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DEVELOPMENT AND DISORDERS OF NEUROCOGNITIVE SYSTEMS FOR ORAL LANGUAGE AND READING

James R. Booth and Douglas D. Burman

Abstract. There are four goals of this article. First, a tentative neurocognitive model of oral language and reading is outlined. Second, our recent functional magnetic resonance imaging studies (fMRI) on the development of oral language and reading are briefly reviewed with reference to this neurocognitive model. Third, brain-imaging research on dyslexia is discussed in light of the neurocognitive model. Fourth, research on the plasticity of neural systems and the implication of this plasticity for studying normative development and disorders is presented.

*JAMES R. BOOTH, Ph.D., is assistant professor, Northwestern University.
DOUGLAS D. BURMAN, Ph.D., is research associate, Northwestern University.*

Reading disorder is the most common form of learning problem in the United States (estimates range from 5-15%) and, therefore, represents a biomedical issue of major importance (Shaywitz, Shaywitz, Fletcher, & Escobar, 1990). Before discussing the neural basis of reading disorders, we need to review the neural representation and development of oral language and reading.

Neurocognitive Model of Oral Language and Reading

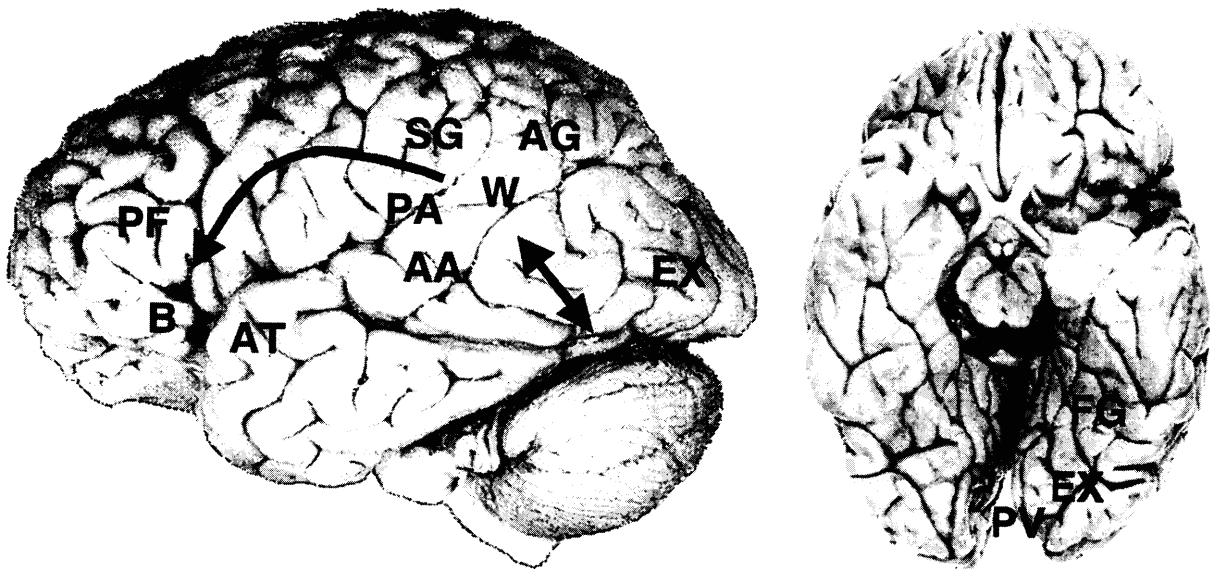
Oral language and reading differ at the most basic level in terms of the nature of perceptual input (see Figure 1). In oral language, auditory input is transmitted from the medial geniculate nucleus in the thalamus to both primary auditory areas (PA) and auditory association areas (AA), the latter of which may contain phonologic representations of words (Binder et al., 1994). In written language, visual input is transmitted from the lateral geniculate nucleus in the thalamus to primary visual areas (PV) in the striate cortex and to secondary visual areas in the extrastriate cortex (EX). From the primary visual area, information has a ventral

“what” projection and a dorsal “where” projection (Mishkin, Ungerleider, & Macko, 1983). The ventral projection includes the unimodal visual area of the fusiform gyrus (FG), which may contain orthographic representations of words (Fujimaki et al., 1999; Herbster, Mintun, Nebes, & Becker, 1997; Nobre, Allison, & McCarthy, 1994). The dorsal projection includes the superior parietal lobule, which may be important in aspects of reading that involve spatial attention.

Wernicke’s area (W) and surrounding areas, including angular gyrus (AG) and supramarginal gyrus (SG), are heteromodal areas that may be responsible for the integration of spoken and written word forms with arbitrary associations that give rise to meaning or semantics (Mesulam, 1998; Pugh et al., 1996). Consistent with this role, Wernicke’s area is interconnected to category-specific areas in the inferior temporal lobe that appear to contain representations of faces, animals and tools (Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996; Di Virgilio & Clarke, 1997).

Figure 1.

Tentative neurocognitive model of oral language and reading. The lateral geniculate nucleus in the thalamus projects to visual areas (PV, EX) and the medial geniculate nucleus in the thalamus projects to auditory areas (PA, AA). Arrows indicate major connections of posterior perisylvian areas (W, AG, SG) with ventral temporal (FG) and anterior perisylvian areas (B, PF, AT). Other connected areas are not indicated in the figure for clarity. AA: auditory association area in superior temporal gyrus; AG: angular gyrus in inferior parietal lobe; AT: anterior temporal region; B: Broca's area in inferior frontal gyrus; EX: extrastriate area in occipital lobe including a dorsal (left figure) and ventral (right figure) projection; FG: fusiform gyrus in ventral temporal region; PA: primary auditory area in transverse temporal gyrus; PF: prefrontal area; PV: primary visual area in occipital lobe; SG: supramarginal gyrus in inferior parietal lobe; W: Wernicke's area in superior temporal gyrus.



Wernicke's area also has massive connections through the arcuate fasciculus with Broca's area (B), which tends to show later peaks of activation in language tasks (Thierry, Boulanouar, Kherif, Ranjeva, & Demonet, 1999). Broca's area includes brain regions for overt (Hagoort et al., 1999) and covert speech production of articulatory word forms involving segmented phonology (Friedman et al., 1998; Paulesu et al., 1996) as well as syntactic processing (Booth et al., 2001b; Caplan, Alpert, & Waters, 1998). The anterior temporal region (AT) is strongly interconnected with Broca's area through the uncinate fiber tract and is also implicated in syntactic processing (Mazoyer et al., 1993; Vorob'ev et al., 1998).

Finally, the prefrontal cortex (PF) may be responsible for modulation of processing in posterior regions such

as Wernicke's area (Frith, Friston, Liddle, & Frackowiak, 1991; Raichle et al., 1994) and/or for maintaining and manipulating verbal information in memory (Gabrieli, Desmond, Demb, Wagner et al., 1996; Jonides et al., 1997). For further details on the functional anatomy of language processing, we refer the reader to chapters in a recent edited book, which presents a critical evaluation of research that is largely consistent with the model outlined above (Hagoort, Brown, & Osterhout, 1999; Price, Indefrey, & van Turennout, 1999).

Developmental Differences in Brain Activation During Reading and Oral Language

We have conducted an fMRI study examining developmental differences between unimpaired children (9- to 12-year-olds) and adults (22- to 31-year-olds) in

brain activation while performing word judgment tasks in the visual and auditory modality (Booth et al., 2001a). Each judgment task tapped into one of four levels of linguistic processing: phonologic, orthographic, semantic and syntactic. These tasks were compared to a control condition matched to the experimental condition in perceptual characteristics, memory demands, and behavioral response criteria.

Our main hypothesis, based on the neurocognitive model outlined above, was that reading and oral language processing become more specialized with development such that unimodal visual areas are more prominently activated when processing written word forms, whereas unimodal auditory areas are more prominently activated when processing spoken word forms. Our results illustrated developmental differences consistent with this developmental hypothesis. Adults showed significantly more activation in fusiform gyrus (FG) during reading tasks and more activation in auditory association areas (AA) during oral language tasks (see Figures 2 and 3). The heavier reliance on these unimodal areas in adults suggests that they are more specialized at visual and auditory word recognition. This interpretation is consistent with cognitive developmental research, which has demonstrated increasing automaticity in the processing of written word forms (Booth, Perfetti, & MacWhinney, 1999).

Our results also showed that children exhibited significantly more activation during processing of written word forms in heteromodal regions of Wernicke's area

(W), in superior parietal lobule and in posterior cerebellum. The activation in cerebellum for children may be associated with less automatic performance. Brain-imaging studies with adults show either a reduction or a shift in the focus of activation in cerebellum, with increasing practice on verbal response selection and motor learning tasks (Raichle et al., 1994; van Mier, Tempel, Perlmuter, Raichle, & Petersen, 1998). The activation for children in superior parietal lobe is consistent with the hypothesis that there is a greater role for spatial attention in less skilled reading (Mesulam, 1990).

The heteromodal regions of Wernicke's area are involved in integrating different sources of information, and our assumption is that integrating different sources of information is a less specialized process. As mentioned, Wernicke's area may be responsible for integrating spoken and written word forms with arbitrary associations that give rise to meaning or semantics (Mesulam, 1998). The greater activation in Wernicke's area for the children in our study is consistent with behavioral findings and computational models showing greater reliance on semantics in younger children (Plaut & Booth, 2000). Most models of the development of reading assume that children initially rely on their semantic knowledge, because grapheme (orthography) to phoneme (phonology) decoding processes are inefficient (Perfetti & Lesgold, 1977; Stanovich, 1980). As development proceeds, phonologic processes play a greater role in word identification, whereas semantic processes play a lesser role (Booth et al., 1999; Plaut & Booth, 2000).

Figure 2.

Activation maps of developmental differences in a visual semantic meaning judgment task. C indicates significantly more activation in children and A indicates significantly more activation in adults. Activation areas not pointed to indicate equal activation in children and adults.

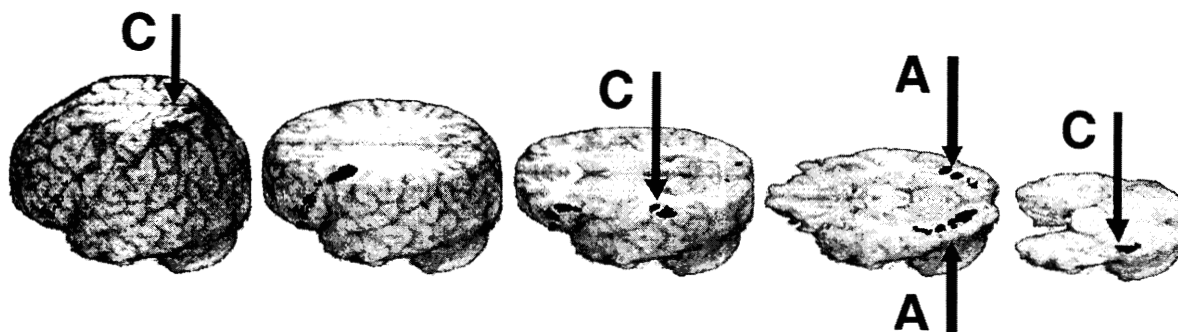
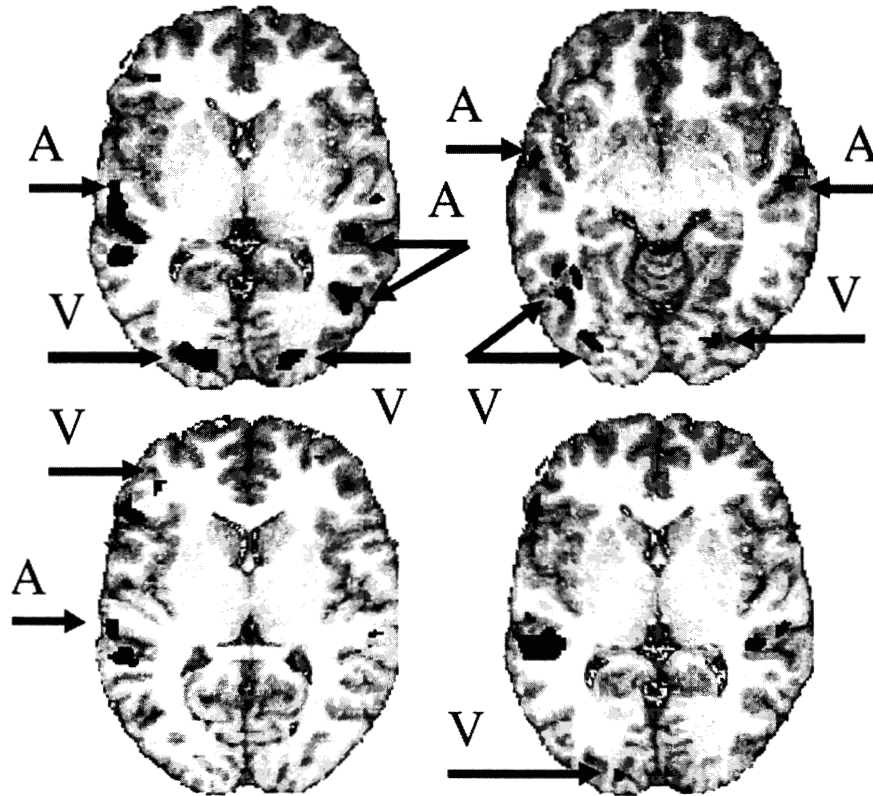


Figure 3.

Activation maps of modality differences for adults (top row) and children (bottom row) in a phonologic rhyming judgment task. The columns represent different axial slices for the adults and children. V indicates significantly more activation in visual modality and A indicates significantly more activation in auditory modality. Activation areas not pointed to indicate equal activation in the visual and auditory modality. The left side of the brain is on the left and the right on the right.



Our hypothesis that children are less specialized than adults at reading and oral language is also supported by the finding that children showed mostly overlap between the visual and auditory word judgment tasks (see Figure 2). In contrast, adults showed selective activation in the unimodal region of the auditory association area (AA) when processing spoken word forms and selective activation in the unimodal visual areas of fusiform gyrus (FG) when processing written word forms. These results are consistent with other findings that suggest a different neural focus in adults for the orthographic and phonologic lexicons (Demonet & Frackowiak, 1993; Howard et al., 1992; Petersen & Fiez, 1993).

Research on Reading Disability

Just as oral language and reading disorders are heterogeneous at a behavioral level, different subtypes of disorders are likely to be associated with different abnormalities at a neural level. The pattern of activation in dyslexics likely involves underactivation in certain brain regions due to inefficient processing and overactivation in other regions reflecting compensatory activity. In this section we will review several brain abnormalities demonstrated in dyslexics with reference to the neurocognitive model outlined above. First, abnormalities have been demonstrated in magnocellular perceptual systems for processing rapidly changing information in both visual and auditory modalities.

Second, underactivation occurs in left fusiform gyrus for processing written word forms, and underactivation occurs in the left tempoparietal region for integrating heteromodal information from the visual and auditory modalities with semantics. Third, the left tempoparietal region is functionally disconnected from fusiform gyrus and Broca's area. Fourth, overactivation is observed in the right tempoparietal region and in Broca's area, suggesting compensatory processes.

Abnormalities in the magnocellular pathway in the visual system. Physiological studies have demonstrated smaller cell bodies in the thalamic lateral geniculate nucleus of dyslexics, which are limited to magnocellular layers (Livingstone, Rosen, Drislane, & Galaburda, 1991). The magnocellular system is important for processing rapidly changing information and projects to both subcortical and cortical brain areas, including the primary visual cortex. Although cell layers in primary visual cortex associated with magnocellular input from the lateral geniculate nucleus do not show consistent differences between dyslexics and unimpaired readers, unimpaired readers, but not dyslexics, have larger neurons in the left than in the right cortex (Jenner, Rosen, & Galaburda, 1999). The magnocellular layers in the primary visual cortex, as well as subcortical visual pathways with magnocellular input, have strong projections to the "where" pathway, including area V5/MT, which is involved in processing visual motion. Despite null findings in one study (Vanni, Uusitalo, Kiesila, & Hari, 1997), most studies have found reduced activity in bilateral V5/MT of dyslexics compared to unimpaired readers (Demb, Boynton, & Heeger, 1998; Eden et al., 1996). Furthermore, the activation in V5/MT is positively correlated with reading rate (Demb, Boynton, & Heeger, 1997). These results suggest that the visual system for processing rapidly changing information in dyslexics may be abnormal. Such abnormality may interfere with reading because of increased visual persistence of information across saccades, which could slow reading rate (Lovegrove, Martin, & Slaghuis, 1986).

Abnormalities in the auditory system pathway. Similar to studies on the visual system, physiological studies have demonstrated that the left thalamic medial geniculate nucleus of dyslexics includes more small and fewer large neurons compared to unimpaired readers (Galaburda, Menard, & Rosen, 1994). This suggests a deficit in processing rapidly changing auditory information (Merzenich et al., 1996; Tallal et al., 1996). Such a deficit may prevent the development of accurate and stable phonologic representations that are essential for learning to read (Bradley & Bryant, 1983). Such neural abnormalities may even be present at birth. Thus, research shows that newborns at familial risk for

dyslexia show abnormal event-related potentials for speech stimuli (Leppanen, Pihko, Eklund, & Lyytinen, 1999; Pihko et al., 1999). Furthermore, event-related potentials recorded in newborns can differentiate between eight-year-old unimpaired readers and dyslexics (Molfese, 2000). Research in adults also shows activation differences between good and poor readers in primary auditory cortex when processing rapidly changing auditory stimuli (Nagarajan et al., 1999), as well as between unimpaired readers and dyslexics in left prefrontal regions that have strong connections with posterior auditory regions (Temple et al., 2000).

Thus, research suggests abnormalities in dyslexics in visual and auditory systems for processing rapidly changing information. However, most brain-imaging research has not distinguished between different subtypes of dyslexia such as surface dyslexics, who have relative orthographic deficits, and phonologic dyslexics, who have relative phonologic deficits (Castles & Coltheart, 1993; Manis, Seidenberg, Doi, McBride-Chang, & Petersen, 1995). A recent study with event-related potentials showed that dyslexics with poor phonetics show a different pattern than those with good phonetics (McPherson, Ackerman, Holcomb, & Dykman, 1998). Recent behavioral research also shows that a deficit in rapid visual processing is more strongly related to orthographic ability whereas a deficit in rapid auditory processing is more strongly related to phonologic ability (Booth, Perfetti, MacWhinney, & Hunt, 2000). Further fMRI research should examine the relation between rapid temporal processing and orthographic and phonologic development.

Underactivation of the inferior temporal region. As reported, unimpaired children exhibit less activity than unimpaired adults in fusiform gyrus when processing written word forms (see Figures 2 and 3). Similarly, several studies demonstrate that when reading, dyslexics show less activation in unimodal visual areas of the inferior occipital temporal cortex, including the fusiform gyrus (Brunswick, McCrory, Price, Frith, & Frith, 1999; Georgiewa et al., 1999; Helenius, Tarkianinen, Cornelissen, Hansen, & Salmelin, 1999; Salmelin, Helenius, & Service, 2000; Salmelin, Service, Kiesila, Uutela, & Salonen, 1996; Shaywitz et al., 1998).

This may reflect dyslexics' lack of development of a specialized system for processing written word forms. Such lack of development may result from an inefficient visual processing system that interferes with the formation of accurate and stable orthographic representations in fusiform gyrus. Alternatively, the lack of a specialized system for processing written word forms may result from abnormalities in the tempoparietal region, which is normally involved in the effective mapping between written and spoken word forms.

This mapping between print and sound may function as a self-teaching mechanism that enables the learner to acquire an autonomous orthographic lexicon (Share, 1995).

Underactivation of the left tempoparietal region.

Compared to unimpaired readers, dyslexics are consistently associated with less activation in the heteromodal region of the left tempoparietal cortex, including Wernicke's area (Helenius, Salmelin, Service, & Connolly, 1999; Rumsey et al., 1992; Rumsey et al., 1997; Shaywitz et al., 1998; Simos, Breier, Fletcher, Foorman et al., 2000). Further, dyslexics have a reduction of gray matter, particularly in the tempoparietal region (Eliez et al., 2000). These findings are consistent with the hypothesis mentioned above that the damaged tempoparietal region interferes with dyslexics' ability to map written words to spoken words, which in turn may interfere with their ability to form an autonomous orthographic lexicon. Interestingly, *higher* reading skill is associated with more activation in the left tempoparietal region in unimpaired readers, whereas *lower* reading skill is associated with more activation in dyslexics (Rumsey et al., 1999). Perhaps unimpaired readers are engaging tempoparietal cortex for comprehension, whereas dyslexics are engaging tempoparietal cortex for mapping between written and spoken word forms. If so, lower reading skill in dyslexia may be associated with more activation because the conversion of graphemes to phonemes is inefficient.

Both unimpaired children and dyslexics are less skilled readers than unimpaired adults. One might therefore predict that unimpaired children, like dyslexics, would show less activation in the tempoparietal area than unimpaired adults. However, our developmental results reported above showed that unimpaired children activate Wernicke's area more than unimpaired adults during visual word judgment tasks (see Figure 1). Unimpaired children may utilize a high degree of integrative processing in Wernicke's area during development to form specialized processing mechanisms in the unimodal areas by adulthood. Adults with reading disorders may have failed to form these systems because they did not have early integrative processing within the tempoparietal region necessary to form specialized systems.

Lack of functional connectivity between the tempoparietal region and other regions. As mentioned, some researchers have interpreted underactivation in the tempoparietal region as an underdeveloped or inefficient posterior reading network involving Wernicke's area, angular gyrus and supramarginal gyrus. Others have interpreted this underactivation as reflecting a disconnection of posterior reading areas from other brain regions involved in reading. Structural imaging

studies show that dyslexics have less white matter in the tempoparietal region than unimpaired readers and that more white matter in this region is associated with higher reading skill (Klingberg et al., 2000). This lack of white matter may limit the communication efficiency of the tempoparietal region with other brain regions. Indeed, research suggests a functional disconnection of the left tempoparietal area from fusiform gyrus and Broca's area. Researchers have found that dyslexics activated Wernicke's area and Broca's area during language tasks but, unlike unimpaired readers, they did not activate them in concert (Paulesu, Frith, & Frackowiak, 1993). Furthermore, dyslexics never activated the insula during these language tasks.

The insula has been shown to be associated with more practiced and automatic performance in language tasks (Raichle et al., 1994). It may also act as an anatomical bridge between anterior and posterior language regions, so the absence of activation in the insula suggests a functional disconnection between language systems. Indeed, morphological research shows that the insula tends to be smaller in dyslexics than in unimpaired readers (Pennington et al., 2000). Researchers have also demonstrated a lower correlation of activation in dyslexics between left angular gyrus, fusiform gyrus, and inferior frontal gyrus (Horwitz, Rumsey, & Donohue, 1998). However, this functional disconnection appears to be limited to visual tasks that require orthographic-to-phonologic conversion (Pugh et al., 2000). Taken together, this research clearly shows that the dyslexic brain is not functionally connected in the same manner as unimpaired brains.

Overactivation of the right tempoparietal region.

The inefficient and disconnected left tempoparietal region of dyslexics may be compensated for by the involvement of the right tempoparietal region. Several researchers have demonstrated overactivation of right tempoparietal areas (Simos, Breier, Fletcher, Foorman et al., 2000). Both unimpaired readers and dyslexics show early activation (about 200 ms) in the left fusiform gyrus. Later activation occurs in the left tempoparietal area for unimpaired readers, whereas later activation occurs in the right tempoparietal area for dyslexics (Simos, Breier, Fletcher, Bergman, & Papanicolaou, 2000). Dyslexics may be engaging the right tempoparietal region to compensate for their inefficient left tempoparietal region. Although research has documented hemispheric differences in linguistic processing for unimpaired adults (Beeman & Chiarello, 1998), at this point it is unclear exactly how the right hemisphere may compensate for the deficient left hemisphere in dyslexics.

Overactivation in the inferior frontal gyrus including Broca's area. Some investigators have found more activation using MEG (magnetoencephalography) or

fMRI among dyslexics in heteromodal regions of the inferior frontal gyrus, including Broca's area, on a reading task visually presented (Salmelin et al., 1996; Shaywitz et al., 1998). Another group found more chemical activity during fMRS (functional magnetic resonance spectroscopy) on a phonological task auditorially presented in left anterior regions not localized to inferior frontal gyrus or Broca's area (Richards et al., 1999). This overactivation in left frontal regions may be a mechanism to compensate for phonologic deficits in left temporo-parietal regions through covert or overt articulatory rehearsal in Broca's area. Indeed, research shows that phonologically based treatment reduces the amount of activation in left frontal regions (Richards et al., 2000). Interestingly, our results reported above indicated no differences in activation between unimpaired adults and children in the inferior frontal gyrus including Broca's area. It may be that the deficit in dyslexia is primarily due to a failure in developing accurate and stable systems for orthographic representations in fusiform gyrus and phonologic representations in the superior temporal gyrus or a failure in mapping between these systems through integration in the tempo-parietal region. In contrast to the studies cited above, some studies have found no difference or reduced activity in the inferior frontal gyrus in dyslexics as compared to unimpaired readers (Georgiewa et al., 1999; Rumsey, Zametkin, Andreason, & Hanahan, 1994). Overactivation may depend on the particular cognitive task employed.

Another potential confound in comparing studies is the heterogeneous dyslexic population both within and between samples. Whereas dyslexia is the most studied reading disorder, other reading disorders are likely to differ in their neural basis. For example, pure dyslexics tend to have little history of oral language disorders and often have decoding deficits in orthography and phonology with smaller deficits in semantics and syntax (Aram, Ekelman, & Nation, 1984; Bishop & Adams, 1990; Silva, Williams, & McGee, 1987). Poor readers, on the other hand, tend to have a significant history of oral language disorders and often have comprehension deficits in semantics and syntax as well as deficits in orthography and phonology (Catts, 1993, 1996; Catts, Fey, Zhang, & Tomblin, 1999). Because orthographic, phonologic, semantic and syntactic processes may use different brain regions, the different cognitive profiles of these reading disorders are likely to be associated with different neural abnormalities (see article by Leonard in this issue). Further research should examine the nature of neural differences in dyslexics versus poor readers.

Neural Development and Implications

Studies have shown nonlinear development in synaptic connections, gray and white matter, glucose

metabolism, and neurotransmitter concentration. Consistent with these studies that show nonlinear patterns of neural development into adolescence, the developmental differences reported above are likely to be due in part to maturational differences and not just differences in reading skill level.

There is an early proliferation of dendrites, axons and synapses until about one to four years of age, followed by a gradual decline in the number of synapses through adolescence (Huttenlocher, 1990; Huttenlocher & de Courten, 1987). There is also decrease in gray matter from about four years of age and an increase in cortical white matter through myelination until about 20 years of age (Pfefferbaum et al., 1994; Yakolev & Lecours, 1967). Recent research has shown that frontotemporal white matter tracks in the left hemisphere demonstrate a prolonged maturation through adolescence, which may be associated with the development of sophisticated linguistic abilities (Paus et al., 1999). Glucose metabolism also rapidly increases until about four years of age and then gradually decreases from about 10 to 18 years of age (Chugani, 1998). Both the neural structure and metabolism data clearly show that developmental changes are not uniform across cortical or subcortical structures (Chugani, Phelps, & Mazziotta, 1987; Huttenlocher & Dabholkar, 1997), and developmental changes in volume for cytoarchitecturally defined regions differ between the hemispheres (Uylings, Malofeeva, Bogolepova, Amunts, & Zilles, 1999). For example, the peak in synaptogenesis tends to occur earlier in primary brain areas (e.g., visual and auditory) than in heteromodal brain areas (e.g., prefrontal).

Nonlinear developmental changes in neural structure and metabolism are paralleled by nonlinear changes in neurotransmitter concentrations. Studies have found complex nonlinear development of cholinergic neurotransmitters and their receptors that differ between brain regions (Court et al., 1997; Court et al., 1993). It seems that there is a cholinergic role in target finding and/or synapse formation for cortical afferents and efferents (Hohmann & Berger-Sweeney, 1998). There is also a nonlinear development of certain dopamine receptors in the basal ganglia and prefrontal cortex with an increase until about adolescence and then a gradual decline (Lewis, 1997; Meng, Ozawa, Itoh, & Takashima, 1999; Rinne, Lonnberg, & Marjamaki, 1990; Seeman et al., 1987; Spear, 2000).

The reduction in synapses, gray matter and metabolism through adolescence is consistent with the hypothesis that cognitive functions are represented in more focal neural regions as development proceeds (Casey et al., 1997; Gaillard et al., 2000; Hertz-Pannier et al., 1997). However, such specialization will likely depend on the cognitive processes and the regions of

the brain involved. This specialization is accompanied by an increase in the efficient transmission of neural signals between regions through enhanced white matter connections. These hypotheses of increasing specialization and efficient connectivity are consistent with computational models of language, which suggest that early in learning there are weak and widespread connections between units, which become stronger and more specialized with development (Harm & Seidenberg, 1999; Plaut & Booth, 2000). The data on nonlinear trends in neural development suggest that the adult pattern of activation for some complex cognitive skills is complete some time in late adolescence, with significant changes occurring over the age range important for oral language and reading acquisition.

All our current knowledge indicates substantial plasticity in development and suggests that reading intervention could influence the organization of neurocognitive networks in children and adults (Richards et al., 2000; Temple et al., 2000). Normative information about patterns of brain activation during cognitive tasks will be critical in the diagnosis of reading disorder subgroups. Eventually, this normative information may be useful for developing intervention programs. Different kinds of remedial intervention may be appropriate for different kinds of reading disorders. For example, an intervention program emphasizing decoding may be of most benefit to dyslexics and may accompany a normalization of activity in orthographic-phonological systems. In contrast, an intervention focusing on semantics and syntax may be of more benefit to poor readers, and may accompany a normalization of activation in semantic-syntactic systems.

However, much more work needs to be done before we can reliably and validly use brain-imaging methods in diagnosis and treatment. To our knowledge, no published fMRI research has addressed developmental differences between younger and older children in patterns of brain activation in an unimpaired population during both reading and oral language processing. Furthermore, no published studies have used longitudinal design to examine developmental differences in brain activation. Therefore, a great need exists for biomedical studies with children that examine the relation between brain activation and the development of reading and oral language abilities.

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Please address all correspondence to: James R. Booth, Department of Communication Sciences and Disorders, Northwestern University, 2299 North Campus Drive, Evanston, IL 60208-3560. (847) 491-2519, fax (847) 491-2494, e-mail j-booth@nwu.edu.