Chapter 29

What Does Reading Have to Tell Us about Writing?

Preliminary Questions and Methodological Challenges in Examining the Neurobiological Foundations of Writing and Writing Disabilities

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Neuroimaging techniques have been employed with increasing frequency in recent years to examine both typical and atypical development in cognitive domains such as language, reading, memory, mathematical reasoning, attention, and executive function (Papanicolaou, Pugh, Simos, & Mencel, 2004). Research aimed at identifying the neural systems (neurocircuitry) that underlie these complex cognitive functions has benefited in recent years from rapid advances in neuroimaging technologies (e.g., positron emission tomography [PET]; functional magnetic resonance imaging [fMRI]; magnetoencephalography [MEG]).

In essence, functional neuroimaging allows us to identify sets of interrelated brain regions that are engaged (activated) when the participant performs a specific cognitive task (see Papanicolaou et al., 2004, for detailed methodological discussion and contrast of different technologies). While we can assume that different cognitive functions will engage many overlapping brain regions, we also might expect domain-specific circuits, and the extant data seem to bear out this expectation. Thus, for instance, some—but not all—brain regions activated during language-processing tasks will be nonoverlapping with regions associated with visual perception, mathematical reasoning, or memory tasks (Frackowiak, Friston, Fruth, Dolan, & Mazziotta, 1997).

In this chapter we consider the kinds of methodological and design challenges that must be met if functional neuroimaging is to be applied fruitfully to the study of composition in writing and its disorders. To date, relatively little neuroimaging research has been conducted in this complex language production domain. However, it can be reasonably assumed from the outset that writing will share with other language functions many overlapping neurobiological systems. Therefore, we begin by considering previous findings on the functional brain organization for spoken and written language perception and production. Berninger, Abbott, Abbott, Graham, and Richards (2002) have conducted extensive behavioral research on the interrelations among all of these language domains, stressing the need to determine how composition in writing and its difficulties relate to general competencies for language by ear (speech perception), mouth (speech production), eye (reading), and hand (writing). Moreover, each of these language domains is complex and hierarchically organized (Inde-
frey & Levelt, 2004); we have previously noted the need to develop methods and experimental designs that will allow us to isolate and examine component subprocesses in each domain (Pugh et al., 1997, 2000). For example, for any modality, we can draw meaningful distinctions between hierarchically organized sublexical, lexical, syntactic, and comprehension-related component processes. To varying degrees, each of these component processes is likely to be shared among the written and spoken language domains.

Behavioral research suggests that disorders of reading and writing are highly comorbid and may therefore share a common etiological basis (Berninger et al., 2002). Because more is known at present regarding the neurobiology of reading development and disability with respect to component process organization, as well as the neurobiological signatures of successful remediation on these processes, this literature is reviewed in some depth to provide a set of preliminary hypotheses about what might be anticipated as we begin to explore writing difficulties and their remediation. We begin however, by considering what is known about the neurobiological substrates for written versus spoken language in general.

**Written Language and Its Relation to Spoken Language**

Both in the history of the human species and the development of the individual child, spoken language capacity emerges prior to the secondary, derived language abilities of reading and writing. Although the cortical and subcortical organization for spoken language perception and production is viewed by many as a biological specialization, reading and writing, by contrast, are certainly not (Liberman, 1992). In contrast to spoken language communication skills, reading and writing must be explicitly taught, and significant numbers of children for whom spoken language communication skills are adequate, will fail to obtain age-appropriate reading and writing levels even with intensive training. When considered from the neurobiological perspective, the acquisition of writing skills requires the integration of visual, motor, language, and associative cortical regions, which can eventually permit bidirectional mapping between the visual forms of words to already well-established spoken language representations (Price, Winterburn, Giraud, Moore, & Noppeney, 2003; Pugh et al., 2000).

Neuroimaging studies that have directly compared spoken with printed word identification have generally found largely overlapping neural networks across the left-hemisphere (LH) cortex (Carpentier et al., 2001; Chee, O'Craven, Bergida, Rosen, & Savoy, 1999; Constable et al., 2004; Howard et al., 1992; Michael, Keller, Carpenter, & Just, 2001; Shaywitz et al., 2001; Simos, Popaniolou, & Breier, 1999). A recent study from our group is illustrative (Constable et al., 2004). Cortical regions engaged by sentence processing in the auditory versus the visual modality were mapped using fMRI. Figure 29.1A demonstrates the influence of input modality: Auditory presentation was associated with relatively higher activity at subregions within the superior temporal gyrus (STG) bilaterally, whereas printed sentences evoked heightened activity at a wider set of mostly posterior sites, including the angular gyrus, supramarginal gyrus, and the fusiform gyrus in the occipitotemporal region within the LH, along with specific loci in the inferior frontal gyrus (IFG). The intersection of these modality-dependent maps (Figure 29.1B), however, revealed many overlapping regions located primarily in the LH, including sites within the IFG, and the STG (see Figure 29.2 for a lateral view of key reading and language zones).

Thus, while reading was associated with a somewhat more broadly distributed posterior circuitry than speech processing (as anticipated by the biological specialization and naturalness argument), the two modalities also show extensive overlap in all major language zones in the LH, including the traditionally defined Broca's area in the IFG, and Wernicke's area in the STG and temporoparietal region (see Figure 29.2). Whereas printed and spoken language processing employ very different sensory level processes (i.e., vision and audition), our focus is on language; accordingly, we employed a subtraction design to control for these non-language differences. The basic logic of subtraction designs is to use control or baseline tasks that share secondary operations with
FIGURE 29.1A. In black are regions with higher activation for printed than for spoken sentences. In white are regions with higher activation for spoken than for printed sentences. Left hemisphere is shown on the right (per radiological convention).

FIGURE 29.1B. In black are regions of maximum overlap for both printed and spoken sentences. Left hemisphere is shown on the right (per radiological convention).

the task of interest (thus, for spoken sentences, we employed an auditory tone judgment control task, and for printed sentences, a visual line judgment control task to isolate language-related activation patterns). In theory, we are able to “subtract away” the brain activation due to sensory processing and are left with the brain activation due to language-specific processing. As seen in figure 29.1B, the overlap within traditional language zones appears to be the most salient feature of this type of contrast. This would certainly motivate speculation that similar patterns with respect to both overlap in traditional language zones with somewhat more diffuse activation for writing relative to speaking due to differences in biological specialization will be evident when written and spoken language production are contrasted with similar designs (controlling for differences in mode of output).

Neural Mechanisms of Language Production: Speaking and Writing

As we begin to map out the brain circuitry for language by eye, ear, mouth, and hand, in order to examine their interdependencies in struggling readers and writers (Berninger et al., 2002), we cannot point to a single experiment that has contrasted all of these pro-
cesses in the same subjects. To explore these complex interrelations in the absence of such studies, Indefrey and Levelt (2004) conducted a large-scale meta-analysis of 82 published neuroimaging experiments in order to identify the neurocircuitry for production of words during varied language tasks, along with the overlap between production and perception. Given the paucity of neurobiological evidence on writing and its various component processes, some consideration of the extant literature on the neurobiology of oral language production may provide some initial insights.

This meta-analysis revealed a complex taxonomy when considering both the location and relative timing of each language process, but several general patterns do emerge. First, large portions of traditionally defined language regions are activated during both spoken language perception and production tasks, including those regions discussed in the preceding section comparing spoken with printed sentence processing: bilateral STG, LH middle temporal gyrus (MTG), and LH IFG. Perhaps this evidence for highly overlapping neural networks for perception and production should not be so surprisingly given the body of behavioral evidence suggesting that speech perception is to some degree, at least, grounded in the mechanisms of speech production (Liberman & Mattingly, 1985).

Second, while revealing tight perception-production links at the neurobiological level of analysis in broad terms, the results of the meta-analysis also suggest that hierarchically organized component processes in spoken language production are partially dissociable within these largely LH language networks. To illustrate this hierarchical organization, one that will have parallels in written language as well, consider the stream of events that need to occur if a participant is presented with pictures of objects and asked to name them aloud. This simple task should engage initially semantic-conceptual processing, followed by lexical selection (finding the word in the mental lexicon), followed by retrieval of the phonological form, and finally phonetic and articulatory planning. These operations are therefore in some sense hierarchically organized, and while they need not be strictly serial, they must logically unfold in a sequential fashion, with, for instance, lexical selection necessarily preceding phonetic and articulatory planning (Levelt, Roelofs, & Meyer, 1999). The meta-analysis included studies using multiple imaging modalities, some of which yield information on spatial location of activation (e.g., PET, fMRI) and others, on the relative timing of these activations (e.g., electroencephalography [EEG], MEG). The analysis suggests that posterior temporal regions (the middle and superior temporal gyri) are active relatively early in naming tasks and likely are associated with lexical and phonological retrieval, while frontal regions, including the supplementary motor area and posterior components of the IFG and insula are activated somewhat later during the naming event and are likely associated with phonetic and articulatory planning relevant to generating the output response. While much more research is needed to gain a precise and fine-grained account of the functional anatomy of spoken language production, and while there is still ongoing debate with respect to precise timing and localization, this posterior to anterior hierarchically organized taxonomy can provide a platform for contrasting written and spoken language output. As with perception, we would anticipate that writing words will overlap speaking at brain regions associated with conceptual, lexical, and phonological processing. On the naturalness argument, we might imagine a less localized pattern for writing relative to speaking, but again, overlap at more abstract levels of processing should be the rule. Differences will no doubt emerge as we isolate later stages of processing relevant phonetic and motor output.

To date, we have few neuroimaging data on the various higher order processes involved in writing (i.e., semantic-conceptual processing, syntax, lexical selection, and phonological coding). But given the evidence discussed in the preceding sections, we might anticipate many overlapping cortical networks for writing and for speaking at more abstract conceptual and linguistic levels of analysis and, hence, the neurobiological model of speaking put forth by Indefrey and Levelt (2004) might serve as an initial framework for generating expectations about the neurocircuitry of writing. Again, in the domain of perception, both spoken and written words and sentences engage largely overlap-
ping neural networks, with some modality-specific regions evident for prelexical input processing stages (Constable et al., 2004; see Figure 29.1).

In the domain of production, lesion studies examining patients with selective deficits in either written or oral spelling suggest that largely overlapping conceptual and lexical systems are likely to be found up to the point at which writing and speaking diverge mechanically, with neural output systems being modality-specific (Croisile et al., 1996; Del Grosso Destreri et al., 2000; Friedman, 1989; Hodges & Marshall, 1992; Miozzo & De Bastiani, 2002). Lesion studies of a relatively rare condition known as pure agraphia have implicated both the superior parietal lobule and middle frontal regions, suggesting a possible role in control of writing behavior for these regions.

A few neuroimaging studies have been conducted to date examining the neural correlates of handwriting. These studies may be thought of as beginning to reveal the neurocircuitry relevant to phonological-to-graphemic and/or graphemic-to-motor planning stages of processing during writing. In one study (Katanoda, Yoshikawa, & Sugishita, 2001), a group of Japanese participants was instructed to write the names of pictured objects, and in a second study (Menon & Desmond, 2001), a group of English speaking participants wrote sentences from dictation. Both studies converge to suggest a role for the regions previously implicated in lesion studies: the LH superior parietal lobule and LH middle to inferior frontal gyri. While the frontal regions would appear to be partially overlapping with areas implicated in speech production (Indefrey & Levelt, 2004) the involvement of the LH superior parietal lobule appears to be more specific to writing (Katanoda et al., 2001). While the tasks employed in these initial studies do not make significant demands on higher order aspects of writing behavior, such as conceptual or grammatical processing, they do suggest neural subsystems that might be crucial to the process of generating written word forms. One might speculate that if handwriting is more compromised than more general phonological and language processes in some clinical cohorts, anomalous activation patterns in these regions might be found. In any event, these studies examining handwriting now set the stage for more elaborate studies, wherein we begin to vary demands made on each of the higher order aspects of writing behavior in order to map out more fully the hierarchically organized neurocircuitry of writing. Again, given the likelihood of many shared neurobiological components with reading, listening, and speaking, studies that examine writing within a broader language context will be very important.

Much remains to be investigated in the functional brain mapping of language by eye, ear, hand, and mouth (especially for those hierarchically arranged processes that constitute composition). Nevertheless, based on our reading of the current literature, we would cautiously suggest that despite differences in input and output mechanisms associated with each of these “end organs,” the brain regions associated with phonological, semantic, syntactic, and pragmatic operations should be highly overlapping and highly interrelated.

With respect to writing deficits, the literature discussed here might be taken to suggest that if an individual has core deficits in any one of these overlapping dimensions, behavioral deficits are likely to manifest similarly in both perception and production (and within production for both speaking and writing). Moreover, given these functionally and anatomically integrated networks, we would also expect complex interactions across hierarchically arranged processing functions: A deficit in one process should result in a processing bottleneck, and all language-based operations that rely on this process (and the network that underlies it) will suffer accordingly. For example, the “bottleneck hypothesis” (Perfetti, 1985), in the domain of reading, has received some support: Slow and labor-prone word identification places severe constraints on subsequent sentence processing and comprehension. We might expect to see an analog of this for writing as well (Berninger et al., 2002); if lexical, phonological, spelling, or handwriting-related networks are compromised, expressing ideas in text composition will be impeded.

As we continue to develop a more comprehensive neurobiological account of how multiple language systems are organized, we can hope to understand better why some deficits tend to co-occur (due to shared networks),
while others dissociate (due to nonoverlapping networks). Such information can also help us to begin to understand subgroup and/or individual differences in cognitive profiles. Knowing that a given subgroup of children shows anomalous development of certain brain systems may allow us to predict where strengths and weaknesses in developing language skills are likely to emerge, and by extension, which skills ought to be targeted in training. In the following section, we discuss in some detail the ways in which these issues have played out in the more extensive literature on reading and reading disability. Implications for writing research are considered in each section.

Behavioral Characteristics of Reading and Writing Disability

Reading disability is characterized by the failure to develop age-appropriate reading skill despite normal intelligence and adequate opportunity for reading instruction. Significant progress has been made in understanding the cognitive and linguistic skills that must be in place to ensure adequate reading development in children (Brady & Shankweiler, 1991; Bruck, 1992; Fletcher et al., 1994; Liberman, Shankweiler, Fischer, & Carter, 1974; Rieben & Perfetti, 1991; Shankweiler et al., 1995; Stanovich & Siegel, 1994). While it has been argued that the reading difficulties experienced by some children may result from difficulties with processing speed (Wolf, Bowers, & Grieg, 1999), rapid auditory processing (Tallal, 1980), general language deficits (Scarborough & Dobrich, 1990), or visual deficits (Cornelissen & Hansen, 1998), there is growing consensus that a core difficulty in reading manifests itself as a deficiency within the language system and, in particular, a deficiency at the level of phonological analysis (e.g., Fletcher et al., 1994; Shankweiler et al., 1995; Stanovich & Siegel, 1994).

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 that of nonimpaired (NI) readers. Many lines of evidence converge on the conclusion that the word- and pseudoword-reading difficulties in RD individuals are, to a large extent, man- ifestations of more basic deficits at the level of rapidly assembling the phonological code represented by a string of letters (Bradley & Bryant, 1983; Liberman, Shankweiler, & Liberman, 1989). In turn, at the earliest stages of literacy training, the failure to develop efficient phonological assembly skills in word and pseudoword reading appears to stem from difficulties in the development of 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 (Brady & Shankweiler, 1991; Bruck, 1992; Fletcher et al., 1994; Liberman et al., 1974; Rieben & Perfetti, 1991; Shankweiler et al., 1995; Stanovich & Siegel, 1994). 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, Cunningham, & Cramer, 1984; Torgesen, Morgan, & Davis, 1992); deficits in phonological awareness consistently separate RD and NI children (Fletcher et al., 1994; Stanovich & Siegel, 1994); phonological deficits persist into adulthood (Bruck, 1992; Felton, Naylor, & Wood, 1990; Shaywitz et al., 1999); and instruction in phonological awareness promotes the acquisition of reading skills (Ball & Blachman, 1991; Bradley & Bryant, 1983; Foorman, Francis, Fletcher, Schatschneider, & Mehta, 1998; Torgesen et al., 1992; Wise & Olson, 1995). For children with adequate phonological skills, the process of phonological assembly in word and pseudoword reading becomes highly automated and 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 (Frost, 1998; Lukatela & Turvey, 1994; Van Orden, Pennington, & Stone, 1990).

Given the high incidence of comorbid reading and writing deficits, and given that input and output likely rely on many overlapping brain systems, we might anticipate that for many poor writers, problems at the phonological level of analysis might undermine development of composition skills. There is some evidence that supports this re-
ational conjecture for many children (see Berninger et al., 2002, for a discussion). Clearly though, if for some children writing problems reside in the more abstract domain of planning and message construction, and not in the phonological coding domain, we might anticipate unique writing problems in the absence of classic reading deficits. Implications of this possible subgrouping dimension for neurobiological analyses are considered later. In the next section, we consider the known neurobiological markers of RD children and how these markers might be expected to have parallels in writing (at least for children with cross-domain deficits) as this research line proceeds.

The Cortical Reading Systems and Their Roles in Skilled Reading

Recently, functional neuroimaging techniques have been employed in the area of reading development, reading disability, and intervention (for reviews, see Pugh et al., 2000; Sarkari et al., 2002). Much research has focused on the processing of words in isolation, because this constitutes a particularly acute deficit in RD. Substantial converging evidence indicates that skilled word recognition requires the development of a highly organized cortical system that integrates processing of visualorthographic, phonological, and lexical–semantic features of words. As illustrated in Figure 29.2, this system includes two posterior subsystems in the LH: a ventral (occipitotemporal) and a dorsal (temporoparietal) system, and a third area anterior to the other two (the IFG).

The ventral system includes a left inferior occipitotemporal–fusiform area and extends anteriorly into the middle and inferior temporal gyri. Importantly, the functional specificity of this region appears to be late developing and critically related to the acquisition of reading skills (Booth et al., 2001; Shaywitz et al., 2002). Although some researchers have suggested that the occipitotemporal (OT) regions function as a presemantic visual word form area (VWFA) (Cohen et al., 2002; but see Price et al., 2003, for an alternative account), we refer to this putative VWFA more neutrally as the ventral “skill zone.” More anterior foci within the ventral system extending into the middle to inferior temporal gyri appear to be semantically tuned (Fiebach, Friederici, Mueller, & von Cramon, 2002; Simos et al., 2002; Tagamets, Novick, Chalmers, & Friedman, 2000). It should be noted that there is some disagreement in the literature about the precise localization of critical subregions comprising the ventral system (Price et al., 2003). Nevertheless, recent studies examining both timing and stimulus-type effects suggest that moving anteriorly through this ventral system, subregions respond to word and word-like stimuli in a progressively abstracted and linguistic manner (Tagamets et al., 2000; Tarkiainen, Cornelissen, & Salmelin, 2003).

The more dorsal temporoparietal system broadly includes the angular gyrus and supramarginal gyrus in the inferior parietal lobule, and the posterior aspect of the superior temporal gyrus (Wernicke’s area). Among their other functions (e.g., attentionally controlled processing), areas within this system seem to be involved in mapping visual percepts of print onto the phonological and semantic structures of language (Black & Behrmann, 1994). In skilled readers, certain regions within the LH temporoparietal system (particularly the supramarginal gyrus) respond with greater activity to pseudowords than to familiar words (Price, Wise, & Frackowiak, 1996; Simos et al., 2002; Xu et al., 2001), and show sensitivity to phonological priming (Mencel et al., submitted). This finding, along with our developmental studies discussed later (Shaywitz et al., 2002), suggests that the temporoparietal system plays a role in the types of phonological analyses that are relevant to learning new material.

An anterior system centered in posterior aspects of the IFG appears to be associated with phonological recoding during reading, among other functions (e.g., phonological memory, syntactic processing); the more anterior aspects of IFG seem to play a role in semantic retrieval (Poldrack et al., 1999). The phonologically relevant components of this multifunctional system have been found to function in silent reading and in overt naming (see Fiez & Peterson, 1998, for review; Pugh et al., 1997). Like the temporoparietal system, the posterior aspect of IFG is more strongly engaged by pseudowords and low-frequency words (particularly, irregular/exception words whose pronunciations deviate from the pronunciation of the majority of
similarly spelled words, e.g., pint vs. mint, hint, lnt, print than by high-frequency words (Fiebach et al., 2002; Fiez & Petersen, 1998). We have speculated that this anterior system operates in close conjunction with the temporoparietal system to decode new words during normal reading development (Pugh et al., 2000).

This initial, speculative taxonomy of three broad LH systems (dorsal, ventral, and anterior) and their computational processing roles is obviously very coarse-grained and underspecified. Indeed, each of these component systems consists of distinct subregions that most likely engage in different types of processing relevant to orthographic, phonological, and semantic integration. In order to refine our basic theoretical framework, we have recently conducted a series of experiments to obtain a more detailed understanding of the information-processing characteristics of the major LH reading-related regions. These recent word recognition experiments have examined phonological priming (Menc & el., submitted), phonological–semantic trade-offs (Frost et al., 2003), and critical factors associated with repetition effects and repetition learning in reading (Katz et al., in press; Sandak et al., 2004a).

These studies have converged on a set of findings that requires us to refine our initial taxonomy (Sandak et al., 2004b). Across these studies, identical loci in the supramarginal gyrus (within the temporoparietal system), posterior aspects of IFG (within the anterior system), and the OT “skill zone” (within the ventral system) showed (1) increased activation for pseudowords relative to words, (2) strong phonological priming effects, and (3) repetition-related reductions that were most salient in a phonologically analytic training condition during repetition learning (Sandak et al., 2004a). This pattern strongly suggests a phonological “tuning” in these subregions. By contrast, the angular gyrus (within the temporoparietal system) and the middle/inferior temporal gyri (within the ventral system) appear to have more abstract lexicosemantic functions across our recent studies (see Price, More, Humphreys, & Wise, 1997, for similar claims). Thus, we might anticipate that individual differences in core deficits will be associated with variability in the locus of dysfunction across different components of the general reading circuitry. Moreover, if deficits are localized to the subsystems that code orthographic and phonological relations in reading (particularly the temporoparietal and inferior frontal learning subsystems), we might anticipate that these deficits will manifest similarly in both reading and writing behaviors.

With respect to reading development in its early stages, of these three broad systems, reading tasks appear predominately to activate the dorsal and anterior systems in normally developing children during initial reading acquisition, while activation in the ventral system, particularly the posterior “skill zone,” increases as children develop greater proficiency in word recognition. We observed that normally developing children younger than 10.5 years of age show strong engagement of dorsal and anterior systems, but limited engagement of the ventral system during reading tasks (Shaywitz et al., 2002). In contrast, children older than 10.5 years of age tend to show increased engagement of the ventral system, which in turn is associated with increasingly skilled reading. Indeed, when we used multiple regression analyses to examine the relation between both age and reading skill (measured by performance on standard reading tests) and activation level in the ventral system, the critical predictor was reading skill: The higher the reading skill level, the stronger the response in the LH ventral cortex (with several other areas showing age- and skill-related reductions). Based on these developmental findings, we have suggested (Pugh et al., 2000) that a beginning reader on a successful trajectory employs a widely distributed cortical system for print processing, including temporoparietal, frontal, and right hemisphere (RH) posterior areas. As reading skill increases, these regions play a somewhat diminished role, while LH ventral sites become more active, and presumably more central to the rapid recognition of printed (word) stimuli (for similar arguments, see Booth et al., 2001; McCandliss, Cohen, & Dehaene, 2003; Tarkkainen et al., 2003; Turkeltaub, Gareau, Flowers, Zeffiro, & Eden, 2003).

It will be quite important to employ developmental imaging designs to examine parallels and differences in neurobiological trajec-
Altered Circuits in Reading Disability

There are clear functional differences between NI and RD readers with regard to activation patterns in dorsal, ventral, and anterior sites during reading tasks. A number of functional imaging studies of RD readers have indicated LH posterior functional dysfunction at both dorsal and ventral sites during phonological processing tasks (Bruns-wick, McCrory, Price, Frith, & Frith, 1999; Paulesu et al., 2001; Pugh et al., 2000; Salmelin, Service, Riesla, Uutela, & Salonen, 1996; Shaywitz et al., 1998, 2002; Temple et al., 2001). This disruption is instantiated as a relative underengagement of these regions, specifically when processing linguistic stimuli (words and pseudowords) or during tasks that require explicit decoding. This functional anomaly in posterior LH regions has been observed consistently in children (Shaywitz et al., 2002) and adults (Salmelin et al., 1996; Shaywitz et al., 1998). Hypoactivation in three key dorsal and ventral sites, including the angular gyrus within the temporoparietal region and the ventral occipitotemporal skill zone, is detectable as early as the end of kindergarten in children who have not reached important milestones in learning to read (Simos et al., 2002). Moreover, this ventral disruption has been seen as a critical signature of reading disability across several languages (Paulesu et al., 2001; Salmelin et al., 1996). Given the critical role for the temporoparietal regions in learning to integrate orthography, phonology, and semantics, we might anticipate similar disruptions in writing behavior.

Many neuroimaging studies have attempted to identify specific brain regions where activation patterns differentiate between RD and NI readers (e.g., Rumsey et al., 1997; Shaywitz et al., 1998; Simos et al., 2002; Temple et al., 2001). However, in order to achieve a deeper understanding of the neurobiology of developmental dyslexia, we must also consider relations among brain regions that function cooperatively as circuits, or networks, to process information during reading; this has been referred to as an issue of functional connectivity (Friston, 1994). Evidence consistent with the notion of a breakdown in functional connectivity within the posterior reading system in RD readers has been reported by Horwitz, Rumsey, and Donohue (1998). Using activation data from the Rumsey et al. (1997) PET study, Horwitz et al. (1998) examined relations between activation levels in the LH angular gyrus and other brain sites during two reading-aloud tasks (exception word and pseudoword reading). Activations in the LH angular gyrus and occipital and temporal lobe sites exhibited strong positive correlations in NI readers, such that when activation increased in the angular gyrus, activation also increased in the occipital and temporal sites. In contrast, the correlations between these sites were weak in RD readers. This finding suggests a breakdown in functional connectivity across the major components of the LH posterior reading system.

We also examined whether the angular gyrus and other LH posterior regions were functionally connected in an examination of a large sample of adult RD and NI readers (Pugh et al., 2000). We looked at connectivity between the angular gyrus and occipital and temporal lobe sites on those tasks that systematically varied demands on phonological assembly. LH connectivity was weaker in RD readers during complex phonological tasks (word category judgment and pseudoword rhyming) (see also Horwitz et al., 1998). However, there appeared to be no dysfunction when readers performed a simple phonological judgment (a single-letter rhyme task) or complex visual-orthographic coding (a case judgment task). These results are most consistent with a specific phonological deficit hypothesis: Our data suggest that communication among these ar-
eases is disrupted only when orthographic-to-
phonological assembly is required. Thus, it is
not the case that functional connectivity in
this system is disrupted across all types of
cognitive behaviors. Moreover, we found
that on the word and pseudoword reading
tasks, RH counterparts or “homologues”
appear to function in a compensatory manner
for RD readers; correlations among these
regions in the RH were strong and stable for
both reading groups, with higher values in
RD readers. Functional connectivity analyses
can help to reveal “system-level” anomalies
in clinical populations; it is critically impor-
tant to include this type of analysis in neuro-
imaging studies as we begin to explore writ-
ing behavior. Again, a parallel with disrupted
connectivity in LH posterior regions during
writing and spelling tasks can be reasonably
anticipated, especially for those individuals
whose writing difficulties appear to reflect
general language-processing deficits.

Potentially Compensatory Processing
in Reading Disability

Behavioral researchers have identified a
number of markers of reading impairment.
Poor readers compensate for their inade-
quate phonological awareness and knowl-
edge of letter–sound correspondences by
overrelying on contextual cues to read indi-
vidual words; their word reading errors tend
to be visual or semantic rather than phonetic
(see Perfetti, 1985, for a review). These
behavioral markers of reading impairment
may be instantiated cortically by compensa-
tory activation of frontal and RH regions. As
noted earlier, previous research by our group
has shown that on tasks that explicitly re-
quire pseudoword and word reading, RD
readers showed a disproportionately greater
engagement of inferior frontal and pre-
frontal dorsolateral sites than did NI readers
(Shaywitz et al., 1998, 2002; for similar
findings, see also Brunswick et al., 1999;
Salmelin et al., 1996). It is noteworthy that
these inferior frontal regions overlap with
those areas shown to be involved in syntactic
processing (discussed earlier) (Caplan, Al-
pert, Waters, & Olivieri, 2000; Constable et
al., 2004). That poor readers show height-
ened reliance on these regions for word iden-
tification suggests a neuroanatomical locus
for the often-reported bottleneck effect in
sentence processing and text comprehension
(Perfetti, 1985; Shankweiler et al., 1995).

Evidence of a second, potentially compen-
satory, shift—in this case, to posterior RH
regions—comes from several findings. Addi-
tionally, using MEG, Sarkari et al. (2002)
found an increase in the apparent engage-
ment of the RH temporoparietal region in
RD children. A more detailed examination
of this trend, using hemodynamic measures,
indicates that hemispheric asymmetries in
posterior temporal and temporoparietal activ-
ation (particularly the middle temporal and
the angular gyrus) vary significantly among
reading groups (Shaywitz et al., 1998):
Greater RH than LH activation was ob-
served in RD readers, but greater LH than
RH activation was observed in NI readers.
Rumsey et al. (1999), who examined the rela-
tionship between RH activation and read-
ing performance in their adult RD and NI
participants, found that RH temporoparietal
activation was correlated with standard
measures of reading performance only for
RD readers (see also Shaywitz et al., 2002).

We hypothesize that the reason why RD
readers tend strongly to engage inferior fron-
tal sites is their increased reliance on covert
pronunciation (articulatory recoding) in an
attempt to cope with their deficient phono-
logical analysis of the printed word. In addi-
tion, their heightened activation of the poste-
rior RH regions, paired with their reduced
activation of the LH homologue, suggests a
process of word recognition that relies on let-
ter-by-letter processing in accessing RH local-
ized visuosemantic representations (or some
other compensatory process) rather than rely-
ing on phonologically structured word recog-
nition strategies. These differential patterns,
especially the increased activation in frontal
regions, might also reflect increased effort
during reading; underengagement of LH pos-
terior areas, particularly ventral sites, would
not be thought to reflect this increased effort,
but rather the failure to engage these areas
likely precipitates any change in effort.
Given the neurobiological overlap evident for
speech and reading, as well as for perception
and production, it would be reasonable to hy-
pothesize similar RH shifts as potential neu-
robiological markers of writing disability, es-
pecially when deficits in phonological and/or
lexical processing are evident for both input and output (e.g., spelling).

**Neurobiological Effects of Successful Reading Remediation**

Converging evidence from several recent studies supports the notion that gains in reading skill resulting from intense reading intervention are associated with a more "normalized" localization of reading processes in the brain. In a recent MEG study, eight young children with severe reading difficulties underwent a brief but intensive phonics-based remediation program (Simos et al., 2002). After intervention, the most salient change observed on a case-by-case basis was a robust increase in the engagement of the LH temporoparietal regions, accompanied by a moderate reduction in the activation of the RH temporoparietal areas. Similarly, Temple et al. (2003) used fMRI to examine the effects of an intervention (FastForward) on the cortical circuitry of a group of 8- to 12-year-old children with reading difficulties. After intervention, increases in activation of LH temporoparietal and inferior frontal sites were observed. Moreover, the LH posterior increases correlated significantly with increased reading scores. Recently, Berninger and her colleagues reported similar LH posterior change following intensive phonological and morphological training (Aylward et al., 2003).

In a recent collaborative study with Benita Blachman of Syracuse University, we conducted a longitudinal study examining three groups of young children (average age was 6.5 years at time 1) with fMRI and behavioral indices (Shaywitz et al., 2004). The three groups consisted of a treatment RD group that received 9 months of intensive, phonics-based intervention (Blachman, Rangel, Ball, Black, & McGraw, 1999) and two control groups: a typically developing group and an RD control group. Relative to RD controls, RD treatment participants showed reliable gains on reading measures (particularly on fluency-related measures; e.g., Gray Oral Reading Test rate scores). When RD groups were compared at time 2 (posttreatment), reliably greater activation increases in LH reading-related sites were seen in the treatment group. Moreover, when pre- and post-treatment activation profiles were directly contrasted for each group, it was evident that both RD treatment and typically developing controls showed reliable increases in LH reading-related sites, while RD controls did not. Prominent differences were seen in the LH IFG, and, importantly, in the LH ventral skill zone. These changes were quite similar to changes observed in the NI controls as they also learned to read, again suggesting that the phonologically analytic intervention led to patterns of activation associated with typically developing readers. Importantly, 1 year after intervention was concluded, the treatment group showed further increases in LH activation, along with further decreases in RH activation.

Thus, initial research on the neurobiological signatures of successful reading remediation are strikingly convergent: increased LH posterior response, with often-reported reductions in RH processing. Focusing on these neurobiological signatures can provide us with highly sensitive markers for those sorts of treatment programs that are likely lead to real and stable cognitive gains. Many important issues remain to be tackled as we continue to explore how treatment modifies brain circuits for reading behavior. For one, studies to date have all contrasted one specific intervention with control conditions. There will always be a subset of children who do not respond to a given intervention; presumably at least some of these children might have a different pattern of deficits than the majority of children who do respond well. It will be desirable to begin to contrast multiple approaches to intervention (within a single study) in RD cohorts who all struggle with language but may differ in the locus of the deficit. This type of study will enable us to begin to explore the issue of whether different types of interventions work better for subgroups of children with distinct neurobiological and behavioral profiles (prior to treatment).

Indeed, the interventions employed in the extant studies have all focused on phonological training to varying degrees. While a majority of children with reading difficulties do struggle at the level of phonological and lexical processing, there may be subgroups of children whose deficits lie in other domains, and for whom alternative approaches may
work better. Neuroimaging techniques might give us a particularly sensitive measure to help in identifying coherent RD subgroups, and to determine which type of approach works best for a given subgroup. By examining reading and writing interventions in parallel and in contrast, we can begin to discriminate language-general from writing-specific effects of training. At present the evidence at least encourages us that the cortical circuitry in struggling readers is directly affected by targeted and intensive treatment. This suggests a high degree of plasticity in this population.

**Implications for Writing Disability and Intervention**

Neuroimaging studies conducted to date have identified both an altered neurocircuitry for reading in RD subjects and a critical neurobiological signature of successful intervention (at least in younger children, most of whom have deficits for phonological and lexical-level processing). This signature appears to be increased engagement of major LH reading-related circuits and reduced compensatory reliance on RH homologues. As noted, this sets up certain plausible expectations for emerging research on writing behavior, its deficits, and effects of specific, targeted interventions.

There is good evidence, at the neurobiological level of analysis, of highly overlapping circuits for core language functions (beyond the specific modality of perception or production), and there is also good evidence, at the behavioral level of analysis, of a high incidence of comorbidity between disorders of reading and writing. For children with both reading and writing deficits, the failure to develop a coherent LH circuitry for reading would lead us to expect parallel neurobiological signatures in writing. A bottleneck associated with the failure to develop fluent lexical access and spelling, for instance, might be associated with increased reliance on RH systems for phonological processing support in both reading and writing. With respect to writing intervention, successful training, focusing on these lexical and phonological skills, would be expected to allow expression of ideas from more abstract conceptual systems to flow through the LH language systems with less RH involvement (thus, a similar signature of successful intervention as in reading for children with general phonological bottleneck difficulties).

Importantly, individual or subgroup differences in the locus of core deficits would complicate this sort of expectation when we are examining writing behavior. For example, if for some children, phonological and general language processing skills are intact and fluent, and if problems instead reside in the more abstract planning and message-generation components of written composition (and possibly in comprehension during reading), expectations are more complicated. We might not observe the RH shift in language-processing regions, and might instead anticipate anomalies in function at those prefrontal regions that have been previously associated with more abstract conceptual processing dimensions (Shaywitz et al., 2001). Of course, we should also anticipate that for such individuals, difficulties will also manifest in any production-related task, whether spoken or written. If these individuals have no demonstrable challenges in the phonological domain, guidance from those reading remediation studies conducted to date might be lacking. Thus, neurobiological signatures of successful remediation are difficult to anticipate in this hypothetical situation; indeed, we will need to acquire a good deal of preliminary data on preintervention differences for those children with good phonological but poor metacognitive skills. One might speculate at the outset, though, that if deficits reside in the metacognitive domain, successful remediation at this level of analysis might not have a straightforward neurobiological signature with respect to hemispheric asymmetries for phonological processing; perhaps changes in prefrontal control-processing regions might be evident as planning and message-generation processes improve. In considering this contrast between subtypes of writing disorders with respect to the locus of the core deficit (e.g., phonological vs. metacognitive), it becomes clear that much needs to be done relative to generating normative data on reading and writing in relation to one another. With such data in hand, however, neuroimaging might begin to serve as a useful tool in making sense of why some approaches work better than others for a given set of deficits.
Task Design in Functional Neuroimaging of Writing Behavior

While it is reasonable to expect many parallels between reading and writing with respect to neurobiological markers of disability (and possibly for those changes associated with improvement through training), this expectation has yet to be put to the test. However, at present, there is evidence that standard imaging techniques and paradigms are able to demarcate the subsystems associated with writing-related behaviors such as handwriting (Katanoda et al., 2001; Menon & Desmond, 2001), and to distinguish these systems from shared language-processing systems. Much basic taxonomic research is therefore needed before clinical issues can be assessed in this domain with neuroimaging. To begin to examine the parallels between reading and writing, it will be necessary at first to conduct comprehensive neuroimaging experiments of skilled readers–writers that (1) compare activation patterns for both reading and writing (as well as speaking and listening) within a single experiment and subject, and (2) systematically vary demands on component processes (e.g., sublexical, lexical, syntactic, pragmatic tasks for both reading and writing). As noted, it is possible to make cross-modality comparisons of more abstract language-processing domains with neuroimaging design when subtractions and controls are employed to factor out gross motor and sensory differences (Constable et al., 2004). As such designs are worked out (and the extant literature already contains good examples applied to one or another domain that explicate component processes), it will then be important to contrast groups with (1) no deficits in either reading or writing, (2) deficits for both, and (3) deficits for one or the other, but not both. We must then move to subgroup comparisons by identifying subgroups whose behavioral profiles suggest different loci of deficits in reading and/or writing (with all possible subgroups compared). Such studies will provide a comprehensive foundation and go a long way toward providing coherent expectations about the neurobiological changes to be anticipated as large-scale training and intervention studies begin. Again, the lessons learned from reading suggest that neuroimaging techniques are very sensitive to detecting neurobiological changes that underlie performance improvement. We have no reason to expect a different state of affairs as we move to the production domain.

Neuroimaging may be of real utility, because it can help us compare connections from the process under investigation to others not expected through shared neural networks. Essentially, links among diverse types of difficulties might emerge as these neurobiological links are revealed; the hope for both broader and deeper theories of childhood disorders is reinforced by the emerging cognitive neuroscience approaches.

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sounds and learning to read—a causal connection. 


