MENTAL RETARDATION AND DEVELOPMENTAL DISABILITIES
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FUNCTIONAL NEUROIMAGING STUDIES OF READING AND READING DISABILITY (DEVELOPMENTAL DYSLEXIA)

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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 consolidated left hemisphere (LH) posterior systems: a dorsal (temporo-parietal) circuit and a ventral (occipito-temporal) circuit. This posterior system is functionally disrupted in developmental dyslexia. Reading disabled readers, 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 dorsal circuit predominates at first, and is associated with analytic processing necessary for learning to integrate orthographic features with phonological and lexical-semantic features of printed words. The ventral circuit constitutes a fast, late-developing, word identification system which underlies fluent word recognition in skilled readers.
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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 and Bryant, 1983; Liberman et al., 1989]. Phonological assembly refers to the decoding operations associated with letter-to-phoneme mapping in printed word identification (Fig. 1). 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 and Shankweiler, 1991; Rieben and Perfetti, 1991; Bruck, 1992; Fletcher et al., 1994; Stanovich and Siegel, 1994; Shankweiler et al., 1995]. 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 et al., 1989; Liberman, 1996; 1998]. 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 and 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 and 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 and Bryant, 1983; Ball and Blachman, 1991; Torgesen et al., 1992; Wise and 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 information continues to serve as an important component in rapid word identification even for mature skilled readers [cf., Van Orden et al., 1990; Lukatela and Turvey, 1994]. Given this

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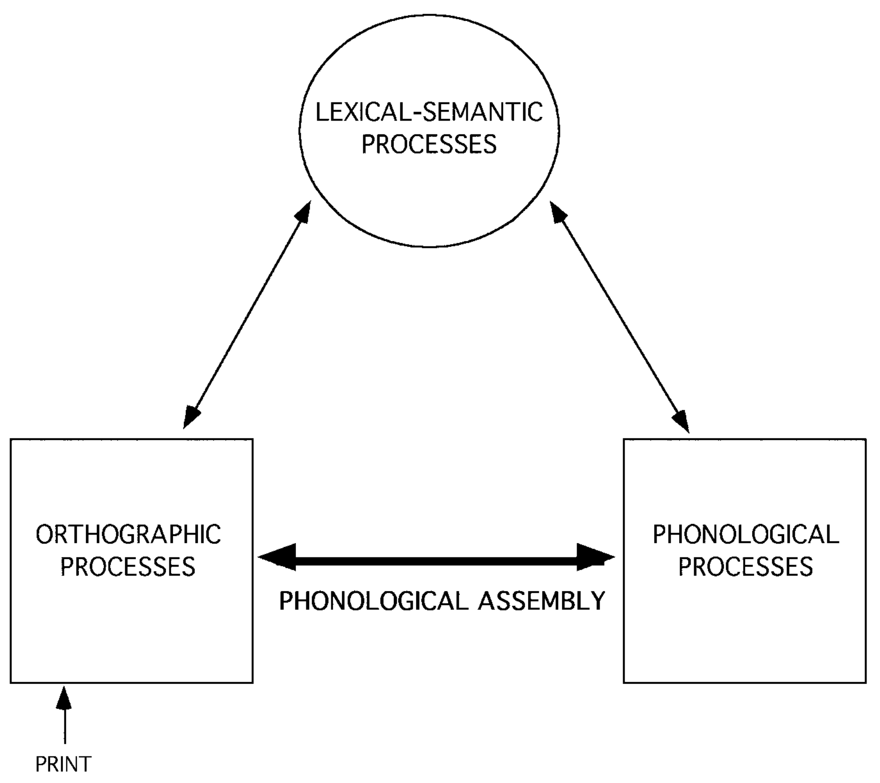

Fig. 1. Component processes for word identification in reading. Evidence suggests that word identification problems in reading disability reflect core deficits at the level of orthographic-to-phonological mapping (shown by the bold lines).

background, our own functional neuroimaging research program and 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 differences between RD and NI groups the reader is referred to Galaburda [1992] and Filipek [1995].

OVERVIEW OF THE MAJOR READING CIRCUITS IN NI AND RD

Converging evidence from a number of laboratories using several imaging technologies [functional magnetic resonance imaging (fMRI), positron emission tomography (PET), and magnetoencephalography (MEG)] indicates that printed word and pseudoword processing implicates a left hemisphere (LH) posterior reading system consisting of both ventral and dorsal components (Fig. 2). The ventral circuit includes lateral extrastriate areas and a left inferior occipito-temporal area where functional imaging studies show robust activation in word and pseudoword reading tasks [reviewed in Henderson, 1986; Frackowiak et al., 1997; Fiez and Petersen, 1998; see also Nobre et al., 1994; Puce et al., 1996; Salmelin et al., 1996; Tarkainen, et al., 1999]. Moreover, findings from a number of functional neuroimaging studies implicate this circuit as dysfunctional in reading disability [Salmelin et al., 1996; Rumsey et al., 1997; Shaywitz et al., 1998; Helenius et al., 1999; Pugh et al., 2000; Helenius et al., in press; Shaywitz et al., personal communication].

The more dorsal circuit 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 circuit 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, 1983; Henderson, 1986], a region considered pivotal in carrying out cross-modal integration necessary for reading (i.e., mapping the visual percept of the print onto the phonologic structures of the language) [Geschwind, 1965; Benson, 1994; Black and Behrmann, 1994]. Converging evidence from functional neuroimaging studies also implicate the temporo-parietal circuit 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; Rumsey et al., 1992; Salmelin et al., 1996; Rumsey et al., 1997; Horwitz et al., 1998; Shaywitz et al., 1998; Pugh et al., 2000; Shaywitz et al., personal communication].

An anterior circuit 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 circuit also is involved in silent reading and naming [reviewed in Pugh et al., 1996; Pugh et al., 1997; Frackowiak et al., 1997; Fiez and Petersen, 1998; Shaywitz et al., 1998]. Evidence from functional imaging studies has implicated this anterior region in RD [Salmelin et al., 1996; Rumsey et al., 1997; Shaywitz et al., 1998; Brunswick et al., 1999; Richards et al., 1999 presumably in compensation for the failure to develop the LH posterior circuits adequately. Before considering the distinct information processing roles that these circuits 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, studies of RD readers using PET, MEG, and fMRI have observed what appears to be LH posterior dysfunction at both dorsal and ventral sites across several reading tasks [Salmelin et al., 1996; Rumsey et al., 1997; Horwitz et al., 1998; Shaywitz et al., 1998; Helenius et al., 1999; Pugh et al., 2000; Shaywitz et al., personal communication]. Essentially, this disruption, in most studies, is characterized by a relative under-engagement of these circuits, specifically during the processing words and pseudowords. Rumsey and colleagues [1992], employing PET reported that NI readers failed to show reliable activation at temporo-parietal sites engaged by NI readers even 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 the first task the 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 task

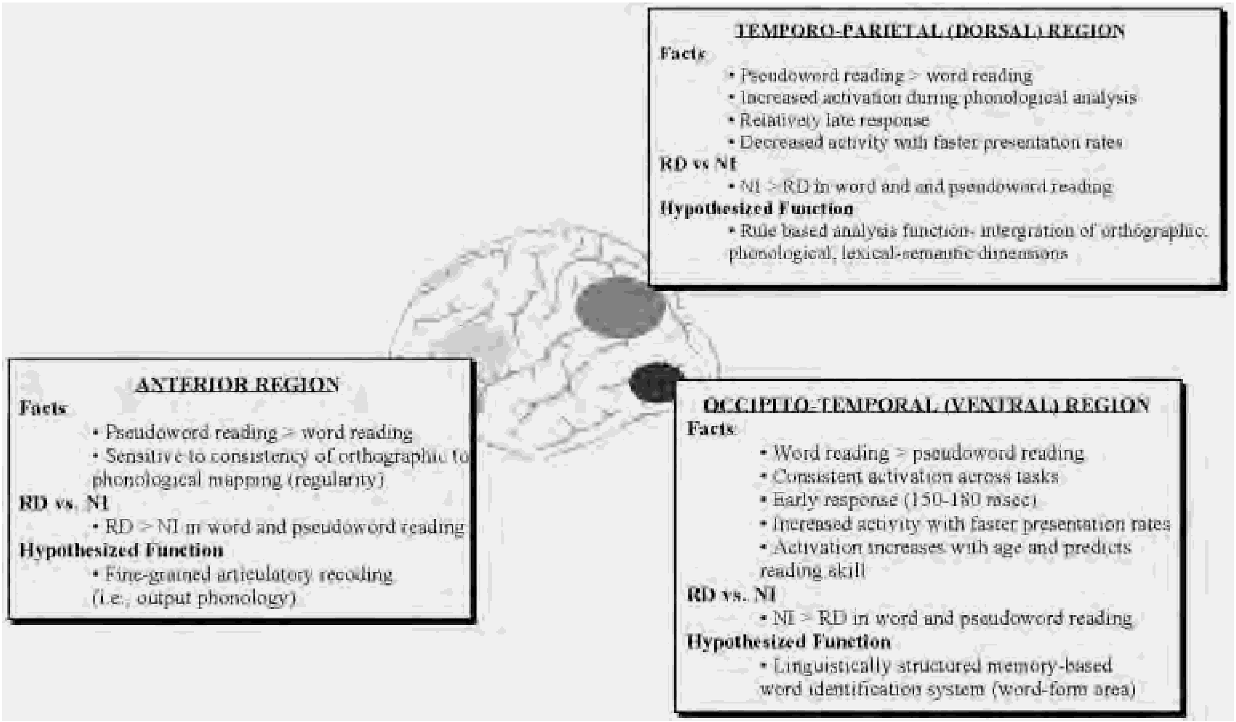

Fig. 2. A general overview of three major reading circuits.

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 circuits both silent reading and pronunciation for words and pseudowords was associated with reduced activation in RD participants. A more recent PET study by Brunswick and colleagues [1999] reinforces this finding. 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 ventral occipito-temporal regions 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; Tarkainen et al., 1999] 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 temporal course of task-related electrophysiological activity. For NI readers print processing was associated with a heightened response relative to nonlinguistic tokens at between 150–200 msec post stimulus onset at the occipito-temporal area. In contrast, RD participants 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 in sentence-processing tasks in the superior temporal gyrus at approximately 250 msec [see Simos et al., in press, for additional evidence of 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 discussed next, wherein we attempted to isolate component systems in word and pseudoword reading [Shaywitz et al., 1998; Pugh et al., 2000].

The aim of our initial investigation [Shaywitz et al., 1998] was to employ a set of hierarchically structured tasks that control the kind of language-relevant coding required (especially including the demand on phonologic analysis) and then to compare the performance and brain activation patterns (as measured by fMRI) of NI and RD readers. We used five tasks that varied in the demands made on: visual-spatial processing, orthographic processing, simple phonologic analysis, phonological assembly, and lexical-semantic processing. We hypothesized 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 (\\\/) and (\\\/) match?], which taps visual-spatial processing, but makes no orthographic demands. Next, the Letter Case 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

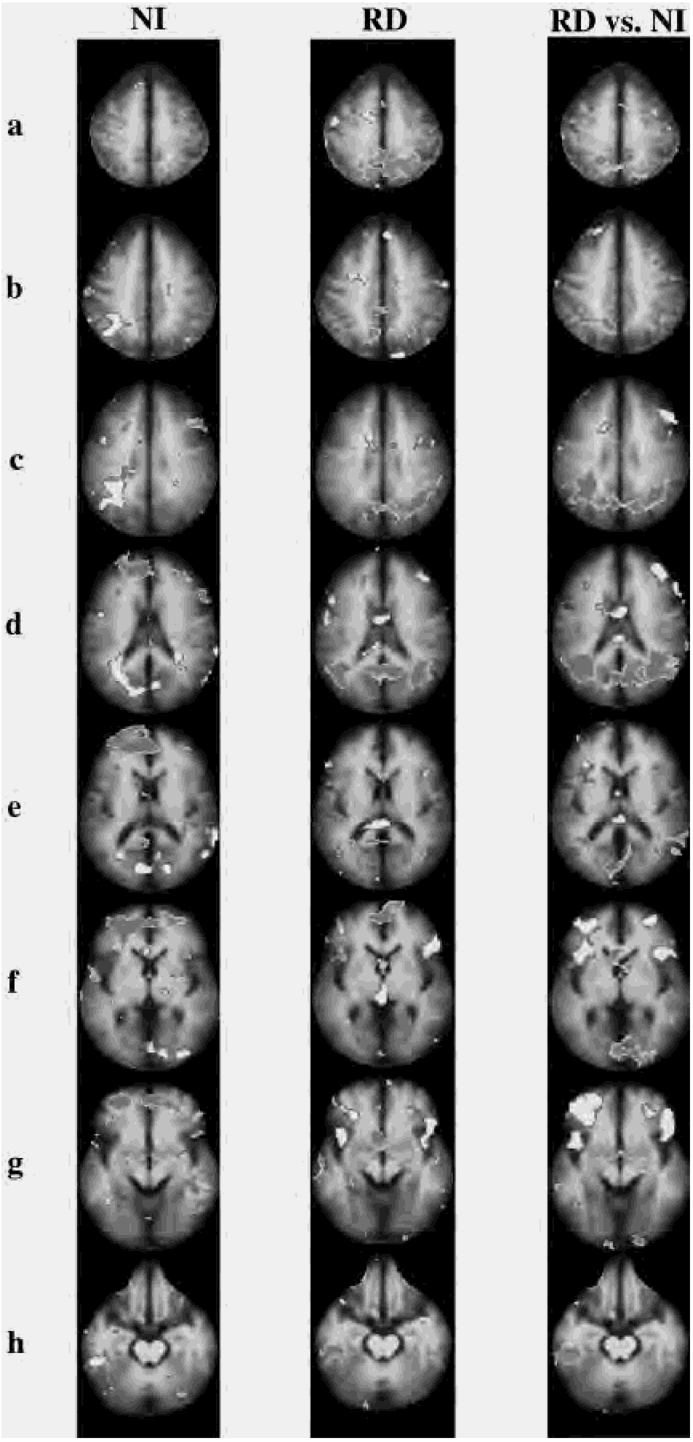

Fig. 3. Activation maps for RD vs. NI readers. Columns 1 and 2 contrast the nonword rhyme task with the case judgment baseline task for each group. Areas in red/yellow show regions of increased activation in the rhyme relative to the case task for each group. Column 3 shows the Group-by-Task interaction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

demands on phonological assembly [Lukatela and Turvey, 1994], but requires in addition that the printed stimulus items activate particular word representations in the readers lexicon to arrive at the words meaning. A common baseline subtraction condition was used in analysis: C, SLR, NWR, and SC tasks contrasted with the non-language 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 and other frontal lobe areas in response to increasing phonological demands. These differences are illustrated in Fig. 3, which shows the contrast of the Case task with Nonword Rhyme (the latter places maximum demands on phonological assembly and analysis).

Although most neuroimaging studies have sought to identify specific brain regions within which activation patterns discriminate DYS from NI readers [e.g., Rumsey et al., 1997; Shaywitz et al., 1998], a deeper understanding of the neurobiology of developmental dyslexia requires that we also consider relations between distinct brain regions which function cooperatively to process information during reading; this issue has been referred to as one of functional connectivity between cortical areas [Friston, 1994; McIntosh and Gonzalez-Lima, 1994]. Evidence consistent with the notion of a breakdown in functional connectivity within the posterior reading system in DYS readers has been recently reported by Horwitz, Rumsey, and Donohue [1998] using activation data from the Rumsey et al. [1997] PET study. They examined correlations (within task/over subjects) between activation levels in the left hemisphere (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 DYS 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]. We looked at functional connectivity between the angular gyrus and occipital and temporal lobe sites using our hierarchical tasks; tasks that systematically varied demands made on phonological assembly. While for DYS readers LH functional connectivity was indeed weak on word and nonword reading tasks as suggested by Horwitz et al. [1998], there appeared to be no dysfunction in the tasks which tap metaphonological judgments only (SLR), or complex visual-orthographic coding only (C) (Fig. 4). 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. The notion of a global lesion, one that would disrupt functional connectivity in this system across all types of cognitive behaviors, is not supported. Moreover, we found that on word and nonword reading tasks right hemisphere homologues appear to function in a compensatory manner for DYS readers; correlations were strong and stable in this hemisphere for both reading groups (see Fig. 4).

As noted, in a presumably compensatory response to LH posterior weaknesses, RD readers show increased reliance on both bihemispheric inferior frontal areas and RH posterior sites including the RH temporo-parietal circuit. 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. 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, Richards et al. [1998] and Brunswick et al. [1999] have shown disproportionately elevated activation 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]. 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. In contrast, they displayed robust correlations at RH homologues of these sites with numerically higher correlations than NI readers [Pugh et al., 2000]. 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., 2000; Shaywitz et al., personal communication]. 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.

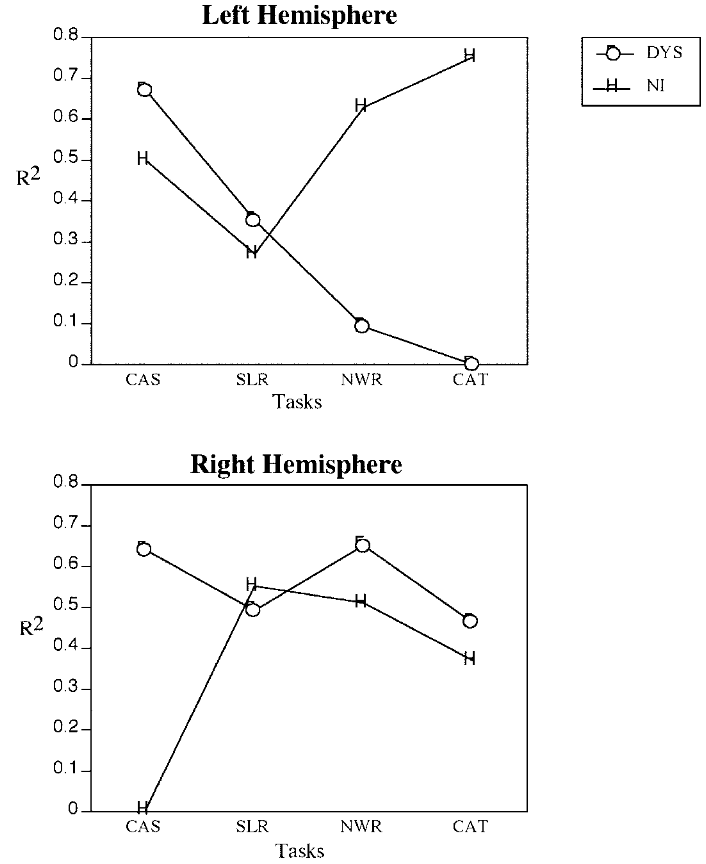

Fig. 4. The results of multiple regression analyses on activation at the angular gyrus by four posterior predictor regions-of-interest are shown for both DYS and NI groups by task and by hemisphere. Proportion of variance accounted for is plotted on the *y*-axis.

COMPUTATIONAL ROLES FOR POSTERIOR AND ANTERIOR CIRCUITS 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 reveal the causes of these differences. For example, the temporo-parietal anomalies detected across studies may suggest an underlying neurological problem at this site (i.e., a developmental lesion), but alternatively the failure of RD readers to develop this circuit could 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. To begin to move 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 circuits 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 word and pseudoword reading. From these findings, which will be discussed next, we propose the following account: the temporo-parietal circuit is associated with rule-based analysis and learning; essentially this system 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 Fig. 2.

We propose that the development of this fast, ventral word form circuit depends on the integrity of analytic processing that occurs in the temporo-parietal or dorsal circuit. There are several lines of evidence that support this proposed relation. In skilled readers, the dorsal circuit responds with greater activation to pseudowords and low-frequency words than to familiar high-frequency words, while the ventral circuit shows the opposite response profile with higher activation to familiar words than to pseudowords [see 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 circuit 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 while dorsal areas 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 circuit is associated with analysis and computation while the ventral circuit 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; Tarkanian et al., 1999] have demonstrated that evoked responses to words and pseudowords diverge from nonlinguistic stimuli early (between 150–180 msec) at the occipito-temporal area; temporo-parietal responses arise later in time (approximately 250 msec). Additionally, our preliminary results from the study of a large group of NI and RD children with a large range in ages (7–17 years) suggests that the LH ventral word form area plays an increasingly important role in skilled word identification along with age and reading experience; activation in the LH occipito-temporal circuit is highly predictive of reading speed and accuracy on a number of standardized measures [Shaywitz et al., personal communications]. Thus, the ventral word form system is fast, relatively late developing, and associated with greater reading fluency.

With respect to the anterior circuit including the LH inferior frontal gyrus, studies indicate that it has a role in speech-gestural articulatory recoding of print. For example, the circuit 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 and Peterson, 1998], a finding that converges with those of Pugh et al. 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 production tasks (output phonology) than in silent reading tasks such as lexical decision, suggesting an important contribution of gestural phonological recoding [Hino and 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 [Zeigler et al., 1997]. Thus the relation between IFG and pronunciation regularity effects suggests a role in speech-gestural or articulatory recoding for this circuit. Finally, in a recent pilot study we observed significantly higher levels of activation at sites within 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 recoding of print.

SUMMARY AND A TENTATIVE MODEL

Posterior reading circuits including both 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 propose the following hypothesis: in NI readers the development of LH posterior reading circuits, particularly the ventral occipito-temporal area, is dependent on a highly organized integration of phonological and lexical-semantic features of words within overlapping neural circuits. Moreover we assume that this integration relies initially on the intactness of processing in the temporo-parietal learning systems; deficient dorsal function will fail to support appropriate development of the fast ventral word form circuit. We suggest that for RD children temporo-parietal difficulties disrupt this developmental trajectory. The shift to the inferior frontal gyrus in RD children reflects an increased reliance on this circuit to support articulatory recoding (covert pronunciation) in an attempt to cope with the demands on phonological analysis. Their RH posterior shift reflects the additional and dissociated development of nonphonological based visuosemantic pattern recognition to support semantic aspects of word reading. Thus a poorly formed occipito-temporal system, itself the result of a disruption of temporo-parietal functioning, underlies the failure to develop skilled reading, while a shift to ancillary systems supports only marginal and nonfluent word reading. This developmental account of the neural circuitry of reading provides a first approximation for the neurobiological substrate of reading and reading disability. 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 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 in dyslexic children. ■

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