

Neuroimaging Studies of Reading Development and Reading Disability*

Kenneth R. Pugh, W. Einar Mencl, Annette R. Jenner, Jun Ren Lee
Yale University School of Medicine; Haskins Laboratories

Leonard Katz, Stephen J. Frost
Haskins Laboratories; University of Connecticut

Sally E. Shaywitz, Bennett A. Shaywitz
Yale University School of Medicine

Abstract. *Converging evidence from a number of neuroimaging studies, including our own, suggest that fluent word identification in reading is related to the functional integrity of two left hemisphere posterior systems: a temporo-parietal system and a ventral occipito-temporal system. These posterior systems are functionally disrupted in developmental dyslexia. Reading disabled, relative to nonimpaired, readers demonstrate heightened reliance on both inferior frontal and right hemisphere posterior regions, presumably in compensation for the LH posterior difficulties. We propose a neurobiological account suggesting that for normally developing readers the temporo-parietal system predominates at first, and is associated with aspects of processing critical in learning to integrate orthography with phonological and lexical-semantic features of printed words. The occipito-temporal system, by contrast, constitutes a fast, late-developing, word-identification system that underlies fluent word recognition in skilled readers.*

A proper understanding of the factors that govern the successful acquisition of literacy skills, and identification of the causes of reading failure, constitutes a high priority for researchers in developmental psychology. Significant progress has been made in understanding the cognitive and linguistic skills that must be in place to ensure adequate reading development in children (Lieberman et al., 1974; Brady, 1991; Rieben & Perfetti, 1991; Bruck, 1992; Shankweiler et al., 1995; Fletcher et al., 1994; Stanovich & Siegel, 1994). Recently, functional neuroimaging technologies, such as Positron Emission Tomography (PET), and functional Magnetic Resonance Imaging (fMRI), have become available, which allow us to begin to map the relation between success or failure in reading development and the neurobiological organization of those brain systems that support this development. Neuroimaging techniques hold much promise for studying both normally developing and clinical populations. The development of reading skill involves processing changes across several different brain systems; neuroimaging techniques can chart this neurobiological developmental trajectory as well as identify deviation from this trajectory in unsuccessful readers. With these trajectories established, we can determine how different factors in the child's educational environment impact the neurobiological substrate and, ultimately, reading performance. Thus, a better understanding of why certain remedial techniques result in improved performance might be facilitated by incorporating neuroimaging techniques.

However, neuroimaging measures are not intrinsically explanatory; they simply describe brain organization at a given point in time or development. A meaningful application of these techniques to developmental psychology requires that imaging studies are guided by principled cognitive theory and method. The studies

* The writing of this manuscript was supported by grants from the National Institute of Child Health and Human Development (PO1 HD-21888 and P50 HD-2580) to Yale School of Medicine and from the National Institute of Child Health and Human Development (HD-01994) to Haskins Laboratories. Portions of the review of the literature and Figures 1 and 2 appeared previously in an article entitled "Functional neuroimaging studies of reading and reading disability (developmental dyslexia)" by Pugh, K. et al., (2000), in *Mental Retardation and Developmental Disabilities Research Reviews*, 6, 207-13, Wiley-Liss Inc., and are reproduced with permission of the publisher.

Requests for reprints should be sent to Kenneth R. Pugh, Department of Pediatrics, Yale University School of Medicine, P.O. Box 3333, New Haven, CT 06510-8064.

discussed in this review focus on comparisons between nonimpaired and reading disabled populations. However, the lessons learned from these contrasts have potential relevance for understanding the neurobiology of reading development across the skill continuum, and also promise to aid in assessing the efficacy of various remedial approaches in children at risk for reading failure.

BEHAVIORAL STUDIES OF READING DISABILITY

Reading disability is characterized by the failure to develop age-appropriate reading skill despite normal intelligence and adequate reading instruction. Behaviorally, deficits are most evident at the level of single word and pseudoword reading; reading disabled (RD) performance is both slow and inaccurate relative to nonimpaired (NI) readers. Many lines of evidence converge on the conclusion that the word and pseudoword reading difficulties in developmental dyslexia are, to a large extent, manifestations of more basic deficits at the level rapidly assembling the phonological code represented by a token letter string (Bradley & Bryant, 1983; Liberman et al., 1989). Phonological assembly refers to the decoding operations associated with letter-to-phoneme mapping in printed word identification. The failure to develop efficient phonological assembly skill in word and pseudoword reading, in turn, appears to stem from difficulties—at the earliest stages of literacy training—in attaining phonological awareness. Phonological awareness is defined as the metalinguistic understanding that spoken words can be decomposed into phonological primitives, which in turn can be represented by alphabetic characters (Liberman et al., 1974; Brady, 1991; Rieben & Perfetti, 1991; Bruck, 1992; Shankweiler et al., 1995; Fletcher et al., 1994; Stanovich & Siegel, 1994). As for why RD readers should have exceptional difficulty developing phonological awareness, there is support for the notion that the difficulty resides in the phonological component of the larger specialization for language (Liberman, 1998; Liberman, 1996; Liberman et al., 1989). If that component is imperfect, its representations will be less than ideally distinct, and therefore harder to bring to conscious awareness.

A large body of evidence directly relates deficits in phonological awareness to difficulties in learning to read: phonological awareness measures predict later reading achievement (Bradley & Bryant, 1983; Stanovich et al., 1984; Torgesen et al., 1994); deficits in phonological awareness consistently separate RD and nondisabled children (Fletcher et al., 1994; Stanovich & Siegel, 1994); phonological deficits persist into adulthood (Felton et al., 1990; Bruck, 1992; Shaywitz et al., 1999), and instruction in phonological awareness promotes the acquisition of reading skills (Bradley & Bryant, 1983; Torgesen et al., 1992; Ball & Blachman, 1991; Wise & Olson, 1995;

Foorman et al., 1998). For children with adequate phonological skill, in contrast, the process of phonological assembly in word and pseudoword reading becomes highly automated, efficient, and, as a growing body of evidence suggests, this phonological decoding continues to serve as an important component in rapid word identification even for mature skilled readers (cf. Lukatela & Turvey, 1994; Van Orden et al., 1990). Given this background, our own functional neuroimaging research program and the studies selected for discussion in this review involve a comparison of RD and NI reading groups on word and pseudoword reading tasks that stress phonological processing. For a discussion of functional neuroimaging studies that have examined sensory-level processing deficits in developmental dyslexia (Eden et al., 1996; Demb et al., 1998), the reader is referred to Eden and Zeffiro (1998). For reviews of research examining anatomical/structural brain differences between RD and NI groups, the reader is referred to Filipek (1995) and Galaburda (1992).

OVERVIEW OF THE MAJOR READING CIRCUITS IN NI AND RD

Converging evidence from a number of laboratories using several imaging technologies (fMRI, PET, and magnetoencephalography (MEG)) indicates that printed word and pseudoword processing involves a left hemisphere (LH) posterior reading system (see Figure 1) consisting of both ventral and dorsal components.¹ The ventral region includes lateral extrastriate areas and a left occipito-temporal area where functional imaging studies show robust activation in word and pseudoword reading tasks (Brunswick et al., 1999; Cohen et al., 2000; Price, ch. 13, in Frackowiak et al., 1997; Nobre et al., 1994; Puce et al., 1996; Rumsey et al., 1997; Salmelin et al., 1996; Shaywitz et al., 1998; Tarkiainen et al., 1999). Moreover, findings from a number of functional neuroimaging studies implicate this system as dysfunctional in reading disability (Brunswick et al., 1999; Helenius et al., 1999a; Rumsey et al., 1997; Salmelin et al., 1996; Shaywitz et al., 1998; Pugh et al., 2000; Shaywitz et al., submitted).

The temporo-parietal system includes the angular gyrus and supramarginal gyrus in the inferior parietal lobule, and the posterior aspect of the superior temporal gyrus (Wernicke's Area). This temporo-parietal system has long been implicated in reading; a large literature on acquired inability to read (alexia) describes neuroanatomic lesions most prominently centered about the angular gyrus (Dejerine, 1891; Damasio & Damasio, 1983; Henderson, 1986), a region considered pivotal in carrying out cross-modal integration

¹ This use of the terms more dorsal and ventral in the LH reading circuitry does not necessarily imply a direct parallel with the traditional dorsal/ventral distinctions in visual processing theory.

A Tentative Model of the Neural Circuitry for Reading

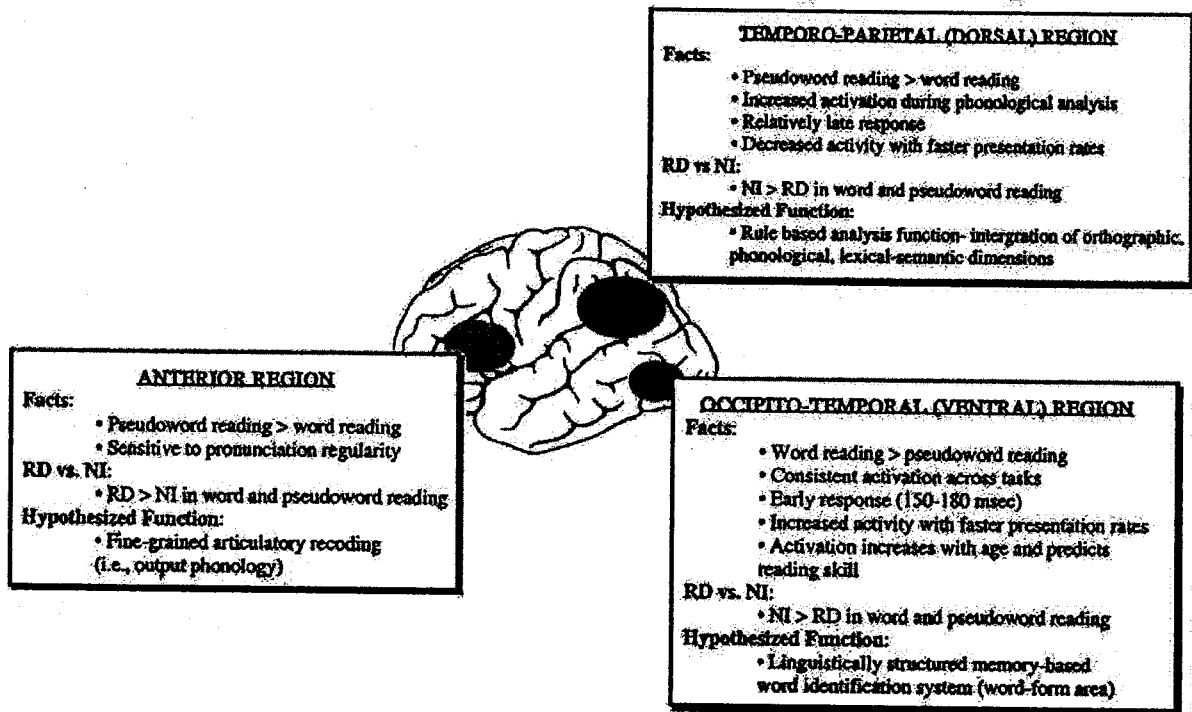


FIGURE 1 A general overview of three major reading circuits.

necessary for reading, i.e., mapping the visual percept of the print onto the phonologic and semantic structures of the language (Benson, 1994; Black & Behrmann, 1994; Geschwind, 1965). Converging evidence from functional neuroimaging studies also implicates the temporo-parietal system in severe reading disability, indicating abnormal activation during language processing tasks when decoding and analysis are taxed (Flowers et al., 1991; Gross-Glenn et al., 1991; Helenius et al., 1999b; Horwitz et al., 1998; Rumsey et al., 1992; Rumsey et al., 1997; Salmelin et al., 1996; Shaywitz et al., 1998; Pugh et al., 2000; Simos et al., 2000; Shaywitz et al., submitted).

An anterior region centered in and around Broca's Area in the inferior frontal gyrus appears to be associated with, among other things, sequencing and control of speech-gestural articulatory recoding and this region is also involved in silent reading and naming (Fiez & Petersen, 1998; Brunswick et al., 1999; Herbster et al., 1997; Pugh et al., 1996; Pugh et al., 1997; Shaywitz et al., 1998). Evidence from functional imaging studies has implicated this anterior region in RD (Brunswick et al., 1999; Richards et al., 1999; Salmelin et al., 1996; Shaywitz et al., 1998). This anterior system appears to be more heavily relied on by RD readers, presumably in compensation for the failure to develop the LH posterior systems adequately. Before considering the distinct

information processing roles that these major regions appear to play in skilled reading, we next describe in more detail the current neurobiological evidence for both disruption and compensation in RD readers.

THE MAJOR READING CIRCUITS IN RD

As noted, in RD readers, studies using PET, MEG, and fMRI have observed what appears to be LH posterior dysfunction at both dorsal and ventral LH areas across a variety of language tasks (Helenius et al., 1999a; Helenius et al., 1999b; Horwitz et al., 1998; Pugh et al., 2000; Rumsey et al., 1997; Salmelin et al., 1996; Shaywitz et al., 1998; Shaywitz et al., submitted). Essentially, this disruption, in most studies, is characterized by a relative under-engagement of these regions, specifically during processing words and pseudowords. Rumsey and colleagues (Rumsey et al., 1992), using PET, reported that RD readers failed to show reliable activation at those temporo-parietal sites engaged by NI readers while performing a simple phonological analysis task (auditory rhyme judgment). Consistent with this finding, Rumsey et al. (1997) again used PET to study 17 RD men and 14 male controls. Subjects performed two pronunciation tasks (low-frequency

irregularly spelled words vs. pseudowords) and two lexical discrimination tasks; in one, subjects judged whether a pseudoword token either sounded like a real word (e.g., a pseudohomophone like BRANE) or did not (e.g., BRONE); in the second, they discriminated real words (e.g., BRAIN) from pseudohomophones. Compared to NI participants, RD readers failed to activate a range of LH posterior areas in both the temporo-parietal and in the occipito-temporal regions on all tasks; thus at both dorsal and ventral sites silent reading and pronunciation was associated with reduced activation in RD participants. A more recent PET study by Brunswick and colleagues (Brunswick et al., 1999) reinforces this. The authors compared six NI adult readers with six readers with a childhood history of RD on simple word naming. NI readers showed robust activation of both occipito-temporal and inferior frontal sites. RD participants, by contrast, showed reduced activation in the occipito-temporal region and an elevated response relative to NI in the inferior frontal gyrus. This type of finding is not unique to hemodynamic measures such as measured by PET. Salmelin and colleagues (Salmelin et al., 1996; Helenius et al., 1999b) contrasted RD and NI readers while passively reading words and nonwords using MEG recordings. MEG has the advantage of providing both information about localization and the temporal course of task-related electrophysiological activity. For NI readers, print processing was associated with a heightened response relative to objects at between 150–200 msec poststimulus onset at the occipito-temporal area. RD participants by contrast showed no evidence of this early ventral response. Interestingly, these readers did display a somewhat earlier response in the inferior frontal gyrus than NI readers, again suggesting a posterior anomaly and heightened reliance on frontal lobe systems. Posterior anomaly was also detected in both lexical and sentence processing tasks in the superior temporal gyrus and temporo-parietal areas at approximately 250 msec (Helenius et al. 1999a; see Simos et al., 2000, for additional evidence of LH temporo-parietal anomaly in RD readers as measured by MEG). The common findings across these different tasks and technologies appear to be a diminished LH posterior response to print stimuli and the suggestion of an anteriorized frontal lobe compensation. This pattern is clearly evident in our own studies of RD vs. NI readers using fMRI. In these studies we attempted to isolate component processing systems in word and pseudoword reading (Shaywitz et al., 1998; Pugh et al., 2000).

In our initial investigation (Shaywitz et al., 1998), we employed a set of hierarchically structured tasks that varied the kind of language-relevant coding required (especially including the demand on phonologic decoding and analysis) and compared the performance and brain activation patterns of NI and RD readers. We used five tasks that varied in the demands made: visual-spatial processing; orthographic processing; simple phonologic analysis; phonological assembly; and lexical-semantic processing. We hypoth-

esized that differences in brain activation patterns would emerge as RD and NI readers were asked to perform tasks that make progressively greater demands on phonologic analysis. The five tasks were: the line orientation (L) judgment task (e.g., Do [W] and [W] match?), which taps visual-spatial processing, but makes no orthographic demands. Next, the letter case (C) judgment task (e.g., Do [bbBb] and [bbBb] match in the pattern of upper and lower case letters?) adds an orthographic processing demand, but makes no phonologic demands, since the stimulus items, which consist entirely of consonant strings, are, therefore, phonotactically impermissible. The third task, single letter rhyme (SLR) (e.g., Do the letters [T] and [V] rhyme?), while orthographically more simple than C, adds a phonologic processing demand, requiring the transcoding of the letters (orthography) into phonologic structures and then, a phonologic analysis of those structures sufficient to determine that they do or do not rhyme. The fourth task, nonword rhyme (NWR) (e.g., Do [leat] and [jete] rhyme?) makes extensive demands on phonological assembly. The final task, semantic category (SC) judgment (e.g., Are [corn] and [rice] in the same category?), also makes substantial demands on phonological assembly (Lukatela & Turvey, 1994), but requires in addition that the printed stimulus items activate particular word representations in the reader's lexicon to arrive at the word's meaning. A common baseline subtraction condition was used in analysis: C, SLR, NWR, and SC tasks contrasted with the nonlanguage line orientation judgment (L) baseline condition.

We found differences between RD and NI readers in the patterns of activation in several critical components of the LH posterior reading system: posterior STG (Wernicke's area), angular gyrus, occipito-temporal areas, and striate cortex. The pattern of group differences was similar at each of these sites: NI readers showed a systematic increase in activation as orthographic-to-phonologic processing demands increased, while RD readers failed to show such systematic modulation in their activation patterns in response to the same task demands. In contrast to findings in the posterior system, RD compared to NI readers demonstrated greater activation in the inferior frontal gyrus (as well as in RH temporo-parietal areas) in response to increasing phonological demands. While the heightened anterior response may reflect, to some degree, the greater effort required by these less-skilled readers in performing these tasks, the paucity of activation at posterior sites cannot be reasonably attributed to differences in effort. These group differences are illustrated in Figure 2, which shows the contrast of the letter case task with nonword rhyme (the latter places maximum demands on phonological assembly and analysis).

Most neuroimaging studies have attempted to isolate specific brain regions where activation patterns discriminate RD from NI readers (e.g., Rumsey et al., 1997; Shaywitz et al., 1998). However, a deeper understanding of the neurobiology of developmental dyslexia

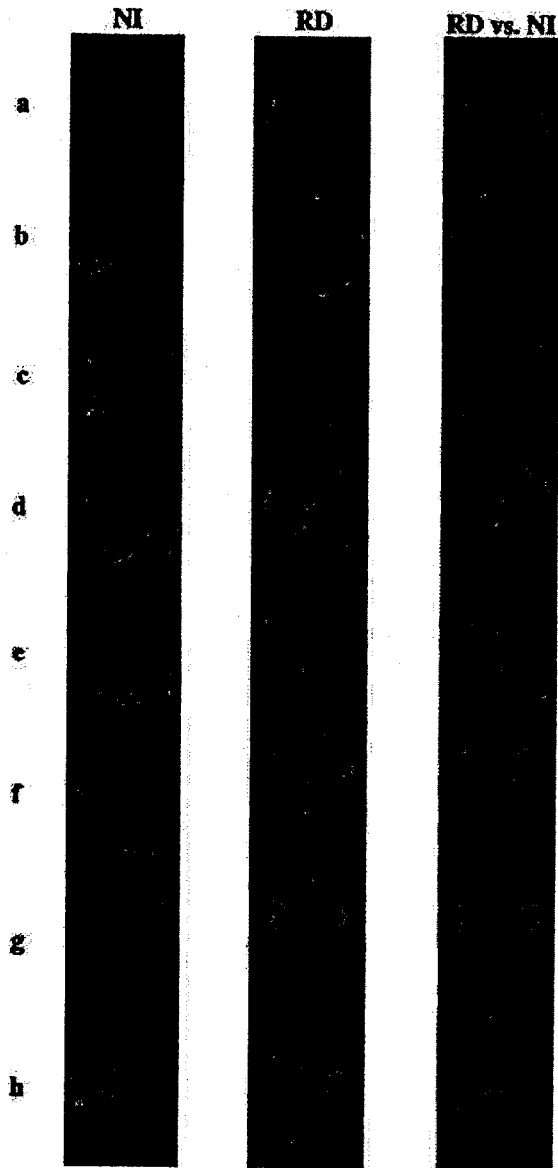


FIGURE 2 Activation maps for RD vs. NI readers. Columns 1 and 2 contrast the nonword rhyme task with the case judgment baseline task for each group. Areas in gray show regions of increased activation in the rhyme relative to the case task for each group. Column 3 shows the group-by-task interaction contrast. Areas shown in gray showed higher rhyme-related increases in RD readers; areas in black showed higher rhyme-related increases in NI readers. The left hemisphere is displayed on the left side of the image.

requires that we also consider relations among distinct brain regions that function cooperatively as circuits to process information during reading; this issue has been referred to as one of functional connectivity (Friston, 1994; McIntosh & Gonzalez-Lima, 1994). Evidence consistent with the notion of a break-

down in functional connectivity within the posterior reading system in RD readers has been recently reported by Horwitz, Rumsey, and Donohue (1998). Using activation data from the Rumsey et al.'s (1997) positron emission tomography (PET) study, these authors examined correlations (within task/over subjects) between activation levels in the LH angular gyrus and other brain sites during two reading aloud tasks (exception word and nonword naming). Correlations between the LH angular gyrus and occipital and temporal lobe sites were strong and significant in NI readers and weak in RD readers. Such a result suggests a breakdown in functional connectivity across the major components of the LH posterior reading system. We also examined functional connectivity between the angular gyrus and other LH posterior regions in our sample of RD and NI readers (Pugh et al., 2000). We looked at functional connectivity between the angular gyrus and occipital and temporal lobe sites on those tasks that systematically varied demands made on phonological assembly. While for RD readers LH functional connectivity was disrupted on word and nonword reading tasks, as reported by Horwitz et al. (1998), there appeared to be no dysfunction on tasks that tap metaphonological judgments only (the single letter rhyme task), or the complex visual-orthographic coding only (the case task) (see Figure 3). The results are most consistent with a specific phonological deficit hypothesis. A breakdown

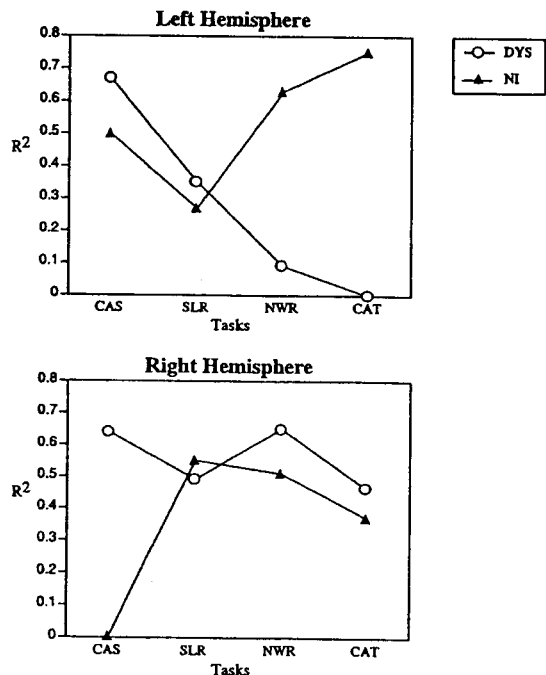


FIGURE 3 The results of multiple regression analyses on activation at the angular gyrus by four posterior predictor regions of interest are shown for both RD and NI groups by task and by hemisphere. Proportion of variance accounted for is plotted on the Y-axis.

in LH posterior systems manifests only when orthographic to phonological assembly is required. The notion of a developmental lesion, one that would disrupt functional connectivity in this system across all types of cognitive behaviors, is not supported by this result. Moreover, we found that on word and nonword reading tasks, right hemisphere homologues appear to function in a compensatory manner for RD readers; correlations were strong and stable in this hemisphere for both reading groups with higher values in RD readers (see Figure 3).

As noted, in a presumably compensatory response to LH posterior difficulties, RD readers show increased reliance on both bihemispheric inferior frontal areas and RH posterior sites including the RH temporo-parietal region. For instance, in our study (Shaywitz et al., 1998) we found that on those tasks that made explicit demands on phonological processing (pseudoword and word tasks), these readers showed a disproportionately greater engagement of inferior frontal gyrus and prefrontal dorsolateral sites than NI readers. As noted, a MEG study by Salmelin et al. (1996) found evidence of a relative early frontal response in RD readers coupled with the occipito-temporal anomaly discussed previously. Recently, both Brunswick et al. (1999) and Richards et al. (1999) found disproportionately elevated activation of the inferior frontal gyrus in RD readers across a number of tasks. Thus fMRI, PET, and MEG studies suggest both a LH posterior anomaly and compensatory shift to frontal sites in RD.

Evidence of an additional RH compensatory reliance in RD readers comes from several findings. In our study (Shaywitz et al., 1998) we observed a significant reading group by hemisphere interaction at the angular gyrus and the middle temporal gyrus indicating greater right than left hemisphere activation in RD readers but greater left than right hemisphere activation in NI readers (see also Barnea et al., 1994). As noted, in the correlational analysis with these same reading tasks, RD readers failed to demonstrate any evidence of functional connectivity between major posterior circuits in the left hemisphere. By contrast, they displayed robust correlations at RH homologues of these sites with numerically higher correlations than NI readers (Pugh et al., 2000). Simos et al. (2000) using MEG found stronger responses in RH than LH temporo-parietal sites in RD children (for NI children the response was strongly LH lateralized). Rumsey et al. (1999) examined brain/behavior correlations in their RD and NI subjects and found that RH temporo-parietal activation was correlated with reading performance on standard measures only for RD readers, suggesting a compensatory function. We observed a similar predictive relation between RH sites and reading skill in our sample of children (Shaywitz et al., submitted). In summary, while NI readers show a strong role of LH posterior circuits in word and pseudoword reading, RD readers show evidence of two, apparently compensatory, responses to their LH posterior dysfunction: increased bihemispheric inferior frontal gyrus activation,

along with an increased functional role for RH posterior sites.

COMPUTATIONAL ROLES FOR POSTERIOR AND ANTERIOR SYSTEMS IN NI READERS

The studies discussed above document neurobiological differences between NI and RD groups on tasks that RD readers find problematic. In this respect the studies are describing the signature neurobiological patterns of reading disability, they do not necessarily reveal the causes of these differences. For example, the temporo-parietal anomalies detected across studies may suggest an underlying neurological problem at this site (see Klingberg et al., 2000 for evidence of anatomical differences in this region) but, alternatively, the failure of RD readers to develop this circuit could also be a consequence of neurological problems elsewhere or more general and nonlocalized dysfunction. The current findings suggest many hypotheses about causal mechanisms but cannot directly address them. As a start in moving beyond description toward explanation we can begin to examine, for instance, how beneficial effects of intensive training and remediation on reading performance alters the underlying neurobiological organization in RD readers. However, in order to know what sorts of training-related changes to look for at the neurobiological level of analysis, a necessary first step is to develop a more precise understanding of the computational roles played by each of the major reading circuits in normally developing readers. Thus, we must construct an adequate neurobiological model of how these reading areas process information in conjunction with one another to support rapid and accurate reading, a process that fails to develop in RD readers.

Extant neuroimaging studies of skilled readers already can provide some guidance toward theory development. A number of studies have demonstrated several important differences between the temporo-parietal (dorsal) and occipito-temporal (ventral) LH posterior regions and the anterior system that allow speculation on their distinctive roles in skilled word and pseudoword reading. From these findings, discussed next, we propose the following account: the temporo-parietal system is associated with rule-based analysis and learning; essentially this system (in cooperation with production-related areas in the inferior frontal gyrus) is critical for extracting the relations between orthography, phonological form, morphological, and lexical-semantic dimensions for printed stimuli, allowing these features to become bound into highly integrated representations (thus basic decoding and analysis skill would rely on intact temporo-parietal function). By contrast, the ventral occipito-temporal area, the point of contact between the ventral visual stream and the middle to inferior temporal lobe, constitutes a linguistically structured, memory-based, word-identification system (i.e., a word form

area) supporting fluent word identification in skilled, but not in impaired, readers. The relevant evidence is summarized in Figure 1.

We propose that the development of this fast ventral word form system depends on the integrity of analytic processing that occurs in the temporo-parietal system working in conjunction with inferior frontal articulatory recoding systems. We assume that the integration of orthographic, phonological, and lexical-semantic features, a process that engages temporo-parietal and frontal areas, will, with experience and training, provide the internal organization of those neural networks that come to support fluent word identification within the ventral system. There are several lines of evidence that support this proposed relation. In skilled readers, the dorsal (and anterior) system responds with greater activation to pseudowords and low frequency words than to familiar high frequency words, whereas sites within the ventral system show the opposite response profile with higher activation to familiar words than to pseudowords (Tagamets et al., 2000; see Price, ch. 13, in Frackowiak et al., 1997, for a review of evidence from PET studies). The increased response to unfamiliar stimuli by the dorsal system suggests that it engages in phonological and semantic analysis relevant to learning; the ventral system by contrast would appear to be associated with a memory-based type of processing in that activation is higher for familiar (i.e., well-learned) stimuli. Additionally, Price et al. (1996) demonstrated that as stimulus presentation rates increased from 20 through 60 words per minute, ventral sites showed increased activation but dorsal sites showed decreased activation, again an opposite profile. Given that at very fast input rates, analysis and computation for a given stimulus is precluded but basic identification processes are intact and engaged, this finding appears consistent with the notion that the dorsal system is associated with analysis and computation while the ventral system is associated with rapid stimulus identification. Finally, as noted above, in skilled readers, but not in RD readers, Salmelin and her colleagues (Salmelin et al., 1996; Helenius et al., 1999a; Tarkanian et al., 1999) demonstrated that evoked responses to words and pseudowords diverge from non-linguistic stimuli early (between 150–180 msec) at the occipito-temporal area; temporo-parietal responses arise later in time (approximately 250 msec). This early, language-specific response of the ventral system suggests very strongly that this region supports fluent word identification in NI readers. Indeed, Booth et al. (1999) found that the occipito-temporal system appears to become increasingly dominant in older skilled readers relative to young children who show heightened activity at temporo-parietal sites. Moreover, our preliminary results from the study of a large group of NI and RD children across a large age range (7–17) suggests that the LH occipito-temporal area plays an increasingly important role in skilled word identification with age and reading experience; activation in this system is highly predictive of reading speed and accuracy on a number of standardized measures (Shaywitz et al., submitted).

Thus, we propose that the ventral word form system is fast, relatively late developing, and is associated with greater reading fluency.

With respect to the anterior system, including the LH inferior frontal gyrus, studies indicate that it has a role in speech-gestural articulatory recoding of print. For example, IFG shows a high degree of sensitivity to the spelling-sound regularity/consistency of words. Pugh et al. (1997) found that interhemispheric variation in IFG activity predicted individuals' sensitivities to regularity effects in silent reading tasks. Low frequency irregularly spelled words elicit higher activation than regular words at this site (Herbster et al., 1997; see also Fiez & Peterson, 1998), a finding that converges with those of Pugh et al. in suggesting a relation between IFG and regularity/consistency effects. Behavioral studies have shown that, on average, regularity/consistency effects are stronger in overt production tasks (output phonology) than in silent reading tasks (i.e., lexical decision), suggesting an important contribution of gestural phonological recoding (Hino & Lupker, 2000) to the effect. Indeed, several studies have shown significant effects in delayed naming tasks, suggesting that at least part of the effect is related to articulatory recoding in overt production tasks (Ziegler et al., 1997). Thus the relation between IFG and pronunciation regularity effects suggests a role in speech-gestural or articulatory recoding for this region. Given that both the temporo-parietal and this anterior region increase activation in response to unfamiliar stimuli that must be decoded, we posit that these two systems normally work in conjunction to integrate perceptual and articulatory features of printed stimuli.

SUMMARY AND A TENTATIVE MODEL

Posterior reading systems including both more dorsal (temporo-parietal) and ventral (occipito-temporal) components are disrupted in RD (indicated both by reduced activation as well as by disrupted functional connectivity between these areas). Additionally, there appear to be two characteristic compensatory patterns responding to this LH posterior anomaly: (1) increased reliance on inferior frontal gyrus (IFG) during reading, and (2) an increased tendency to engage the RH homologues of these disrupted LH posterior circuits.

We suggest the following account of the neurological basis of skilled reading and reading disability. As shown, substantial evidence suggests that in NI readers, skilled reading performance is related to the development of a highly organized cortical system that integrates orthographic, phonological, and lexical-semantic features of words. This system involves two consolidated left hemisphere (LH) posterior reading systems, a dorsal (temporo-parietal) region and a ventral (occipito-temporal) region. Whereas the dorsal region performs the function of learning to decode print for normally developing young readers, the ventral region develops

with reading experience into a system that recognizes printed words in a fast, automatic manner. In contrast, for RD readers, this pattern of consolidation is disrupted, reflecting a dissociation in processing of the orthographic, phonological, and lexical-semantic features of words. This dissociation is evident both cognitively and neurobiologically, and is characterized by the increased reliance on the inferior frontal gyrus (IFG) and the right hemisphere (RH) homologues of the disrupted LH posterior systems. Frontal and RH developments are apparently compensatory and may reflect the inability to use linguistic information appropriately (specifically, phonological and morphological aspects of the spoken language and their relationships to writing). Our findings suggest that the disproportionate shift to inferior frontal sites in RD readers reflects an increased reliance on articulatory recoding (covert pronunciation) in an attempt to cope with phonological analysis. In addition, the RH shift might reflect the dissociated development of nonphonological-based visuo-semantic pattern recognition in order to support semantic aspects of word reading.

With respect to reading acquisition we propose that the normally developing reader initially depends on the temporo-parietal circuit to learn to decode and integrate orthography, phonology, and lexical-semantic features; this paves the way for the development of a fast word-recognition system built around the occipito-temporal area. We propose that this ventral system, which before reading instruction is specialized for rapid visual and auditory integration, becomes entrained to the linguistic structure processed by the dorsal system, acquiring that system's sensitivity to phonological and morphological as well as lexical-semantic information. The result is a word-recognition system in which processing is fast because linguistic knowledge is encapsulated in highly efficient pattern-recognizing templates. In contrast, the RD reader fails to develop a structured temporo-parietal system that can decode effectively, resulting in a failure to establish adequate linkages between phonology, orthography, and meaning. Because the temporo-parietal system does not develop normally, the RD reader subsequently fails to develop a highly integrated word form system in the ventral LH occipito-temporal area.

IMPLICATIONS AND NEW DIRECTIONS

Further studies are needed to test this account and to more precisely reveal the information-processing characteristics of major reading systems in NI and of the altered circuitry engaged by RD readers. We also must begin to examine whether these neurobiological anomalies can be altered by contextual and/or experiential factors that have known ameliorative effects on word reading in RD children. Are these ameliorative factors associated with increased processing efficiency in poorly developed, but not fundamentally disrupted,

posterior LH systems that support skilled reading or do these factors simply affect processing efficiency within the frontal and RH posterior networks relied on by RD readers? These ameliorative variables include the adaptive learning response associated with practice and training on specific words and word types, the use of contextual cues in reading, and, especially, training in phonological awareness and decoding skills.

As our understanding of the neurobiology of reading develops we can begin to provide a means for the evaluation and monitoring of interventions and reading remediation programs. For example, investigators might choose to focus on training-related changes in the activation of the LH ventral system as a target for interventions that could be expected, in turn, to lead to improved word-reading skill in children with early reading difficulties. Neuroimaging measures taken before and after full-scale interventions should further our understanding of the neurobiological modifications associated with varied approaches to the remediation of reading failure; ultimately such findings can lead to more efficient and more effective approaches to treatment. In sum, by further understanding the connections between neurobiological function and reading behaviors, we may be able to determine in what ways RD children are constrained by their neurobiological development and by what neural processes training and remediation might address those limitations.

REFERENCES

- Ball, E. W., & Blachman, B. A. (1991). Does phoneme awareness training in kindergarten make a difference in early word recognition and developmental spelling? *Reading Research Quarterly*, 26(1), 9-66.
- Barnea, A. O., Lamm, R., Epstein, R., & Pratt, H. (1994). Brain potentials from dyslexic children recorded during short-term memory tasks. *International Journal of Neuroscience*, 74, 227-37.
- Benson, D. F. (1994). *The neurology of thinking*. New York: Oxford University Press.
- Black, S. E., Behrmann, M. (1994) Localization in alexia. In A. Kertesz (Ed.), *Localization and neuroimaging in neuropsychology* (pp. 331-76). New York: Academic Press.
- Booth, J. R., MacWhinney, B., Thulborn, K. R., Sacco, K., Voyvodic, J., & Feldman, H. M. (1999). Functional organization of activation patterns in children: Whole brain fMRI imaging during three different cognitive tasks. *Progress in Neuro-Psychopharmacology & Biological Psychiatry*, 23, 669-82.
- Bradley, L., & Bryant, P. E. (1983). Categorizing sounds and learning to read—A causal connection. *Nature*, 301, 419-21.
- Brady, S. A. (1991). The role of working memory in reading disability. In S. A. Brady, & D. P. Shankweiler (Eds.), *Phonological processes in literacy, A tribute to Isabelle Y. Liberman* (pp. 129-52). Hillsdale, NJ: Lawrence Erlbaum.
- Bruck, M. (1992). Persistence of dyslexics' phonological awareness deficits. *Developmental Psychology*, 28(5), 874-86.
- Brunswick, N. E., McCrory, E., Price, C., Frith, C. D., & Frith, M. (1999). Explicit and implicit processing of words and

- pseudowords by adult developmental dyslexics: A search for Wernicke's wortschatz? *Brain*, 122, 1901-17.
- Cohen, L., Dehaene, S., Naccache, L., Lehéricy, S., Dehaene-Lambertz, G., Hénaff, M.-A., & Michel, F. (2000). The visual word form area: spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. *Brain*, 123, 291-307.
- Damasio, A. R., & Damasio, H. (1983). The anatomic basis of pure alexia. *Neurology*, 33, 1573-83.
- Dejerine, J. (1891). Sur un cas de cécité verbale avec agraphie, suivi d'autopsie. *C. R. Société du Biologie*, 43, 197-201.
- Demb, J. B., Boynton, G. M., Heeger, D. J. (1998). Functional magnetic resonance imaging of early visual pathways in dyslexia. *Journal of Neuroscience*, 18, 6939-51.
- Eden, G. F., Vanmeter, J. W., Rumsey, J. M., Maisog, J. M., Woods, R. P., & Zeffiro, T. A. (1996). Abnormal processing of visual motion in dyslexia revealed by functional brain imaging. *Nature*, 382, 66-69.
- Eden, G. F., & Zeffiro, T. A. (1998). Neural systems affected in developmental dyslexia revealed by functional neuroimaging. *Neuron*, 21, 279-82.
- Felton, R. H., Naylor, C. E., & Wood, F. B. (1990). Neuropsychological profile of adult dyslexics. *Brain and Language*, 39, 485-97.
- Fiez, J. A., & Petersen, S. E. (1998). Neuroimaging studies of word reading. *Proceedings of the National Academy of Sciences*, 95, 914-21.
- Filipek, P. A. (1995). Neurobiologic correlates of developmental dyslexia: How do dyslexics brains differ from those of normal readers? *Journal of Child Neurology*, 10(Supp. 1), S62-S69.
- Fletcher, J. M., Shaywitz, S. E., Shankweiler, D. P., Katz, L., Liberman, I., Stuebing, K., Francis, D. J., Fowler, A., & Shaywitz, B. (1994). Cognitive profiles of reading disability: Comparisons of discrepancy and low achievement definitions. *Journal of Educational Psychology*, 86(1), 6-23.
- Flowers, D. L., Wood, F. B., & Naylor, C. E. (1991). Regional cerebral blood flow correlates of language processes in reading disability. *Archives of Neurology*, 48, 637-43.
- Foorman, B. R., Francis, D. J., Fletcher, J. M., Schatsneider, C., & Mehta, P. (1998). The role of instruction in learning to read: Preventing reading failure in at-risk children. *Journal of Educational Psychology*, 90, 37-55.
- Frackowiak, R., Friston, K., Frith, R., Dolan, R., & Mazziotta, J. (1997). *Human brain function*. New York: Academic Press.
- Friston, K. J. (1994). Functional and effective connectivity: A synthesis. *Human Brain Mapping*, 2, 56-78.
- Galaburda, A. M. (1992). Neurology of developmental dyslexia. *Current Opinion in Neurology and Neurosurgery*, 5(1), 71-76.
- Geschwind, N. (1965). Disconnection syndromes in animals and man: Part I. *Brain*, 88, 237-94.
- Gross-Glenn, K., Duara, R., Barker, W. W., Loewenstein, D., Change, J.-Y., Yoshii, F., Apicella, A., Pascal, S., Boothes, T., Sevush, S., Jallad, B., Novoa, L., & Lubs, H. (1991). Positron emission tomographic studies during serial word-reading by normal and dyslexic adults. *Journal of Clinical and Experimental Neuropsychology*, 13(4), 531-44.
- Helenius, P., Salmelin, R., Service, E., & Connolly, J. (1999a). Semantic cortical activation in dyslexic readers. *Journal of Cognitive Neuroscience*, 11, 535-50.
- Helenius, P., Tarkiainen, P., Cornelissen, P., Hansen, P., & Salmelin, R. (1999b). Dissociation of normal feature analysis and deficient processing of letter-strings in dyslexic adults. *Cerebral Cortex*, 4, 476-83.
- Henderson, V. (1986). Anatomy of posterior pathways in reading: A reassessment. *Brain and Language*, 29, 119-33.
- Herbster, A. M., Mintun, R., Nebes, R., & Bekcer, J. (1997). Regional cerebral blood flow during word and nonword reading. *Human Brain Mapping*, 5, 84-92.
- Hino, Y., & Lupker, S. J. (2000). Effects of word frequency and spelling-to-sound regularity in naming with and without preceding lexical decision. *Journal of Experimental Psychology: Human Perception and Performance*, 26, 166-84.
- Horwitz, B., Rumsey, J. M., & Donohue, B. C. (1998). Functional connectivity of the angular gyrus in normal reading and dyslexia. *Proceedings of the National Academy of Sciences*, 95, 8939-44.
- Klingberg, T., Hedehus, M., Temple, E., Salz, T., Gabrieli, J. D., Moseley, M. E., & Poldrack, R. A. (2000). Microstructure of temporo-parietal white matter as a basis for reading ability: Evidence from diffusion tensor magnetic resonance imaging. *Neuron*, 25(2), 493-500.
- Lieberman, A. M. (1998). *Reading and spelling: Development and disorders*. Mahwah, NJ: Lawrence Erlbaum.
- Lieberman, A. M. (1996). *Speech: A special code*. Cambridge, MA: MIT Press.
- Lieberman, I. Y., Shankweiler, D., Fischer, W., & Carter, B. (1974). Explicit syllable and phoneme segmentation in the young child. *Journal of Child Psychology*, 18, 201-12.
- Lieberman, I. Y., Shankweiler, D., Liberman, A. M. (1989). The alphabetic principle and learning to read. In D. Shankweiler, & I. Y. Liberman (Eds.), *Phonology and reading disability: Solving the reading puzzle* (pp. 1-33). Ann Arbor, MI: University of Michigan Press.
- Lukatela, G., & Turvey, M. T. (1994). Visual lexical access is initially phonological 1: Evidence from associative priming words, homophones, and pseudohomophones. *Journal of Experimental Psychology*, 123, 107-28.
- McIntosh, A. R., & Gonzalez-Lima, F. (1994). Structural equation modeling and its application to network analysis of functional brain imaging. *Human Brain Mapping*, 2, 2-22.
- Nobre, A. T., Allison, J., & McCarthy, G. (1994). Word recognition in the human inferior temporal lobe. *Nature*, 372, 260-63.
- Paulesu, E. U., Frith, M., Snowling, M., Gallagher, A., Morton, J., & Frith, C. D. (1996). Is developmental dyslexia a disconnection syndrome? Evidence from PET scanning. *Brain*, 119, 143-57.
- Puce, A. T., Allison, M., Asgari, J., Gore, J., & McCarthy, G. (1996). Differential sensitivity of human visual cortex to faces, letter-strings, and textures: A functional magnetic resonance imaging study. *Cerebral Cortex*, 6, 600-11.
- Pugh, K. R., Mencl, W. E., Shaywitz, B. A., Shaywitz, S., Fulbright, R., Constable, R., Skudlarski, P., Marchione, K., Jenner, A., Fletcher, J., Liberman, A., Shankweiler, D., Katz, L., Lacadie, C., & Gore, J. (2000). The angular gyrus in developmental dyslexia: Task-specific differences in functional connectivity in posterior cortex. *Psychological Science*, 11, 51-56.
- Pugh, K. R., Shaywitz, B. A., Shaywitz, S. E., Contable, R. T., Skudlarski, P., Fulbright, R. K., Bornien, R. A., Shankweiler, D. P., Katz, L., Gletcher, J., & Gore, J. C. (1996). Cerebral organization of component processes in reading. *Brain*, 119, 1221-38.
- Pugh, K. R., Shaywitz, B. A., Shaywitz, S. E., Shankweiler, D. P., Katz, L., Fletcher, J. M., Skudlarski, P., Fulbright, R. K., Constable, R. T., Bornien, R. A., Lacadie, C., & Gore, J. C. (1997). Predicting reading performance from neuroimaging profiles: The cerebral basis of phonological effects in printed word identification. *Journal of Experimental Psychology: Human Perception and Performance*, 23, 1-20.
- Richards, T. P., Dager, S. R., Corina, D., Serafini, S., Heide, A., Steury, K., Strauss, W., Hayes, C., Abbott, R., Craft, S., Shaw, D., Posse, S., & Berninger, V. (1999). Dyslexic children have

- abnormal brain lactate response to reading-related tasks. *American Journal of Neuroradiology*, 20(8), 1393-98.
- Rieben, L., & Perfetti, C. A. (1991). *Learning to read: Basic research and its implications*. Hillsdale, NJ: Lawrence Erlbaum.
- Rumsey, J. M., Andreason, P., Zametkin, A. J., Hanahan, A., Hamburger, S., Aquino, T., King, C., Pikus, A., & Cohen, R. (1992). Failure to activate the left temporo-parietal cortex in dyslexia: An oxygen 15 positron emission tomographic study. *Archives of Neurology*, 49, 527-34.
- Rumsey, J. M., Horwitz, B., Donohue, B., Nace, K., Maisog, J., & Anderson, P. (1997). Phonological and orthographic components of word recognition a PET-rCBF study. *Brain*, 120, 739-59.
- Rumsey, J. M., Horwitz, B., Donohue, B. C., Nace, K. L., Maisog, J. M., & Anderson, P. A. (1999). Functional lesion in developmental dyslexia: left angular gyral blood flow predicts severity. *Brain*, 120, 187-204.
- Salmelin, R. E., Service, P., Kiesila, P., Uutela, K., & Salonen, O. (1996). Impaired visual word processing in dyslexia revealed with magnetoencephalography. *Annals of Neurology*, 40, 157-62.
- Shankweiler, D., Crain, S., Katz, L., Fowler, A. E., Liberman, A. M., Brady, S. A., Thornton, R., Lundquist, E., Dreyer, L., Fletcher, J. M., Stuebing, K. K., Shaywitz, S. E., & Shaywitz, B. A. (1995). Cognitive profiles of reading-disabled children: Comparison of language skills in phonology, morphology and syntax. *Psychological Science*, 6, 149-56.
- 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, 1-9.
- Shaywitz, S. E., Shaywitz, B. A., Pugh, K. R., Fulbright, R., Constable, R., Mencl, W., Shankweiler, D., Liverman, Q., Skudlarski, P., Fletcher, J., Katz, L., Marchione, K., Lacadie, C., Gatenby, C. L., & Gore, J. (1998). Functional disruption in the organization of the brain for reading in dyslexia. *Proceedings of the National Academy of Sciences*, 95, 2636-41.
- Shaywitz, B., Shaywitz, S. E., Pugh, K. R., Mencl, W., Fulbright, R., Skudlarski, P., Constable, T., Marchione, K. E., Fletcher, J., Lyon, G. R., & Gore, J. (Submitted). Disruption of posterior brain systems in children with developmental dyslexia.
- Simos, P., Breier, J., Fletcher, J. M., Bergman, E., & Papanicolaou, A. (2000). Cerebral mechanisms involved in word reading in dyslexic children: A magnetic source imaging approach. *Cerebral Cortex*, 10, 809-16.
- Stanovich, K. E., Cunningham, A. E., & Cramer, B. B. (1984). Assessing phonological awareness in kindergarten children: Issues of task comparability. *Journal of Experimental Child Psychology*, 38, 175-90.
- Stanovich, K. E., & Siegel, L. S. (1994). Phenotypic performance profile of children with reading disabilities: A regression-based test of the phonological-core variable-difference model. *Journal of Educational Psychology*, 86(1), 24-53.
- Tagamets, M. A., Novick, J. M., Chalmers, M. L., & Friedman, R. B. (2000). A parametric approach to orthographic processing in the brain: An fMRI study. *Journal of Cognitive Neuroscience*, 12(2), 281-97.
- Tarkiainen, A. P., Helenius, P., Hansen, P., Cornelissen, P., & Slamenin, R. (1999). Dynamics of letter string perception in the human occipito-temporal cortex. *Brain*, 122, 2119-32.
- Torgesen, J. K., Wagner, R. K., & Rashotte, C. A. (1994). Longitudinal studies of phonological processing and reading. *Journal of Learning Disabilities*, 27(5), 276-86.
- Van Orden, G., Pennington, B., & Stone, G. (1990). Word identification in reading and the promise of subsymbolic psycholinguistics. *Psychological Review*, 97, 488-522.
- Wise, B. W., & Olson, R. K. (1995). Computer-based phonological awareness and reading instruction. *Annals of Dyslexia*, 45, 99-122.
- Ziegler, J. C., Montant, M., & Jacobs, A. M. (1997). The feedback consistency effect in lexical decision and naming. *Journal of Memory and Language*, 37, 533-54.