child. The superior temporal gyrus (STG) ROI in the left hemisphere and right hemisphere are outlined on the MNE map. B) MEG source waveforms. The estimated source strength as a function of time, as obtained from the MNE averaged across all subjects in the good and poor reader groups are shown for the left and right STG ROIs. The zero level for each curve is indicated by a horizontal line in the prestimulus period. The shading indicates the 200-300 ms time range where there were significant differences between the conditions and groups. The dashed vertical line indicates the onset of the final word in a sentence.

To examine whether the amplitude or latency of the peak MEG response in the early (70-120 ms) time range differed between the two groups, repeated measures ANOVAs were conducted for the STG ROIs, with condition (*congruent, phonologically similar, phonologically dissimilar*) as the repeated within subjects factor and group as the between subjects factor. The dependent measure was either the peak MNE value or the latency of the peak MNE value within the 70-120 ms time window. No main effects or group x condition interactions for the peak MNE value or peak latency within the early time window were observed. These findings suggest that the groups did not process the acoustic properties of the stimuli differently.

Repeated-measures ANOVAs were conducted within each ROI and time bin for the two subtraction contrasts (*phonologically similar - congruent, phonologically dissimilar - congruent*) to examine group differences in MNE activation within the later time bins (200-300 ms, 300-500 ms, 500-700 ms). A group x condition interaction, $F(1,28) = 4.5$, $p < 0.05$, was observed in the left STG during the 200-300 ms time bin. Post-hoc *t*-tests revealed two trends contributing to the interaction (Fig. 4.6). First, poor readers appeared to show more activation in the *phonological dissimilar* contrast than the *phonologically similar* contrast ($p = 0.1$), whereas the good readers showed no difference between the conditions. Second, the poor readers appeared to show more activation in the *phonologically dissimilar* contrast than the good readers ($p = 0.07$), whereas the amount of activation in the *phonologically similar* contrast did not differ between the two groups. No other comparisons in the left hemisphere or right hemisphere were significant.

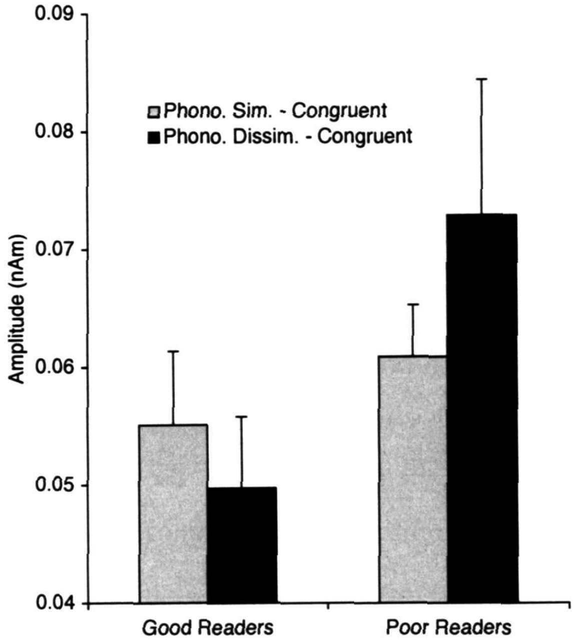

Figure 4.6: Magnitude of the group-averaged MNE activation in the left STG ROI (200-300 ms) for the two subtraction conditions.

Pearson product-moment correlations were calculated to examine the relationship between standardized testing measures (PM, RN) and mean MNE activation (*phonologically similar - congruent, phonologically dissimilar - congruent*) within ROIs and the three later time bins for all subjects combined, and for each group separately. To control for the potential increase in Type 1 errors arising from multiple comparisons (2 ROIs, 3 time bins), only correlations that achieved a significance level of $p = 0.05/6 = 0.0083$ were considered. No correlations between standardized test scores and brain activation were significant. We also calculated correlations between behavioral performance (RT, accuracy) for each semantically incongruent condition (*phonologically similar*, *phonologically dissimilar*) and the associated mean MNE activation (e.g., *phonologically similar - congruent* for *phonologically similar* RT) within all ROIs and time bins. No significant correlations were observed for either accuracy or RTs.

As the same critical words were used in Experiment 1 and Experiment 2, we wanted to investigate group differences in how the presence of sentence context affected the perception of words that differed in degrees of phonological contrast. To this end, we plotted the difference in the accuracy and reaction time measures between the conditions (*phonologically dissimilar - phonologically similar*) for both tasks and all subjects (Fig. 4.7). The critical element in the figure is the distance of each point (corresponding to an individual subject) from the diagonal line, which represents an equal difference in performance between the *phonologically similar* and *phonologically dissimilar* conditions on the two tasks. If the difference for a particular subject were equal for the two tasks, the point for that subject would fall on the diagonal. If the difference were larger for the sentence task, the point would tend toward the lower right corner of the graph, whereas if the difference were larger for the discrimination task, the point would tend toward the upper left corner of the graph. To quantify the effect of task on the perception of words with different degrees of phonological contrast, the distances from each point to the diagonal line were calculated and compared across groups. Distances for points below the diagonal line were considered to be negative (Fig. 4.7: shaded region), whereas distances for points above the line were considered to be positive. For accuracy, the mean distance to the equal performance line was –2.8 for good readers and –2.5 for poor readers. For RTs, the mean distance to the equal performance line was 28 for good readers and 11 for poor readers. Two-tailed *t*-tests revealed that there were no group differences in distance to the equal performance line for either the accuracy or the RT data. However, for accuracy, distances were significantly different from zero in the negative (shaded region, below the diagonal line) direction regardless of group (paired *t*-test, $p < 0.01$), indicating that both groups were affected by sentence context. Distances were not significantly different than zero for the reaction time data.

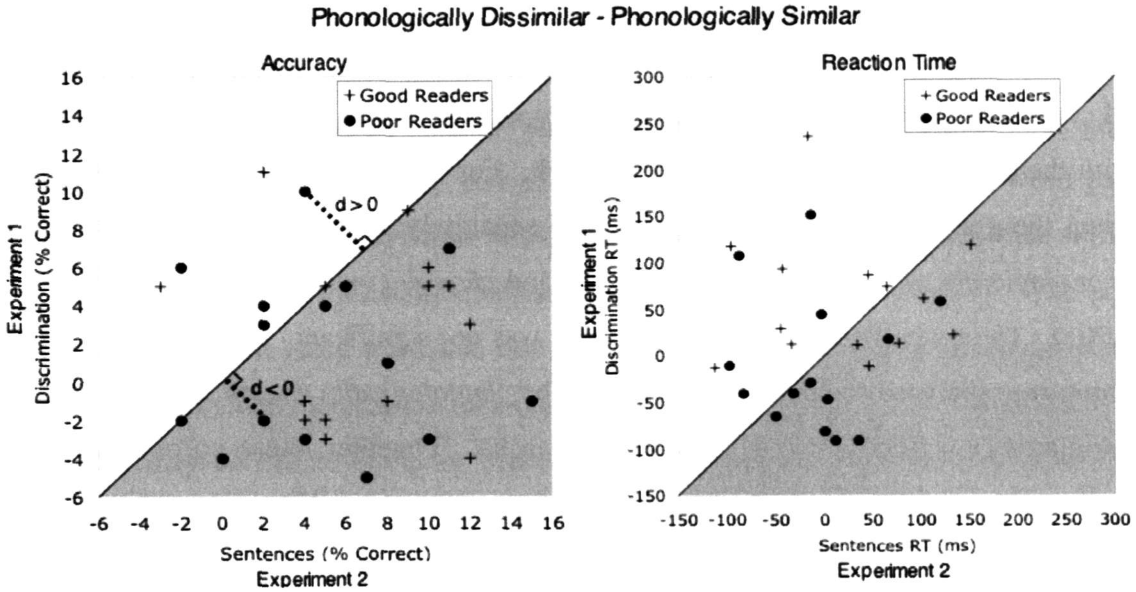

Figure 4.7: Comparison of behavioral performance (Left: accuracy, Right: reaction time (RT)) on Experiment 1 (discrimination task) and Experiment 2 (sentence task). Each point on the plots represents one subject in the good reader group (crosses) or poor reader group (circles). Values along each axis represent the accuracy (left) or RT (right) difference between the two phonological contrasts (i.e., *phonologically dissimilar - phonologically similar*) for the discrimination task (vertical axis) and the sentence task (horizontal axis). Distances (dashed lines) were calculated for each point to the equal performance line (diagonal line). Distances in the shaded region were considered negative.

Correlations between distances to the equal performance line (accuracy, RTs) and performance on standardized tests (PM, RN) were calculated for all subjects and for each group separately. For RTs, a significant correlation ($r = 0.74$, $p < 0.01$) was observed between distance to the equal performance line and phonological memory scores for the poor readers, suggesting that poor readers with lower phonological memory scores also relied more on sentence context, as evidenced by more subjects in the shaded region (Fig. 7). No other correlations were significant.

Correlations were also computed to examine the relationship between performance (accuracy and RT) on the discrimination and sentence tasks. When all subjects were taken together, overall accuracy on the discrimination task correlated ($r =$

0.52, $p < 0.01$) with overall accuracy on the sentence task. Additionally, overall RT, *phonologically similar* RT, and *phonologically dissimilar* RT on the discrimination task all correlated ($r = 0.68$, $p < 0.001$; $r = 0.62$, $p < 0.001$; $r = 0.70$, $p < 0.001$ respectively) with their RT counterpart in the sentence task. For RTs, this pattern was also observed when the good readers group was analyzed separately; overall ($r = 0.81$, $p < 0.001$), *phonologically similar* ($r = 0.75$, $p < 0.001$), and *phonologically dissimilar* ($r = 0.73$, $p < 0.001$). The overall correlation for accuracy was not significant. When the poor reader group was analyzed separately, the RTs for the *phonologically dissimilar* condition were correlated ($r = 0.65$, $p < 0.01$) for the two tasks. Together, these correlation results suggest that children that performed poorly (e.g., with longer RTs or lower accuracy) on one task also performed poorly on the other.

4.5 Discussion

Perception of auditory words that varied in the degree of phonological contrast was examined in good and poor readers. The words were presented in pairs (Experiment 1: discrimination task) or in sentence context (Experiment 2: sentence task). Both groups were less accurate in the *phonologically similar* condition than the *phonologically dissimilar* condition on the two tasks; however this effect was larger for the sentence task. Additionally, good readers responded faster to phonologically similar items than phonologically dissimilar items in the discrimination task, whereas the poor readers showed no difference. On the sentence task, despite the similar performance, the MEG source analysis revealed different patterns of brain activation for the two groups as a function of phonological contrast. Poor readers appeared to show less activation in left STG between 200-300 ms for the *phonologically similar* contrast than the *phonologically dissimilar* contrast, whereas good readers showed no difference between the conditions.

Experiment 1 was designed to stress the phonological processing abilities of good readers and poor readers by varying the degree of phonetic contrast of auditory word pairs to be recalled. Early research in phonological working memory has shown good readers' recall performance to be adversely affected for items that were phonetically similar than those that were phonetically dissimilar (Liberman et al., 1977; Mark et al., 1977). Poor readers, in contrast, appeared to be less affected by the phonetic characteristics of the stimulus list to be recalled. Liberman and colleagues attributed these findings to the impaired readers' poor phonological coding abilities. The good readers in the present study were less accurate on *phonologically similar* word pairs relative to *phonologically dissimilar* word pairs, consistent with the idea that skilled readers are susceptible to phonetic confusability effects in working memory. The poor readers in the present study were also less accurate on the *phonologically similar* items than the *phonologically dissimilar* items, unlike the poor readers in the Liberman et al. study; this may be due to our poor readers being slightly older (Liberman et al.: 7-8 years-old, present study: mean 10.4 years-old). The results of the present experiment suggest that good readers' superior phonological encoding abilities may have helped them key in on subtle phonetic differences yielding superior (i.e., faster) performance on the *phonologically similar* than the *phonologically dissimilar* condition. Poor readers, in contrast, did not show any difference in their performance on the two conditions, perhaps due to their weaker coding of phonological distinctions. Below, we discuss the differences in brain activity between the two groups under phonologically similar and phonologically dissimilar conditions in sentence context to better understand differences in phonological processing between good and poor readers.

Top-down information provided by sentence context is normally facilitatory during everyday speech perception; however, reliance on context in our sentence task was designed to be detrimental to impaired readers' performance if they have poorly coded phonological representations. Both groups appeared to be affected by sentence context, evident in the larger difference in accuracy between the two conditions on the sentence task compared to the discrimination task. However, performance on the sentence task allowed us to examine the extent to which poor readers relied on top-down influences to compensate for phonological processing deficits in this task compared to the good readers, especially under phonologically demanding conditions. Manipulating the phonetic similarity between congruent and incongruent sentence terminal words permitted us to investigate the extent to which the two groups used sentence context to disambiguate between phonologically confusing words to determine sentence plausibility. When the terminal word in a sentence is semantically incongruent with the preceding context, the brain typically elicits a negative response about 400 ms after the stimulus, referred to as the N400 (Kutas & Iragui, 1998). In behavioral studies, this takes the form of a delayed plausibility judgment to the incongruent condition compared to the congruent condition (McElree & Griffith, 1995), as was also seen in our subjects.

Insofar as poor readers have difficulty with phonological coding, they may attempt to compensate by using semantic information provided by sentence context (Perfetti, 1995; Stanovich & West, 1981). In the present study, we made the plausibility judgment more difficult by increasing the phonological similarity of the sentence final word to the congruent word. Consequently, poor readers needed to make the judgment in the presence of conflicting top-down (sentence context) and bottom-up (phonological) cues. Both groups were less accurate in the *phonologically similar* condition, indicating that good and poor readers were more apt to incorrectly accept these stimuli as being semantically congruent with the preceding context. Despite this similarity in behavioral performance, the brain activation patterns suggest differences in the processing of auditory words in sentence context between good and poor readers as a function of phonological contrast.

Based on the MEG results, poor readers appeared to show less activation in left STG between 200-300 ms for the *phonologically similar* contrast than the *phonologically dissimilar* contrast, whereas good readers showed no difference between the conditions. Poor readers' reduced activation in the phonologically demanding condition in the time range associated with phonological processing (Connolly & Phillips, 1994; Kujala et al., 2004) may thus reflect their difficulties with phonological coding.

Examination of the dSPM revealed additional activation in brain regions that were not captured by our omnibus ROI analysis. The omnibus ROI-based approach provided us with an unbiased method to quantify differences between groups and conditions with statistics. However, these ROIs were defined only for regions that show consistent activation across the subjects and conditions. The dSPM complemented the ROI approach by providing statistical maps of cortical activation that may be qualitatively compared across conditions and groups. Both groups showed strong responses in left STG between 300-500 ms for the *phonologically dissimilar* condition, consistent with previous N400 studies (Halgren et al., 2002; Helenius, Salmelin, Service et al., 2002;

Maess, Herrmann, Hahne, Nakamura, & Friederici, 2006; Simos et al., 1997). Additional activation in the left IFG for the poor readers but not the good readers may represent articulatory recoding of the stimuli, as overactivation of the left IFG has been observed in poor readers versus good readers (Pugh et al., 2000; Shaywitz et al., 1998). When the discrimination was difficult, i.e., for the *phonologically similar* condition, poor readers showed abnormally early right posterior temporal activation and weaker and later left hemisphere activation, consistent with a previous MEG study of speech perception in reading-disabled children (Breier et al., 2003).

In summary, children with reading impairments do worse than their normal-reading peers on speech perception tasks that emphasize phonological processing (Bradley & Bryant, 1991; Brady et al., 1983; Godfrey et al., 1981; Reed, 1989). Good readers' superior phonological coding abilities appear to have facilitated their performance on the phonologically demanding (viz., *phonologically similar*) condition in the discrimination task, whereas the poor readers showed no difference between the *phonologically similar* versus *phonologically dissimilar* conditions. This difference between the groups, however, was not observed when the phonological contrasts to be perceived were presented in sentence context. Based on the MEG data, sentence context appears to have differentially affected the response of the two groups to the two contrasts. More specifically, context appears to have exacerbated poor readers' phonological processing problems: their reduced activation in the *phonologically similar* condition compared to the *phonologically dissimilar* condition suggests that the poor readers may have processed the phonologically similar words like the congruent words. In contrast, good readers intact phonological representations made them less vulnerable to the effects of context, regardless of the degree of phonological contrast between the congruent and incongruent sentence terminal words. The overall findings appear to support a phonological account of reading disability.

4.6 Conclusion

All the children in the present study used a combination of bottom-up phonological encoding and top-down sentence context cues during speech perception. However, poor readers' impaired phonological processing skills, appear to have led them to rely more on sentence context under phonologically demanding conditions. Poor readers showed less brain activation in the left STG between 200-300 ms in the *phonologically similar* condition than in the *phonologically dissimilar* condition, whereas good readers showed no difference. As such, poor readers' reduced activation in the phonologically demanding (i.e., *phonologically similar*) reflect their difficulties with perceiving small phonological differences, and may be viewed as consistent with a phonological core deficit account of reading disability.

Appendix 4.A: Stimuli for Experiments 1 and 2

Sentence stem (*congruent, phonologically similar, phonologically dissimilar*)

On their head, all of the baseball players wore a (*cap, gap, lap*).
Because of missing steps on the ladder, there was a large (*gap, cap, map*).
Billy's favorite dessert at Thanksgiving was the pumpkin (*pie, tie, sigh*).
For the wedding, Joe wore a suit and (*tie, pie, guy*).
After she heard a buzz, the girl was stung by a (*bee, pea, knee*).
The round vegetable was a (*pea, bee, sea*).
Another name for a pig is a (*hog, fog, log*).
It was hard to see the mountains through the thick (*fog, hog, dog*).
The apples were not ripe enough to (*pick, kick, thick*).
In soccer, you use your feet to (*kick, pick, lick*).
To relax her muscles, Julie took a soak in the (*tub, cub, hub*).
The sad mother bear lost her (*cub, tub, rub*).
She drives the children to school in a (*van, fan, can*).
The cool air came from the spinning (*fan, van, man*).
After eating, the baby had food all over her (*face, vase, case*).
She put the flowers in a (*vase, face, race*).
The man drove to work in an old (*car, tar, bar*).
The road was repaired with new (*tar, car, jar*).
The cowboy shot the bank robber with a (*gun, bun, sun*).
The hot dog was too long for the (*bun, gun, run*).
Suzie wore mittens and a hat when it became (*cold, gold, mold*).
The fancy jewelry was made of silver and (*gold, cold, hold*).
For cutting wood, a saw is a useful (*tool, pool, fool*).
Betty went swimming in her friend's new (*pool, tool, rule*).
At the beach, we walked in the (*sand, hand, band*).
Bob threw the ball with his right (*hand, sand, land*).
The woodpecker made a hole in the tree with its long (*beak, peak, leak*).
The top of the mountain is called the (*peak, beak, cheek*).
The doctor told the patient to take a (*pill, bill, gill*).
Without any money, Bob couldn't pay the (*bill, pill, hill*).
The book was missing a (*page, cage, rage*).
The tiger escaped from the (*cage, page, wage*).
The frightened woman thought she saw a (*ghost, coast, toast*).
The fisherman lived along the (*coast, ghost, roast*).
The beach surrounded a large (*bay, day, ray*).
The weatherman said tomorrow will be a rainy (*day, bay, hay*).
The army soldier slept on a (*cot, pot, knot*).
He stirred the soup in the (*pot, cot, shot*).
To make the train go faster, the workers shoveled (*coal, goal, hole*).
To score a point, Billy kicked the ball into the (*goal, coal, roll*).
The old man couldn't hear the dog (*bark, park, mark*).

Mary read her book on a bench in the (*park, bark, shark*).
He poured cereal into a (*bowl, pole, toll*).
The fireman slid down the (*pole, bowl, sole*).
The wrong key did not (*fit, sit, knit*).
Tommy liked to stand rather than (*sit, fit, lit*).
The large waves tipped over the small (*boat, goat, coat*).
The animals on the farm were three sheep and one (*goat, boat, note*).
Without his watch, Frank didn't know the (*time, dime, lime*).
The lollipop cost only two nickels and a (*dime, time, rhyme*).
The potatoes came in a (*sack, shack, back*).
The small house in the woods was a (*shack, sack, rack*).
To open the soda, Jill pulled on the (*tab, cab, jab*).
Because his car broke down, Sam took a (*cab, tab, lab*).
After walking so much, John had tired (*feet, seat, meat*).
The bicycle had an uncomfortable (*seat, feet, wheat*).
After the car was in a crash it had a big (*dent, tent, rent*).
When they went camping they slept in a (*tent, dent, vent*).
Plastics and paper should be separated in the recycling (*bin, pin, fin*).
The dress was held together with a safety (*pin, bin, chin*).
In the afternoon the queen had biscuits and (*tea, key, fee*).
He couldn't open the lock because he lost the (*key, tea, she*).
The boy rolled the (*ball, doll, hall*).
Barbie was the girl's favorite (*doll, ball, wall*).
The colorful bird swimming in the pond was a (*duck, buck, puck*).
The only money she had left was one (*buck, duck, luck*).
Before putting on his shoes, he put on (*socks, fox, rocks*).
The small furry animal Larry saw was a (*fox, socks, box*).
During the test, Jody couldn't remember what she had been (*taught, caught, fought*).
The football was thrown too high to be (*caught, taught, thought*).
The only fruit at the small store was some apples and a (*pear, bear, hair*).
Jimmy's favorite zoo animal was the (*bear, pear, chair*).
The sailor lived on a big (*ship, hip, lip*).
The old lady fell and broke her (*hip, ship, tip*).
The slimy animal Jimmy picked up was a (*toad, code, road*).
To open the door, he had to enter a (*code, toad, load*).
The dirty laundry was collected in a (*pile, tile, mile*).
The bathroom floor was made entirely of (*tile, pile, file*).
To think, you must use your (*brain, grain, crane*).
The horses ate oats and (*grain, brain, train*).
For breaking the law, Jim had to pay a (*fine, vine, line*).
Grapes grow on a twisty (*vine, fine, sign*).
On his whole family, the witch put a (*curse, purse, nurse*).
The lady's money was in her (*purse, curse, verse*).
My grandmother keeps her band-aids in a safety (*kit, pit, hit*).
The seed inside of a peach is also called a (*pit, kit, mitt*).
To wash the floor, you need a mop and a (*pail, tail, hail*).

A pig has a small curly (*tail, pail, whale*).
The time we always eat lunch is (*noon, moon, June*).
Neil Armstrong was the first astronaut on the (*moon, noon, tune*).
Tennis is played on a (*court, port, fort*).
The big ship sailed into the (*port, court, short*).
The princess was held prisoner in the highest (*tower, power, shower*).
The king got rid of his enemies to gain more (*power, tower, sour*).
With the hammer, Jack hit the rusty (*nail, mail, jail*).
She sent the letter in the (*mail, nail, sail*).
My uncle's favorite drink is (*beer, deer, cheer*).
The men enjoyed hunting rabbits and (*deer, beer, fear*).
The thief ran away from the (*cop, top, mop*).
The bubbles in the boiling water always rise to the (*top, cop, shop*).

Filler sentences

The mother held the baby in her *lap.*
The location of the buried treasure was marked on the *map.*
The sleepy man let out a big *sigh.*
Another name for a man is a *guy.*
The girl fell down and scraped her *knee.*
You can often smell the salty air near the *sea.*
In the river there was a floating *log.*
Every morning, Kim walked the *dog.*
The dough was hard to stir because it was so *thick.*
The lollipop was fun to *lick.*
A wheel has spokes attached to a *hub.*
After the long drive, Mary gave John a back *rub.*
Rex stirred the paint in the *can.*
Steve helped others because he was a nice *man.*
When Sam wasn't wearing his glasses, he kept them in a *case.*
The fastest runner won the *race.*
Sandy met Will for lunch at the neighborhood *bar.*
Pickles are usually sold in a *jar.*
It was too hot standing in the *sun.*
The old man was no longer able to *run.*
The old bread had started to grow *mold.*
The frying pan was too hot to *hold.*
Since Jill made bad choices, people called her a *fool.*
To play fairly was the only *rule.*
Megan played the trumpet in the *band.*
Turtles can swim in water and walk on *land.*
The rusty pipe began to *leak.*
The man kissed the woman on the *cheek.*
A fish breathes through a *gill.*
The tree was at the top of the *hill.*

The angry tiger was full of *rage.*
Greg's job paid a low *wage.*
Jack spread butter on the *toast.*
For dinner they had potatoes and a *roast.*
The sun cast a bright *ray.*
The horse ate from a large pile of *hay.*
The rope was tied into a *knot.*
The basketball player made the winning *shot.*
The old sweater had more than one *hole.*
Jeff spread butter on his dinner *roll.*
Debbie used the pencil to make a *mark.*
The black fin in the water was from a *shark.*
To cross the bridge we paid a *toll.*
The bottom of the shoe had a worn out *sole.*
My grandmother taught me how to *knit.*
The candle would not stay *lit.*
When it was cold outside, Jim wore a warm *coat.*
Suzie wrote Billy a short *note.*
Some soda has lemon and *lime.*
Poems have lines that *rhyme.*
Lifting heavy objects gave the man a painful *back.*
The red jacket hung from the coat *rack.*
Ron punched the wall with a short *jab.*
The scientist works in a big *lab.*
The grill was used for cooking the *meat.*
The farmer planted the field with corn and *wheat.*
The student's apartment cost a lot of money to *rent.*
The fresh air flowed out of the *vent.*
The dolphin had a large gray *fin.*
The man's face had a square *chin.*
The museum charged a small *fee.*
The boy was older than *she.*
At school students walked down the *hall.*
John hung a picture on the *wall.*
Hockey is played with a small black *puck.*
Winning the lottery requires a lot of *luck.*
The mountainside was full of sharp *rocks.*
The new toy came in a large cardboard *box.*
The two girls who didn't like each other often *fought.*
To escape the jail was the prisoner's only *thought.*
The bald man did not have any *hair.*
The child sat down on the little *chair.*
Gary's mouth hurt because he had a cut on his upper *lip.*
The marker wouldn't write with a broken *tip.*
The car drove along a bumpy *road.*
The truck could not carry such a heavy *load.*

The race distance was one *mile.*
The papers were put in the student's permanent *file.*
The construction workers used a large *crane.*
There were forty cars on the long *train.*
To buy tickets for the movie, we had to wait in *line.*
The name of the road was marked with a *sign.*
The doctor gave the girl's medicine to the *nurse.*
The song only had one *verse.*
The popular song was a big *hit.*
To catch the ball, the player wore a large *mitt.*
The weather became bad and it started to *hail.*
The largest animal in the sea is the *whale.*
The month after May is *June.*
The bad singer sang out of *tune.*
The army was safe inside of the *fort.*
The rope wouldn't reach because it was too *short.*
To get clean, Ralph took a *shower.*
The candy tasted very *sour.*
The guilty man was sent to *jail.*
The wind filled up the boat's large *sail.*
The fans all stood up and began to *cheer.*
The brave child showed no *fear.*
To clean the floor, use a wet *mop.*
They bought the table at a small *shop.*

Appendix 4.B: EEG results

Analysis of the EEG data was not included in the submitted paper, as our focus was on the MEG source analysis. We report and discuss the EEG results here for completeness.

4.B.1 EEG analysis method

Grand-averaged EEG waveforms for the two groups were constructed by averaging responses at each electrode location for all subjects (Fig. 4.B.1). All electrodes were referenced to an electrode placed on the nose. One subject in the good reader group was excluded due to poor quality of their EEG data. Individual electrodes with poor data quality were identified from the EEG responses for each subject, and were excluded from the grand average. Excluded electrodes were rare and accounted for only 2.5% of the data. For consistency with the MEG analysis, we used the same time windows (70-120 ms, 200-300 ms, 300-500 ms, 500-700 ms) for comparisons between the conditions and groups. The frontal (Fz) and parietal (Pz) midline electrodes were selected for statistical comparisons, based on the previous literature showing the largest EEG responses at these locations. For the early time range (70-120 ms), we determined the maximum value for each condition (*congruent, phonologically similar, phonologically dissimilar)* and subject. For the later time ranges (200-300 ms, 300-500 ms, 500-700 ms), we calculated the mean value in the time window for each condition (*congruent, phonologically similar, phonologically dissimilar*) and subject. These values were subjected to repeated-measures ANOVAs with condition as the repeated factor and group as the between subjects factor.

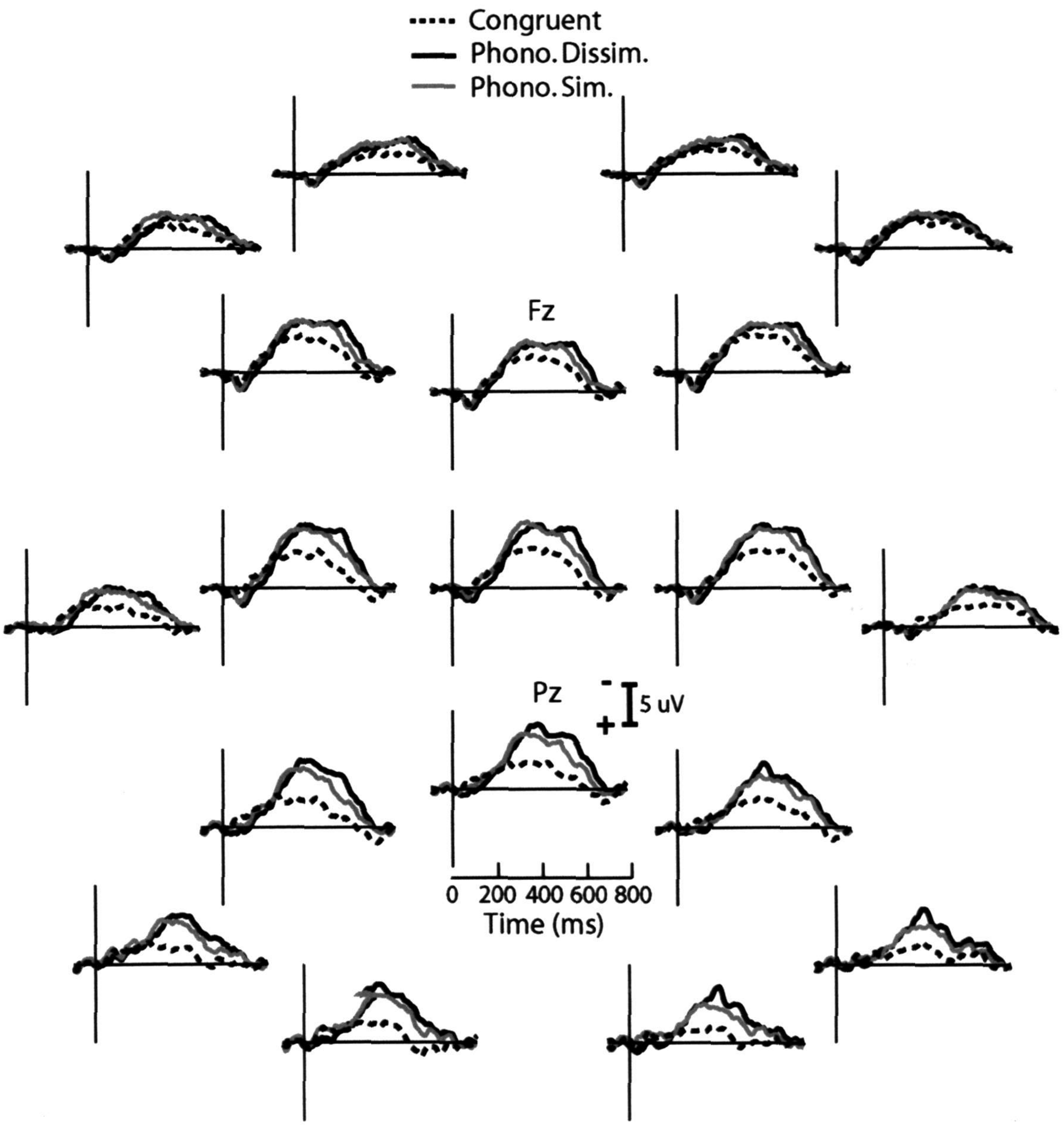

Figure 4.B.1: Grand-average EEG waveforms for the three conditions for all electrodes. Statistical comparisons between conditions and groups were performed on a frontal midline electrode (Fz) and a parietal midline electrode (Pz).

4.B.2 EEG results

No main effects or group x condition interactions were significant for either the Fz or Pz electrode in the early time range (70-120 ms). For the later time ranges, no main effects of group or group x condition interactions were significant. However, for Fz, there was a main effect of condition between 300-500 ms, $F(2,52) = 14.245$, $p < 0.001$, and between 500-700 ms, $F(2,52) = 27.513$, $p < 0.001$. For both time ranges, post-hoc *t*-tests revealed that the response to the *congruent* condition was significantly smaller, than to the *phonologically similar* condition ($p < 0.0001$) and the *phonologically dissimilar* condition ($p < 0.0001$). Similarly, for Pz there was a main effect of condition between 300-500 ms, $F(2,52) = 23.408$, $p < 0.001$, and between 500-700 ms, $F(2,52) = 14.281$, $p < 0.001$. For both time ranges, post-hoc *t*-tests revealed that the response to the *congruent* condition was significantly smaller, than to the *phonologically similar* condition ($p < 0.01$) and the *phonologically dissimilar* condition ($p < 0.0001$). Additionally, for Pz there was also a main effect of condition between 200-300 ms, $F(2.52) = 3.983$, $p < 0.03$. Post-hoc *t*-tests revealed that the response to the *congruent* condition was smaller than to the *phonologically similar* condition ($p < 0.01$). These results are summarized in Fig. 4.B.2.

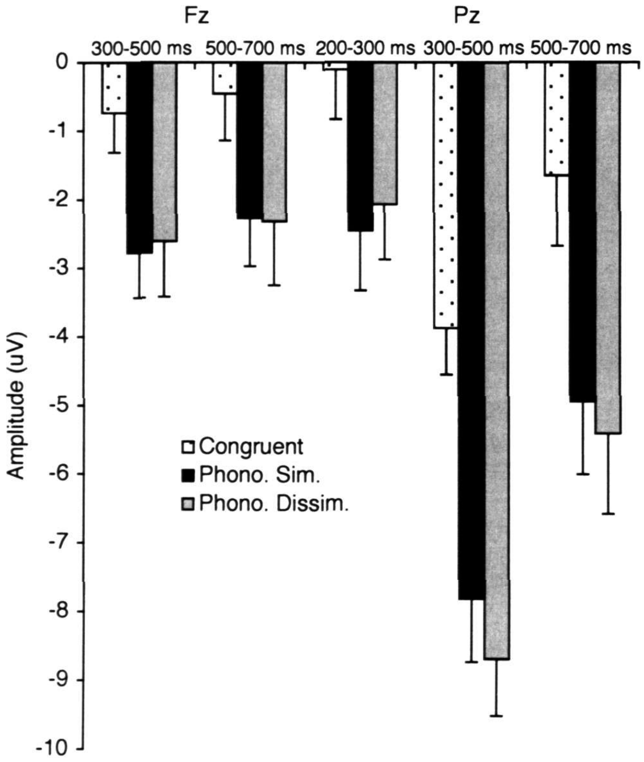

Figure 4.B.2: Mean EEG amplitude for the three conditions for a frontal midline electrode (300-500 ms, 500-700 ms), and a parietal midline electrode (200-300 ms, 300-500 ms, 500-700 ms). The two incongruent conditions were significantly different than the congruent condition ($p < 0.01$) for both electrode locations (Fz, Pz) and all time bins.

4.B.3 Discussion

Both groups showed a large N400 response to semantically incongruent sentence final words, regardless of their phonological characteristics. This response showed a widespread scalp distribution and was maximal at posterior electrode locations. Similar to the MEG data, we found no evidence for group differences in the N400 time range (300-500 ms), suggesting that both groups detected the semantically anomalous words. However, in contrast to the MEG data, we did not observe any group differences in the earlier time range associated with phonological processing (200-300). The lower sensitivity of EEG compared with MEG at detecting the subtle differences in brain activation related to the phonological manipulation in this task may be related to the fewer number of EEG channels (19 electrodes) than MEG channels (306 channels) used in this study, or the fact that EEG and MEG provide different information about the underlying brain currents (for a discussion, see Appendix A).

Chapter 5: General discussion

The work presented in this thesis aimed at understanding the phonological processing deficits in reading-impaired children by examining good and poor readers' discrimination of auditory words in isolation, in word pairs, and in sentence context. In this chapter, we first discuss similarities and differences between good and poor readers in the three speech perception studies conducted in this thesis. We then note how our results support the idea that both good and poor readers use semantic information from sentence context during auditory word perception, albeit to different degrees. Finally, we interpret our results in light of the phonological theory of dyslexia.

5.1 Similarities between good and poor readers

Despite the different paradigms used in the three speech perception experiments, a similar pattern of behavioral results was observed for these tasks. In Chapter 3, we saw that both good and poor readers missed more deviants and took longer to discriminate the phonologically similar word *bat* than the phonologically dissimilar word *rat* from the repeated standard word, *pat*. Similarly, in the word-pair discrimination and the sentence tasks (Chapter 4), both good and poor readers performed worse on the phonologically similar condition than the phonologically dissimilar condition. Therefore, it appears that the discrimination abilities of both groups were sensitive to the degree of phonological contrast, such that all children performed better when the discrimination was easy (2 or 3 phonetic feature difference), than when it was difficult (1 phonetic feature difference). Insofar as poor readers are known to have known difficulty with processing small phonological contrasts (Godfrey et al., 1981; Mody et al., 1997), we hypothesized that they would show this pattern of results. However, since good readers did not do significantly better on the phonologically dissimilar words than the phonologically similar words, some of the phonological representations of the children who were good readers in our sample, were yet to be fully developed. This is consistent with the premise that the process of lexical restructuring is slow (Metsala & Walley, 1998; Nittrouer, 1992; Nittrouer & Studdert-Kennedy, 1987). Furthermore, both groups' poorer performance (lower accuracy and/or longer RTs) on phonologically demanding contrasts in all three studies provides strong evidence that this finding is not epiphenomenal.

In Chapter 2, we discussed how lexical restructuring (Metsala & Walley, 1998) may explain the development of phonological representations. The smaller lexicons of younger 7 year-old children may therefore result in phonological representations that are not fully developed (Charles-Luce & Luce, 1990). To this end, however, the good and poor readers in our study did not differ on the Peabody Picture Vocabulary Test (PPVT-III) (Dunn & Dunn, 1997), a standardized measure of vocabulary.

Alternatively, words with one-feature phonological contrasts in the present study may have been more difficult to discriminate than words with multiple-feature contrasts. The phonologically similar word pairs had initial phonemes that were stops (e.g., /b/, /p/, /k/), fricatives (e.g., /s/, /f/, /v/) or nasals (e.g., /n/, /m/) and that differed in either voicing or place of articulation. In contrast, the phonologically dissimilar word pairs also included words with initial phonemes that were approximants (e.g., /w/, /r/), or affricates (e.g., /ch/), which usually differed in manner of articulation, and either voicing and/or place of articulation. As such, phonologically dissimilar words may have differed in their acoustic and phonetic properties compared to phonologically similar words. The stimuli were carefully constructed to minimize acoustic differences (e.g., duration of the initial phoneme), though, some acoustic differences between the stimuli are unavoidable as they are inherent to the different phonetic categories the stimuli belong to, e.g., greater responses to *bat* than to the other deviants (*cat*, *rat*), in the early time range associated with acoustic processing (65-115 ms). Second, the limited vocabulary of 7-13 year-old children and the large number of sentence stimuli required to achieve an adequate signal-to-noise ratio for MEG, prevented us from using a more restricted set of stimuli. However, the stimuli were the same for the two groups, and insofar as the primary motivation for the thesis was to investigate differences between good and poor readers, one way to separate the effects of acoustic versus phonetic contrast is to examine the time ranges where group differences were observed using MEG.

Neither of the MEG studies in this thesis revealed differences between good and poor readers in the amplitude or latency of activation in the early time range (oddball: 65-115 ms, sentences: 70-120 ms) associated with acoustic processing (Hari, 1990; Näätänen

& Picton, 1987), suggesting that the groups did not differ in their processing of the acoustic properties of the stimuli. On the contrary, the differences between good and poor readers were observed in the time range associated with phonological processing (Connolly et al., 2001; Kujala et al., 2004) for both MEG studies (oddball: 140-240 ms, sentences: 200-300 ms). This provides strong evidence that the observed group differences in the MEG data reflect the ability of good versus poor readers to discriminate words with small phonetic contrasts rather than suggesting differences in acoustic processing between the two groups.

5.2 Differences between good and poor readers

Although good and poor readers showed similar patterns of behavioral performance for the two MEG studies (oddball and sentence), the reaction times for the two groups differed in the behavioral word-pair discrimination study as a function of phonological contrast. This study was particularly challenging for poor readers, as it required precise encoding, storage, and retrieval of phonological forms; phonological processes that have been shown to be disrupted in reading-impaired children (Brady et al., 1983; Godfrey et al., 1981). Good readers' performance differed as a function of phonological contrast, whereas poor readers were not affected by the phonological manipulation, consistent with previous research (Liberman et al., 1977; Mann et al., 1980; Mark et al., 1977). This reduced effect of phonological contrast in poor readers has been taken as evidence that poor readers employ phonological codes less often, or less efficiently than good readers. Others have suggested that these results may be accounted for by floor effects, such that poor readers performed so poorly that effects of phonological contrast could not be observed (Macaruso, Locke, Smith, & Powers, 1996). However, this explanation does not hold for our study, as both good and poor readers performed the task with higher than 75% accuracy (clearly above chance level).

Good readers responded faster to the phonologically similar words compared to the phonologically dissimilar words, contrary to our expectations. If good readers discovered that phonologically similar words were more difficult, they might have focused on detecting words in this phonologically demanding condition, evidenced by shorter reaction times to these stimuli. In contrast, the task may have been difficult for the poor readers, thereby preventing them from using a similar high-level strategy. The MEG data also support the notion that good readers but not poor readers, took advantage of the amount of phonological contrast. Both groups took longer to respond to the phonologically demanding deviant *bat* than the phonologically dissimilar deviant *rat* on the oddball task, yet only the good readers showed a significant difference in brain activation between these two conditions during the time range associated with phonological processing (150-300 ms). Additionally, poor readers compared to good readers also showed greater activation in the left superior temporal gyrus (STG) in the phonologically easier contrast for both MEG studies (oddball: *rat-pat*, sentence: *phonologically dissimilar - congruent*), suggesting that both groups used phonological coding to perform the tasks. However, under phonologically demanding conditions, the poor readers' phonological processing difficulties became apparent, with less activation in the left STG for both MEG tasks.

Although additional areas of brain activation differences were observed between good and poor readers using dSPM (Figures 3.4 and 4.4), some of these were not captured by our region of interest (ROI) analysis approach. This might be because the omnibus ROI analysis we employed was rather conservative, as it assumed that the same regions of cortex were activated across conditions and subjects, albeit with different magnitudes and time courses. As a first approximation, it was not unreasonable to make this assumption, particularly since the previous literature investigating the auditory P1/N1, N2/PMN and N4 evoked response components has suggested that neural sources contributing to these components were most reliably localized to the superior temporal cortex, the area captured by our ROI analysis.

Relatively small group differences were observed for the easy phonological contrasts (oddball: *rat-pat*, sentence: *phonologically similar-congruent*); however, poor readers showed signs that their processing of easy contrasts deviated from "normal", in that they showed bilateral sustained activation in the oddball task, and activation in the left inferior frontal cortex with weak responses in the right hemisphere in the sentence task. Excessive brain activation during cognitive tasks is often interpreted as inefficient processing (Goldsberry, O'Leary, Hichwa, & Nopoulos, 2006; Ramsey et al., 2002), due to the inability to inhibit ongoing processes or the need to engage additional cortical regions. Poor readers' sustained activation for all contrasts in the oddball task, and activation in left inferior frontal regions in the sentence task may reflect their general difficulties with phonological processing. It is particularly interesting that poor readers but not good readers, engaged the left inferior frontal cortex, as this area has also been implicated in phonological processing (Gold & Buckner, 2002), and has shown increased activation in reading-impaired children (Pugh et al., 2001). A possible interpretation might be that poor readers required more effortful phonological processing compared to good readers, perhaps needing to engage subvocal articulatory mechanisms to perform the task.

As expected, the greatest differences in brain activation between the two groups were observed to the most demanding phonological contrasts in both MEG tasks (oddball: *bat-pat*, sentence: *phonologically similar-congruent*). A common finding to both studies was delayed and weaker activation in the left hemisphere coupled with abnormal right hemisphere brain activation for the poor readers. Poor readers, compared to good readers, often show less activation in left posterior brain regions and more activation in homologous regions of the right hemisphere during phonological processing tasks (Breier et al., 2003; Pugh et al., 2001; Shaywitz et al., 1998). In the present studies, the amount of right hemisphere activation in poor readers was modulated as a function of the degree of phonological contrast. Although speculative, one might hypothesize that phonological representations of words that are less segmental could be represented in more "holistic" right hemisphere systems, whereas well-defined phonological representations of words could be represented by the same left hemisphere posterior systems that are activated during grapheme to phoneme conversion during reading. Representations of words in the mental lexicon can be thought of as distributed neuronal assemblies that contain connections to their phonological, semantic, and syntactic content (Pulvermüller, 1999). Therefore, one could imagine a shift in activation from the right to the left hemisphere as the phonological representations of words become more segmental via lexical restructuring either through vocabulary growth or the development of spelling and reading skills. If this lexical restructuring does not occur as rapidly in poor readers as it does in good readers, right hemisphere activation may persist for words with underspecified phonological representations. Longitudinal studies examining the neural basis of lexical restructuring may be necessary to assess the validity of these claims.

5.3 Semantic influences on phonological processing

The availability of top-down semantic information provided by sentence context may influence bottom-up phonological encoding processes during speech perception. We examined the effect of phonological contrast on auditory word perception with and without sentence context in good and poor reader groups. The results were consistent with our expectation that both good and poor readers use semantic information provided by sentence context during speech perception, albeit to different extents. Both groups showed more negative EEG responses to the semantically incongruent conditions than to the congruent condition, consistent with previous studies investigating the N400(m) in children (Coch & Holcomb, 2003; Holcomb et al., 1985; Juottonen et al., 1996), although no reliable group differences were observed in the EEG data.

The MEG ROI source analysis provided a more detailed picture of brain activation differences between good and poor readers in the left superior temporal gyrus (STG), an area implicated in phonologically processing. Poor readers' reliance on sentence context was most evident under phonologically demanding conditions, possibly due to deficiencies in their low-level phonological coding skills. Poor readers showed less activation for words that were phonologically similar than phonologically dissimilar to an expected congruent word in the left STG during a time range associated with phonological processing (200-300 ms), but not in a later time range associated with semantic processing (300-500 ms), consistent with previous studies investigating sentence context effects in speech perception for good and poor readers (Bonte & Blomert, 2004; Helenius, Salmelin, Service et al., 2002). Furthermore, poor readers with lower phonological memory scores (CTOPP: nonword repetition and memory for digits subtests) also relied more on sentence context than poor readers with higher phonological memory scores. This is consistent with the idea that the extent to which one relies on sentence context is related to difficulties with phonological processing.

It is not surprising that semantic and phonological information interacted during spoken word recognition in our sentence task given that previous research showed that semantic context can both facilitate and inhibit the recognition of phonologically ambiguous words (Gaskell & Marslen-Wilson, 2002; Zwitserlood, 1989). A recent study examining context effects on categorical perception (*bath-path* continuum) in good and poor reading children found that both good and poor readers were affected by context (Chiappe et al., 2004), although to different degrees. Chiappe and colleagues found good readers only showed a contextual bias when the first segment of the word to be identified was near a phoneme boundary (more phonologically demanding condition), but not when the word was at an endpoint of the continuum (less phonologically demanding condition). In contrast, poor readers were equally affected by context at all points along the continuum including the endpoints. Both groups in our studies appeared to be affected by context in the phonologically similar condition, although only the poor readers showed less activation in this phonologically demanding condition. Results from our studies and those of Chiappe et al. (2004) can be explained in terms of the quality of phonological representations in the two groups. Whereas good readers are able to take advantage of the their superior phonological coding abilities under phonologically demanding conditions (e.g., at a category boundary, or phonetically similar stimuli), poor readers cannot, leading to a greater reliance on sentence context to resolve phonologically ambiguous words.

5.4 Implications for the phonological theory of dyslexia

The results in this thesis are consistent with the notion that poor readers have underdeveloped phonological representations. On the one hand, good readers were sensitive to the phonological characteristics of words presented without sentence context, which was evidenced by greater brain activation (Chapter 3: oddball task) and faster reaction times (Chapter 4: discrimination task) to phonologically similar contrasts relative to phonologically dissimilar contrasts. On the other hand, poor readers did not show differential effects of varying phonological contrast on their neural (oddball task) or behavioral (discrimination task) responses, consistent with poorly coded phonological representations. In fact, poor readers were less accurate or had slower reaction times in the most demanding phonological, i.e., phonologically similar, condition in all three speech perception studies, and also showed less brain activation in a time range (200-300 ms) and brain region (left STG) associated with phonological processing in the sentence study. Poor readers' greater susceptibility to semantically incongruent but phonetically similar words presented in sentence context, evidenced by their lower accuracy and reduced brain activation for this phonologically demanding contrast, further provides evidence for underspecified phonological representations in reading-impaired children.

Chapter 6: Conclusions and Future Work

6.1 Final remarks

In a series of three speech perception experiments, we have demonstrated the usefulness of MEG to detect subtle differences in speech perception abilities between normal and reading-impaired children. Despite similar behavioral profiles and EEG responses for the two groups, MEG with an ROI approach revealed small yet significant differences in the patterns of brain activation during auditory word perception for the two groups. Our data support the view that both good and poor readers use similar phonological coding mechanisms during auditory word perception, although poor readers appear to do so less efficiently. The impaired bottom-up phonological processing abilities of poor readers forced them to rely more on top-down sentence context during speech perception, evident as lower accuracy and less brain activation in the phonologically demanding, i.e., phonologically similar condition. Taken together the results from the three experiments are consistent with a phonological account of dyslexia in which the phonological representations of poor readers are underspecified.

6.2 Suggestions for future studies

We did not observe group differences in behavioral performance in either of the two MEG tasks. One reason might be that the tasks did not place high enough phonological coding demands on the poor readers to elicit significant group differences. Future studies that could stress the phonological processing system, yet limit the memory resources required to perform the task may prove more sensitive to behavioral differences between good and poor reading children. For example by shortening the interstimulus interval (ISI) between sequentially presented words, or by making the interval between successive word-pairs to be recalled longer, one might be able to make the tasks sufficiently more challenging, yet still doable for the poor readers

Differences were observed in the brain activation patterns between the normal and reading-impaired children under phonologically demanding conditions, i.e., for the phonologically similar stimuli, although our studies were not designed to examine the locus of the phonological deficit in poor readers (e.g., whether the phonological representations themselves or rather access to them is impaired). Future studies targeted at different aspects (e.g., encoding, storage, retrieval) of the phonological representation may be necessary to better understand the precise nature of the phonological deficit in poor readers.

The region of interest (ROI) approach that we employed to test for significant group differences may have been too conservative to reveal slight differences in brain activation between the two groups. In addition, although this method provides an unbiased way of selecting ROIs, it may unduly yield false negatives when the same brain regions are not consistently activated across all conditions and groups. Future research exploring new ways to quantify the differences in MEG activation with fewer assumptions is suggested.

Finally, we have chosen to study children who are already of reading age (7-13 years old). Therefore, our studies do not directly address the development of underspecified representations in good and poor readers. Neuroimaging studies with younger children at risk for reading difficulties are already beginning to appear in the literature, and it is likely that such studies will continue to be critical towards our understanding of the role of developing phonological representations in reading outcomes.

Appendix A: MEG theory and methods

Several excellent reviews exist on various aspects of magnetoencephalography (MEG) methods (Hämäläinen et al., 1993; Paetau, 2002; Sato, Balish, & Muratore, 1991). In this appendix we briefly describe the basics of MEG theory and methodology to provide the reader with a framework in which to interpret the data presented in this thesis.

Neurophysiological basis of MEG signal

MEG measures weak magnetic fields (on the order of 10^{-14} Tesla) arising from thousands of synchronously active neurons in the brain. According to Maxwell's equations, a moving electric charge always generates a magnetic field oriented perpendicularly to the direction of the movement. The sources of MEG signals are thought to be post-synaptic currents within the apical dendrites of pyramidal neurons in the cerebral cortex (Fig. A.1). These so called primary currents, $\bar{j}^{p}$, are oriented perpendicular to the cortical surface. Sources that are radial, that is oriented perpendicular to the skull surface, do not produce an appreciable magnetic field outside of the head; The percentage of sources that are strictly radial is small.

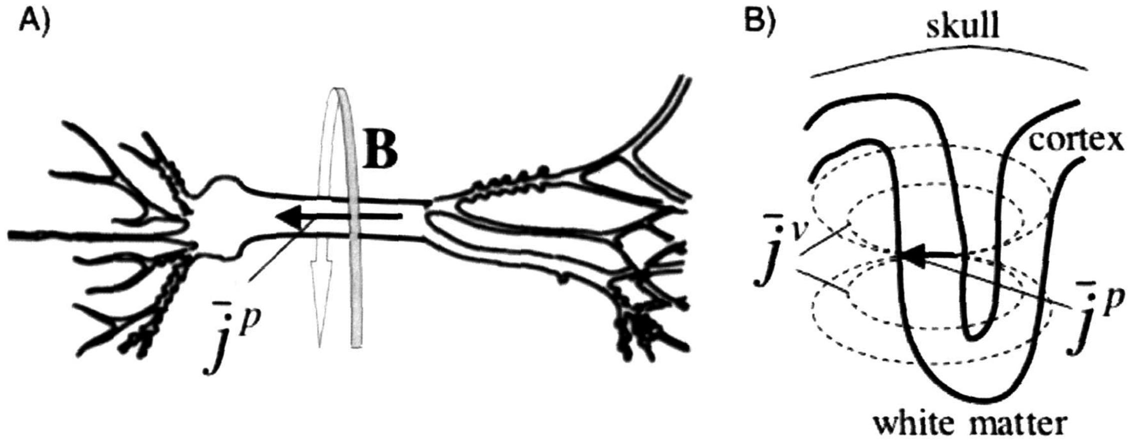

Figure A.1: A) The intracellular current, $\bar{j}^p$, in an apical dendrite of a pyramidal cell surrounded with a surrounding magnetic field **B**. B) The externally recorded magnetic signals arise from the active primary currents ($\bar{j}^p$) as well as the associated passive (ohmic) volume currents ($\bar{j}^v$) [Adapted from Paetau, 2002].

MEG methods

MEG signals from the brain are much smaller than the magnetic fields generated by external environmental sources. Hence, MEG measurements are usually carried out in a magnetically shielded room using sensitive detectors of magnetic flux called superconducting quantum interference devices (SQUIDs) (Zimmerman, Thiene, & Harding, 1970). The first MEG measurement of brain activity using a SQUID sensor was conducted at MIT (Cohen, 1972).

In modern whole-head MEG devices, several hundreds of sensors are immersed in a liquid helium dewar, which is helmet-shaped and encloses most of the head (Fig. A.2A). This arrangement of MEG sensors allows for identification of simultaneous signals from multiple brain regions. The sensors are typically 3-4 cm from the cortical surface depending on the subject's head position. Most MEG systems are designed for use with adults. Hence, the distance between the MEG sensors and the cortical sources may be further in children with smaller head sizes. Each of the 102 sensor elements in the MEG device used in the present thesis (Fig. A.2B: squares) contained one axial magnetometer and two orthogonally-oriented planar gradiometers.

Gradiometers are differential sensors, which maximally detect signals from sources directly below the sensors, and are generally insensitive to sources far away from the sensors. In contrast, magnetometers are more sensitive to deep sources than gradiometers are.

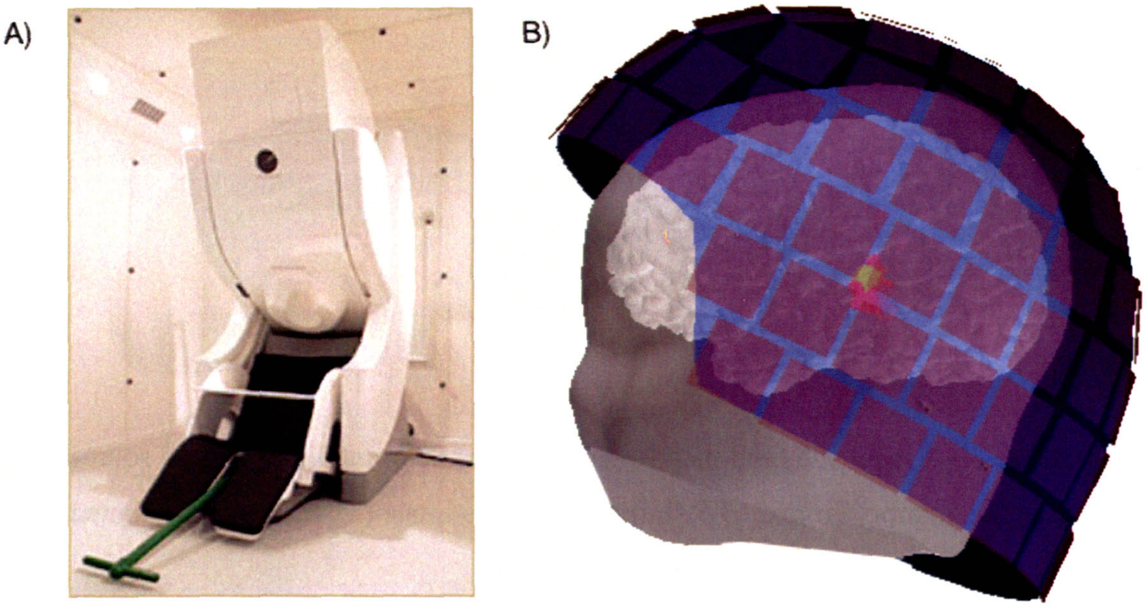

Figure A.2: A) The Elekta-Neuromag™ 306-channel MEG device. B) The scalp surface for a child is shown within a representation of a helmet-shaped array of MEG sensor elements (purple squares). The scalp surface is transparent to reveal the estimated brain activation in the left superior temporal cortex.

MEG experiments are typically designed to examine either spontaneous activity, e.g., for detection of epileptic spikes, or evoked activity that is time-locked to the presentation of a stimulus (as in the present thesis). An important goal of MEG data analysis is to estimate the spatiotemporal distribution of the neural currents giving rise to the observed MEG signals by solving the 'inverse problem'. The inverse problem is ill-posed as there are an infinite number of primary (source) current distributions that result in the same field pattern (Sarvas, 1987). Therefore, the brain sources must be appropriately modeled and additional constraints must be employed, e.g., obtained from magnetic resonance imaging (MRI), to eliminate unrealistic solutions. An equivalent current dipole (ECD) is a good approximation for a small region of activated cortex (Fig. A.3A). More complicated source configurations can be modeled using multi-dipole models. Alternatively, a distributed solution such as the minimum norm estimate (MNE) (Hämäläinen & Ilmoniemi, 1994), may provide a better approximation of widespread activation (Fig A.3B). The location of an ECD or MNE activation can be viewed on a subject's MRI. Fiducial points on the head are usually digitized at the beginning of the experiment for alignment of the MEG data with the MRI.

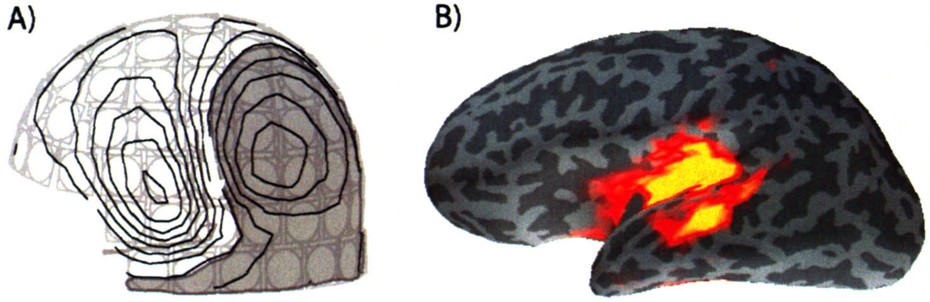

Figure A.3: A) A magnetic field map for an equivalent current dipole (ECD) source located in the auditory cortex. B) Minimum norm estimate (MNE) for a distributed source in the superior temporal cortex.

Differences between MEG and EEG

Although both MEG and EEG signals reflect activity from similar sources in the brain, the two methods are complementary in that they sample the underlying primary currents differently (Cohen, 1999). For example, MEG is primarily sensitive to tangentially-oriented sources, whereas EEG is sensitive to both tangential and radial sources. In addition, the EEG signal is more susceptible to spatial distortion due to the inhomogeneous tissue conductivities of different brain layers such as the cerebrospinal fluid, skull, and scalp. In contrast, the magnetic fields are not distorted as they pass through the head, and the MEG signals are less affected by inhomogeneities in the skull. Head movements may occur when recording from children, particularly if the head is considerably smaller than the measurement helmet containing the MEG sensors. An advantage of EEG is that the electrodes are fixed to the head, and therefore EEG, unlike MEG is insensitive to head motion during the recording. Together these differences between EEG and MEG suggest that simultaneous EEG and MEG recordings are warranted whenever possible.

Bibliography

Ackerman, P. T., & Dykman, R. A. (1993). Phonological processes, confrontation naming, and immediate memory in dyslexia. *Journal of Learning Disabilities, 26*, 597-609.

Adlard, A., & Hazan, V. (1998). Speech perception in children with specific reading difficulties (dyslexia). *Quarterly Journal of Experimental Psychology A, 51*, 153-177.

Alho, K., Winkler, I., Escera, C., Huotilainen, M., Virtanen, J., Jääskeläinen, I. P., Pekkonen, E., & Ilmoniemi, R. J. (1998). Processing of novel sounds and frequency changes in the human auditory cortex: magnetoencephalographic recordings. *Psychophysiology, 35*, 211-224.

Annett, M. (1970). A classification of hand preference by association analysis. *British Journal of Psychology, 61*, 303-321.

ANSI. (1989). Specifications for audiometers, *S3.6*. New York: American National Standards Institute.

Berger, H. (1929). Uber das Elektrekephalogramm des Menschen. *Archiv fur Psychiatrie und Nervenkrankheiten, 87*, 527-570.

Bernal, J., Harmony, T., Rodriguez, M., Reyes, A., Yanez, G., Fernandez, T., Galan, L., Silva, J., Fernandez- Bouzas, A., Rodriguez, H., Guerrero, V., & Marosi, E. (2000). Auditory event-related potentials in poor readers. *International Journal of Psychophysiology, 36*, 11-23.

Binder, J. R., Frost, J. A., Hammeke, T. A., Bellgowan, P. S., Springer, J. A., Kaufman, J. N., & Possing, E. T. (2000). Human temporal lobe activation by speech and nonspeech sounds. *Cerebral Cortex, 10*, 512-528.

Bird, J., & Bishop, D. V. (1992). Perception and awareness of phonemes in phonologically impaired children. *European Journal of Disorders of Communication, 27*, 289-311.

Bishop, D. V., Carlyon, R. P., Deeks, J. M., & Bishop, S. J. (1999). Auditory temporal processing impairment: neither necessary nor sufficient for causing language impairment in children. *Journal of Speech, Language, and Hearing Research, 42*, 1295-1310.

Blalock, J. W. (1982). Persistent auditory language deficits in adults with learning disabilities. *Journal of Learning Disabilities, 15*, 604-609.

Boada, R., & Pennington, B. F. (2006). Deficient implicit phonological representations in children with dyslexia. *Journal of Experimental Child Psychology, 95*, 153-193.

Bonte, M. L., & Blomert, L. (2004). Developmental dyslexia: ERP correlates of anomalous phonological processing during spoken word recognition. *Brain Research: Cognitive Brain Research, 21*, 360-376.

Bonte, M. L., Poelmans, H., & Blomert, L. (2007). Deviant neurophysiological responses to phonological regularities in speech in dyslexic children. *Neuropsychologia, 45*, 1427-1437.

Bowers, P. G., Sunseth, K., & Golden, J. (1999). The route between rapid naming and reading progress. *Scientific Studies of Reading, 3*, 31-53.

Bowers, P. G., & Swanson, L. B. (1991). Naming speed deficits in reading disability: multiple measures of a singular process. *Journal of Experimental Child Psychology, 51*, 195-219.

Bradley, L., & Bryant, P. (1983). Categorizing sounds and learning to read - a causal connection. *Nature, 301*, 419-421.

Bradley, L., & Bryant, P. (1991). Phonological skills before and after learning to read. In S. Brady & D. Shankweiler (Eds.), *Phonological processes in literacy: A tribute to Isabelle Y. Liberman* (pp. 37-45). Hillsdale, N.J.: Erlbaum.

Bradlow, A. R., Kraus, N., Nicol, T. G., McGee, T. J., Cunningham, J., Zecker, S. G., & Carrell, T. D. (1999). Effects of lengthened formant transition duration on discrimination and neural representation of synthetic CV syllables by normal and learning-disabled children. *Journal of Acoustical Society of America, 106*, 2086-2096.

Brady, S., Mann, V., & Schmidt, R. (1987). Errors in short-term memory for good and poor readers. *Memory and Cognition, 15*, 444-453.

Brady, S., Shankweiler, D., & Mann, V. (1983). Speech perception and memory coding in relation to reading ability. *Journal of Experimental Child Psychology, 35*, 345-367.

Brandt, J., & Rosen, J. J. (1980). Auditory phonemic perception in dyslexia: categorical identification and discrimination of stop consonants. *Brain and Language, 9*, 324-337.

Breier, J. I., Gray, L., Fletcher, J. M., Diehl, R. L., Klaas, P., Foorman, B. R., & Molis, M. R. (2001). Perception of voice and tone onset time continua in children with dyslexia with and without attention deficit/hyperactivity disorder. *Journal of Experimental Child Psychology, 80*, 245-270.

Breier, J. I., Simos, P. G., Fletcher, J. M., Castillo, E. M., Zhang, W., & Papanicolaou, A. C. (2003). Abnormal activation of temporoparietal language areas during phonetic analysis in children with dyslexia. *Neuropsychology, 17*, 610-621.

Breznitz, Z., & Meyler, A. (2003). Speed of lower-level auditory and visual processing as a basic factor in dyslexia: electrophysiological evidence. *Brain and Language, 85*, 166-184.

Brown, C. M., Hagoort, P., & Chwilla, D. J. (2000). An event-related brain potential analysis of visual word priming effects. *Brain and Language, 72*, 158-190.

Brown, L., Sherbenou, R. J., & Johnsen, S. K. (1997). Test of Nonverbal Intelligence, Third Edition. Austin, TX: PRO-ED, Inc.

Brown, W. E., Eliez, S., Menon, V., Rumsey, J. M., White, C. D., & Reiss, A. L. (2001). Preliminary evidence of widespread morphological variations of the brain in dyslexia. *Neurology, 56*, 781-783.

Bruck, M. (1992). Persistence of dyslexics' phonological awareness deficits. *Developmental Psychology, 28*, 874-886.

Buchel, C., Price, C., & Friston, K. (1998). A multimodal language region in the ventral visual pathway. *Nature, 394*, 274-277.

Byrne, B., & Shea, P. (1979). Semantic and phonetic memory codes in beginning readers. *Memory and Cognition, 7*, 333-338.

Castillo, E. M., Simos, P. G., Davis, R. N., Breier, J., Fitzgerald, M. E., & Papanicolaou, A. C. (2001). Levels of word processing and incidental memory: dissociable mechanisms in the temporal lobe. *Neuroreport, 12*, 3561-3566.

Catts, H. W. (1989). Speech production deficits in developmental dyslexia. *Journal of Speech & Hearing Disorders, 54*, 422-428.

Catts, H. W., Gillispie, M., Leonard, L. B., Kail, R. V., & Miller, C. A. (2002). The role of speed of processing, rapid naming, and phonological awareness in reading achievement. *Journal of Learning Disabilities, 35*, 509-524.

Celesia, G. G. (1976). Organization of auditory cortical areas in man. *Brain, 99*, 403-414.

Ceponiene, R., Rinne, T., & Näätänen, R. (2002). Maturation of cortical sound processing as indexed by event-related potentials. *Clinical Neurophysiology, 113*, 870-882.

Charles-Luce, J., & Luce, P. A. (1990). Similarity neighbourhoods of words in young children's lexicons. *Journal of Child Language, 17*, 205-215.

Chiappe, P., Chiappe, D. L., & Gottardo, A. (2004). Vocabulary, Context, and Speech Perception Among Good and Poor Readers. *Educational Psychology, 24*, 825-843.

Chiappe, P., Chiappe, D. L., & Siegel, L. S. (2001). Speech perception, lexicality, and reading skill. *Journal of Experimental Child Psychology, 80*, 58-74.

Chomsky, N., & Halle, M. (1968). *The sound pattern of English*. New York: Harper & Row.

Coch, D., Grossi, G., Coffey-Corina, S., Holcomb, P. J., & Neville, H. J. (2002). A developmental investigation of ERP auditory rhyming effects. *Developmental Science, 5*, 467-489.

Coch, D., & Holcomb, P. J. (2003). The N400 in beginning readers. *Developmental Psychobiology, 43*, 146-166.

Coch, D., Maron, L., Wolf, M., & Holcomb, P. J. (2002). Word and picture processing in children: an event-related potential study. *Developmental Neuropsychology, 22*, 373-406.

Cohen, D. (1972). Magnetoencephalography: detection of the brain's electrical activity with a superconducting magnetometer. *Science, 175*, 664-666.

Cohen, D. (1999). Magnetoencephalography (neuromagnetism). In G. Adelman & B. H. Smith (Eds.), *Elsevier's Encyclopedia of Neuroscience* (2nd enlarged and revised edition ed., pp. 1079-1083): Elsevier Science B.V.

Cole, R. A., & Perfetti, C. A. (1980). Listening for mispronunciations in a children's story: The use of context by children and adults. *Journal of Verbal Learning and Verbal Behavior, 19*, 297-315.

Connolly, J. F., & Phillips, N. A. (1994). Event-related potential components reflect phonological and semantic processing of the terminal word of spoken sentences. *Journal of Cognitive Neuroscience, 6*, 256-266.

Connolly, J. F., Phillips, N. A., Stewart, S. H., & Brake, W. G. (1992). Event-related potential sensitivity to acoustic and semantic properties of terminal words in sentences. *Brain and Language, 43*, 1-18.

Connolly, J. F., Service, E., D'Arcy, R. C., Kujala, A., & Alho, K. (2001). Phonological aspects of word recognition as revealed by high-resolution spatio-temporal brain mapping. *Neuroreport, 12*, 237-243.

Connolly, J. F., Stewart, S. H., & Phillips, N. A. (1990). The effects of processing requirements on neurophysiological responses to spoken sentences. *Brain and Language, 39*, 302-318.

Corina, D. P., Richards, T. L., Serafini, S., Richards, A. L., Steury, K., Abbott, R. D., Echelard, D. R., Maravilla, K. R., & Berninger, V. W. (2001). fMRI auditory language differences between dyslexic and able reading children. *Neuroreport, 12*, 1195-1201.

D'Arcy, R. C., Connolly, J. F., Service, E., Hawco, C. S., & Houlihan, M. E. (2004). Separating phonological and semantic processing in auditory sentence processing: a high-resolution event-related brain potential study. *Human Brain Mapping, 22*, 40-51.

Dale, A. M., Fischl, B., & Sereno, M. I. (1999). Cortical surface-based analysis. I. Segmentation and surface reconstruction. *Neuroimage, 9*, 179-194.

Dale, A. M., Liu, A. K., Fischl, B. R., Buckner, R. L., Belliveau, J. W., Lewine, J. D., & Halgren, E. (2000). Dynamic statistical parametric mapping: combining fMRI and MEG for high-resolution imaging of cortical activity. *Neuron, 26*, 55-67.

de Gelder, B., & Vroomen, J. (1991). Phonological deficits: beneath the surface of reading acquisition. *Psychological Research, 53*, 88-97.

de Jong, P. F., & Olson, R. K. (2004). Early predictors of letter knowledge. *Journal of Experimental Child Psychology, 88*, 254-273.

Deacon, D., Hewitt, S., Yang, C., & Nagata, M. (2000). Event-related potential indices of semantic priming using masked and unmasked words: evidence that the N400 does not reflect a post-lexical process. *Brain Research: Cognitive Brain Research, 9*, 137-146.

Dell, G. S. (1986). A spreading-activation theory of retrieval in sentence production. *Psychological Review, 93*, 283-321.

Diaz, M. T., & Swaab, T. Y. (2006). Electrophysiological differentiation of phonological and semantic integration in word and sentence contexts. *Brain Research.*

Dunn, L. M., & Dunn, L. M. (1997). Peabody Picture Vocabulary Test, Third Edition. Circle Pines, MN: American Guidance Service, Inc.

Edwards, M. L. (1974). Perception and production in child phonology. *Journal of Child Language, 1*, 205-219.

Elbro, C. (1998). When reading is "readn" or somthn. Distinctness of phonological representations of lexical items in normal and disabled readers. *Scandinavian Journal of Psychology, 39*, 149-153.

Elbro, C., Borstrøm, I., & Petersen, D. K. (1998). Predicting dyslexia from kindergarten: The importance of distinctness of phonological representations of lexical items. *Reading Research Quarterly, 33*, 36-60.

Elbro, C., & Jensen, M. N. (2005). Quality of phonological representations, verbal learning, and phoneme awareness in dyslexic and normal readers. *Scandinavian Journal of Psychology, 46*, 375-384.

Ellis, N. (1981). Visual and name coding in dyslexic children. *Psychological Research, 43*, 201-218.

Farmer, M. E., & Klein, R. M. (1995). The evidence for a temporal processing deficit linked to dyslexia: A review. *Psychonomic Bulletin and Review, 2*, 460-493.

Fawcett, A. J., & Nicolson, R. I. (1992). Automatisation deficits in balance for dyslexic children. *Perceptual and Motor Skills, 75*, 507-529.

Fawcett, A. J., & Nicolson, R. I. (1994). Naming speed in children with dyslexia. *Journal of Learning Disabilities, 27*, 641-646.

Fawcett, A. J., & Nicolson, R. I. (1999). Performance of Dyslexic Children on Cerebellar and Cognitive Tests. *Journal of Motor Behavior, 31*, 68-78.

Fischl, B., Sereno, M. I., & Dale, A. M. (1999). Cortical surface-based analysis. II: Inflation, flattening, and a surface-based coordinate system. *Neuroimage, 9*, 195-207.

Fletcher, J. M., Shaywitz, S. E., Shankweiler, D. P., Katz, L., Liberman, I. Y., Stuebing, K. K., Francis, D. J., Fowler, A. E., & Shaywitz, B. A. (1994). Cognitive profiles of reading disability: Comparisons of discrepancy and low-achievement definitions. *Journal of Educational Psychology, 86*, 6-23.

Flowers, D. L. (1995). Neuropsychological profiles of persistent reading disability and reading improvement. In C. K. Leong & R. M. Joshi (Eds.), *Developmental and acquired dyslexia* (pp. 61-77). Dordrecht: Kluwer Academic Publishers.

Fowler, A. E. (1991). How early phonological development might set the stage for phoneme awareness. In S. Brady & D. Shankweiler (Eds.), *Phonological processes in literacy: A tribute to Isabelle Y. Liberman* (pp. 97-117). Hillsdale, NJ: Erlbaum.

Fowler, A. E., & Swainson, B. (2004). Relationships of naming skills to reading, memory, and receptive vocabulary: evidence for imprecise phonological representations of words by poor readers. *Annals of Dyslexia, 54*, 247-280.

Foy, J. G., & Mann, V. (2001). Does strength of phonological representations predict phonological awareness in preschool children? *Applied Psycholinguistics, 22*, 301-325.

Francis, W. N., & Kucera, H. (1982). *Frequency analysis of english usage: Lexicon and grammar*. Boston: Houghton Mifflin.

Friederici, A. D., Gunter, T. C., Hahne, A., & Mauth, K. (2004). The relative timing of syntactic and semantic processes in sentence comprehension. *Neuroreport, 15*, 165-169.

Frith, U., & Snowling, M. (1983). Reading for meaning and reading for sound in autistic and dyslexic children. *British Journal of Developmental Psychology, 1*, 329-342.

Galaburda, A. M., Menard, M. T., & Rosen, G. D. (1994). Evidence for aberrant auditory anatomy in developmental dyslexia. *Proceedings of the National Academy of Sciences USA, 91*, 8010-8013.

Gallagher, A. M., Laxon, V., Armstrong, E., & Frith, U. (1996). Phonological difficulties in high-functioning dyslexics. *Reading and Writing: An Interdisciplinary Journal, 8*, 499-509.

Garlock, V. M., Walley, A. C., & Metsala, J. L. (2001). Age-of-acquisition, word frequency and neighborhood density effects on spoken word recognition: Implications for the development of phoneme awareness and early reading ability. *Journal of Memory and Language, 45*, 468-492.

Garnica, O. K. (1973). The development of phonemic speech perception. In T. E. Moore (Ed.), *Cognitive development and the acquisition of language* (pp. 215-222). New York: Academic Press.

Gaskell, M. G., & Marslen-Wilson, W. D. (2002). Representation and competition in the perception of spoken words. *Cognitive Psychology, 45*, 220-266.

Georgiewa, P., Rzanny, R., Hopf, J. M., Knab, R., Glauche, V., Kaiser, W. A., & Blanz, B. (1999). fMRI during word processing in dyslexic and normal reading children. *Neuroreport, 10*, 3459-3465.

Geschwind, N. (1965). Disconnection syndromes in animals and man. *Brain, 88*, 237-294.

Giard, M. H., Perrin, F., Pernier, J., & Bouchet, P. (1990). Brain generators implicated in the processing of auditory stimulus deviance: a topographic event-related potential study. *Psychophysiology, 27*, 627-640.

Godfrey, J. J., Syrdal-Lasky, A. K., Millay, K. K., & Knox, C. M. (1981). Performance of dyslexic children on speech perception tests. *Journal of Experimental Child Psychology, 32*, 401-424.

Gold, B. T., & Buckner, R. L. (2002). Common prefrontal regions coactivate with dissociable posterior regions during controlled semantic and phonological tasks. *Neuron, 35*, 803-812.

Goldsberry, G., O'Leary, D., Hichwa, R., & Nopoulos, P. (2006). Functional abnormalities in the neural circuitry of reading in men with nonsyndromic clefts of the lip or palate. *The Cleft-palate-craniofacial journal, 43*, 683-690.

Goodman, K. S. (1976). Reading: A psycholinguistic guessing game. In H. Singer & R. Ruddell (Eds.), *Theoretical models and processes of reading* (2nd Ed. ed.). Newark, Del: International Reading Association.

Goswami, U. (2000). Phonological representations, reading development and dyslexia: towards a cross-linguistic theoretical framework. *Dyslexia, 6*, 133-151.

Goswami, U. (2003). Phonology, learning to read and dyslexia: A cross-linguistic analysis. In V. Csepe (Ed.), *Dyslexia: Different brain, different behavior* (Vol. 23, pp. 1-40). New York: Kluwer Academic Publishers.

Goswami, U., & Bryant, P. (1990). *Phonological Skills and Learning to Read.* Hillsdale, NJ: Erlbaum.

Griffiths, Y. M., & Snowling, M. (2002). Predictors of exception word and nonword reading in dyslexic children: the severity hypothesis. *Journal of Educational Psychology, 1*, 34-43.

Grosjean, F. (1980). Spoken word recognition processes and the gating paradigm. *Perception and Psychophysics, 28*, 267-283.

Hagoort, P., & Brown, C. M. (2000). ERP effects of listening to speech: semantic ERP effects. *Neuropsychologia, 38*, 1518-1530.

Hahne, A., Eckstein, K., & Friederici, A. D. (2004). Brain signatures of syntactic and semantic processes during children's language development. *Journal of Cognitive Neuroscience, 16*, 1302-1318.

Halgren, E., Dhond, R. P., Christensen, N., Van Petten, C., Marinkovic, K., Lewine, J. D., & Dale, A. M. (2002). N400-like magnetoencephalography responses modulated by semantic context, word frequency, and lexical class in sentences. *Neuroimage, 17*, 1101-1116.

Halle, M. (1990). Features. In W. Bright (Ed.), *Oxford international encyclopedia of linguistics*. New York: Oxford University Press.

Halle, P. A., & de Boysson-Bardies, B. (1996). The format of representation of recognized words in the infants' early receptive lexicon. *Infant Behavior and Development, 19*, 463-481.

Hämäläinen, M. S., Hari, R., Ilmoniemi, R., Knuutila, J., & Lounasmaa, O. V. (1993). Magnetoencephalography - theory, instrumentation, and applications to noninvasive studies of the working human brain. *Reviews of Modern Physics, 65*, 413-497.

Hämäläinen, M. S., & Ilmoniemi, R. J. (1994). Interpreting magnetic fields of the brain: minimum norm estimates. *Medical and Biological Engineering and Computing, 32*, 35-42.

Hämäläinen, M. S., & Sarvas, J. (1989). Realistic conductivity geometry model of the human head for interpretation of neuromagnetic data. *IEEE Transactions on Biomedical Engineering, 36*, 165-171.

Hansen, J., & Bowey, J. (1994). Phonological analysis skills, verbal working memory, and reading ability in second grade children. *Child Development, 54*, 938-950.

Hari, R. (1990). The neuromagnetic method in the study of the human auditory cortex. In F. Grandori, M. Hoke & G. Romani (Eds.), *Auditory Evoked Magnetic Fields and Potentials: Advances in Audiology* (Vol. 6, pp. 222-282). Basel, Switzerland: Karger.

Heim, S., Eulitz, C., & Elbert, T. (2003). Altered hemispheric asymmetry of auditory N100m in adults with developmental dyslexia. *Neuroreport, 14*, 501-504.

Heim, S., Eulitz, C., Kaufmann, J., Fuchter, I., Pantev, C., Lamprecht-Dinnesen, A., Matulat, P., Scheer, P., Borstel, M., & Elbert, T. (2000). Atypical organisation of the auditory cortex in dyslexia as revealed by MEG. *Neuropsychologia, 38*, 1749-1759.

Helenius, P., Salmelin, R., Richardson, U., Leinonen, S., & Lyytinen, H. (2002). Abnormal auditory cortical activation in dyslexia 100 msec after speech onset. *Journal of Cognitive Neuroscience, 14*, 603-617.

Helenius, P., Salmelin, R., Service, E., & Connolly, J. F. (1998). Distinct time courses of word and context comprehension in the left temporal cortex. *Brain, 121 (Pt 6)*, 1133-1142.

Helenius, P., Salmelin, R., Service, E., & Connolly, J. F. (1999). Semantic cortical activation in dyslexic readers. *Journal of Cognitive Neuroscience, 11*, 535-550.

Helenius, P., Salmelin, R., Service, E., Connolly, J. F., Leinonen, S., & Lyytinen, H. (2002). Cortical activation during spoken-word segmentation in nonreading-impaired and dyslexic adults. *Journal of Neuroscience, 22*, 2936-2944.

Hill, H., Strube, M., Roesch-Ely, D., & Weisbrod, M. (2002). Automatic vs. controlled processes in semantic priming--differentiation by event-related potentials. *International Journal of Psychophysiology, 44*, 197-218.

Holcomb, P. J. (1993). Semantic priming and stimulus degradation: implications for the role of the N400 in language processing. *Psychophysiology, 30*, 47-61.

Holcomb, P. J., Ackerman, P. T., & Dykman, R. A. (1985). Cognitive event-related brain potentials in children with attention and reading deficits. *Psychophysiology, 22*, 656-667.

Holcomb, P. J., Coffey, S. A., & Neville, H. J. (1992). Visual and auditory sentence processing: A developmental analysis using event-related brain potentials. *Developmental Neuropsychology, 8*, 203-241.

Hulme, C. (1988). The implausibility of low-level visual deficits as a cause of children's reading difficulties. *Cognitive Neuropsychology, 5*, 369-374.

Hulme, C., & Snowling, M. J. (1992). Deficits in output phonology: An explanation of reading failure? *Cognitive Neuropsychology, 9*, 47-72.

Hurford, D. R., & Sanders, R. E. (1990). Assessment and remediation of a phonemic discrimination deficit in reading disabled second and fourth graders. *Journal of Experimental Child Psychology, 50*, 396-415.

Jakobson, R., Fant, C. G. M., & Halle, M. (1952). *Preliminaries to speech analysis: The distinctive features and their correlates* (No. 13). Cambridge, MA: Massachusetts Institute of Technology.

Johannes, S., Kussmaul, C. L., Munte, T. F., & Mangun, G. R. (1996). Developmental dyslexia: passive visual stimulation provides no evidence for a magnocellular processing defect. *Neuropsychologia, 34*, 1123-1127.

Jorm, A. F. (1983). Specific reading retardation and working memory: a review. *British Journal of Psychology, 74 (Pt 3)*, 311-342.

Juottonen, K., Revonsuo, A., & Lang, H. (1996). Dissimilar age influences on two ERP waveforms (LPC and N400) reflecting semantic context effect. *Brain Research: Cognitive Brain Research, 4*, 99-107.

Jusczyk, P. W., & Aslin, R. N. (1995). Infants' detection of the sound patterns of words in fluent speech. *Cognitive Psychology, 29*, 1-23.

Katz, L., Healy, A. F., & Shankweiler, D. (1983). Phonetic coding and order memory in relation to reading proficiency: A comparison of short term memory for temporal and spatial order information. *Applied Psycholinguistics, 4*, 229-250.

Katz, R. B. (1986). Phonological deficiencies in children with reading disability: evidence from an object-naming task. *Cognition, 22*, 225-257.

Katz, R. B., Shankweiler, D., & Liberman, I. Y. (1981). Memory for item order and phonetic recording in the beginning reader. *Journal of Experimental Child Psychology, 32*, 474-484.

Klatt, D. (1980). Software for a cascade/parallel formant synthesizer. *Journal of the Acoustical Society of America, 67*, 971-995.

Kraus, N., McGee, T. J., Carrell, T. D., Zecker, S. G., Nicol, T. G., & Koch, D. B. (1996). Auditory neurophysiologic responses and discrimination deficits in children with learning problems. *Science, 273*, 971-973.

Kronbichler, M., Hutzler, F., & Wimmer, H. (2002). Dyslexia: verbal impairments in the absence of magnocellular impairments. *Neuroreport, 13*, 617-620.

Kucera, H., & Francis, W. (1967). *Computational analysis of present-day American English.* Providence: Brown University Press.

Kujala, A., Alho, K., Service, E., Ilmoniemi, R. J., & Connolly, J. F. (2004). Activation in the anterior left auditory cortex associated with phonological analysis of speech input: localization of the phonological mismatch negativity response with MEG. *Brain Research: Cognitive Brain Research, 21*, 106-113.

Kuriki, S., & Murase, M. (1989). Neuromagnetic study of the auditory responses in right and left hemispheres of the human brain evoked by pure tones and speech sounds. *Experimental Brain Research, 77*, 127-134.

Kuriki, S., Okita, Y., & Hirata, Y. (1995). Source analysis of magnetic field responses from the human auditory cortex elicited by short speech sounds. *Experimental Brain Research, 104*, 144-152.

Kurtzberg, D., Vaughan, H. G., Jr., Kreuzer, J. A., & Fliegler, K. Z. (1995). Developmental studies and clinical application of mismatch negativity: problems and prospects. *Ear and Hearing, 16*, 105-117.

Kutas, M., & Hillyard, S. A. (1980). Reading senseless sentences: brain potentials reflect semantic incongruity. *Science, 207*, 203-205.

Kutas, M., & Iragui, V. (1998). The N400 in a semantic categorization task across 6 decades. *Electroencephalography and Clinical Neurophysiology, 108*, 456-471.

Kutas, M., Neville, H. J., & Holcomb, P. J. (1987). A preliminary comparison of the N400 response to semantic anomalies during reading, listening and signing. *Electroencephalography and Clinical Neurophysiology Supplement, 39*, 325-330.

Lachmann, T., Berti, S., Kujala, T., & Schroger, E. (2005). Diagnostic subgroups of developmental dyslexia have different deficits in neural processing of tones and phonemes. *International Journal of Psychophysiology, 56*, 105-120.

Lahiri, A., & Marslen-Wilson, W. (1991). The mental representation of lexical form: a phonological approach to the recognition lexicon. *Cognition, 38*, 245-294.

Lawson, E. A., & Gaillard, A. W. (1981). Mismatch negativity in a phonetic discrimination task. *Biological Psychology, 13*, 281-288.

Leonard, C. M., Eckert, M. A., Lombardino, L. J., Oakland, T., Kranzler, J., Mohr, C. M., King, W. M., & Freeman, A. (2001). Anatomical risk factors for phonological dyslexia. *Cerebral Cortex, 11*, 148-157.

Leppänen, P. H., Richardson, U., Pihko, E., Eklund, K. M., Guttorm, T. K., Aro, M., & Lyytinen, H. (2002). Brain responses to changes in speech sound durations differ between infants with and without familial risk for dyslexia. *Developmental Neuropsychology, 22*, 407-422.

Liberman, A. M. (1973). Segmentation of the spoken word. *Bulletin of the Orton Society, 23*, 65-77.

Liberman, I. Y., Shankweiler, D., Liberman, A. M., Fowler, C., & Fischer, F. W. (1977). Phonetic segmentation and recoding in the beginning reader. In A. S. Reber & D. Scarborough (Eds.), *Toward a psychology of reading: The proceedings of the CUNY Conference*. Hillsdale, N.J.: Erlbaum.

Liegeois-Chauvel, C., Musolino, A., Badier, J. M., Marquis, P., & Chauvel, P. (1994). Evoked potentials recorded from the auditory cortex in man: evaluation and topography of the middle latency components. *Electroencephalography and Clinical Neurophysiology, 92*, 204-214.

Lin, F. H., Belliveau, J. W., Dale, A. M., & Hämäläinen, M. S. (2006). Distributed current estimates using cortical orientation constraints. *Human Brain Mapping, 27*, 1-13.

Lin, F. H., Witzel, T., Ahlfors, S. P., Stufflebeam, S. M., Belliveau, J. W., & Hämäläinen, M. S. (2006). Assessing and improving the spatial accuracy in MEG source localization by depth-weighted minimum-norm estimates. *Neuroimage, 15*, 160-171.

Livingstone, M. S., Rosen, G. D., Drislane, F. W., & Galaburda, A. M. (1991). Physiological and anatomical evidence for a magnocellular defect in developmental dyslexia. *Proceedings of the National Academy of Sciences USA, 88*, 7943-7947.

Lutkenhoner, B., & Steinstrater, O. (1998). High-precision neuromagnetic study of the functional organization of the human auditory cortex. *Audiology and Neurootology, 3*, 191-213.

Macaruso, P., Locke, J. L., Smith, S. T., & Powers, S. (1996). Short-term memory and phonological coding in developmental dyslexia. *Journal of Neurolinguisitics, 9*, 135-146.

Maess, B., Herrmann, C. S., Hahne, A., Nakamura, A., & Friederici, A. D. (2006). Localizing the distributed language network responsible for the N400 measured by MEG during auditory sentence processing. *Brain Research, 1096*, 163-172.

Makela, A. M., Makinen, V., Nikkila, M., Ilmoniemi, R. J., & Tiitinen, H. (2001). Magnetoencephalographic (MEG) localization of the auditory N400m: effects of stimulus duration. *Neuroreport, 12*, 249-253.

Manis, F. R., McBride-Chang, C., Seidenberg, M. S., Keating, P., Doi, L. M., Munson, B., & Petersen, A. (1997). Are speech perception deficits associated with developmental dyslexia? *Journal of Experimental Child Psychology, 66*, 211-235.

Mann, V. A., Liberman, I. Y., & Shankweiler, D. (1980). Children's memory for sentences and word strings in relation to reading ability. *Memory and Cognition, 8*, 329-335.

Marinkovic, K., Dhond, R. P., Dale, A. M., Glessner, M., Carr, V., & Halgren, E. (2003). Spatiotemporal dynamics of modality-specific and supramodal word processing. *Neuron, 38*, 487-497.

Mark, L. S., Shankweiler, D., Liberman, I. Y., & Fowler, C. (1977). Phonetic recoding and reading difficulty in beginning readers. *Memory and Cognition, 5*, 623-629.

Marslen-Wilson, W., & Tyler, L. K. (1980). The temporal structure of spoken language understanding. *Cognition, 8*, 1-71.

McAnally, K. I., Hansen, P. C., Cornelissen, P. L., & Stein, J. F. (1997). Effect of time and frequency manipulation on syllable perception in developmental dyslexics. *Journal of Speech, Language, and Hearing Research, 40*, 912-924.

McBride-Chang, C. (1995). Phonological Processing, Speech Perception, and Reading Disability: An Integrative Review. *Educational Psychologist, 30*, 109-121.

McCardle, P., Scarborough, H. S., & Catts, H. W. (2001). Predicting, explaining, and preventing children's reading difficulties. *Learning Disabilities Research & Practice, 16*, 230-239.

McCarthy, G., Nobre, A. C., Bentin, S., & Spencer, D. D. (1995). Language-related field potentials in the anterior-medial temporal lobe: I. Intracranial distribution and neural generators. *Journal of Neuroscience, 15*, 1080-1089.

McDougall, S., Hulme, C., Ellis, A., & Monk, A. (1994). Learning to read: the role of short-term memory and phonological skills. *Journal of Experimental Child Psychology, 58*, 112-133.

McElree, B., & Griffith, T. (1995). Syntactic and thematic processing in sentence comprehension: Evidence for a temporal dissociation. *Journal of Experimental Psychology: Learning Memory and Cognition, 21*, 134-157.

McGuinness, D. (2005). *Language Development and Learning to Read.* Cambridge, MA: MIT Press.

McPherson, W. B., Ackerman, P. T., Holcomb, P. J., & Dykman, R. A. (1998). Event-related brain potentials elicited during phonological processing differentiate subgroups of reading disabled adolescents. *Brain and Language, 62*, 163-185.

Metsala, J. L. (1997). Spoken word recognition in reaing disabled children. *Journal of Educational Psychology, 89*, 159-169.

Metsala, J. L., & Walley, A. C. (1998). Spoken vocabulary growth and the segmental restructuring of lexical representations: Precursors to phonemic awareness and early reading ability. In J. L. Metsala & L. C. Ehri (Eds.), *Word Recognition in Beginning Literacy* (pp. 89-120). Mahwah, NJ: LEA.

Miles, T. (1974). *Understanding dyslexia.* London: Priory Press.

Mody, M. (2003). Phonological basis in reading disability: A review and analysis of the evidence. *Reading and Writing: An Interdisciplinary Journal, 16*, 21-39.

Mody, M. (2004). Neurobiological Correlates of Language and Reading Impairments. In C. A. Stone, E. Silliman, B. Ehren & K. Apfel (Eds.), *Handbook of Language and Literacy: Development and Disorders* (pp. 49-72). New York, NY: Guilford Press.

Mody, M., Studdert-Kennedy, M., & Brady, S. (1997). Speech perception deficits in poor readers: auditory processing or phonological coding? *Journal of Experimental Child Psychology, 64*, 199-231.

Morais, J. (2003). Levels of phonological representation in skilled reading and in learning to read. *Reading and Writing: An Interdisciplinary Journal, 16*, 123-151.

Morrison, F. J., Giordani, B., & Nagy, J. (1977). Reading disability: an information-processing analysis. *Science, 196*, 77-79.

Muter, V., Hulme, C., Snowling, M. J., & Stevenson, J. (2004). Phonemes, rimes, vocabulary, and grammatical skills as foundations of early reading development: evidence from a longitudinal study. *Developmental Neuropsychology, 40*, 665-681.

Näätänen, R. (1992). *Attention and brain function.* Hillsdale, NJ: Erlbaum.

Näätänen, R., & Picton, T. (1987). The N1 wave of the human electric and magnetic response to sound: a review and an analysis of the component structure. *Psychophysiology, 24*, 375-425.

Näätänen, R., & Picton, T. W. (1986). N2 and automatic versus controlled processes. *Electroencephalography and Clinical Neurophysiology Supplement, 38*, 169-186.

Nagarajan, S., Mahncke, H., Salz, T., Tallal, P., Roberts, T., & Merzenich, M. M. (1999). Cortical auditory signal processing in poor readers. *Proceedings of the National Academy of Sciences USA, 96*, 6483-6488.

Nation, K., & Snowling, M. J. (1998). Individual differences in contextual facilitation: evidence from dyslexia and poor reading comprehension. *Child Development, 69*, 996-1011.

Nation, K., & Snowling, M. J. (2004). Beyond phonological skills: broader language skills contribute to the development of reading. *Journal of Research in Reading, 27*, 342-356.

Neville, H. J., Coffey, S. A., Holcomb, P. J., & Tallal, P. (1993). The Neurobiology of Sensory and Language Processing in Language-Impaired Children. *Journal of Cognitive Neuroscience, 5*, 235-253.

Neville, H. J., Nicol, J., Brass, A., Forster, K. I., & Garrett, M. F. (1991). Syntactically based processing clauses: evidence from event-related potentials. *Journal of Cognitive Neuroscience, 3*, 151-165.

Newman, R. L., Connolly, J. F., Service, E., & McIvor, K. (2003). Influence of phonological expectations during a phoneme deletion task: evidence from event-related brain potentials. *Psychophysiology, 40*, 640-647.

Nicolson, R. I., & Fawcett, A. J. (1990). Automaticity: a new framework for dyslexia research? *Cognition, 35*, 159-182.

Nicolson, R. I., & Fawcett, A. J. (1996). Impaired performance of children with dyslexia on a range of cerebellar tasks. *Annals of Dyslexia, 46*, 259-283.

Nicolson, R. I., Fawcett, A. J., & Dean, P. (2001). Developmental dyslexia: the cerebellar deficit hypothesis. *Trends in Neuroscience, 24*, 508-511.

Nittrouer, S. (1992). Age-related differences in perceptual effects of formant transitions within syllables and across syllable boundaries. *Journal of Phonetics, 20*, 351-382.

Nittrouer, S. (1999). Do temporal processing deficits cause phonological processing problems? *Journal of Speech, Language, and Hearing Research, 42*, 925-942.

Nittrouer, S., & Studdert-Kennedy, M. (1987). The role of coarticulatory effects in the perception of fricatives by children and adults. *Journal of Speech, Language, and Hearing Research, 30*, 319-329.

Nobre, A. C., & McCarthy, G. (1995). Language-related field potentials in the anterior-medial temporal lobe: II. Effects of word type and semantic priming. *Journal of Neuroscience, 15*, 1090-1098.

Okada, K., & Hickok, G. (2006). Identification of lexical-phonological networks in the superior temporal sulcus using functional magnetic resonance imaging. *Neuroreport, 17*, 1293-1296.

Opitz, B., Mecklinger, A., Von Cramon, D. Y., & Kruggel, F. (1999). Combining electrophysiological and hemodynamic measures of the auditory oddball. *Psychophysiology, 36*, 142-147.

Paavilainen, P., Alho, K., Reinikainen, K., Sams, M., & Näätänen, R. (1991). Right hemisphere dominance of different mismatch negativities. *Electroencephalography and Clinical Neurophysiology, 78*, 466-479.

Paetau, R. (2002). Magnetoencephalography in pediatric neuroimaging. *Developmental Science, 5*, 361-370.

Paulesu, E., Frith, U., Snowling, M., Gallagher, A., Morton, J., Frackowiak, R. S., & Frith, C. D. (1996). Is developmental dyslexia a disconnection syndrome? Evidence from PET scanning. *Brain, 119 (Pt 1)*, 143-157.

Pennington, B. F., Van Orden, G. C., Smith, S. D., Green, P. A., & Haith, M. M. (1990). Phonological processing skills and deficits in adulty dyslexics. *Child Development, 61*, 1753-1778.

Perfetti, C. A. (1985). *Reading ability*. New York: Oxford University Press.

Perfetti, C. A. (1995). Cognitive research can inform reading education. *Journal of Research in Reading, 18*, 106-115.

Perfetti, C. A., Goldman, S. R., & Hogaboam, T. W. (1979). Reading skill and the identification of words in discourse context. *Memory and Cognition, 7*, 273-282.

Perfetti, C. A., & Roth, S. F. (1981). Some of the interactive processes in reading and their role in reading skill. In A. M. Lesgold & C. A. Perfetti (Eds.), *Interactive Processes in Reading*. Hillsdale, NJ: Lawrence Erlbaum Associates.

Perrin, F., & Garcia-Larrea, L. (2003). Modulation of the N400 potential during auditory phonological/semantic interaction. *Brain Research: Cognitive Brain Research, 17*, 36-47.

Phillips, N. A., Klein, D., Mercier, J., & de Boysson, C. (2006). ERP measures of auditory word repetition and translation priming in bilinguals. *Brain Research, 1125*, 116-131.

Poeppel, D., Yellin, E., Phillips, C., Roberts, T. P., Rowley, H. A., Wexler, K., & Marantz, A. (1996). Task-induced asymmetry of the auditory evoked M100 neuromagnetic field elicited by speech sounds. *Brain Research: Cognitive Brain Research, 4*, 231-242.

Poldrack, R. A., Temple, E., Protopapas, A., Nagarajan, S., Tallal, P., Merzenich, M., & Gabrieli, J. D. (2001). Relations between the neural bases of dynamic auditory processing and phonological processing: evidence from fMRI. *Journal of Cognitive Neuroscience, 13*, 687-697.

Poldrack, R. A., Wagner, A. D., Prull, M. W., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. (1999). Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. *Neuroimage, 10*, 15-35.

Praamstra, P., Meyer, A. S., & Levelt, W. J. M. (1994). Neurophysiological Manifestations of Phonological Processing - Latency Variation of a Negative Erp Component Timelocked to Phonological Mismatch. *Journal of Cognitive Neuroscience, 6*, 204-219.

Price, C. J., & Devlin, J. T. (2004). The pro and cons of labelling a left occipitotemporal region: "the visual word form area". *Neuroimage, 22*, 477-479.

Pugh, K. R., Mencl, W. E., Jenner, A. R., Katz, L., Frost, S. J., Lee, J. R., Shaywitz, S. E., & Shaywitz, B. A. (2000). Functional neuroimaging studies of reading and reading disability (developmental dyslexia). *Mental Retardation and Developmental Disability Research Reviews, 6*, 207-213.

Pugh, K. R., Mencl, W. E., Jenner, A. R., Katz, L., Frost, S. J., Lee, J. R., Shaywitz, S. E., & Shaywitz, B. A. (2001). Neurobiological studies of reading and reading disability. *Journal of Communication Disorders, 34*, 479-492.

Pulvermüller, F. (1999). Words in the brain's language. *Behavioral and Brain Sciences, 22*, 253-279; discussion 280-336.

Rack, J. P., Snowling, M. J., & Olson, R. K. (1992). The nonword reading deficit in developmental dyslexia: A review. *Reading Research Quarterly, 27*, 29-53.

Radeau, M., Besson, M., Fonteneau, E., & Castro, S. L. (1998). Semantic, repetition and rime priming between spoken words: behavioral and electrophysiological evidence. *Biological Psychology, 48*, 183-204.

Ramsey, N. F., Koning, H. A., Welles, P., Cahn, W., van der Linden, J. A., & Kahn, R. S. (2002). Excessive recruitment of neural systems subserving logical reasoning in schizophrenia. *Brain, 125*, 1793-1807.

Ramus, F. (2001). Dyslexia. Talk of two theories. *Nature, 412*, 393-395.

Ramus, F., Rosen, S., Dakin, S. C., Day, B. L., Castellote, J. M., White, S., & Frith, U. (2003). Theories of developmental dyslexia: insights from a multiple case study of dyslexic adults. *Brain, 126*, 841-865.

Reed, M. A. (1989). Speech perception and the discrimination of brief auditory cues in reading disabled children. *Journal of Experimental Child Psychology, 48*, 270-292.

Renvall, H., & Hari, R. (2002). Auditory cortical responses to speech-like stimuli in dyslexic adults. *Journal of Cognitive Neuroscience, 14*, 757-768.

Ritter, W., Simpson, R., Vaughan, H. G., Jr., & Friedman, D. (1979). A brain event related to the making of a sensory discrimination. *Science, 203*, 1358-1361.

Roodenrys, S., & Stokes, J. (2001). Serial recall and nonword repetition in reading disabled children. *Reading and Writing: An Interdisciplinary Journal, 14*, 379-394.

Rossell, S. L., Price, C. J., & Nobre, A. C. (2003). The anatomy and time course of semantic priming investigated by fMRI and ERPs. *Neuropsychologia, 41*, 550-564.

Ruff, S., Marie, N., Celsis, P., Cardebat, D., & Demonet, J. F. (2003). Neural substrates of impaired categorical perception of phonemes in adult dyslexics: an fMRI study. *Brain and Cognition, 53*, 331-334.

Rumsey, J. M., Andreason, P., Zametkin, A. J., Aquino, T., King, A. C., Hamburger, S. D., Pikus, A., Rapoport, J. L., & Cohen, R. M. (1992). Failure to activate the left temporoparietal cortex in dyslexia. An oxygen 15 positron emission tomographic study. *Archives of Neurology, 49*, 527-534.

Sabisch, B., Hahne, A., Glass, E., von Suchodoletz, W., & Friederici, A. D. (2006). Auditory language comprehension in children with developmental dyslexia: evidence from event-related brain potentials. *Journal of Cognitive Neuroscience, 18*, 1676-1695.

Salmelin, R., Service, E., Kiesila, P., Uutela, K., & Salonen, O. (1996). Impaired visual word processing in dyslexia revealed with magnetoencephalography. *Annals of Neurology, 40*, 157-162.

Samuel, A. G. (2001). Knowing a word affects the fundamental perception of the sounds within it. *Psychological Science, 12*, 348-351.

Sarvas, J. (1987). Basic mathematical and electromagnetic concepts of the biomagnetic inverse problem. *Physics in Medicine and Biology, 32*, 11-22.

Sato, S., Balish, M., & Muratore, R. (1991). Principles of magnetoencephalography. *Journal of Clinical Neurophysiology, 8*, 144-156.

Savage, R. (2004). Motor skills, automaticity and dyslexia: a review of the research literature. *Reading and Writing: An Interdisciplinary Journal, 17*, 301-324.

Savage, R., Frederickson, N., Goodwin, R., Patni, U., Smith, N., & Tuersley, L. (2005). Evaluating current deficit theories of poor reading: role of phonological processing, naming speed, balance automaticity, rapid verbal perception and working memory. *Percept Mot Skills, 101*, 345-361.

Scherg, M., Vajsar, J., & Picton, T. (1989). A source analysis of the late human auditory evoked potentials. *Journal of Cognitive Neuroscience, 1*, 336-355.

Schulte-Korne, G., Deimel, W., Bartling, J., & Remschmidt, H. (1998). Auditory processing and dyslexia: evidence for a specific speech processing deficit. *Neuroreport, 9*, 337-340.

Scott, S. K., Blank, C. C., Rosen, S., & Wise, R. J. (2000). Identification of a pathway for intelligible speech in the left temporal lobe. *Brain, 123 Pt 12*, 2400-2406.

Scott, S. K., & Johnsrude, I. S. (2003). The neuroanatomical and functional organization of speech perception. *Trends in Neuroscience, 26*, 100-107.

Serniclaes, W., Sprenger-Charolles, L., Carre, R., & Demonet, J. F. (2001). Perceptual discrimination of speech sounds in developmental dyslexia. *Journal of Speech, Language, and Hearing Research, 44*, 384-399.

Shankweiler, D., Lundquist, E., Katz, L., Stuebing, K. K., Fletcher, J. M., Brady, S., Fowler, A., Dreyer, L. G., Marchione, K. E., Shaywitz, S. E., & Shaywitz, B. A. (1999). Comprehension and Decoding: Patterns of Association in Children With Reading Difficulties. *Scientific Studies of Reading, 3*, 69-94.

Shaywitz, B. A., Shaywitz, S. E., Pugh, K. R., Mencl, W. E., Fulbright, R. K., Skudlarski, P., Constable, R. T., Marchione, K. E., Fletcher, J. M., Lyon, G. R., & Gore, J. C. (2002). Disruption of posterior brain systems for reading in children with developmental dyslexia. *Biological Psychiatry, 52*, 101-110.

Shaywitz, S. E. (1998). Dyslexia. *New England Journal of Medicine, 338*, 307-312.

Shaywitz, S. E., Fletcher, J. M., Holahan, J. M., Shneider, A. E., Marchione, K. E., Stuebing, K. K., Francis, D. J., Pugh, K. R., & Shaywitz, B. A. (1999). Persistence of dyslexia: the Connecticut Longitudinal Study at adolescence. *Pediatrics, 104*, 1351-1359.

Shaywitz, S. E., & Shaywitz, B. A. (2005). Dyslexia (specific reading disability). *Biological Psychiatry, 57*, 1301-1309.

Shaywitz, S. E., Shaywitz, B. A., Pugh, K. R., Fulbright, R. K., Constable, R. T., Mencl, W. E., Shankweiler, D. P., Liberman, A. M., Skudlarski, P., Fletcher, J. M., Katz, L., Marchione, K. E., Lacadie, C., Gatenby, C., & Gore, J. C. (1998). Functional disruption in the organization of the brain for reading in dyslexia. *Proceedings of the National Academy of Sciences USA, 95*, 2636-2641.

Shvachkin, N. K. (1973). The development of phonemic speech perception in early childhood. In C. Ferguson & D. Slobin (Eds.), *Studies of child development* (pp. 91-127). New York: Holt, Rinehart, and Winston.

Siegel, L. S., & Ryan, E. B. (1988). Development of grammatical-sensitivity, phonological, and short-term memory skills in normally achieving and learning disabled children. *Developmental Psychology, 24*, 28-37.

Simos, P. G., Basile, L. F., & Papanicolaou, A. C. (1997). Source localization of the N400 response in a sentence-reading paradigm using evoked magnetic fields and magnetic resonance imaging. *Brain Research, 762*, 29-39.

Simos, P. G., Breier, J. I., Fletcher, J. M., Bergman, E., & Papanicolaou, A. C. (2000). Cerebral mechanisms involved in word reading in dyslexic children: a magnetic source imaging approach. *Cerebral Cortex, 10*, 809-816.

Simos, P. G., Breier, J. I., Fletcher, J. M., Foorman, B. R., Bergman, E., Fishbeck, K., & Papanicolaou, A. C. (2000). Brain activation profiles in dyslexic children during non-word reading: a magnetic source imaging study. *Neuroscience Letters, 290*, 61-65.

Simos, P. G., Breier, J. I., Zouridakis, G., & Papanicolaou, A. C. (1998). Identification of language-specific brain activity using magnetoencephalography. *Journal of Clinical Experimental Neuropsychology, 20*, 706-722.

Sivonen, P., Maess, B., & Friederici, A. D. (2006). Semantic retrieval of spoken words with an obliterated initial phoneme in a sentence context. *Neuroscience Letters, 408*, 220-225.

Sivonen, P., Maess, B., Lattner, S., & Friederici, A. D. (2006). Phonemic restoration in a sentence context: evidence from early and late ERP effects. *Brain Research, 1121*, 177-189.

Sjolander, K., & Beskow, J. (2000). *Wavesurfer - An open source speech tool.* Paper presented at the ICSLP, Beijing, China.

Skoyles, J., & Skottun, B. C. (2004). On the prevalence of magnocellular deficits in the visual system of non-dyslexic individuals. *Brain and Language, 88*, 79-82.

Smith, F. (1971). *Understanding reading*. New York: Holt, Rinehart and Winston.

Smith, M. E., Stapleton, J. M., & Halgren, E. (1986). Human medial temporal lobe potentials evoked in memory and language tasks. *Electroencephalography and Clinical Neurophysiology, 63*, 145-159.

Snowling, M. (2000). *Dyslexia* (2nd ed.). Oxford: Blackwell.

Snowling, M. J. (1981). Phonemic deficits in developmental dyslexia. *Psychological Research, 43*, 219-234.

Snowling, M. J., Gallagher, A., & Frith, U. (2003). Family risk of dyslexia is continuous: individual differences in the precursors of reading skill. *Child Dev, 74*, 358-373.

Snowling, M. J., Goulandris, N., Bowlby, M., & Howell, P. (1986). Segmentation and speech perception in relation to reading skill: a developmental analysis. *Journal of Experimental Child Psychology, 41*, 489-507.

Stager, C. L., & Werker, J. F. (1997). Infants listen for more phonetic detail in speech perception than in word-learning tasks. *Nature, 388*, 381-382.

Stanovich, K. E. (1980). Toward an interactive-compensatory model of individual differences in the development of reading fluency. *Reading Research Quarterly, 1*, 32-71.

Stanovich, K. E. (1982). Individual differences in the cognitive processes of reading: I. Word decoding. *Journal of Learning Disabilities, 15*, 485-493.

Stanovich, K. E. (1986). Matthew effects in reading: some consequences of individual differences in the acquisition of literacy. *Reading Research Quarterly, 21*, 360-407.

Stanovich, K. E. (1992). Speculations on the causes and consequences of individual differences in early reading acquisition. In P. B. Gough, L. C. Ehri & R. Treiman (Eds.), *Reading Acquisition* (pp. 307-342). Hillsdale, NJ: Erlbaum.

Stanovich, K. E., & Siegel, L. S. (1994). Phenotypical performance profile of children with reading disabilities: A regression-based test of the phonological-core variable-difference model. *Journal of Educational Psychology, 86*, 24-53.

Stanovich, K. E., & West, R. F. (1979). Mechanisms of sentence context effects in reading: Automatic activation and conscious attention. *Memory and Cognition, 7*, 77-85.

Stanovich, K. E., & West, R. F. (1981). The effect of sentence context on on-going word recognition: Tests of a two-process theory. *Journal of Experimental Psychology: Human Perception and Performance, 7*, 658-672.

Stein, J., & Walsh, V. (1997). To see but not to read; the magnocellular theory of dyslexia. *Trends in Neuroscience, 20*, 147-152.

Stevens, K. N. (1998). *Acoustic Phonetics*. Cambridge, MA: MIT Press.

Stone, B. H., & Brady, S. A. (1995). Evidence for phonological processing deficits in less-skilled readers. *Annals of Dyslexia, 45*, 51-78.

Swan, D., & Goswami, U. (1997). Picture naming deficits in developmental dyslexia: the phonological representations hypothesis. *Brain and Language, 56*, 334-353.

Swingley, D. (2003). Phonetic detail in the developing lexicon. *Language and Speech, 46*, 265-294.

Takeshita, K., Nagamine, T., Thuy, D. H., Satow, T., Matsuhashi, M., Yamamoto, J., Takayama, M., Fujiwara, N., & Shibasaki, H. (2002). Maturational change of parallel auditory processing in school-aged children revealed by simultaneous recording of magnetic and electric cortical responses. *Clinical Neurophysiology, 113*, 1470-1484.

Tallal, P. (1980). Auditory temporal perception, phonics, and reading disabilities in children. *Brain and Language, 9*, 182-198.

Tarkiainen, A., Helenius, P., Hansen, P. C., Cornelissen, P. L., & Salmelin, R. (1999). Dynamics of letter string perception in the human occipitotemporal cortex. *Brain, 122 (Pt 11)*, 2119-2132.

Taylor, M. J., & Keenan, N. K. (1990). Event-related potentials to visual and language stimuli in normal and dyslexic children. *Psychophysiology, 27*, 318-327.

Temple, E., Poldrack, R. A., Salidis, J., Deutsch, G. K., Tallal, P., Merzenich, M. M., & Gabrieli, J. D. (2001). Disrupted neural responses to phonological and orthographic processing in dyslexic children: an fMRI study. *Neuroreport, 12*, 299-307.

Thomson, J. M., Richardson, U., & Goswami, U. (2005). Phonological similarity neighborhoods and children's short-term memory: typical development and dyslexia. *Memory and Cognition, 33*, 1210-1219.

Tonnquist-Uhlen, I. (1996). Topography of auditory evoked long-latency potentials in children with severe language impairment: the P2 and N2 components. *Ear and Hearing, 17*, 314-326.

Uutela, K., Taulu, S., & Hämäläinen, M. (2001). Detecting and correcting for head movements in neuromagnetic measurements. *Neuroimage, 14*, 1424-1431.

van Daal, V., & van der Leij, A. (1999). Developmental dyslexia: Related to specific or general deficits. *Annals of Dyslexia, 49*, 71-104.

van den Brink, D., Brown, C. M., & Hagoort, P. (2001). Electrophysiological evidence for early contextual influences during spoken-word recognition: N200 versus N400 effects. *Journal of Cognitive Neuroscience, 13*, 967-985.

van den Brink, D., & Hagoort, P. (2004). The influence of semantic and syntactic context constraints on lexical selection and integration in spoken-word comprehension as revealed by ERPs. *Journal of Cognitive Neuroscience, 16*, 1068-1084.

van der Leij, A., & van Daal, V. H. (1999). Automatization aspects of dyslexia: speed limitations in word identification, sensitivity to increasing task demands, and orthographic compensation. *Journal of Learning Disabilities, 32*, 417-428.

Van Petten, C., Coulson, S., Rubin, S., Plante, E., & Parks, M. (1999). Time course of word identification and semantic integration in spoken language. *Journal of Experimental Psychology: Learning Memory and Cognition, 25*, 394-417.

Van Petten, C., & Kutas, M. (1987). Ambiguous words in context: an event-related potential analysis of the time course of meaning activation. *Journal of Memory and Language, 26*, 188-208.

Vellutino, F. R. (1979). *Dyslexia: Theory and research.* Cambridge, MA: MIT Press.

Vellutino, F. R., Fletcher, J. M., Snowling, M. J., & Scanlon, D. M. (2004). Specific reading disability (dyslexia): what have we learned in the past four decades? *J Child Psychol Psychiatry, 45*, 2-40.

Victor, J. D., Conte, M. M., Burton, L., & Nass, R. D. (1993). Visual evoked potentials in dyslexics and normals: failure to find a difference in transient or steady-state responses. *Visual Neuroscience, 10*, 939-946.

Vukovic, R. K., & Siegel, L. S. (2006). The double-deficit hypothesis: a comprehensive analysis of the evidence. *Journal of Learning Disabilities, 39*, 25-47.

Wagner, R. K., & Torgesen, J. K. (1987). The nature of phonological processing and Its causal role in the acquisition of reading skills. *Psychological Bulletin, 101*, 192-212.

Wagner, R. K., Torgesen, J. K., & Rashotte, C. A. (1994). Development of Reading-Related Phonological Processing Abilities: New Evidence of Bidirectional Causality From a Latent Variable Longitudinal Study. *Developmental Psychology, 30*, 73-87.

Wagner, R. K., Torgesen, J. K., & Rashotte, C. A. (1999). Comprehensive Test of Phonological Processing. Austin, TX: PRO-ED, Inc.

Walker, M. M. (2002). Visual and lexical factors in naming speed by children with reading disorders. *Perceptual and Motor Skills, 95*, 1196-1198.

Walley, A. C. (1993). The role of vocabulary development in children's spoken word recognition and segmentation ability. *Developmental Review, 13*, 286-350.

Walley, A. C., Metsala, J. L., & Garlock, V. M. (2003). Spoken vocabulary growth: It's role in the development of phoneme awareness and early reading ability. *Reading and Writing: An Interdisciplinary Journal, 16*, 5-20.

Warren, R. M. (1970). Perceptual restoration of missing speech sounds. *Science, 167*, 392-393.

Watson, B. U., & Miller, T. K. (1993). Auditory perception, phonological processing, and reading ability/disability. *Journal of Speech and Hearing Research, 36*, 850-863.

Wehner, D. T., Ahlfors, S. P., & Mody, M. (in press). The influence of semantic processing on phonological decisions in children and adults: A magnetoencephalography (MEG) study. *Journal of Speech, Language, and Hearing Research.*

Werker, J. F., & Tees, R. C. (1987). Speech perception in severely disabled and average reading children. *Canadian Journal of Psychology, 41*, 48-61.

West, R. F., & Stanovich, K. E. (1978). Automatic contextual facilitation in readers of three ages. *Child Development, 49*, 717-727.

Wolf, M., & Bowers, P. G. (1999). The double deficit hypothesis for the developmental dyslexias. *Journal of Educational Psychology, 91*, 1-24.

Wolf, M., Bowers, P. G., & Biddle, K. (2000). Naming-speed processes, timing, and reading: a conceptual review. *Journal of Learning Disabilities, 33*, 387-407.

Woodcock. (1987). *Woodcock reading mastery test: revised.* Circle Pines, MN: American Guidance Services.

Yap, R. L., & van der Leij, A. (1993). Word processing in dyslexics: An automatic decoding deficit? *Reading and Writing: An Interdisciplinary Journal, 5*, 261-279.

Yap, R. L., & van der Leij, A. (1994). Testing the automatization deficit hypothesis of dyslexia via a dual-task paradigm. *Journal of Learning Disabilities, 27*, 660-665.

Zatorre, R. J., Evans, A. C., Meyer, E., & Gjedde, A. (1992). Lateralization of phonetic and pitch discrimination in speech processing. *Science, 256*, 846-849.

Zimmerman, J. E., Thiene, P., & Harding, J. T. (1970). Design and operation of stable rf-biased superconducting point-contact quantum devices and a note on the properties of perfectly clean metal contacts. *Journal of Applied Physics, 41*, 1572-1580.

Zwitserlood, P. (1989). The locus of the effects of sentential-semantic context in spoken-word processing. *Cognition, 32*, 25-64.