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11 Neuroimaging and the Phonological Deficit Hypothesis

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Neuroimaging technology has provided researchers with access to the brain on multiple dimensions, including anatomy and functional activity. Advances in this technology have vastly improved our knowledge of the neural circuitry related to reading, and the role of phonological processing in reading skill. The phonological deficit hypothesis (PDH; I. Y. Liberman, Shankweiler, & A. M. Liberman, 1989; Shankweiler & Crain, 1986; Shankweiler et al., 1995) is a theory that posits deficits in phonological processing; connecting phonemes to letters is the core deficit of reading disability (RD). In this chapter, we present an overview of what imaging tells us about the reading circuit in the brain. We then take a look at the history of neuroimaging research on skilled and impaired reading, and examine how the PDH has facilitated the progression of knowledge in this area. Finally, we address current and future directions of research, including emerging research on precursors to reading skills and deficits, cross-cultural studies, and reading interventions.

THE READING CIRCUIT

The neural structures and functions involved in skilled reading and the acquisition of that skill (hereafter “the reading circuit”) have been outlined in several reviews (Frost, Landi, Mencl, Sandak, Fulbright, Tejada, et al., 2009; Pugh, Mencl, Jenner,

et al., 2000; Pugh, Sandak, Frost, Moore, & Mencl, 2005; Vellutino, Fletcher, Snowling, & Scanlon, 2004). Here, we provide a brief summary of these findings.

There appear to be three major components in the reading circuit: (a) an anterior system primarily in the posterior portion of the inferior frontal gyrus, (b) a posterior dorsal system in temporo-parietal cortex, and (c) a posterior ventral system in occipito-temporal cortex and adjacent areas. Systematic research suggests that each of these areas has a specialized role in the reading process. The anterior system is tuned to syntactic and phonological processing in reading, and is hypothesized to be particularly important for speech-motor coding and learning new words (T. T. Brown et al., 2005; Church, Coalson, Lugar, Petersen, & Schlaggar, 2008; Pugh, Mencl, Shaywitz, et al., 2000; Pugh et al., 1996). The posterior dorsal system, which includes posterior portions of the superior temporal gyrus (Wernicke's area) and extends into the angular and supramarginal gyri in the inferior parietal lobule, is important for learning to read new words. Its specific functions appear to involve mapping orthography onto phonology and binding them together with semantic features (Price, Winterburn, Giraud, Moore, & Noppeney, 2003). The posterior ventral system includes extrastriate areas, portions of the middle and inferior temporal gyrus, and a left inferior occipito-temporal/fusiform region known as the visual word form area (Cohen & Dehaene, 2004; Cohen et al., 2000, 2002). Engagement of this area appears to be a late-developing signature for skilled and fluent word identification (B. A. Shaywitz et al., 2002; S. E. Shaywitz et al., 2003).

Research has shown that these areas are differently engaged by the act of reading as a function of reader skill and the presence/absence of RD. Skilled readers tend to have lateralized left hemisphere activity on reading tasks (see Pugh et al., 1996, among many others). Beginning readers appear to rely on the anterior and posterior dorsal systems more heavily, whereas skilled readers rely on the posterior ventral system when presented with familiar material (T. T. Brown et al., 2005; Church et al., 2008; B. A. Shaywitz et al., 2002; S. E. Shaywitz et al., 2003). In contrast, it is reported that individuals with RD tend to exhibit underactivation of the left hemisphere posterior structures compared to non-impaired controls and to exhibit right hemisphere and frontal activation, perhaps reflecting compensation for deficient phonological processing (Pugh, Mencl, Shaywitz, et al., 2000; Rippon & Brunswick, 2000; S. E. Shaywitz et al.). Individuals with RD also fail to show a developmental trend of increased specialization of the ventral left hemisphere areas for print (B. A. Shaywitz et al.).

In general, the areas in the brain that have been implicated in reading show significant overlap with traditional left-lateralized language areas (such as Broca's area and Wernicke's area). More specifically, reading performance (behaviorally and neurally) reflects the difficulties of phonological processing, which has long been thought to play a crucial role in RD. In the following section, we describe how neuroimaging has further underscored the importance of phonological processing in reading. Moreover, we highlight how the advancement in our knowledge of how printed material is processed in the brain has been facilitated by the PDH and the methodological paradigms driven by it.

HISTORICAL PERSPECTIVE ON NEUROIMAGING AND THE READING CIRCUIT

In order to understand how neuroimaging and the PDH have mutually influenced each other, it is important to put the current state of research and theory in a historical context. This section tracks the relationship between the PDH and our understanding of the neural processes involved in reading through several decades of methodological developments in neuroimaging.

THEORIES THAT PREDATE NEUROIMAGING

Behavioral research over the past few decades has consistently emphasized the importance of phonological processing for reading skill acquisition (I. Y. Liberman et al., 1989; Shankweiler & Crain, 1986; Shankweiler et al., 1995; Vellutino et al., 2004). From both neurobiological and sociocultural perspectives, it is not surprising (but also not inevitable) that spoken language has primacy over written language, both in time of development and in utilization (A. M. Liberman, 1992; Schlaggar & McCandliss, 2007). Spoken language is mastered naturally by almost all individuals without direct instruction, but reading skill is more variable, with failure occurring in significant numbers of children within every language community that has a written form. Moreover, written language is essentially the spoken language written down; alphabetic writing systems represent phonological language forms. Successful reading requires a mastery of the internal phonological structure of language in relation to the orthography (i.e., the alphabetic principle; I. Y. Liberman et al.). Therefore, it follows that deficits in phonological systems that support spoken language would also affect an individual's ability to learn to read. Similarly, it is likely that neurobiological systems for reading rely on existing areas that support the spoken language abilities that have previously developed.

At about the time neuroimaging was emerging as a useful tool, there were a number of theories of the mechanisms underlying reading disorders based on behavioral findings. These theories included (but were not limited to) ones that hypothesized deficits in auditory discrimination (Tallal, Miller, & Fitch, 1993), motor timing (Wolff, Cohen, & Drake, 1984), verbal working memory (Hulme & Roodenrys, 1995), visual processing and the magnocellular deficit hypothesis (Eden, VanMeter, Rumsey, Maisog, & Zeffiro, 1996), and phonological awareness and the PDH (Goswami & Bryant, 1990; I. Y. Liberman et al., 1989; Shankweiler & Crain, 1986). Deficits in phonological awareness were the most consistent findings across research groups and often constituted the strongest single predictor of literacy acquisition (Fletcher et al., 1994; Goswami & Bryant; Shankweiler et al., 1995; Share, Jorm, Maclean, & Matthews, 1984; Stanovich & Siegel, 1994). Thus, it was argued that reading deficits were primarily a result of a general weakness in phonological processing (Olson, Wise, Connors, & Rack, 1990; Shankweiler et al.; Vellutino & Scanlon, 1991; Wagner, Torgesen, Laughon, Simmons, & Rashotte, 1993); however, debate continued as to whether this deficit might be a downstream consequence of some other underlying factor.

NEUROANATOMY

Early Anatomical Discoveries: Soft Signs, Lesions, and Postmortem Discoveries

Even before neuroimaging methods became widely used, it was thought that neurological abnormalities were present in RD (see Vellutino et al., 2004, for a review). One type of evidence came from clinical indications, or “soft signs,” of neurological dysfunction, including perceptual difficulties and motor clumsiness, among others (Vellutino et al.). There were also established associations between reading impairment and specific aspects of phonological processing such as poor retention of phonological information in verbal working memory (Brady, 1991; Shankweiler, Liberman, Mark, Fowler, & Fischer, 1979).

Before neuroimaging, the postmortem examination of individuals with brain damage was one of the only available methods for understanding the neurobiology of normal and impaired cognitive functioning. Some individuals with focal brain lesions displayed dissociations of reading abilities from other skills, and this led to early hypotheses about what brain regions might be involved in RD (Vellutino et al., 2004). Based on such data, Dejerine (1891) was one of the first to report that lesions in the angular gyrus might be related to the reading deficits in individuals with acquired dyslexia. Later, Henschelwood (1917) conjectured that the same area might be related to developmental dyslexia.

Early postmortem studies revealed neuroanatomical atypicalities in the brains of individuals with reading difficulties. One region of interest was the planum temporale of the left temporal lobe, an area thought to support aspects of language functioning. In non-impaired adults, postmortem examination revealed that the planum temporale area tended to be larger in the left hemisphere (Geschwind & Levitsky, 1968). Individuals with dyslexia, however, usually did not show this asymmetry (and in some cases showed a reversal of asymmetry), a finding that seemed to implicate language-related structures in reading (Galaburda, Sherman, Rosen, Aboitiz, & Geschwind, 1985; Humphreys, Kaufmann, & Galaburda, 1990). Recently, Galaburda (2006) has used postmortem histological findings to argue that individuals with RD may have a congenital abnormality of brain structure, possibly as a result of errors in neuronal migration, which precedes reading (and perhaps) language development (e.g., Galaburda & Cestnick, 2003). For a review of findings beyond those highlighted in this section, see Galaburda (2006).

Anatomical Neuroimaging

Neuroimaging has provided a new tool for probing the neuroanatomy of individuals with neurodevelopmental disorders. Magnetic resonance imaging (MRI) allows the examination of brain structures *in vivo*. Findings from MRI studies of individuals with RD were more mixed than the early postmortem research. For example, although some postmortem studies had found a reversal of asymmetry in the planum temporale, some MRI studies on RD found left hemisphere–right hemisphere symmetry (Hynd, Semrud-Clikman, Lorys, Novey, & Eliopoulos, 1990; Larsen, Høien, Lundberg, & Odegarrd, 1990), some found no differences

(Rumsey et al., 1997; Schultz et al., 1994), whereas others replicated the postmortem findings of the increased right hemisphere size (Hynd et al.). Studies that examined cortical differences in the corpus callosum and temporo-parietal areas were also inconsistent, and even when differences between individuals with RD and non-impaired controls were present, the differences were relatively small (Pennington, 1999; Schultz et al.; Vellutino et al., 2004). Still, a growing number of studies have found structural differences between individuals with and without RD that show a pronounced overlap with regions identified as being important for reading, including temporo-parietal (Brambati et al., 2004; W. E. Brown et al., 2001), inferior frontal (W. E. Brown et al.; Eckert et al., 2003), and (less consistently) occipito-temporal sites (Kronbichler et al., 2008).

Some recent studies have suggested that individual differences in anatomy might predict reading and oral language impairments (Leonard, Eckert, Givens, Berninger, & Eden, 2006). Recently, Hoeft et al. (2007) used voxel-based morphometry to measure gray and white matter structure, and found that the presence of greater gray matter density in the right fusiform gyrus and greater white matter density in the left superior temporal and inferior parietal regions predicted later decoding ability. Although the findings summarized here are intriguing, it is as yet unclear why the pattern of morphological differences is inconsistent across studies. See Eckert (2004) and Leonard et al. (2001) for reviews.

The use of diffusion tensor imaging (DTI) has shown promise as an approach to examining white matter tracts. Results from a number of studies using DTI have indicated that individuals with dyslexia have less white matter development in left hemisphere, language-related areas, including reduced myelination in left temporo-parietal regions that are implicated in language processing (Beaulieu et al., 2005; Klingberg et al., 2000; Niogi & McCandliss, 2006). A study of a group of children with a range of reading abilities, Deutsch et al. (2005) showed that white matter volume in the left hemisphere was positively correlated with reading performance. Furthermore, Dougherty et al. (2007) have used DTI data to show that interhemispheric connectivity in the temporal-collosal pathway was positively correlated with phonemic awareness.

Neuroanatomical research has provided insight into the neural basis of reading in RD. The most consistent finding demonstrates group differences in areas traditionally thought to be devoted to language. Recent technological advances, including DTI, will be important for identifying major neuroanatomical differences that could be a signature of RD.

Functional Neuroimaging

Over the past decade, there has been a growing interest in online measures of brain function in order to achieve better understanding of the neural circuitry involved in reading. The expectation was that functional neuroimaging would enable identification of cortical networks related to reading. The identification of cortical networks was especially important for understanding RD because reading theories had developed to a level of complexity that involved interactive processes and networks of activity that would not necessarily be confined to a

specific area (Horwitz, Rumsey, & Donohue, 1998; Pugh, Mencl, Shaywitz, et al., 2000). Two main classes of functional neuroimaging techniques have emerged. The first is based on electrophysiological indicators of brain activity, including electro-encephalography (EEG) and magneto-encephalography (MEG). The second is based on hemodynamic measures of brain activity and includes functional MRI (fMRI) and positron emission tomography (PET).

Electrophysiological Imaging

Electrophysiological measures of brain activity, starting with EEG, were among the first measures to allow researchers to associate behavior with neural responses. These measures have the advantage of possessing fine-grained temporal resolution, which is particularly important for exploring the dynamic nature of reading and language processing. They do, however, lack the spatial resolution of fMRI or PET. EEG, and more recently MEG, have proven to be sensitive to the temporal progression of activity in language-specific areas even with simple language tasks (e.g., Breier, Simos, Zouridakis, & Papanicolaou, 1998; Papanicolaou et al., 1999; Simos et al., 1999).

Nonetheless, electrophysiological studies (EEG, MEG, and evoked response potentials) have provided support for the involvement of core-language areas in RD, particularly areas involved in phonological processing. In one study, children with dyslexia did not engage or were much slower to engage the temporo-occipital region when passively viewing words, whereas controls showed pronounced activation (Salmelin, Service, Kiesila, Uutela, & Salonen, 1996). When the task targeted phonological processing, group differences in neural activity became most pronounced (Duffy, Denckla, Bartels, & Sandini, 2004; Spironelli, Penolazzi, & Angrilli, 2008; Spironelli, Penolazzi, Vio, & Angrilli, 2006). For example, when both phonological and visual processing were measured separately, individuals with RD showed increased frontal activity only during the phonological task, and also showed a right hemisphere shift in parieto-occipital activity in both tasks when compared to controls (Rippon & Brunswick, 2000). This provides further support for left hemisphere dysfunction, and right hemisphere compensation for this deficit. There are also several studies that have found differences in intra- and interhemispheric coherence (Arns, Peters, Breteler, & Verhoeven, 2007; Leisman & Ashkenazi, 1980; Sklar, Hanley, & Simmons, 1972), although the involvement of specific cortical areas or regions is often difficult to interpret. Other studies have examined activation patterns relative to subtypes of RD, although the delineation and categorization of subtypes is a matter of significant debate (Arns et al.).

Although electrophysiological methods show great sensitivity to temporal changes in processing, one disadvantage is the lack of spatial sensitivity of these measures, which is why electrophysiological studies often refer to hemispheres and quadrants rather than specific neural structures or functional areas. By contrast, hemodynamic measures of neural activity tend to have good spatial resolution and poor temporal resolution, and the presence of these complementary strengths/limitations accentuates the need for both measures. Still,

electrophysiological data provide compelling and replicated evidence for the role of language areas in the left hemisphere in reading tasks, and reduced activity patterns in these areas during tasks that specifically tax phonological processing in individuals with RD. For findings from electrophysiological research in addition to those we have highlighted in this section, see recent reviews (Goswami, 2008; Pammer, 2009).

Hemodynamic Measures of Neural Activity

The earliest hemodynamic measure of neural activity was PET. It involves the injection of a radioactive tracer, which emits gamma rays as the result of neural metabolic activity as a signal of the functional involvement of brain areas. PET provided the first opportunity for researchers to isolate neuroanatomical areas engaged during specific cognitive tasks. (e.g., Fox & Mintun, 1989; Mintun, Fox, & Raichle, 1989; Petersen, Fox, Posner, Mintun, & Raichle, 1989; Petersen, Fox, Snyder, & Raichle, 1990). The advent of fMRI, which does not require a tracer, made it possible, with a noninvasive procedure, to detect the location and magnitude of activity with better spatial resolution than PET (Constable, McCarthy, Allison, Anderson, & Gore, 1993; Ogawa, Lee, Nayak, & Glynn, 1990; Ogawa et al., 1992; B. A. Shaywitz et al., 1995). As with all functional imaging measures, task design is crucial to the relevance of fMRI findings to inferences about brain-behavior connections that researchers are attempting to make. One approach is cognitive subtraction, which involves using a series of tasks thought to differ minimally on a single characteristic of interest. The “cognitive subtraction” of the results of one task from the results of another putatively isolates the neural activity related to the desired behavior. Cognitive subtraction provides strong evidence for localization of function. In this section, we highlight some of the major findings in this area, focusing on how methodology has shaped the way we understand the processing of printed material in skilled and impaired readers. For the purposes of this chapter, we focus mainly on the work that is directly relevant to the PDH.

An important step in understanding neural markers for reading disorder was the identification of the cortical regions functionally involved in reading. Although early fMRI studies found group differences in left hemisphere activation between individuals with RD and controls (Rumsey et al., 1992; Wood, Flowers, Buchsbaum, & Tallal, 1991), the cortical regions involved in specific aspects of word reading—orthographic, phonological, and lexical-semantic processing—were not identified until later (Pugh et al., 1996). Initial studies attempting to localize component processes utilized a series of hierarchical subtractions (see Table 11.1). For example, by subtracting activation for a visuospatial task from activation for a task involving both visuospatial and orthographic processing, Pugh et al. were able to isolate a unique activation for orthographic processing in lateral extrastriate cortex. They also found that phonological processing for both real words and nonwords engaged the inferior frontal gyrus as well as temporal regions. Lexical-semantic processing was found to engage middle and superior temporal gyri. The results of Pugh

TABLE 11.1
Model for Functional Neuroimaging Studies of Dyslexia to Allow for Comparisons Between Orthographic, Lexical–Semantic, and Phonological Processes

Condition Levels	Task Demands ^a	Stimulus Example
1. Visuospatial	Identify whether two line patterns are the same or different	Same = <i>N/</i> and <i>N/</i> Different = <i>/N</i> and <i>N/</i>
2. Visuospatial + orthographic	Identify whether two consonant strings are the same or different, where capitalization is the differentiating characteristic	Same = bbCb and bbCb Different = bbCb and bBcb
3. Visuospatial + orthographic + phonological ^{b,c}	Identify whether two single letters rhyme	Same = B and C Different = B and F
4. Visuospatial + orthographic + phonological ^d	Identify whether two pseudo-words rhyme	Same = lete and jeat Different = lete and jiff
5. Visuospatial + orthographic + phonological + semantic	Identify whether two words are in the same semantic category	Same = corn and rice Different = corn and cart

^a Participant pushed a button for every pair that was the same visually (1 and 2), rhymed (3 and 4), or was in the same semantic category (5). Children were told not to respond if stimulus did not meet these criteria.

^b This component was not used until S. E. Shaywitz et al. (1998).

^c This component places a smaller demand on orthography, in comparison to #4.

^d This component places a greater demand on orthography, in comparison to #3.

et al. have been replicated in MEG using the same cognitive subtraction method (Breier, Simos, Zouridakis, & Papanicolaou, 1999) and PET (Herbster, Mintun, Nebes, & Becker, 1997).

An important methodological advance was the application of brain–behavior analyses. For example, Pugh et al. examined correlations between task-dependent BOLD activation and a behavioral measure of phonological processing (Pugh et al., 1997). Participants had performed a lexical decision task outside of the MRI scanner, providing behavioral measures of sensitivity to grapheme–phoneme regularity (a marker of phonological processing). These findings were then analyzed with previously collected brain activation patterns from fMRI using the paradigm in Table 11.1. Individual differences in lexical decision performance were found to correlate with the magnitude of left-lateralized activation in the inferior frontal gyrus. Specifically, an increased regularity effect was associated with more nearly bilateral activity, and participants who were less sensitive to the regularity effect exhibited more left-lateralized activation. This finding confirmed the role of the inferior frontal gyrus in phonological processing.

As the neural signature for skilled reading became better understood, the next step was to identify how these areas were disrupted in adults with developmental reading disorders (S. E. Shaywitz et al., 1998). S. E. Shaywitz et al. argued that inconsistencies in previous functional imaging studies (Eden et al., 1996; Flowers, Wood, & Naylor, 1991; Gross-Glenn et al., 1991; Paulesu et al., 1996; Rumsey et al., 1992, 1997; Salmelin et al., 1996) were the result of a methodology that measured multiple overlapping reading processes, failing to systematically isolate each of the components. S. E. Shaywitz et al. used a design similar to that of Pugh et al. (1996) but added a letter rhyme identification task to the paradigm (level #3, see Table 11.1) to examine further the role of orthography in reading. They found that adults with dyslexia failed to engage posterior cortical structures (Wernicke's area, angular gyrus, occipito-temporal cortex) and tended to over-engage anterior structures (e.g., inferior frontal gyrus and related areas), and importantly that group differences in these areas increased as the demands for phonological processing became greater. These findings have held up fairly well in subsequent studies (e.g., Brunswick, McCrory, Price, Frith, & Frith, 1999; Rumsey et al., 1997).

Shaywitz et al. then extended their findings to a large cross-sectional sample of RD and non-impaired children aged 7–17 years, looking at developmental changes in the reading circuit (B. A. Shaywitz et al., 2002). The paradigm in Table 11.1 was used, although case matching for single letters was used rather than letter strings. Brain activation was correlated with chronological age to examine development, and also with reading skill (after age was covaried). Increases in reading skill were associated with increased specialization for print of the ventral left hemisphere occipito-temporal areas, which indicated that this area is important for skilled reading. Children with RD tended to have greater activation in frontal areas (left and right inferior frontal gyrus) than non-impaired children, especially as they grew older. This study was one of the first to provide empirical support for the long-held idea that developmental and acquired dyslexia had similar neural disruptions. It also suggested the possibility of neurodevelopmental changes in RD indicating that there may be plasticity in the brain that is amenable to intervention. Recent studies have shown similar results that support the role of temporo-parietal regions and lateral frontal regions in printed word learning in children and temporo-occipital (visual word form area) regions in skilled reading in several different types of reading paradigms (e.g., T. T. Brown et al., 2005; Church et al., 2008). Moreover, findings indicate that there are divergent neurodevelopmental patterns in individuals with RD, some of whom have persistent reading difficulties, and others that show marked improvement in reading skill (S. E. Shaywitz et al., 2003).

In addition to isolating the language-related areas involved in skilled and disabled reading, studies have also highlighted relationships between phonological awareness and patterns of brain activity during both language and reading tasks. Frost, Landi et al. (2009) examined the relationship between phonological awareness and brain activation patterns in children aged 6–10 years, both for print and for speech. Individual differences in behavioral measures of phonological

awareness were correlated with activation differences for modality (print vs. speech) and pronounceability (printed pseudo-words vs. consonant strings) in several language-related areas, particularly the superior temporal gyrus. The findings showed that greater phonological awareness was associated with activation by print of areas primarily active for speech, and, further, that the response to print in speech areas was selective; these were activated by phonologically well-structured print tokens but not by unpronounceable consonant strings. The findings underline the importance of phonological processing in early reading development and suggest that differences in the magnitude of activation in speech areas may serve as an early predictor of reading outcome (cf. Turkeltaub, Lynn, Flowers, Zeffiro, & Eden, 2003).

In total, this series of studies suggests that neural systems involved in reading are subject to systematic developmental change in both typical and atypical development, and that phonological awareness is linked to neural activity in reading and language tasks, highlighting its importance for the development of skill in reading. Children rely chiefly on phonological processing mechanisms in anterior and temporo-parietal regions when they are first learning to read, and that phonological processing appears to play a role in the development of a left hemisphere occipito-temporal region that is important for skilled reading (Pugh et al., 2001). A fuller account of the neural signature of RD will require focus not only on within-region group differences, but also on group differences in patterns of interregional correlations or functional connectivity (Friston, 1994; Horwitz, 1994; Horwitz et al., 1992; McIntosh & Gonzalez-Lima, 1994; Pugh, Mencl, Shaywitz, et al., 2000) to determine how these putative reading areas interact with each other during the processing of text.

An appreciation for the interaction between brain regions, or functional connectivity, involved in reading will allow a deeper understanding of RD (Pugh, Mencl, Shaywitz, et al., 2000). Functional connectivity is typically measured as correlations in activation levels among brain regions during a task. Horwitz et al. (1998), using PET, were the first to note disruptions in functional connectivity in adults with dyslexia between areas traditionally thought to be involved in reading (left angular gyrus, visual association areas, and Wernicke's area), although it was unclear whether the reduced connectivity was specific to areas associated with reading, or part of a more global deficit in connectivity.

Pugh, Mencl, Shaywitz, et al. (2000) asked directly whether differences in connectivity could be derived from predictions derived from the PDH. Using the paradigm in Table 11.1 to compare adults with RD and non-impaired readers, Pugh et al. found that connectivity in adults with RD was deficient only on tasks that relied on phonological assembly. For example, non-impaired readers displayed robust functional connectivity on all tasks, but the RD group demonstrated functional connectivity only on the letter-case and single-letter rhyming tasks, which did not require complex phonological assembly. Reduced left hemisphere functional connectivity was found only when phonological processing was important (e.g., nonword rhyming vs. semantic category judgment). Importantly, the

RD group appeared to show increased right hemisphere activation in homologous structures, suggesting a rightward compensatory shift in neural engagement.

In another study using a line judgment task, a nonword rhyming task, and a semantic category judgment task (levels 1, 4, and 5 in Table 11.1), a group of adults with persisting RD was compared to a group who were poor readers as children but had improved with age and to a non-impaired group of adults (S. E. Shaywitz et al., 2003). An interesting developmental pattern emerged. Similar to Pugh, Mencl, Shaywitz, et al. (2000), the results indicated that the RD group who had shown improvement in reading abilities tended to show connectivity between left hemisphere ventral (temporo-occipital) region and right hemisphere regions typically associated with working memory, whereas the non-impaired group showed the expected left hemisphere connectivity between reading areas. This suggested that readers who had improved (but were not skilled readers) were relying on compensatory strategies for poor basic reading skills, possibly involving working memory, instead of the typical phonologically based processing networks. In addition, persistently poor readers failed to activate posterior regions associated with learning new words when presented with pseudo-words. This contrasts with the pattern displayed by skilled readers, who show strong connections between the left occipito-temporal (visual word form area) region and Broca's area, and weak connections between areas thought to be involved in word learning (e.g., left angular gyrus and Broca's area, T. T. Brown et al., 2005; Church et al., 2008; S. E. Shaywitz et al., 2003).

Intervention as an Experiment

Several studies have shown that phonologically based interventions for individuals with RD can lead to improvements in reading skill and concomitant changes in brain activation patterns to more closely resemble those of individuals with normal reading skills (Simos et al., 2002; Temple et al., 2003). Furthermore, the effects of phonologically mediated reading intervention have been shown to remain stable one year post-intervention (B. A. Shaywitz et al., 2004). Varying the treatment conditions within subjects can also be used to test questions relating to the PDH. In a word learning study on a normative sample, Sandak et al. (2004) investigated the relative efficacy of phonological, orthographic, and semantic cues. Participants were instructed to attend to one of the three cue types when attempting to learn pseudo-words. Findings indicated that phonological and semantic cues similarly facilitated learning as indexed through behavioral (accuracy) measures. However, words acquired through phonologic or semantic training yielded distinct brain activation patterns. Phonological training supported increased sensitivity of the visual word form area to the phonological structure of words, whereas semantic training was associated with greater bilateral activation in superior and medial temporal gyri, regions that are involved in the formation and recall of semantic representations. Both training regimens were effective in the remediation of RDs, but each acted on a distinct system that was important for skilled reading. This study highlights the mutually supporting roles of

well-designed treatment studies for understanding basic neural mechanisms in reading and, for evaluating changes resulting from the treatment of neurodevelopmental reading disorders.

SUMMARY OF NEUROIMAGING FINDINGS

In sum, neuroanatomical and functional neuroimaging studies using a variety of techniques have been important for understanding the role of phonological processing in reading, and also for creation of a neurological model of the relationship between phonological processing and reading, including disabled reading. Skilled and impaired readers have contrasting developmental patterns of activation and connectivity. Impaired readers show frontward and rightward shifts in activation, relative to skilled readers, a finding that suggests less reliance on phonological processing and more on visual processing or other right hemisphere-based faculties. A crucial point is that progress would not have been made in these research areas without the development of neurobehavioral paradigms that could be replicated across studies, across research groups, and across populations.

CURRENT AND FUTURE DIRECTIONS

Several ongoing areas of research will be crucial to improving our knowledge of reading disabilities. These include further investigations of (a) the role that phonological awareness and phonological deficits play in initial reading acquisition, (b) determining what cross-linguistic studies can tell us about the PDH, and (c) determining how we can improve reading interventions and, at the same time, how treatment studies can experimentally test the PDH.

Although most current research on reading development uses cross-sectional designs, there is a need to examine development longitudinally with integrated brain and behavior designs. First, a major question in the field that requires longitudinal study is to identify the behavioral and neurobiological preconditions for successful literacy acquisition. It will be important to examine children at risk for reading failure using research designs that relate multiple levels of analysis through time, including behavior, genetics, neuroanatomy, neurochemistry, and neurocircuitry. Second, we know that phonemic awareness scores reflect reading readiness, but how do children with higher reading readiness differ in initial brain organization? Recent research reviewed in this chapter suggests that children who are developing normally in phonological skills utilize brain systems specialized for spoken language processing to process visual graphemes (e.g., Frost, Sandak, Mencl, Landi, Rueckl, Katz et al., 2009; Petersson, Reis, Askelöf, Castro-Caldas, & Ingvar, 2000; Petersson, Silva, Castro-Caldas, Ingvar, & Reis, 2007). What are the preconditions that allow phonological processing systems acquired for spoken language to adapt to different (but related) forms of communication (as in printed language)?

Cross-linguistic research affords comparisons between systems of writing that differ in orthographic depth (i.e., the ease by which a reader can access pronunciation from spelling) in order to determine what aspects of RD are universal and

what aspects might be culturally driven. Important, research has found substantial overlap in the neural signature for skilled and impaired reading across languages (Paulesu et al., 2000, 2001). Still, there may be language-specific differences that arise from the complexity of the mapping between phonology and orthography for a given language (although see Bergmann & Wimmer, 2008, for different findings). For example, research is starting to show that for readers of Mandarin Chinese (where the writing system lacks direct phoneme-to-grapheme mappings) orthographic processing is more important for the development of skilled reading than for English readers (Tan, Spinks, Eden, Perfetti, & Siok, 2005). Moreover, Chinese readers who have RD show differences in frontal activation but do not show the differences in posterior activation seen in readers of alphabetic writing systems with RD (Siok, Niu, Jin, Perfetti, & Tan, 2008). This indicates that different writing systems can tax different brain systems based on the amount and kind of phonological processing the writing system requires. Future research that looks at writing systems with varying orthographic depth can further illuminate the relationship of phonological processing to reading acquisition by allowing researchers to explore the implications of variation in the phoneme-to-grapheme correspondence.

Some of the most socially valuable research currently being conducted relates to intervention for reading disorders. One significant question is whether or not remediation can work by normalizing the developmental trajectory, and if these changes can be measured by changes in neural activity. Additionally, can treatment of phonological skills such as phonological awareness improve outcomes in children at risk for reading disorders when initially learning to read? Also, do different treatments work better for different brain “subtypes”?

Although the PDH's influence on our understanding of skilled and impaired reading is profound, it is important to pay attention to other sources of variation that may interact with phonological processing to interfere with the normal acquisition of reading skill. In a recent article, Pugh et al. (2008) found that factors known to facilitate reading performance (e.g., imageability of word, frequency of occurrence, repetition of exposure) led to decreased activation in reading-related areas in non-impaired readers, but resulted in *increased* activation for these sites in individuals with RD. The study confirmed that these facilitative factors were helpful to both groups in supporting word reading accuracy, yet they generated different neural activity between groups. Specifically, in children with RD these tasks activated neural areas associated with reading, suggesting that the reading circuit may be intact but poorly trained. Stated differently, even when the phonological systems are activated, learning and consolidation may pose additional problems for individuals with RD.

It is important to investigate potential compensatory strengths that individuals with RD might possess (Geschwind & Galaburda, 1987; Winner, 2000). There are many clinical and anecdotal reports of visual processing strengths in individuals with dyslexia (see Gilger & Hynd, 2008; Winner). Unfortunately, there are very few published research studies in this area, and results have not been consistent in finding visual processing strengths among RD individuals (e.g., Bannatyne, 1971; Winner et al., 2001). Still, there are experimental data that suggest a

compensatory shift in favor of visual-spatial processing for some individuals with language and reading disability (von Karolyi, Winner, Gray, & Sherman, 2003), or indications that visual-spatial information is processed differently in this population (Riccio & Hynd, 1996). This is an area where neuroimaging studies could provide unique insight into the neural underpinnings of these putative visual processing differences. It is an area that merits further exploration.

GENERAL SUMMARY

Neuroimaging techniques have allowed our field to make tremendous strides in understanding skilled and impaired reading. In particular, when this technology has been exploited with sound methodology to probe subcomponents of reading, the result has been consistent support for the centrality of phonological processing in reading, and the importance of phonological deficits in RD. Important areas for future research include longitudinal studies of children at risk for RD, cross-linguistic studies using writing systems that exploit phonology in different ways including different phoneme-to-grapheme correspondences, treatment studies, and studies looking at general resources of learning and consolidation, which, in addition to the phonological processing, could influence reading skill. It will be especially important to take a multilevel-analysis approach that incorporates genetics, neuroanatomy, neurochemistry, and neurocircuitry, and also to combine the strengths of the different neuroimaging techniques. Finally, it will be important to better understand differences between individuals and subgroups of children with RD in order to identify more accurately the factors that lead to different developmental trajectories and more effective treatments.

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