

Mapping the Word Reading Circuitry in Skilled and Disabled Readers

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Research on the neurocognitive foundations of reading in typically and atypically developing readers has benefited in recent years from rapid advances in several neuroimaging technologies (see Papanicolaou, Pugh, Simos, & Mencl, 2004 for a review). In this chapter,¹ we describe recent studies from our lab, and from others, that were designed to generate data not only on the localization of reading-related brain activation, but also to examine patterns of interactions and dynamic tradeoffs among these distributed reading-related systems. Acquiring data of this sort is necessary, in our view, if we are to begin to construct neurobiological models of skilled word identification that can speak to the complexities and dynamics of reading performance. Indeed, computational models of reading in the behavioral domain stand or fall, not by their capacity to account for main effects of isolated variables (e.g., lexicality, frequency, consistency, concreteness, and the like), but rather by whether they can seamlessly account for complex interactions among them (Harm & Seidenberg, 1999). Ultimately, the same criteria must be applied to neurobiologically grounded models as well. Thus, it is critical that we begin to look beyond simply more and more fine-tuned localization and consider also a systems-level approach. Research on systems appears to be a realistic possibility at this stage in the development of these new technologies, given the evidence that extant neurophysiological measures are amenable to sophisticated psycholinguistic designs (Frost et al., 2005; Sandak et al., 2004a;

Dehaene et al., 2004). When we add to all this the clinically oriented goal of better understanding what those demonstrated differences in activation patterns for struggling readers imply about core deficits and optimal remediation, the need to develop dynamic accounts becomes all the more pressing (Pugh et al., 2005). We focus here primarily on studies of word identification in reading, given that this stage of processing appears to be crucial in discriminating fluent from reading disabled (RD) cohorts (Pugh et al., 2000a).

We begin with a review of relevant behavioral studies of component processing in fluent reading, with particular emphasis on the role of early (sublexical) phonology; this operation appears to be most compromised in RD cohorts. We then discuss the current literature on the neurobiology of skilled and disabled reading, along with consideration of a series of recent studies from our lab that aim to capture brain correlates of component processing, again with an emphasis on phonological processing, adaptive learning, and complex tradeoffs and interactions. In each section we also note relevant cross-linguistic studies. Indeed, an adequate neurobiological theory will need to make sense of both cross-language variance and invariance in both typical and atypical reading trajectories. Finally, we take stock of what we consider to be crucial next steps (both technical and theoretical) in the emerging cognitive neuroscience of reading and its disorders.

Behavioral Studies of Skilled Reading

An important issue in studies of reading concerns the question of whether prelexical phonological processing plays an important role in printed skilled and fluent word identification. Clearly, acquiring behavioral data on this question is crucial if we are to correctly interpret observed patterns of activation across the reading circuitry. Different classes of models have been put forward to address this question. Purely orthographic access models (Baron, 1973), and phonological coherence models (Van Orden & Goldinger, 1994; Van Orden, Pennington, & Stone, 1990) each assume singular lexical access codes; graphemic in the former, and phonologically mediated in the latter. By contrast, dual-process accounts usually posit two independent mechanisms or routes for accessing meaning: (1) by mapping from spelling to the lexicon and then obtaining phonological information through a lexical lookup procedure or (2) by mapping from spelling to a phonological code and then to the lexicon ("phonologically mediated access") (Coltheart, 1978; Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001; Paap & Noel, 1991). A number of alternative models do not assume multiple independent mechanisms, but instead posit interactive bidirectional links with a cooperative division of labor among orthographic, phonological, and semantic processes to support efficient

word recognition (Harm & Seidenberg, 1999; Plaut, McClelland, Seidenberg, & Patterson, 1996; Seidenberg & McClelland, 1989).

With regard to the evidence for the role of prelexical phonology in skilled word recognition, many studies have now demonstrated that phonological access is early and automatic (see R. Frost, 1998 for review). Using a semantic categorization task, Van Orden found that participants produced more false-positive responses to words that were homophones or pseudohomophones of category exemplars than for spelling foils (e.g., categorizing ROWS/ROZE as a flower more often than the control foil ROBS/REEZ) (Van Orden, 1987; Van Orden et al., 1988). This effect persisted, even at brief exposure durations, indicating that phonological recoding occurred early in processing and mediated activation of meaning. Moreover, because pseudohomophones are not represented lexically, Van Orden and colleagues concluded that the effect must occur before lexical access.

Findings using brief exposure paradigms, such as backward masking and priming, point to an early and robust influence of phonology on lexical access (Lesch & Pollatsek, 1993; Lukatela, Frost, & Turvey, 1999; Lukatela & Turvey, 1994a, 1994b; Perfetti & Bell, 1991; Perfetti, Bell & Delany, 1988). For example, Perfetti and colleagues found significantly better identification rates when briefly presented target words were followed by pseudoword masks that were phonemically similar, than when they were graphemically similar, suggesting that phonological information was automatically extracted from the pseudoword mask and contributed to the identification of the target (Perfetti & Bell, 1991; Perfetti et al., 1988). Furthermore, Lukatela and Turvey (1994a; see also Lesch & Pollatsek, 1993) observed associative priming, pseudoassociative priming, and pseudohomophonic associative priming relative to matched controls. At a short prime-target interval, robust priming of the target word FROG was obtained for TOAD, TOWED, and TODE. At a long interval both TOAD and TODE effects were observed, but TOWED effects were eliminated. The authors concluded that the initial access code must be phonological in nature, with orthographic constraints coming into play relatively late.

Cross-language studies have provided additional evidence indicating that the assembly of prelexical phonological codes mediates lexical access. A unique feature of Serbo-Croatian is that it has one spoken form, but two written alphabets (the Roman and Cyrillic) that share characters, some of which are pronounced the same in both alphabets (i.e., common letters) and some of which are pronounced differently in the two alphabets (i.e., phonologically ambiguous letters). This feature allows researchers to combine the characters such that letter strings have one or more phonological interpretations, depending on whether the phonologically ambiguous characters are interpreted as Cyrillic or Roman. Studies of readers who are competent in both written forms produce slower word naming and lexical decision latencies

for letter strings composed of phonologically ambiguous and common letters compared to letter strings composed of phonologically unique and common letters (Lukatela, Popadic, Ognjenovic, & Turvey, 1980), and the size of the effect is positively correlated with the number of phonologically ambiguous letters (Feldman & Turvey, 1983). Moreover, this phonological ambiguity effect can be reduced by using an alphabetic prime composed of phonologically unique letters that effectively specify the target's script (Lukatela, Feldman, et al., 1989). There is also growing evidence that readers of Mandarin are sensitive to the sublexical phonological information contained in the phonetic components of compound words (see Perfetti, Liu, & Tan, 2005 for review). Studies have shown that homophone characters that are unrelated in meaning produce slower decision latencies and higher error rates than control stimuli in semantic similarity judgments (Perfetti & Zhang, 1995). Experiments in Chinese using the backward masking paradigm have shown that briefly exposed target words are better identified when a following mask is a homophone (Tan, Hoosain, & Peng, 1995), paralleling results in English (Perfetti et al., 1988). Although language differences have been reported relative to the size or type of phonological unit that governs lexical access (e.g., see the German/English comparison study of Ziegler et al., 2001; Goswami, Ziegler, et al., 2003), the key point is that the findings converge to indicate that word recognition in skilled adult readers does not appear to differ in fundamental ways across languages and orthographies, despite differences in the complexity of the mapping between a language's written form and its spoken form (Carello, Turvey, & Lukatela, 1992; R. Frost, 1998; Perfetti, 1985). Such language invariance has direct implications for our expectations regarding neurobiological similarities across different orthographies (Pugh et al., 2005).

Behavioral Studies of Reading Disability

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 et al., 1974; Rieben & Perfetti, 1991; Shankweiler et al., 1995; Stanovich & Siegel, 1994). With regard to reading disability, it has been argued that the reading difficulties experienced by some children may result from difficulties with processing speed (Wolf & Bowers, 1999), rapid auditory processing (Tallal, 1980), general language deficits (Scarborough & Dobrich, 1990), or visual deficits (Cornelissen & Hansen, 1998). However, there is growing consensus that, for the majority of struggling readers, a core difficulty in reading manifests itself as a deficiency within the language system and, in particular, a deficiency at

the level of phonological representation and processing (Liberman, 1992; Liberman et al., 1974; Goswami & Zeigler, 2005).

Deficits in behavioral performance are most evident at the level of single word and pseudoword reading; RD individuals are 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 RD individuals are, to a large extent, manifestations of more basic deficits at the level of rapidly assembling the phonological code represented by a token letter string (Bradley & Bryant, 1983; Liberman et al., 1989). *Phonological assembly* refers to the operations associated with mapping from the orthographic to the phonological form in printed word identification. The failure to develop efficient phonological assembly skills in word and pseudoword reading, in turn, appears to stem from difficulties—at the earliest stages of literacy training—in attaining fine-grained phonemic awareness. Phonological awareness in general 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).

As for why RD readers should have exceptional difficulty developing phonological awareness, the etiological underpinnings of this difficulty are still actively being investigated and the question of whether such language-level challenges might, in some children at least, be linked to more basic deficits in one of the above-mentioned domains is much debated. Nonetheless, a large body of evidence directly relates deficits in phonological awareness to difficulties in learning to read: phonological awareness measures predict later reading achievement (Bradley & Bryant, 1983; Stanovich et al., 1984; Torgesen et al., 1994); deficits in phonological awareness consistently separate RD and NI children (Fletcher et al., 1994; Stanovich & Siegel, 1994); phonological deficits persist into adulthood (Bruck, 1992; Shaywitz et al., 1999); and instruction in phonological awareness promotes the acquisition of reading skills (Ball & Blachman, 1991; Bradley & Bryant, 1983; Foorman et al., 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, efficient, and, as the just-mentioned evidence suggests, continues to serve as an important component in rapid word identification even for mature skilled readers (R. Frost, 1998).

Despite some developmental variability across languages and orthographies, we anticipate that RD will likewise show universality. Regardless of the writing system, RD often has a genetic basis (Grigorenko, 2001) and has been associated with a common neurobiological marker—the failure to develop a functionally specialized visual word form area (VWFA) in the left

hemisphere (LH) ventral cortex (Paulesu et al., 2001; Shaywitz, Shaywitz, Pugh et al., 2002). Behavioral manifestations of RD seem to differ somewhat across languages, however. Whereas slow word identification is a hallmark of RD in all orthographies, inaccuracy of mapping is seen predominantly in irregular systems like English (Wimmer & Mayringer, 2002; Ziegler & Goswami, 2005). This difference in manifest symptoms is nonetheless consistent with a common etiology. Given the virtually one-to-one mapping between phonemes and graphemes in highly regular alphabetic orthographies like Finnish and German, once a student is able to associate letters with their corresponding sounds (and to blend those sounds together), word recognition can be achieved. When reading accuracy is measured, therefore, errors are rare; wide individual differences occur in reading speed, however, and the slowest readers are considered to have RD (Landerl et al., 1997; Wimmer & Mayringer, 2002). Like disabled readers in English, many RD readers in orthographies with very consistent grapheme-phoneme correspondences: (a) have a family history of RD (Lyytinen, 2004a, 2004b); (b) show the larger lexicality, length, and grain size effects relative to typically developing (TD) controls that also characterizes RD in English (Ziegler et al. 2003); and (c) exhibit signs of reduced distinctiveness (precision) in their phonological representations in the lexicon (Elbro, 1998; Elbro et al., 1998; Goswami, 2000; Ziegler & Goswami, 2005). Furthermore, their reading difficulties are predicted from younger ages by measures of similar skills that antedate RD outcomes in English-speaking samples (e.g., letter knowledge, phonological awareness, vocabulary), except that rapid serial naming skill at age 5–6 years appears to be a somewhat stronger predictor in Finnish and German than in English (Lyytinen, et al., 2004a; Wimmer et al., 2002). Recall, however, that rapid naming becomes the strongest prognostic measure for RD in English-speaking learners by about age 8 years (Meyer et al., 1998; Scarborough, 1998b). Thus, it may be that naming speed becomes important for predicting fluency among children who have already learned the sounds of letters, an accomplishment that is attained earlier in development when regular orthographies are being acquired.

From the extant evidence showing many similarities and a few differences in profiles of RD across orthographies, the hypothesis that RD is attributable to the same core phonological deficit in all languages is tenable. Indeed, Goswami (2000; Ziegler & Goswami, 2005), in line with previous theoretical work at Haskins (Fowler, 1991), has proposed that reduced precision in representing and processing phonological information may be the universal hallmark of RD. As noted earlier, the development of fine-grained representations (tapped by phonemic awareness and naming tasks), necessary for linking letters with phonemes and spellings with known words, both shapes and is shaped by growth in literacy. The transparency of the O > P correspondences

in regular orthographies like Finnish, allows the yoked processes of phonemic awareness and decoding to develop earlier and more fully (even in RD) than is possible given the additional challenges faced when a more irregular orthography must be deciphered. Even though decoding will be more accurate by RD children in regular orthographies, the imprecision (and potentially reduced accessibility) of their stored phonological knowledge about words still impedes routinization and subsequent fluency.

Functional Imaging Studies of Skilled Reading

Given the importance of phonological information evidenced from behavioral studies of skilled and impaired reading, identifying the neuroanatomical correlates of phonology and their interactions with orthographic, morphological, and lexico-semantic component processes represents an important step toward understanding the functional architecture of reading and reading failure. Evidence from functional imaging studies indicates that skilled word recognition in general requires the development of a highly organized cortical system that integrates the processing of orthographic, phonological, and lexico-semantic features of words (see Pugh et al., 2000a and Sarkari et al., 2002 for reviews). This system broadly appears to include two posterior subsystems in the left hemisphere: a ventral (occipitotemporal) and a dorsal (temporoparietal) system, and a third area, anterior to the other two, centered in and around the inferior frontal gyrus.

The ventral system includes extrastriate areas, a left inferior occipitotemporal/fusiform area, and appears to extend anteriorly into the middle and inferior temporal gyri (MTG, ITG). It has been suggested that the occipitotemporal region functions as a presemantic VWFA by some researchers (c.f., Cohen et al., 2002, but see Price et al., 2003 for an alternative conceptualization). Importantly, the functional specificity of sites along the ventral pathway for reading appears to be late developing and critically related to the acquisition of reading skill, as discussed later (Booth et al., 2001; see Shaywitz et al., 2002, discussed later). More anterior foci within the ventral system extending into the MTG to ITG appear to be semantically tuned (Fiebach et al., 2002; Simos et al., 2002; Tagamets et al., 2000). The ventral system, particularly the posterior aspects thought to be prelexical and presemantic, is also fast-acting in response to orthographic stimuli in skilled readers but not in RD individuals (Salmelin et al., 1996). There is still a good deal of disagreement in the literature about the precise taxonomy of critical subregions comprising the ventral system (Cornelissen et al., 2003; Dehaene et al., 2004; Price et al., 2003). Nevertheless, recent studies examining both timing and stimulus-type effects suggest in general terms that moving anteriorly along the ventral pathways, subregions respond to

word and word-like stimuli in a progressively abstracted and linguistic manner (Dehaene et al., 2004; Tagamets et al., 2000; Tarkiainen et al., 2003). Later, we describe several experiments suggesting potential distinctions between phonological and lexical-semantic tuning along the ventral pathway.

The temporoparietal system responding to reading tasks broadly includes the angular gyrus (AG) and supramarginal gyrus (SMG) 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) subregions within this system seem to be involved in mapping visual percepts of print onto the phonological and semantic structures of language (Black & Behrmann 1994; Price et al., 2003). In skilled readers, certain regions within the LH temporoparietal system (particularly the SMG) respond with greater activity to pseudowords than to familiar words, and to print more than pictures (Price et al., 1996; Simos et al., 2002; Xu et al., 2001; Sandak et al., 2004b). This finding, along with our own developmental studies (Shaywitz et al., 2002) suggests that temporoparietal regions play a critical role in the types of phonological analyses that are relevant to learning new material (Pugh et al., 2000a).

The anterior system is centered in posterior aspects of the inferior frontal gyrus (IFG) and appears to be associated with phonological recoding during reading, among other functions (e.g., phonological memory, syntactic processing); more anterior aspects of the 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 naming (see Fiez & Petersen, 1998 for review; Pugh et al., 1997) and, like the temporoparietal system, is more strongly engaged by low-frequency words (particularly, words with irregular/inconsistent spelling-to-sound mappings) and pseudowords than by high-frequency words (Fiebach et al., 2002; Fiez & Peterson, 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., 2000a).

Of these three systems, the dorsal and anterior systems appear to predominate during initial reading acquisition in normally developing beginning readers, with an increased ventral response to print stimuli as proficiency in word recognition increases. We observed (Shaywitz, Shaywitz, Pugh et al., 2002) that normally developing children younger than 10.5 years of age show robust engagement of temporoparietal and anterior systems, but limited engagement of the ventral system during pseudoword and real-word reading tasks. In contrast, children older than 10.5 years of age tend to show increased engagement of the ventral system, which in turn is correlated with increasingly skilled reading. Indeed, when multiple regression analyses examined both age and reading skill (measured by performance on standard reading tests), the critical predictor was reading skill level: the higher the reading skill,

the stronger the response in the LH ventral cortex (with several other areas including RH and frontal lobe sites showing age- and skill-related reductions). RD readers by contrast showed age-related increases in a widely distributed set of regions across both LH and RH. Based on these cross-sectional developmental findings, we suggest that a beginning reader on a successful trajectory employs a widely distributed cortical system for print processing, including temporoparietal, frontal, and RH posterior areas. As reading skill increases, LH ventral sites become more active, and presumably more central to the rapid recognition of printed (word) stimuli (see Booth et al., 2001; Turkeltaub et al., 2003; Tarkianien et al., 2003 for similar arguments).

Each writing system has unique challenges depending on how the script encodes phonology, morphology, and semantics. The functional neuroanatomy of visual word recognition in reading has also been investigated in mature readers in a variety of written languages (which employ both alphabetic and nonalphabetic writing systems) (e.g., Chee et al., 1999; Fiebach et al., 2002; Kuo et al., 2003, 2004; Paulesu et al., 2000; Salmelin et al., 1996). Neuroimaging studies of alphabetic languages broadly implicate the same set of LH cortical regions (including occipitotemporal, temporoparietal, and inferior frontal networks) identified in English-language studies (see Pugh et al., 2005). These common networks are almost always engaged by skilled readers irrespective of the specific language and/or writing system under investigation. Language-specific differences usually appear to be a matter of degree, not of kind. That is, in one language, the reading-relevant constituents of a neural network might be more or less activated than in another language, but the general circuitry appears similar in its taxonomic organization (Paulesu et al., 2000). Recent work with nonalphabetic writing systems also suggests similarities. For example, Kuo and colleagues (2003) examined covert naming of high- and low-frequency Chinese characters and observed greater activation in left premotor/inferior frontal regions and the left insula for low-frequency characters relative to high-frequency characters. These areas have been implicated in phonological processing in English; in particular, the inferior frontal gyrus is more strongly engaged by low-frequency words and pseudowords than by high-frequency words (Fiebach et al., 2002; Fiez & Peterson, 1998). Moreover, high-frequency characters produced greater activation in the middle temporal/angular gyrus, which have been implicated in lexical-semantic processing in neuroimaging studies of English word recognition (Fiebach et al., 2002; Price et al., 1997; Simos et al., 2002) and the precuneus, previously implicated in visual imagery (Fletcher et al., 1996). In a subsequent study, Kuo and colleagues had participants perform homophone judgments and physical judgments on real characters, pseudocharacters (novel combinations of legal semantic and phonetic radicals that follow the positional architecture of Chinese characters), and Korean-like nonsense figures

(Kuo et al., 2004). A number of regions important for orthographic-to-phonological mapping in English were also more active for the homophone judgment relative to the character judgment in Chinese. These regions included the inferior frontal gyrus, inferior parietal lobule/supramarginal gyrus, and the fusiform gyrus. Note that some important differences have been reported for Mandarin reading, with increased reading-related activation at both superior parietal (Kuo et al., 2003) and especially left middle frontal regions; the middle frontal region is also implicated in reading disability in Chinese (Tan et al., 2001; Siok et al., 2004). Nonetheless, overall the reading networks appear to be largely similar to those observed for alphabetic writing systems (Kuo et al., 2003, 2004) with a few key differences. Again, we would argue that the universal demand of rapid contact with phonological systems for print stimuli results in the brain “choosing” largely invariant pathways when constructing the reading circuitry.

Functional Imaging Studies of Reading Disability

Evidence for Altered Circuits in Reading Disability

Clear functional differences exist between NI and RD readers with regard to activation patterns in dorsal, ventral, and anterior sites during reading tasks. In disabled readers, a number of functional imaging studies have observed LH posterior functional disruption, at both dorsal and ventral sites during phonological processing tasks (Brunswick et al., 1999; Paulesu et al., 2001; Pugh et al., 2000b; Salmelin et al., 1996; Shaywitz et al., 1998; 2002; Temple et al., 2001). This disruption is instantiated as a relative under-engagement of these regions, specifically when processing linguistic stimuli (words and pseudo-words) or during tasks that require 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 cortex within the temporoparietal region, the angular gyrus, 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). Posterior disruption is evident both in measures of activation and in analysis of functional connectivity (Horwitz et al., 1998; Pugh et al., 2000b).

Because the evidence from neuroimaging studies of skilled reading indicates that different languages and orthographies engage common circuits during reading, and given the argument for common phonological deficits, we might expect language-invariant neurobiological signatures to be associated with reading disability as well. The evidence to date from alphabetic languages is supportive of this expectation (Paulesu et al., 2001; Salmelin et al., 1996;

Shaywitz et al., 2002). Functional disruptions in LH posterior cortex (particularly the occipitotemporal region) in RD individuals performing reading tasks during neuroimaging have been found in several languages that vary in the complexity of mappings between printed and spoken forms (English, Finnish, German, French, and Italian). This common neurobiological signature, within a largely language-invariant circuitry for reading in the LH, reinforces the notion of universality in RD. A recent study of Chinese RD readers (Siok et al., 2004) reported a language-specific difference in the RD signature (specifically, diminished activation of middle frontal regions for RD readers relative to controls). This finding has not been reported in alphabetic languages. However, these authors also found diminished activation in RD readers at the same LH ventral region previously reported by Paulesu and others in RD within alphabetic languages in their word reading task (Brunswick et al., 1999; Paulesu et al., 2001; Salmelin et al., 1996; Shaywitz et al., 2002).

Potentially Compensatory Processing in Reading Disability

Behaviorally, poor readers compensate for their inadequate phonological awareness and knowledge of letter–sound correspondences by over-relying on contextual cues to read individual words; their word reading errors tend to be visual or semantic rather than phonetic (see Perfetti, 1985 for review). These behavioral markers of reading impairment may be instantiated cortically by compensatory activation of frontal and RH regions. In our studies (Shaywitz et al., 1998, 2002), we observed processing in RD readers that we interpret as compensatory. We found that on tasks that made explicit demands on phonological processing (pseudoword and word reading tasks), RD readers showed a disproportionately greater engagement of IFG and prefrontal dorsolateral sites than did NI readers (see also Brunswick et al., 1999; Salmelin et al., 1996 for similar findings). Evidence of a second, potentially compensatory, shift—in this case to posterior RH regions—comes from several findings. Using magnetoencephalography (MEG), Sarkari and colleagues (2002) found an increase in the apparent engagement of the RH temporoparietal region in RD children. More detailed examination of this trend, using hemodynamic measures, indicates that hemispheric asymmetries in activity in posterior temporal and temporoparietal regions (MTG and AG) vary significantly among reading groups (Shaywitz et al., 1998): there was greater right than left hemispheric activation in RD readers but greater left than right hemispheric activation in NI readers. Rumsey and colleagues (1999) examined the relationship between RH activation and reading performance in their adult RD and NI participants and found that RH temporoparietal activation was correlated with standard measures of reading performance only for RD readers (see also Shaywitz et al., 2002). In summary, initial adult and cross-sectional developmental studies have identified reading

group differences in both functional neuroanatomical and behavioral trajectories; NI children develop a left hemispheric posterior (ventral) reading system capable of supporting fluent word identification, whereas RD readers, failing to master component reading skills, demonstrate presumably compensatory trajectories toward both RH posterior and frontal lobe regions. Although imaging studies have established group differences in developmental trajectories at two correlated levels of analysis, they are nonetheless descriptive. We must begin to conduct studies aimed at gaining a better understanding of key behavioral, neurobiological, and genetic etiological factors that may be responsible for this divergence in circuitry between NI and RD cohorts; such work is critical to establish a proper causal account.

Refining Our Account of Neurobiology of Skilled Word Recognition

In a preliminary model (Pugh et al., 2000a), we speculated that the temporoparietal and anterior systems are critical in learning to integrate orthographic, phonological, and semantic features of words, whereas the ventral system develops, as a consequence of adequate learning during reading acquisition, to support fluent word identification in normally developing, but not RD, individuals. This general taxonomy however, is both coarse-grained and underspecified. To explore functional subspecialization further, we have recently conducted a series of experiments with skilled readers as participants (Frost et al., 2005; Katz et al., 2005; Mencl et al., 2002; Sandak et al., 2004a; summarized in depth by Sandak et al., 2004b). We examined: phonological priming (Mencl et al., 2002), phonological/semantic tradeoffs (Frost et al., 2005), and critical factors associated with repetition effects (Katz et al., 2005) and adaptive learning (Sandak et al., 2004a). This line of research is aimed at providing more information on both subspecialization with the major LH regions, and how different component systems modulate processing in relation to one another in response to varied stimuli and at different stages during adaptive learning. Given the importance of the ventral pathway in the development of fluent reading, we are particularly interested in assessing both the tuning characteristics of the skilled, correlated occipitotemporal region (along with remote areas most closely linked to processing within this ventral area).

Phonological Priming

We have recently completed a functional magnetic resonance imaging (fMRI) study of phonological and orthographic priming effects in printed word recognition (Mencl et al., 2002). Participants performed a primed lexical decision task. Word prime–target pairs were either (a) both orthographically and phonologically

similar (bribe–TRIBE); (b) orthographically similar but phonologically dissimilar (couch–TOUCH); or (c) unrelated (lunch–SCREEN). Results revealed that targets primed by phonologically dissimilar words evoked more activation than did targets primed by phonologically similar words in several LH cortical areas hypothesized to underlie phonological processing: this modulation was seen in the IFG, Wernicke's area, and the SMG. Notably, this phonological priming effect was also obtained within the early-activating LH occipitotemporal skill zone, consistent with the claim from behavioral priming research that phonologically analytic processing occurs early in lexical access. Whether these phonological effects within the ventral word form system we have observed occur early or late in processing, however, awaits replication of this experiment with real-time measures such as electroencephalograph (EEG) or MEG, where more precise temporal relations between activated systems can be uncovered.

Tradeoffs Between Phonology and Semantics

Many previous studies have attempted to identify the neural substrates of orthographic, phonological, and semantic processes in NI (Fiebach et al., 2002) and RD (Rumsey et al., 1997) cohorts. RD readers have acute problems in mapping from orthography to phonology and appear to rely on semantic information to supplement deficient decoding skills (Plaut & Booth, 2000). NI readers too, appear to show a tradeoff between these component processes. Strain and colleagues (1996) provided behavioral confirmation of this, demonstrating that the standard consistency effect on low-frequency words (longer naming latencies for words with inconsistent spelling-to-sound mappings such as PINT relative to words with consistent mappings such as MILL) is attenuated for words that are highly imageable/concrete. Importantly, this interaction reveals that semantics can facilitate the processes associated with orthographic-to-phonological mapping in word recognition.

Using fMRI, we sought to identify the neurobiological correlates of this tradeoff between semantics and phonology (Frost et al., 2005). A go/no-go naming paradigm was employed in an event-related fMRI protocol, with word stimuli representing the crossing of frequency, imageability, and spelling-to-sound consistency. Higher activation for high-imageable words was found in middle temporal and posterior parietal sites. In contrast, higher activation for inconsistent relative to consistent words was found in the IFG, replicating findings by Fiez and colleagues (1999) and Herbster and colleagues (1997). Critically, analyses revealed that imageability was associated with reduced consistency-related activation in the IFG, SMG, and occipitotemporal, but increased posterior parietal (AG) and middle temporal activation; this appears to be the principal neural signature of the behavioral tradeoff between semantics and phonology revealed by Strain and colleagues. These findings provide

clear evidence that skilled performance results from complementary, cooperative processing involving different components of the reading circuitry.

Adaptive Learning

Previous studies have demonstrated that both increased familiarity with specific words and increased reading skill are associated with a shift in the relative activation of the cortical systems involved in reading, from predominantly dorsal to predominantly ventral. In another line of research, we are carrying out functional neuroimaging experiments in order to provide a more precise characterization of the means by which practice with unfamiliar words results in this shift, and to gain insights into how these systems learn to read new words. In one study from our group (Katz et al., 2005), we found evidence for this shift as skilled readers acquired familiarity for words via repetition. In that study, we examined repetition effects (comparing activation for thrice-repeated tokens relative to unrepeated words) in both lexical decision and overt naming. Across tasks, repetition was associated with facilitated processing, as measured by reduced response latencies and errors. Many sites, including the IFG, SMG, supplementary motor area, and cerebellum, showed reduced activation for highly practiced tokens. Critically, a dissociation was observed within the ventral system: the occipitotemporal skill zone showed practice-related reduction (like the SMG and IFG sites), whereas more anterior ventral sites, particularly the MTG, were stable or even showed increased activation with repetition. Thus, we concluded that a neural signature of increased efficiency in word recognition signals more efficient processing in dorsal, anterior, and posterior ventral sites, with stable or increased activation in more anterior middle and inferior temporal sites.

A second experiment (Sandak et al., 2004a) examined whether the type of processing engaged in when learning a new word mediates how well that word is learned, and the cortical regions engaged when that word is subsequently read. We suspected that repetition alone is not sufficient to optimize learning; rather, we hypothesized that the quality of the lexical representations established when new words are learned is affected by the type of processing engaged in during learning. Specifically, we predicted that, relative to attending to the orthographic features of novel words, learning conditions that stress phonological or semantic analysis would speed naming and, in turn, cortical activation patterns similar to those characteristic of increased familiarity with words (as seen in Katz et al., 2005). Prior to MRI scanning, participants completed a behavioral session in which they acquired familiarity for three sets of pronounceable pseudowords while making orthographic (consonant/vowel pattern), phonological (rhyme), or semantic (category) judgments. Note that in the semantic condition, participants learned a novel

semantic association for each pseudoword. Following training, participants completed an event-related fMRI session in which they overtly named trained pseudowords, untrained pseudowords, and real words.

As predicted, we found that the type of processing (orthographic, phonological, or semantic) engaged in when learning a new word influences both how well that word is learned and the cortical regions engaged when that word is subsequently read. Behaviorally, phonological and semantic training resulted in speeded naming times relative to orthographic training. Of the three training conditions, we found that only phonological training was associated with both facilitated naming and the pattern of cortical activations previously implicated as characteristic of increased efficiency for word recognition (Katz et al., 2005). We suggest that for phonologically trained items, learning was facilitated by engaging in phonological processing during training; this in turn resulted in efficient phonological processing (instantiated cortically as relatively reduced activation in IFG and SMG) and efficient retrieval of presemantic lexical representations during subsequent naming (instantiated cortically as relatively reduced activation in the occipitotemporal skill zone). Semantic training also facilitated naming but was associated with increased activation in areas previously implicated in semantic processing, suggesting that the establishment and retrieval of semantic representations compensated for less efficient phonological processing for these items.

Implications of Recent Findings

Our recent experiments examining phonological priming, phonological/semantic tradeoffs, and critical factors associated with adaptive learning in reading have yielded findings that allow for the development of a more fine-grained picture of the functional neuroanatomy and subspecializations within these systems, and we have begun to acquire information on learning-related modulation and tradeoffs among component regions. Across these studies identical sites in the SMG (within the temporoparietal system), IFG (within the anterior system) and the occipitotemporal skill zone (within the ventral system) showed (a) increased activation for pseudowords relative to words, (b) strong phonological priming effects, and (c) repetition-related reductions that were most salient in the phonologically analytic training condition. This converging pattern with regard to phonological variables strongly suggests a phonological “tuning” in these subregions. (It is particularly noteworthy that the developmentally critical occipitotemporal skill zone—the putative VWFA—by these data, appears to be phonologically tuned. It makes good sense that this region should be so structured, given the failure to develop this system in RD when phonological

deficits are one of the core features of this population). By contrast, the angular gyrus (within the temporoparietal system) and the MTG/ITG (within the ventral system) appear to have more abstract lexico-semantic functions across our studies (see Price et al. 1997 for similar claims).

From these findings, we speculate that subregions within the SMG and IFG operate in a yoked fashion to bind orthographic and phonological features of words during learning; these systems also operate in conjunction with the AG, in which these features are further yoked to semantic knowledge systems distributed across several cortical regions. Adequate binding, specifically adequate orthographic-phonological integration, enables the development of the presemantic occipitotemporal skill zone into a functional pattern identification system. As words become better learned, this area becomes capable of efficiently activating lexico-semantic subsystems in the MTG/ITG, thus enabling the development of a rapid ventral word identification system. RD individuals, with demonstrable anomalies in temporoparietal function (and associated difficulties with phonologically analytic processing on behavioral tests), fail to adequately "train" ventral subsystems (particularly the occipitotemporal skill zone) and thus develop compensatory responses in frontal and RH systems.

In our view, this developing account better lends itself to the architectural assumptions put forward in interactive models (e.g., Harm and Seidenberg, 1999) than to the classic dual-route models. The findings on stimulus-type effects, and especially the data on adaptive learning, do not readily support the notion of, for instance, independent dorsal and ventral reading pathways, with each coding different information. Instead, they suggest a set of phonologically or semantically tuned subsystems that are widely distributed across both dorsal and ventral cortex and appear to act cooperatively during fluent word reading and in adaptive learning. Developmentally, there is good evidence that a ventral reading specialization depends on the intactness of processing across this distributed system.

Cross-linguistic studies will be critical in expanding our account. In the newly funded study involving a collaboration between Haskins Laboratories, the University of Jyväskylä, and the National Yang-Ming University, we will longitudinally contrast typical and atypical reading development in English with Finnish and Mandarin Chinese. Relative to English, Finnish has a rather transparent orthographic-to-phonological mapping, whereas Mandarin is more opaque with regard to how phonology is coded in the writing system. Importantly, as noted, data suggest that skilled adult readers in all three languages appear to develop a common neurobiological circuit for reading (Pugh et al., 2005), suggesting very strong biological constraints on the neural pathways that will emerge as reading competence is acquired (even for very different orthographies).

However, we might anticipate that the initial neurocircuitry for reading might be rather different in each language, reflecting the different challenges that these writing systems place on orthography, phonology, morphology, visual memory, and the like. This would imply that, whereas a common ventral reading specialization should eventually develop for each language, the computational organization of this common neural pathway will differ somewhat as a function of the language-specific challenges (statistical properties of the writing system) during early reading development. An adequate neurobiologically grounded reading theory must be able to account for both language variance (with respect to computational factors) and language invariance (with respect to common neural pathways) over the course of development. With regard to ventral cortex (VWFA), we might expect that the tuning of this region, as well as its developmental course, will vary somewhat in orthographies that differ in orthographic depth. These anticipated language differences, along with our progressive studies of component processing tradeoffs during adaptive learning, will continue to drive the conceptual and computational development of neurobiological theories in the next phase of our research.

Conclusion

We conclude with a note on next steps in our research. Although neurobiological studies of word recognition, particularly those identifying the neurobiological signatures of RD, have generated a good deal of enthusiasm, it should be remembered that functional neuroimaging measures are not intrinsically explanatory; they simply describe brain organization at a given point in development. Links between multiple indices of reading (dis)ability including genetic polymorphisms, brain structure and function, and cognitive deficits promise to constitute the core scientific foundation for our understanding of neurodevelopmental disorders in the coming years, which aims to progress from descriptive neurobiological findings to potentially explanatory models. To that end, in a new project in our lab we are using a longitudinal design to characterize reading development in NI and RD cohorts of children by measuring developmental changes in reading performance (obtained during the early stages of reading acquisition through to the point where fluent reading is anticipated) using multimodal functional imaging (fMRI and event-related potentials [ERPs]), neurochemistry measured with magnetic resonance spectroscopy (MRS), and genetic analyses. By establishing meaningful links between behavioral/cognitive skills that must be in place to read and neuroanatomical, neurochemical, and genetic measures, we can begin to develop an explanatory account of neurocognitive

divergences in typically developing and RD children (Grigorenko, 2001; Pugh et al., 2000a). That is, we believe that designs of this type will allow specifications of the biological *pathways* predisposing for risk for the development of RD and explorations of elements of these pathways that might be most suitable for pharmacological and behavioral intervention. Although the goal of linking genetics, neurochemistry, functional neuroanatomy, and behavior in reading development is both ambitious and, to some extent, exploratory, the goal of developing an adequate explanatory model of observed divergences in RD with respect to brain and behavior requires such links to be made.

Finally, as discussed, much behavioral research supports the notion that word recognition engages common processes across languages and orthographies; however, at present there is much less cross-linguistic neuroimaging research on reading development, disability, and the effects of intervention. Although the initial evidence has provided support for a common neurobiological signature of both skilled and impaired reading, some differences have been observed (Siok et al., 2004). Given the significant variability in orthographic form, orthographic-to-phonological mappings, methods of reading instruction, and manifestations of RD across languages and cultures, more work needs to be done in the area of cross-linguistic studies of reading, both in order to identify the neurobiological universals of reading and to understand how the functional organization of reading varies with language-specific features. Cross-linguistic neurocognitive research has the potential, we believe, to enhance significantly our current understanding of universal influences on learning to read.

Acknowledgments

This research was funded by NICHD grants F32-HD42391 to Rebecca Sandak, R01-HD40411 to Kenneth R. Pugh, and P01-HD01994 to Haskins Laboratories.

Note

1. A few sections of this chapter have appeared recently in:
 Frost, S.J. et al. (2008). Neurobiological studies of skilled and impaired word reading. In E.L. Grigorenko & A.J. Naples (Eds.). *Single-word reading: Behavioral and biological perspectives*, pp. 355–376. New York: Lawrence Erlbaum.
 Pugh, K.R. et al. (2006). Neurobiological studies of skilled and impaired reading: A work in progress. In G.R. Rosen (Ed.). *The dyslexic brain: New pathways in neuroscience discovery*, 21–47. Mahwah, NJ: Lawrence Erlbaum.

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