

Neurobiological studies of reading and reading disability

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Received 4 May 2001; received in revised form 25 June 2001; accepted 25 June 2001

Abstract

Evidence from neuroimaging studies, including our own, suggest that skilled word identification in reading is related to the functional integrity of two consolidated left hemisphere (LH) posterior systems: a dorsal (temporo-parietal) circuit and a ventral (occipito-temporal) circuit. This posterior system appears to be functionally disrupted in developmental dyslexia. Relative to nonimpaired readers, reading-disabled individuals 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 dorsal circuit predominates at first, and in conjunction with premotor systems, is associated with analytic processing necessary for learning to integrate orthographic with phonological and lexical-semantic features of printed words. The ventral circuit constitutes a fast, late-developing, word form system, which underlies fluency in word recognition.

Learning outcomes: As a result of this activity, (1) the participant will learn about a model of lexical processing involving specific cortical regions. (2) The participant will learn about evidence which supports the theory that two dorsal LH systems may be disrupted in developmental dyslexia. (3) The participant will learn that individuals with

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reading impairment may rely on other regions of the brain to compensate for the disruption of posterior function. © 2001 Elsevier Science Inc. All rights reserved.

Keywords: Dyslexia; Neuroimaging; Reading; Lexical processing; Phonology

1. Introduction

Theories of reading disability have been proposed based on putative deficiencies of several kinds of processing: the visual system (Stein & Talcott, 1999; Stein, 1993), the language system (Shankweiler, Liberman, Mark, Fowler, & Fischer, 1979), and the fine-grained temporal processing of auditory stimuli (Stein & Walsh, 1997; Tallal & Stark, 1982). However, there is now a good consensus among reading researchers that whatever the contributions of other systems and processes may be, the core difficulty in reading disability manifests itself as a deficiency within the language system and, in particular, a deficiency at the level of phonological analysis. To learn to read, a child must first develop an appreciation of the segmental nature of speech and come to realize that spoken words are composed of the smallest of these segments — the phoneme. This appreciation of the segmental nature of speech is termed *phonemic awareness*. Subsequently, the beginning reader must also understand that written words, too, possess an internal phonological structure that is the same as the spoken word. It is phonemic awareness and the understanding that the constituents of a printed word bear a relationship to phonemes that allows the reader to connect printed words to the corresponding words in his/her speech lexicon.

As many studies have shown, phonemic awareness is largely missing in reading-disabled (RD) children and adults (Brady & Shankweiler, 1991; Bruck, 1992; Fletcher et al., 1994; Rieben & Perfetti, 1991; Shankweiler et al., 1995; Shaywitz et al., 1999; Stanovich & Siegel, 1994). As to why RD readers should have exceptional difficulty developing phonemic awareness, there is support for the notion that the difficulty resides in the phonological component of the larger specialization for spoken language (Liberman, 1998; Liberman, Shankweiler, & Liberman, 1989). If that component is imperfect in an individual, the individual's perception of phonemes will be less than ideally distinctive. Therefore, it will be harder to bring their distinctiveness to conscious awareness, as must be done when learning the "sounds that letters make," i.e., in memorizing the correspondences between letters and letter clusters, on one hand, and the phonemes and syllables that they represent, on the other. As noted above, there is now overwhelming evidence that phonological awareness is characteristically deficient (or lacking) in RD readers who, as a consequence, have difficulty mapping the alphabetic characters of print onto the spoken word. For example, measures of phonemic awareness predict later reading achievement

(Bradley & Bryant, 1983; Stanovich, Cunningham, & Cramer, 1984); deficits in phonemic awareness consistently separate RD and nondisabled children (Fletcher et al., 1994; Stanovich & Siegel, 1994); phonological processing deficits persist into adulthood (Bruck, 1992; Felton, Naylor, & Wood, 1990; Shaywitz et al., 1999) and instruction in phonemic awareness promotes the acquisition of reading skills (Ball & Blachman, 1991; Bradley & Bryant, 1983; Foorman, Francis, Fletcher, Schatschneider, & Mehta, 1998; Torgesen, Morgan, & Davis, 1992; Wise & Olson, 1995). Given this background, our own functional neuroimaging research program and studies selected for discussion in this review involve a comparison of RD and nonimpaired (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 (e.g., Demb, Boynton, & Heeger, 1998; Eden et al., 1996), the reader is referred to Eden and Zeffiro (1998). For reviews of research examining anatomical/structural differences between RD and NI groups, the reader is referred to Filipek (1995) and Galaburda (1992).

2. Neurobiological studies: the posterior and anterior reading circuits

There is substantial converging evidence that identification of printed words implicates a posterior cortical reading system with both ventral and dorsal components. The ventral circuit includes lateral extrastriate areas and a left inferior occipito-temporal area where functional imaging studies show robust activation in word-reading tasks, and where electrophysiological studies reveal the earliest source of temporal dissociation (approximately 150–180 ms) in signal between printed words and pseudowords, on one hand, and nonlinguistic visual materials, on the other (Fiez & Petersen, 1998; Frackowiak, Friston, Frith, Dolan, & Mazziotta, 1997; Henderson, 1986; see also Nobre, Allison, & McCarthy, 1994; Puce, Allison, Asgari, Gore, & McCarthy, 1996; Salmelin, Service, Kiesila, Uutela, & Salonen, 1996; Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999). Evidence from a number of functional imaging studies finds this circuit to be disrupted in RD individuals (Brunswick, McCrory, Price, Frith, & Frith, 1999; Helenius, Tarkiainen, Cornelissen, Hansen, & Salmelin, 1999; Helenius, Uutela, & Hari, 1999; Pugh et al., 2000; Rumsey et al., 1997; Salmelin et al., 1996; Shaywitz et al., 1998, submitted).

A more dorsal reading-related system contains the angular gyrus and supra-marginal gyrus in the inferior parietal lobule, and the posterior aspect of the superior temporal gyrus (Wernicke's Area). The temporo-parietal circuit has long been implicated in reading and writing disorders. Indeed, a large literature on acquired dyslexia indicates that lesions centered about the angular gyrus are strongly predictive of this malady (Damasio & Damasio, 1983; Dejerine, 1891; Friedman, Ween, & Albert, 1993; Henderson, 1986). On several accounts, this

region is considered relevant in mapping the visual percepts of print onto the phonological structures of language (Benson, 1994; Black & Behrmann, 1994; Geschwind, 1965). Converging findings from functional imaging studies also implicate the temporo-parietal circuit in RD, indicating abnormal activation during reading-related tasks when decoding and when other linguistic analyses are taxed (Flowers, Wood, & Naylor, 1991; Gross-Glenn et al., 1991; Horwitz, Rumsey, & Donohue, 1998; Pugh et al., 2000; Rumsey et al., 1992, 1997; Salmelin et al., 1996; Shaywitz et al., 1998, submitted; Simos et al., 2000).

Anterior sites centered in and around Broca's Area in the inferior frontal gyrus (IFG) appears to be associated with fine-grained, speech-gestural (articulatory), phonological recoding. This circuit also functions in silent reading and naming (reviewed in Fiez & Petersen, 1998; Frackowiak et al., 1997; Pugh et al., 1996, 1997). Functional imaging studies implicate this inferior frontal region in RD (Brunswick et al., 1999; Paulesu et al., 1996; Rumsey et al., 1997; Shaywitz et al., 1998, submitted). Several findings suggest that the anterior system appears to be more heavily used by RD than normal readers, perhaps in compensation for their failure to develop the posterior reading system adequately (Pugh et al., 2000; Shaywitz et al., 1998).

3. Functional roles for posterior and anterior circuits in NI

Neuroimaging studies reveal several important differences between the temporo-parietal (dorsal) and occipito-temporal (ventral) left hemisphere (LH) posterior regions, which allow speculation on their distinctive roles in skilled word and pseudoword reading. From these findings, we suggest that the temporo-parietal circuit is associated with slow decoding, i.e., a rule-based analysis of the printed word that makes heavy use of attentional resources. This system is critical for extracting and learning the relationships between orthography and its phonological forms, connecting these to morphological and lexical-semantic information. With repeated experience of a particular word, all these elements become bound into highly integrated representations. Thus, basic decoding and analysis skills rely on an intact temporo-parietal organization.

The ventral circuit lies at the point of contact between the ventral visual stream and the middle to inferior temporal lobe. Our cross-sectional study of children indicates that the ventral word form area plays an increasingly important role in word identification for young NI readers as they become skilled (Shaywitz et al., submitted). In contrast to the dorsal circuit, the ventral occipito-temporal area responds rapidly in word identification and may, we conjecture, respond automatically, without heavy dependence on attentional resources. We suggest that the information coded by the ventral circuit is linguistically structured orthographic form. Note, however, that although the ventral system appears to process information that is orthographic (i.e., in the visual modality), we propose that this information is structured perceptually in linguistic terms, i.e., in

orthographic units that correspond to the phonological and morphological units of the speech form of the word. Such sensitivity to phonological and morphological structure could be the legacy of the slower dorsal circuit decoding process, the system that initially learned how to recognize a particular printed word. Thus, we propose that the earlier developing dorsal circuit guides and shapes the development of the ventral circuit. The development of the ventral word form circuit may depend on the integrity of the word-analytic temporo-parietal (dorsal) circuit that precedes it.

What is the evidence that supports this distinction between the dorsal and ventral circuits? In skilled readers, the dorsal circuit responds with greater activation to pseudowords and low-frequency words (words that must be decoded effortfully) than to familiar high-frequency words (see Frackowiak et al., 1997 for discussion). The ventral system shows the opposite response profile with higher activation to familiar words than to pseudowords (Tagamets, Novick, Chalmers, & Friedman, 2000; see Frackowiak et al., 1997 for a review of evidence from positron emission tomography (PET) studies regarding these systems). The increased response to unfamiliar stimuli by the dorsal system suggests that it is engaging in decoding, an effortful phonological analysis. By contrast, the ventral circuit appears to support a type of processing that depends strongly on familiarity (i.e., memory): activation is higher for well-learned words. Further evidence that suggests this distinction shows that simple word identification tasks make maximum demands on ventral sites with limited demands on dorsal sites (Brunswick et al., 1999), while tasks that involve phonological or semantic analysis show heightened dorsal responses (Pugh et al., 1996, 2000; Rumsey et al., 1997; Shaywitz et al., 1998). Additionally, Price, Moore, & Frackowiak (1996) demonstrated that as stimulus presentation rates increased from 20 through 60 words/min, ventral areas showed increased activation while dorsal areas showed decreased activation, again an opposite profile. It is plausible that analysis and computation for a given stimulus are precluded at very fast input rates, but basic visual pattern identification processes are intact. This is consistent with the notion that the dorsal circuit maps letters to phonology via effortful decoding (a computational or algorithmic process) while the ventral circuit is associated with rapid stimulus identification in which a stimulus that is perceived as a structured pattern is matched to a similar pattern in memory. Finally, the ventral circuit responds more rapidly. As noted above, Salmelin and her colleagues (Salmelin et al., 1996; Tarkiainen et al., 1999), using MEG, demonstrated that evoked responses to words and pseudowords diverge from nonlinguistic visual stimuli early (between 150 and 180 ms) at the occipito-temporal area; temporo-parietal responses arise later in time (approximately 250 ms). Further, this difference occurred in skilled readers but not in RD readers.

With respect to the anterior circuit including the LH IFG, studies indicate that it is active in silent reading (Fiez & Petersen, 1998; Price et al., 1996; Pugh et al., 1996, 1997), and is more strongly engaged by low-frequency words and

pseudowords than by high-frequency words; in this regard, it mirrors the dorsal circuit (Fiez & Petersen, 1998). A number of findings suggest that the anterior system has a role in the speech–gestural (articulatory) recoding of print. For example, we observed significantly higher levels of activation in IFG during word- and pseudoword-naming than during silent reading of the same stimuli — another indication of a role for this anterior circuit in gestural phonological recoding (Pugh et al., in preparation). Further, the circuit shows a high degree of sensitivity to the spelling–sound regularity (or perhaps 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 (e.g., PINT) elicited higher activation than regular words (e.g., MINT) at this site (Herbster, Mintun, Nebes, & Becker, 1997; see also Fiez & Petersen, 1998), a finding that converges with those of Pugh et al. (1997) in suggesting a relation between the IFG circuit and regularity/consistency effects. Behavioral studies have shown that, on average, regularity/consistency effects are stronger in overt speech production tasks (output phonology) than in silent reading tasks such as lexical decision, suggesting an important contribution of gestural phonological recoding to this effect (Hino & Lupker, 2000). 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 (Inhoff, Briihl, & Schwartz, 1996; Ziegler, Montant, & Jacobs, 1997).

4. Altered functions for posterior and anterior circuits in RD

There are clear functional differences between NI and RD readers with regard to the dorsal, ventral, and anterior sites we have been discussing. In RD readers, a number of functional imaging studies have observed LH posterior dysfunction, at both dorsal and ventral sites during phonological processing tasks (Brunswick et al., 1999; Helenius, Tarkiainen, et al., 1999; Helenius, Uutela, et al., 1999; Pugh et al., 2000; Rumsey et al., 1992, 1997; Salmelin et al., 1996; Shaywitz et al., 1998, submitted; Simos et al., 2000). This disruption is reflected by a relative underengagement of these circuits specifically in processing words and pseudowords where decoding is required, suggesting a disruption of this region in RD readers. For instance, in our study of adults (Shaywitz et al., 1998), we observed 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. As noted above, in the Salmelin studies using MEG, skilled readers show a response to

printed tokens between 150 and 180 ms poststimulus onset at the occipito-temporal area, but this early ventral response is not seen in adult developmental dyslexics, suggesting disruption here for them. Additionally, in our recent examination of children (Shaywitz et al., submitted), we observed anomalous activation in RD readers at both dorsal and ventral LH sites during word- and pseudoword-reading tasks, confirming our findings from an earlier adult sample (Shaywitz et al., 1998). Importantly, this posterior anomaly was confined to tasks that tapped word- and pseudoword-reading only, for both adults and children. In contrast, on tasks that did not require phonological decoding, no group differences were seen.

While most neuroimaging studies have sought to identify those brain regions within which activation patterns discriminate RD from NI readers, implicating the dorsal and ventral aspects of LH posterior cortex, a more complete understanding of the neurobiology of developmental dyslexia requires that we also consider relations between the distinct brain regions, which function cooperatively to process information during reading. This relational processing issue has been referred to as one of functional connectivity between cortical areas. Evidence consistent with the notion of a breakdown in functional connectivity within the posterior reading system in RD readers has been recently reported by Horwitz et al. (1998) using activation data from the Rumsey et al. (1997) PET study. These authors examined correlations between activation levels in the LH angular gyrus and other brain sites during two reading-aloud tasks. 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 posterior reading system. We recently extended the analysis of our initial sample of adults to examine functional connectivity between LH posterior regions in these two groups (Pugh et al., 2000). As in the Horwitz et al. study, we looked at functional connectivity between the angular gyrus and occipital and temporal lobe sites, but using a hierarchically organized set of tasks — tasks that systematically varied demands made on phonological assembly. While for RD readers LH functional connectivity was indeed weak on word- and nonword-reading tasks as suggested by Horwitz et al., there appeared to be no dysfunction in the tasks which tap metaphonological judgments only, or complex visual–orthographic coding only. The results are most consistent with a specific phonological deficit hypothesis: A breakdown in LH posterior systems manifests only when orthographic to phonological assembly is required. Moreover, we found that on word- and nonword-reading tasks, right hemisphere (RH) homologues appear to function in a compensatory manner for RD readers; correlations were strong and stable in this hemisphere for both reading groups.

In our studies (Pugh et al., 2000; Shaywitz et al., 1998, submitted), we also observed reading disability processing that appears to be compensatory. We found that on those tasks that made explicit demands on phonological

processing (pseudoword and word tasks), RD readers showed a disproportionately greater engagement of IFG and prefrontal dorsolateral sites than did NI readers. Rumsey et al. (1997) found the same pattern of posterior disruption and inferior frontal reliance with PET. 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 and, more recently, Brunswick et al. (1999) and Richards et al. (1999) have shown disproportionately elevated frontal activation in RD readers across several different tasks. Thus fMRI, PET, and MEG studies converge to suggest that there is a LH posterior anomaly and an apparent compensatory shift to frontal sites in reading disability.

Evidence of a second apparent compensatory shift (in this case, to posterior RH), comes from several findings. In Shaywitz et al. (1998), we observed a significant interaction of hemisphere by reading group in angular gyrus and middle temporal gyrus. The effect showed greater RH, than LH, activation in NI readers, but greater LH, than RH, activation in RD readers (see also Barnard-Lamm, Epstein, & Pratt, 1994). As noted, in the correlational analysis with the same reading tasks, RD readers failed to demonstrate any evidence of functional connectivity between major posterior circuits in the LH. In contrast, NI readers displayed strong correlations at reading disability homologues of these sites that were numerically higher than the correlations of RD readers (Pugh et al., 2000). Rumsey et al. (1999) examined the relationship between RH activation and reading performance in their RD and NI subjects and found that RH temporoparietal activation was correlated with standard measures of reading performance only for RD readers, suggesting a compensatory function for the shift to RH. We observed a similar predictive relation between RH sites and reading skill in our samples of children (Shaywitz et al., submitted). In summary, NI readers show strong functioning LH posterior circuit in word- and pseudoword-reading, but RD readers do not. Instead, they show evidence of two, apparently compensatory responses to their LH posterior dysfunction: increased bi-hemispheric IFG activation and an increased functional role for RH posterior sites (Pugh et al. 2000; Shaywitz et al., 1998).

5. Summary and a tentative model

Posterior reading circuits including both dorsal (temporo-parietal) and ventral (occipito-temporal) components are disrupted in people who are RD, as indicated by reduced activation as well as by disrupted functional connectivity between these areas. Additionally, there appear to be two characteristic compensatory patterns in response to this LH posterior anomaly: (1) increased reliance on IFG during reading, and (2) an increased tendency to rely on the RH homologues of the dysfunctional LH posterior circuits. Our cross-sectional imaging studies of children suggest the following model.

In the normally developing NI reader, the development of the LH posterior reading circuits, particularly the ventral occipito-temporal area, is dependent on an organized integration of phonological, morphological, and lexical–semantic processing of words within highly overlapping neural circuits. We assume that this integration relies initially on the intactness of processing in the temporo-parietal circuit (presumably via feedforward and feedback resonance with articulatory recoding sites in the frontal lobe). Deficient dorsal function will fail to support appropriate ventral development. Thus, in the RD reader, temporo-parietal difficulties disrupt this developmental trajectory. The shift to inferior frontal sites in the RD child reflects a compensatory reliance on these circuits to support articulatory recoding (covert pronunciation) in an attempt to cope with a problematic phonological analysis of printed words. A second compensatory shift, from posterior LH to posterior RH, likely reflects the development of an additional word recognition process that is essentially visual–perceptual; graphemic patterns in the printed word are associated directly with entries in the RD reader’s mental lexicon. Thus, these visual patterns do not code the phonological or morphological information that the NI reader perceives within the printed word, but instead represent the printed word as a nonlinguistic visuo-semantic icon. This developmental account of the neural circuitry of reading (Fig. 1) provides a first approximation for the neurobiological substrate of reading and RD. As the model 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

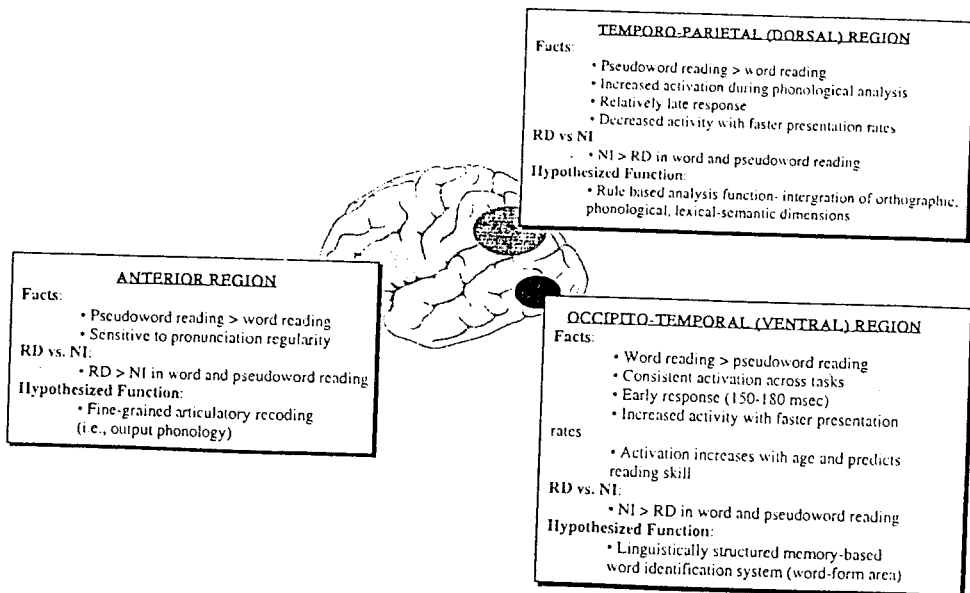


Fig. 1. A tentative model of the neural circuitry for reading.

on training-related changes in the activation of the LH ventral circuit as a target for interventions that could be expected in turn to lead to improved word-reading skill in dyslexic children.

Acknowledgments

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 by National Institute of Child Health and Human Development grant HD-01994 to Haskins Laboratories. This paper is dedicated to the memory of our dear friend and colleague, Professor Alvin Liberman, whose intellectual guidance and boundless love of truth was, and will continue to be, a driving force behind our program of research.

Appendix A. Continuing education

1. Reading impairment in the majority of individuals with dyslexia appears attributable to
 - a. visual confusions
 - b. letter confusions
 - c. phonological decoding problems
 - d. vocabulary deficits
 - e. syntactic deficits

2. The posterior ventral reading circuit appears to support
 - a. identification of printed words
 - b. identification of sentence context
 - c. identification of word meanings
 - d. phonological decoding
 - e. syntactic decoding

3. Reading-disabled subjects may attempt to compensate for poor reading through
 - a. increased reliance of the ventral posterior regions of the brain
 - b. increased reliance on the dorsal posterior regions of the brain
 - c. increased reliance on the superior frontal regions of the brain
 - d. increased reliance on the inferior frontal regions of the brain
 - e. increased reliance on the RH

4. The dorsal reading circuit appears to support
 - a. phonological analysis
 - b. syntactic analysis

- c. morphological analysis
 - d. high-frequency words
 - e. all of the above
5. The inferior frontal region of the brain tends to be active in tasks requiring
- a. decoding of pseudowords
 - b. decoding of low-frequency words
 - c. articulatory recoding of print
 - d. silent reading
 - e. nonreading control tasks

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0003-1682(200109)34:6:1-0 Volume 34, Number 6, November/December 2001
ISSN 0021-8922

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