1162

Research Report

THE ANGULAR GYRUS IN DEVELOPMENTAL DYSLEXIA: Task-Specific Differences in Functional Connectivity Within Posterior Cortex

Kenneth R. Pugh,[1,2] W. Einar Mencl,[1,2] Bennett A. Shaywitz,[1,3] Sally E. Shaywitz,[1] Robert K. Fulbright,[4] R. Todd Constable,[4] Pawel Skudlarski,[4] Karen E. Marchione,[1] Annette R. Jenner,[1,2] Jack M. Fletcher,[5] Alvin M. Liberman,[2] Donald P. Shankweiler,[2] Leonard Katz,[2] Cheryl Lacadie,[4] and John C. Gore[4,6]

[1]Department of Pediatrics, Yale University School of Medicine; [2]Haskins Laboratories; [3]Department of Neurology, Yale University School of Medicine; [4]Department of Diagnostic Radiology, Yale University School of Medicine; [5]Department of Pediatrics, University of Texas Medical School-Houston; and [6]Department of Applied Physics, Yale University

Abstract—*Converging evidence from neuroimaging studies of developmental dyslexia reveals dysfunction at posterior brain regions centered in and around the angular gyrus in the left hemisphere. We examined functional connectivity (covariance) between the angular gyrus and related occipital and temporal lobe sites, across a series of print tasks that systematically varied demands on phonological assembly. Results indicate that for dyslexic readers a disruption in functional connectivity in the language-dominant left hemisphere is confined to those tasks that make explicit demands on assembly. In contrast, on print tasks that do not require phonological assembly, functional connectivity is strong for both dyslexic and nonimpaired readers. The findings support the view that neurobiological anomalies in developmental dyslexia are largely confined to the phonological-processing domain. In addition, the findings suggest that right-hemisphere posterior regions serve a compensatory role in mediating phonological performance in dyslexic readers.*

Many lines of evidence converge on the conclusion that word and nonword reading difficulties in developmental dyslexia are, to a large extent, manifestations of more basic deficits at the level of phonological assembly (Bradley & Bryant, 1983; Gough & Tunmer, 1986; Liberman, Shankweiler, & Liberman, 1989). Phonological assembly refers to an analytic decoding process associated with context-sensitive grapheme-to-phoneme mapping routines (Coltheart, Curtis, Atkins, & Haller, 1993). Problems in developing phonological awareness (i.e., the metalinguistic understanding that spoken words can be decomposed into phonological primitives, which in turn can be represented by alphabetic characters) at the early stages of literacy training result in the failure to properly develop phonological assembly routines (Bruck, 1992; Fletcher et al., 1994; Shankweiler et al., 1995). By contrast, phonological assembly is performed in an automated manner by skilled readers, and, as a growing body of research confirms, this decoding operation serves as a fundamental code used in lexical access for these readers (Lukatela & Turvey, 1994; Van Orden, Pennington, & Stone, 1990).

Functional neuroimaging techniques can provide insight into the neurobiological underpinnings of developmental disabilities, but only if task designs are analytic and guided by cognitive research and theory. Finding a brain region where two groups activate differently is informative only to the extent that investigators can experimentally determine the specific sorts of computational operations that this region (and related sites) actually supports, and establish activation-performance links (Pugh et al., 1997). In a recent investigation (Shaywitz et al., 1998), we used functional magnetic resonance imaging (fMRI) to contrast brain activation patterns of nonimpaired (NI) and dyslexic (DYS) adult readers who were performing a set of hierarchically organized print tasks that systematically varied demands on phonological assembly. On those tasks that made explicit demands on assembly (e.g., nonword rhyming), DYS readers showed a relative underengagement of posterior brain regions including the angular gyrus in the inferior parietal lobule, Wernicke's area in the superior temporal gyrus, and striate and extrastriate regions of the occipital lobe, coupled with a disproportionately greater engagement of frontal lobe sites than NI readers. These findings—revealed by significant Group × Task interactions across important dimensions of lexical processing—suggest a functional deficit in those posterior brain systems that are engaged by reading and, perhaps, a compensatory reliance on Broca's area in the inferior frontal gyrus and other frontal lobe sites. Similar findings implicating the angular gyrus and surrounding cortex in developmental dyslexia have been reported by other groups who have exploited functional mapping techniques to study aspects of phonological processing (cf. Rumsey et al., 1997; Salmelin, Service, Kiesila, Uutela, & Salonen, 1996).

Neuroimaging results implicating the region of the angular gyrus raise the issue of a possible parallel between the anatomy of developmental and acquired dyslexia. In the last century, Dejerine (1891) showed that lesions implicating the angular gyrus may result in acquired dyslexia. Hinschelwood (1917) suggested that this region could also be implicated in developmental dyslexia. Parallel symptomatology does not, of course, imply a similar neurobiological etiology for acquired and developmental dyslexia (e.g., Benton, 1975). Nevertheless, that the common cause is an anatomical lesion or malformation has been suggested recently (Eden & Zeffiro, 1998) by the finding of dysfunction in developmental dyslexics in MT/V5, a region in proximity to the angular gyrus, even on simple motion-detection tasks (Demb, Boynton, & Heeger, 1998; Eden et al., 1996). A first step in addressing the issue is to determine whether dysfunction of the angular gyrus (and related sites) is, in fact, evident across multiple cognitive or perceptual domains, as a lesion account would imply, or is largely confined to phonological processing. If the latter is the case, a more subtle functional disturbance is indicated.

Address correspondence to Kenneth R. Pugh, Department of Pediatrics, Yale University School of Medicine, P.O. Box 3333, New Haven, CT 06510-8064.

FUNCTIONAL CONNECTIVITY IN READING

Although most neuroimaging studies have sought to identify specific brain regions within which activation patterns discriminate DYS from NI readers (e.g., Rumsey et al., 1997; Shaywitz et al., 1998), a deeper understanding of the neurobiology of developmental dyslexia requires that one consider relations between distinct brain regions that function cooperatively to process information during reading; we refer to this issue as one of functional connectivity between cortical areas (Friston, 1994; McIntosh & Gonzalez-Lima, 1994). Consider, for instance, the classical account of the neurology of reading, which views the angular gyrus as serving a mediational role, relating the output from orthographic processing at extrastriate sites (e.g., the lingual gyrus) to lexical and linguistic representations in and around the posterior aspect of the superior temporal gyrus (Geschwind, 1965). In an intact brain, these areas should be functionally connected.

Evidence consistent with a breakdown in functional connectivity between the angular gyrus and related posterior regions in DYS readers was reported recently by Horwitz, Rumsey, and Donohue (1998). In this positron emission tomography (PET) study, the authors examined correlations (within task, between subjects) between activation in the left angular gyrus and other brain sites during two reading-aloud tasks, exception word naming and nonword naming. Correlations between a reference site in the angular gyrus and occipital and superior temporal lobe sites were strong and significant in NI readers but weak in DYS readers. This finding suggests a disruption in functional connectivity between the angular gyrus and related posterior cortical regions during the reading of words and nonwords, but leaves open the question of whether this disruption is specific to the phonological assembly engaged by reading tasks. Conceivably, the failure to show evidence of functional connectivity in DYS readers might be obtained for a variety of tasks, linguistic and nonlinguistic, and hence would represent a global deficit. A global deficit would be anticipated if there is a structural malformation of the angular gyrus. A more limited proposal, and one that is compatible with behavioral findings (Fletcher et al., 1994; Shankweiler et al., 1995), would posit that abnormal functional connectivity in the posterior system is confined to those tasks that make explicit demands on phonological assembly. The phonological-deficit hypothesis would lead us to anticipate that on print tasks not requiring phonological assembly, the angular gyrus and related sites will behave in a functionally connected manner for DYS readers.

In this report, we compare the global-deficit and phonological-deficit accounts. To accomplish this, we contrast functional connectivity, operationalized as correlations between the angular gyrus and related posterior reading areas (Horwitz et al., 1998), in four tasks that vary in demands on orthographic, phonological, and lexical-semantic processing (see Table 1 for details). The tasks include a nonword rhyming task (NWR) and a word semantic-category task (SC), both of which engage phonological assembly. Two other tasks that do not engage assembly were also employed. The single-letter rhyming task (SLR) shares with the NWR task a similar metaphonological demand; both tasks involve the same rhyme judgment on monosyllabic tokens ("Do these two stimuli rhyme?"), but SLR does not engage context-sensitive grapheme-to-phoneme assembly whereas NWR does. We also included an orthographic case judgment task (C) consisting of strings of consonants; this task places demands on orthographic coding similar to the orthographic demands of the NWR task, but does not engage phonological assembly. Thus, C shares orthographic characteristics with NWR, and SLR shares metaphonological characteristics with NWR, but each differs from NWR with respect to demands on context-sensitive grapheme-to-phoneme mapping (phonological assembly).

METHOD

Subjects

Subjects were 29 DYS readers (14 men, 15 women; ages 16–54 years) and 32 NI readers (16 men, 16 women; ages 18–63 years). Reading performance in the DYS subjects was significantly impaired: The mean standard score on a measure of nonword reading (Woodcock Johnson–Revised word attack) was 81 ± 1.9 (mean ± *SEM*) in DYS readers, compared with 114 ± 1.5 in NI readers, with no overlap between groups (see Shaywitz et al., 1998, for details).

Tasks and Image Analysis

In this fMRI study, subjects were scanned with echo-planar imaging on a 1.5-T Signa MR imaging system. For each task performed during scanning, the subject viewed two displays, one above the other, and made a same/different judgment on the stimulus pair, pressing the appropriate key (see Table 1 for illustrative stimuli from each task). The line-orientation (L) judgment task served as a baseline subtraction condition and taps visual-spatial processing, but makes no explicit language demands. The C task adds an orthographic-processing demand, but makes no phonological demands because the stimulus items, which consist entirely of consonant strings, are, therefore, phonotactically impermissible. The third task, SLR, although orthographically more simple than C, requires a metaphonological analysis sufficient to determine that the tokens do or do not rhyme; the fourth task, NWR, requires extensive phonological assembly, but shares the same metaphonological judgment as SLR. The final task, SC judgment, also makes substantial demands on assembly (Lukatela & Turvey, 1994), but requires in addition that the printed stimulus items

Table 1. *Task description and illustrative stimuli*

Task	Stimuli	Description
Line orientation (L)	//\/*//\/	Same/different judgment on line displays; baseline condition
Letter case (C)	BtbT * BtbT	Same/different judgment on pattern of case alternation
Single-letter rhyming (SLR)	B * T	Same/different letter-rhyme judgment
Nonword rhyming (NWR)	LEAT * JETE	Same/different nonword-rhyme judgment
Semantic category (SC)	CORN * RICE	Same/different category judgment

activate particular word representations in the reader's lexicon, so that the reader arrives at the words' meanings.

The primary analysis was a common baseline subtraction: C, SLR, NWR, and SC tasks contrasted with the nonlanguage L task; the primary dependent measure was a count of significantly activated voxels ($t > 2.0$) in a given task and region (for details on trials and imaging protocols, see Shaywitz et al., 1998). For NI subjects, error rates (percentage errors) during the fMRI session on the L, C, SLR, NWR, and SC tasks were 3.0 ± 0.8 , 2.6 ± 0.5, 1.2 ± 0.5, 9.3 ± 1, and 4.6 ± 0.7; the corresponding mean error rates for DYS subjects were 5.1 ± 1.3, 7.6 ± 1.5, 11.0 ± 2.3, 31.5 ± 2.3, and 13.8 ± 1.8. Analysis of error rates revealed a significant Reading Group × Task interaction. $F(4, 228) = 24.98$, $p < .0001$. DYS and NI readers did not differ significantly on the L task, but did on all others.

Regression Analysis

In order to examine the correlational structure between angular gyrus and other posterior sites implicated in reading, we used multiple regression analyses (see Table 2 for details). For each subject, we used activation scores in four regions of interest as predictors of activation at BA 39 (angular gyrus) within the inferior parietal lobule. These four regions were BA 17 (primary visual cortex), BA 18/19 medial (lingual gyrus), BA 18/19 lateral (lateral extrastriate) in the occipital lobe, and BA 22 posterior in the superior temporal gyrus (Wernicke's area); these cortical sites constitute critical components of the posterior reading system (see Shaywitz et al., 1998, for details on the regions of interest). The analysis was performed separately for left-hemisphere and right-hemisphere regions of interest for each of the four reading tasks.

RESULTS

Table 2 shows that for the left hemisphere in NI readers, the model was significant for all tasks; the highest R^2 values occurred on the NWR and SC tasks (.63 and .75, respectively). Thus, for all tasks, and particularly the NWR and SC tasks, variance in the angular gyrus is well accounted for by covariance at occipital and temporal sites. By contrast, for DYS readers, the model was significant for the C and SLR tasks, but not for the NWR and SC tasks. Right-hemisphere analyses showed a different pattern: For both reading groups, the model was significant for the SLR, NWR, and SC tasks; for the C task, the model was nonsignificant for NI readers. (In Fig. 1, we illustrate group differences with the simple correlations between the angular gyrus and each of the four predictor sites on the critical NWR task; the anatomic locations of these regions are shown in the top panel of the figure.)

DISCUSSION

Regression analyses examined evidence for functional connectivity between angular gyrus and related posterior sites in both hemispheres. In the left hemisphere, on tasks that demand substantial phonological assembly, NI readers displayed robust functional connectivity (high R^2 values), but DYS readers did not. This finding is consistent with that of Horwitz et al. (1998), who also examined word and nonword reading.

However, both NI and DYS readers demonstrated functional connectivity in the left hemisphere on the SLR and C tasks. Consider first the SLR task. The judgment is nearly identical to that of the NWR task at the level of metaphonological analysis; each requires the reader to generate a monosyllabic phonological form (either the letter name in SLR or the assembled nonword form in NWR). When coping with the SLR task, the DYS subjects demonstrated significant correlations between angular gyrus and occipital and temporal lobe sites (R^2 is actually numerically higher on the SLR task for these readers than for NI readers). Thus, when the demand on phonological assembly was low, DYS readers showed robust functional connectivity.

Next consider the C task, which is matched with the NWR task on the number of to-be-coded letters in the displays. Neither the task itself nor the stimulus type (consonant strings) requires phonological assembly; however, demands on visual-orthographic analysis are as

Table 2. *Regression analyses by task, hemisphere, and reading group*

Task	Dyslexic subjects			Nonimpaired subjects		
	$F(4, 28)$	p	R^2	$F(4, 31)$	p	R^2
			Left hemisphere			
Letter case (C)	15.06	.0001	.67	7.31	.001	.50
Single-letter rhyming (SLR)	4.76	.01	.35	3.86	.01	.27
Nonword rhyming (NWR)	1.65	n.s.	.09	13.92	.0001	.63
Semantic category (SC)	0.68	n.s.	.00	23.59	.0001	.75
			Right hemisphere			
Letter case (C)	13.51	.0001	.64	1.03	n.s.	.004
Single-letter rhyming (SLR)	7.83	.001	.49	10.30	.0001	.55
Nonword rhyming (NWR)	14.07	.0001	.65	8.97	.0001	.51
Semantic category (SC)	7.01	.001	.46	5.57	.01	.37

Note. The table shows results of multiple regression analysis of activation in the four predictor regions on activation in the angular gyrus. Shown are F values, along with corresponding p values and proportion of variance accounted for. Adjusted R^2 is reported, to control for the slightly different numbers of subjects in the two groups.

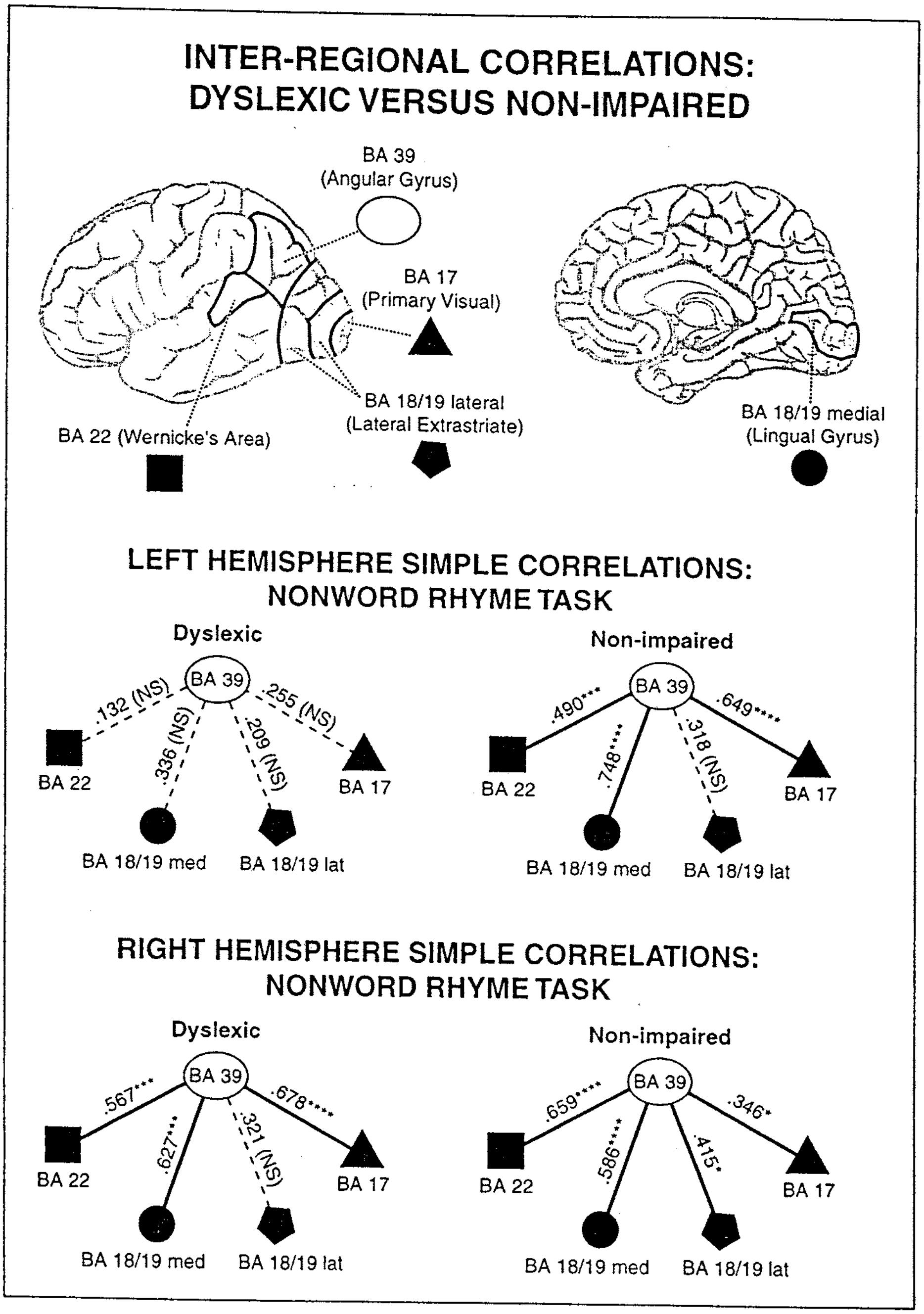

Fig. 1. Anatomic location of the regions of interest and simple correlation values in the critical nonword rhyming task. The top panel shows the anatomic location of each of the relevant regions of interest included in the analyses, with a lateral view on the left and a medial view on the right. In the middle and bottom panels, simple correlation values (with significance levels denoted by asterisks) between the angular gyrus and BA 22 posterior, BA 18/19 medial, BA 18/19 lateral, and BA 17 in the nonword rhyming task are shown schematically. $^*p < .05$. $^{***}p < .001$. $^{****}p < .0001$.

great, or even greater, in the C as in the NWR task. A global-deficit hypothesis, which posits a lesion capable of interfering with visual motion processing (Demb et al., 1998; Eden et al., 1996) in addition to phonological processing in reading, would predict a breakdown in left-hemisphere functional connectivity on this orthographically complex task. In fact, the DYS readers in the current study showed strong functional connectivity in the left hemisphere on the C task, with a numerically higher R^2 value than was obtained for NI readers.

The most plausible explanation for these left-hemisphere findings is the hypothesis, derived from many cognitive studies of DYS readers, positing a basic weakness in phonological representations. This linguistic deficit limits DYS readers' ability to build efficient structures within the angular gyrus that link orthographic codes computed in the extrastriate areas of the occipital lobe to phonological codes represented in the superior temporal gyrus. Thus, when phonological assembly is not required—even when phonological judgments are required, as in the SLR task—patterns of functional connectivity between the angular gyrus and these sites appear normal. Although this conclusion cannot be reached definitively from correlational data alone, we believe that the weight of behavioral evidence further suggests its plausibility (see Shaywitz, 1998, for a review). At minimum, these findings imply that the angular gyrus is not globally dysfunctional in DYS readers; when phonological assembly is not required by the task, DYS readers engage the posterior system in a cohesive, functionally connected manner.

Note that on the same tasks on which DYS readers failed to demonstrate any evidence of functional connectivity in the left hemisphere (NWR and SC), they displayed robust correlations at right-hemisphere homologues (with numerically higher R^2 values than NI readers). In our earlier report that focused on within-region activation patterns by these subjects (Shaywitz et al., 1998), we observed a significant Reading Group × Hemisphere interaction at the angular gyrus, indicating greater right- than left-hemisphere activation in DYS readers but greater left- than right-hemisphere activation in NI readers. Other imaging studies have also observed a rightward shift in activation in the inferior parietal lobule in DYS readers during language-processing tasks (Rumsey et al., 1992). Those results, together with the current finding of increased functional connectivity between angular gyrus and related sites in the right hemisphere, raise the possibility of compensatory reliance on these right-hemisphere systems in developmental dyslexia (see Galaburda, Sherman, Rosen, Aboitiz, & Geschwind, 1985).

A comment on the problem of remediation and retraining, which is in the public eye (Lyon, 1995), is perhaps in order. The global-deficit and phonological-deficit accounts make different predictions concerning the way in which intensive (phonologically based) remediation might affect left-hemisphere function in compensated DYS readers. The global-deficit account indicates that improvements associated with intensive phonological training must come about by subjects learning to bypass the malformed left posterior sites. The current finding of robust functional connectivity on a simple phonological task like SLR permits a speculation that with sufficient training the angular gyrus and related left-hemisphere regions would begin to function as a cohesive system for words and nonwords, as they do for single-letter displays. Obviously, an adequate test of this hypothesis would require examination of younger readers in the context of a longitudinal study with a specific intervention component; we are currently engaged in such a project. Indeed, a highly promising use of neuroimaging techniques will be to determine how treatments of various sorts affect functional brain organization.

CONCLUSIONS

Functional connectivity between angular gyrus and occipital and temporal lobe sites was assessed with tasks that systematically varied demands made on phonological assembly. For DYS readers, left-hemisphere functional connectivity was disrupted on word and nonword reading tasks that tax phonological assembly. By contrast, there appeared to be no dysfunction in a task that taps metaphonological judgments based on letter names, or in a task requiring complex visual-orthographic coding that does not implicate phonology. The results go against a global-deficit hypothesis but are entirely consistent with the phonological-deficit hypothesis: A functional breakdown in left-hemisphere posterior systems is manifest only when orthographic-to-phonological assembly is required. Moreover, when phonological assembly is required, right-hemisphere homologues may function in a potentially compensatory manner for DYS readers.

Acknowledgments—This research was supported by grants from the National Institute of Child Health and Human Development (PO1 HD-21888 and P50 HD-2580). The participation of Kenneth Pugh, Leonard Katz, Don Shankweiler, and Al Liberman was also supported by National Institute of Child Health and Human Development Grant HD-01994 to Haskins Laboratories. We thank Carol Fowler, Carmel LaPore, John Holahan, Ram Frost, Sally Andrews, and the staff at the Yale Center for the Study of Learning and Attention for their contributions to this project.

REFERENCES

Benton, A.L. (1975). Developmental dyslexia: Neurological aspects. In W.J. Friedlander (Ed.), *Advances in neurology, Vol. 7* (pp. 1–47). New York: Raven Press.

Bradley, L., & Bryant, P.E. (1983). Categorizing sounds and learning to read—A causal connection. *Nature, 301*, 419–421.

Bruck, M. (1992). Persistence of dyslexics' phonological awareness deficits. *Developmental Psychology, 28*, 874–886.

Coltheart, M., Curtis, B., Atkins, P., & Haller, M. (1993). Models of reading aloud: Dual-route and parallel-distributed-processing approaches. *Psychological Review, 100*, 589–608.

Dejerine, J. (1891). Sur un cas eccite verbale avec agraphie, suivi d'autopsie. *C.R. Societe du Biologie, 43*, 197–201.

Demb, J.B., Boynton, G.M., & Heeger, D.J. (1998). Functional magnetic resonance imaging of early visual pathways in dyslexia. *The Journal of Neuroscience, 18*, 6939–6951.

Eden, G., VanMeter, J.W., Rumsey, J.M., Maisog, J.M., Woods, R.P., & Zeffiro, T.A. (1996). Abnormal processing of visual motion in dyslexia revealed by functional brain imaging. *Nature, 382*, 66–69.

Eden, G., & Zeffiro, T.A. (1998). Neural systems affected in developmental dyslexia revealed by functional neuroimaging. *Neuron, 21*, 279–282.

Fletcher, J.M., Shaywitz, S.E., Shankweiler, D.P., Katz, L., Liberman, I.Y., Stuebing, K.K., Francis, D.J., Fowler, A.E., & Shaywitz, B.A. (1994). Cognitive profiles of reading disability: Comparisons of discrepancy and low achievement definitions. *Journal of Educational Psychology, 86*, 1–23.

Friston, K.J. (1994). Functional and effective connectivity: A synthesis. *Human Brain Mapping, 2*, 56–78.

Galaburda, A.M., Sherman, S.F., Rosen, G.D., Aboitiz, F., & Geschwind, N. (1985). Developmental dyslexia: Four consecutive patients with cortical anomalies. *Annals of Neurology, 18*, 222–233.

Geschwind, N. (1965). Disconnection syndromes in animals and man: Part I. *Brain, 88*, 237–294.

Gough, P.B., & Tunmer, W.E. (1986). Decoding, reading, and reading disability. *Remedial and Special Education, 7*, 6–10.

Hinschelwood, J. (1917). *Congenital word blindness*. London: H.K. Lewis.

Horwitz, B., Rumsey, J.M., & Donohue, B.C. (1998). Functional connectivity of the angular gyrus in normal reading and dyslexia. *Proceedings of the National Academy of Sciences, USA, 95*, 8939–8944.

Liberman, I.Y., Shankweiler, D., & Liberman, A.M. (1989). The alphabetic principle and learning to read. In D. Shankweiler & I.Y. Liberman (Eds.), *Phonology and reading disability, solving the reading puzzle* (International Academy for Research in Learning Disabilities Monograph Series, No. 6, pp. 1–33). Ann Arbor: University of Michigan Press.

Lukatela, G., & Turvey, M.T. (1994). Visual lexical access is initially phonological 1: Evidence from associative priming words, homophones, and pseudohomophones. *Journal of Experimental Psychology: General, 123*, 107–128.

Lyon, G.R. (1995). Research initiatives in learning disabilities: Contributions from scientists supported by the National Institute of Child Health and Human Development. *Journal of Child Neurology, 10*(Suppl. 1), 120–126.

McIntosh, A.R., & Gonzalez-Lima, F. (1994). Structural equation modeling and its application to network analysis of functional brain imaging. *Human Brain Mapping, 2*, 2–22.

Pugh, K., Shaywitz, B., Shaywitz, S., Shankweiler, D., Katz, L., Fletcher, J., Constable, T., Skudlarski, P., Fulbright, R., Bronen, R., & Gore, J. (1997). Predicting reading performance from neuroimaging profiles: The cerebral basis of phonological effects in printed word identification. *Journal of Experimental Psychology: Human Perception and Performance*, *23*, 299–318.

Rumsey, J.M., Andreason, P., Zametkin, A.J., Hanahan, A.P., Hamburger, S.D., Aquino, T., King, C., Pikus, A., & Cohen, R.M. (1992). Failure to activate the left temporoparietal cortex in dyslexia: An oxygen 15 positron emission tomographic study. *Archives of Neurology*, *49*, 527–534.

Rumsey, J.M., Nace, K., Donohue, B., Wise, D., Maisog, J.M., & Andreason, P. (1997). A positron emission tomographic study of impaired word recognition and phonological processing in dyslexic men. *Archives of Neurology*, *54*, 562–573.

Salmelin, R., Service, E., Kiesila, P., Uutela, K., & Salonen, O. (1996). Impaired visual word processing in dyslexia revealed with magnetoencephalography. *Annals of Neurology*, *40*, 157–162.

Shankweiler, D., Crain, S., Katz, L., Fowler, A.E., Liberman, A.M., Brady, S.A., Thornton, R., Lundquist, E., Dreyer, L., Fletcher, J.M., Stuebing, K.K., Shaywitz, S.E., & Shaywitz, B.A. (1995). Cognitive profiles of reading-disabled children: Comparison of language skills in phonology, morphology, and syntax. *Psychological Science*, *6*, 149–156.

Shaywitz, S., Shaywitz, B., Pugh, K., Fulbright, R., Constable, R., Mencl, W., Shankweiler, D., Liberman, A., Skudlarski, P., Fletcher, J., Katz, L., Marchione, K., Lacadie, C., Gatenby, C., & Gore, J. (1998). Functional disruption in the organization of the brain for reading in dyslexia. *Proceedings of the National Academy of Sciences, USA*, *95*, 2636–2641.

Shaywitz, S.E. (1998). Current concepts: Dyslexia. *New England Journal of Medicine*, *338*, 307–312.

Van Orden, G.C., Pennington, B.F., & Stone, G.O. (1990). Word identification in reading and the promise of subsymbolic psycholinguistics. *Psychological Review*, *97*, 488–522.

(RECEIVED 11/30/98; ACCEPTED 2/16/99)