Predicting Reading Performance From Neuroimaging Profiles: The Cerebral Basis of Phonological Effects in Printed Word Identification

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This study linked 2 experimental paradigms for the analytic study of reading that heretofore have been used separately. Measures on a lexical decision task designed to isolate phonological effects in the identification of printed words were examined in young adults. The results were related to previously obtained measures of brain activation patterns for these participants derived from functional magnetic resonance imaging (fMRI). The fMRI measures were taken as the participants performed tasks that were designed to isolate orthographic, phonological, and lexical-semantic processes in reading. Individual differences in the magnitude of phonological effects in word recognition, as indicated by spelling-to-sound regularity effects on lexical decision latencies and by sensitivity to stimulus length effects, were strongly related to differences in the degree of hemispheric lateralization in 2 cortical regions.

Recent advances in functional neuroimaging technology and the development of analytic measures of cognitive function have made it possible, in principle, to isolate cortical regions associated with component processing operations of complex cognitive tasks (Demonet, Price, Wise, & Frackowiak, 1994; Petersen, Fox, Posner, Mintun, & Raichle, 1989; Petersen & Fiez, 1993; Shaywitz, Pugh, et al., 1995; Shaywitz, Shaywitz, et al., 1995; Wise et al., 1991; Zatorre, Evans, Meyer, & Gjedde, 1992). We exploited these advances to investigate basic processes of word identification in reading. We examined whether individual differences in phonological processing during word recognition can be accounted for by differences in patterns of cerebral activity in language-relevant regions of the brain. Specifically, we used functional magnetic resonance imaging (fMRI) techniques to examine the relation between an individual reader's sensitivity to regularity of spelling–sound relations in a lexical decision task (performed out of the magnet) and patterns of cortical activation in orthographic, phonological, and semantic networks during the on-line performance (in the magnet) of tasks designed to isolate these functions. We believed that the coordinated use of neuroimaging and cognitive–behavioral approaches, as used in the current study, would present an unparalleled opportunity to further the basic understanding of cognitive systems for reading in both normal and impaired populations.

Linking Functional Activation of the Brain With Dimensions of Reading Performance

We examined the interconnections between the results of two experiments (the first of which has been presented elsewhere [Pugh et al., 1996]) performed on the same group

of normal young adults who were fluent readers. In the first experiment, Pugh et al. used echoplanar fMRI[1] to study patterns of cerebral activation in tasks designed to decompose visual word recognition into its component processes and to isolate the cortical regions most closely implicated in orthographic, phonological, and lexical-semantic processing, respectively. The results were strikingly clear-cut, showing partially nonoverlapping foci associated with each aspect of the word identification process. In the experiment reported in this article, we investigated the role of regularity of word spelling, word frequency, and stimulus length on speed of lexical decision in the same participants, now tested out of the magnet. The focus of this article is on the relations between the two data sets. Thus, we treat the fMRI results as predictor variables for a lexical decision experiment designed to study modes of word identification involving the occurrence of phonological recoding in which individuals are thought to differ (Bernstein & Carr, 1996; Pugh, Rexer, & Katz, 1994). We wanted to find out whether individual patterns of phonological sensitivity exhibited behaviorally in the lexical decision task can be associated with specific distributions of cerebral activation in the same participants.

Summary of fMRI Results

We begin by reviewing the previously reported findings (Pugh et al., 1996) on cortical localization of separable components of the reading process. Pugh et al. examined whether distinct visual and linguistic processes engage specific cortical regions. Using echoplanar fMRI procedures, we examined performance on four same–different matching tasks for 38 neurologically normal adults (19 men and 19 women). The primary dependent variable was the sum of voxels (a voxel corresponds to $3.12 \times 3.12 \times 8$ mm volume of brain tissue) in specific regions of interest that differed significantly between control and experimental conditions (computed for each participant in each subtraction condition). This measure provided information about the spatial extent of significant activation (signal changes) within a specific cortical region. The tasks, consisting of line, letter case, nonword rhyme, and semantic category judgments (summarized in Table 1), share decision and response characteristics but differed systematically in the types of linguistic processing demands they entailed. In the line judgment task, participants viewed two displays (each consisting of four slanted lines with right or left orientations), one above the other, and judged whether the upper and lower displays had the same pattern of left–right alternation. This task should primarily engage visual-spatial (featural) information processing. In the letter case judgment task, two sets of consonant strings were displayed, and participants determined whether these consisted of the same pattern of letter case (upper and lower) alternation. This task engages both visual-spatial and orthographic (letter) processing. With nonpronounceable consonant strings, both phonological and lexical-semantic processing should be minimal. In the rhyme judgment task, participants judged whether two non-

sense word strings rhymed. This task engages visual-spatial, orthographic, and assembled phonological processing (i.e., mapping letters onto phonological structures). The use of phonotactically legal nonwords forces assembled phonological processing and minimizes spurious lexical-semantic processing. Finally, in the semantic category task, participants judged whether two words came from the same semantic category. This task engages visual, orthographic, phonological (to the degree that such coding mediates real word reading), and lexical-semantic information processing.

Brain activation maps for all possible subtraction conditions were computed separately for each participant (see Pugh et al., 1996; Shaywitz, Pugh, et al., 1995; Shaywitz, Shaywitz, et al., 1995; for a more detailed description of image processing techniques). Six specific task subtractions were used to isolate orthographic, phonological, and lexical-semantic networks (Table 1 shows each of the subtraction conditions and the processes thought to be isolated in each). The procedure generated a set of scores for each participant by counting the number of significantly activated voxels (evaluated by a t test) in each region of interest and for each subtraction condition. These activation scores for each participant then were entered into appropriate repeated measures analyses of variance (ANOVAs), with participants as the unit of analysis. In the one-step subtractions, case minus line isolated orthographic processing, rhyme minus case isolated phonological processing, and the use of nonword stimuli precluded using lexical memory; it forced assembled phonological processing), and category minus rhyme isolated lexical-semantic processing. Furthermore, various two- and three-step subtractions were used as converging measures to isolate a given process using different baselines, experimental conditions, or both. The use of multiple baselines, experimental conditions, or both, which logically isolate comparable processes, increased the confidence with which Pugh et al. (1996) tested hypotheses about the func-

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[1] Echoplanar functional magnetic resonance imaging (fMRI) is an imaging technique that permits acquisition of a sufficient number of images in a short period of time to perform separate statistical analyses on the brain activation data for each individual participant. With interpretable data for each participant, one then can assess how individual differences in reading performance are associated with individual differences in the functional organization of the brain. The fMRI technique is sensitive to changes in the local concentration of deoxyhemoglobin. As first demonstrated in vivo by Ogawa, Lee, Nayak, and Glynn (1990) and Ogawa et al. (1992), the oxygenation state of hemoglobin influences the transverse magnetization decay time, T2*, of brain tissue water, a property that offers the potential for detecting the effects of altered blood flow and oxygen balance in tissues. As the concentration of deoxyhemoglobin decreases, the intensity of the tissue magnetic resonance (MR) signal increases because deoxyhemoglobin acts as an endogenous susceptibility contrast agent that shortens T2*. Studies (Blamire et al., 1992; Kwong et al., 1992; Ogawa et al., 1992) using this technique have used either ultrafast (echoplanar) MR imaging or a high field strength to demonstrate brain activation in response to different sensory stimuli and task requirements (see also Constable, McCarthy, Allison, Anderson, & Gore, 1993; McCarthy, Blamire, Rothman, Bruetter, & Shulman, 1993; Schad, Trostt, Knopp, Muller, & Lorenz, 1993).

Table 1
Task Design and Subtractions

Task	Stimuli	Processes engaged	Processes isolated
Line	/ / \ / / / \ /	Visual-spatial	
Case	BtBT BtBT	Visual-spatial + orthographic	
Rhyme	LETE JEAT	Visual-spatial + orthographic + phonological	
Category	CORN RICE	Visual-spatial + orthographic + phonological + semantic	
Subtractions			
Case minus line			Orthographic
Rhyme minus line			Orthographic + phonological
Rhyme minus case			Phonological
Category minus line			Orthographic + phonological + semantic
Category minus rhyme			Semantic
Category minus case			Phonological + semantic

tional role of a given cortical region. If, for example, a given subtraction produced an artifactual activation caused by a spurious difference between the experimental and control conditions, one would not expect similar activation to be observed in subsequent subtractions with different experimental and control conditions. Given the potential ambiguities of subtraction approaches (see, e.g., McClelland, 1979; Sergent, 1994), the use of multiple subtractions to isolate a given function achieves validation by convergence.

Six broad regions of interest were examined, including areas that traditionally have been implicated in language function. In the frontal lobe, these included the inferior frontal gyrus (centered in Broca's area), the prefrontal dorsolateral, and the orbital gyrus. In the temporal lobe, the superior temporal gyrus and the middle temporal gyrus were examined, and within the occipital lobe the extrastriate region was examined (this also was further divided into lateral and medial subregions).

The results showed that orthographic processing made maximum demands on the extrastriate region across subtraction conditions. Subtractions that isolated orthographic processing (e.g., case minus line, rhyme minus line, and semantic category minus line) activated this region significantly more than subtractions that did not (e.g., rhyme minus case, semantic category minus case, semantic category minus rhyme; see Figure 1). In addition, a difference between lateral and medial subregions was observed. Although the lateral aspect showed equivalent patterns of activation in case minus line, rhyme minus line, and semantic category minus line, the medial aspect showed a small but reliable increase in activation to the real word stimuli used in the semantic category minus line subtraction (see Petersen, Fox, Snyder, & Raichle, 1990, for related results).

Assembled phonological processing activated the inferior frontal gyrus (primarily centered in Brodman's area 44–45 within this region) as indicated by reliable differences on those subtractions that isolated phonology (e.g., rhyme minus case) from those that did not (see Figure 2). A sex

difference emerged in the inferior frontal gyrus; normal male participants showed, on average, greater left hemisphere (LH) than right hemisphere (RH) activation for phonology, whereas normal female participants showed equivalent LH and RH activation on average.[2] This highly robust difference, which has been discussed by Shaywitz, Shay-

[2] In the one-step subtraction analysis (case minus line, rhyme minus case, and semantic category minus rhyme), hemisphere interacted with sex, $F(1, 36) = 14.14, p < .001$. The right hemisphere (RH) and left hemisphere (LH) mean numbers of activated voxels were 3.4 versus 10.4 for men and 7.9 versus 7.6 for women. The hemisphere difference was significant for men, $F(1, 18) = 19.09, p < .001$, but not for women ($F < 1.0$). Furthermore, as discussed earlier, the rhyme minus case subtraction produced reliably stronger activation than either case minus line or semantic category minus rhyme, specifically implicating a phonological function for the region. For instance, in the one-step analyses, there was a main effect of task, $F(2, 72) = 11.39, p < .001$. The means for the case minus line, rhyme minus case, and semantic category minus rhyme subtractions were 5.0, 13.2, and 4.2, respectively. Rhyme significantly differed from both case, $F(1, 72) = 16.28, p < .001$, and semantic category, $F(1, 72) = 17.84, p < .001$, whereas case and semantic category did not differ significantly ($F < 1.0$). The means for the rhyme minus case subtraction alone for men were 4.1 and 16.4 in the RH and LH, respectively. The corresponding RH and LH means for women were 17.0 and 15.5. To explore this sex difference further, we examined the ratio of RH to LH activation in the inferior frontal region for each participant. Eleven of 19 women, but no men, had an RH-to-LH ratio of .70 or more; in fact, for 9 of these 11 women, the RH-to-LH ratio was 1.0 or more. Thus, more than half of the women produced strong bilateral activation in the inferior frontal region; by contrast, no men showed this pattern. Reliable Sex × Hemisphere interactions were not in general obtained in other regions, although the pattern of left dominance for men and the tendency toward bilateral activation in women was marginally significant in the extrastriate region. These hemispheric differences served as predictors in the experiment reported here.
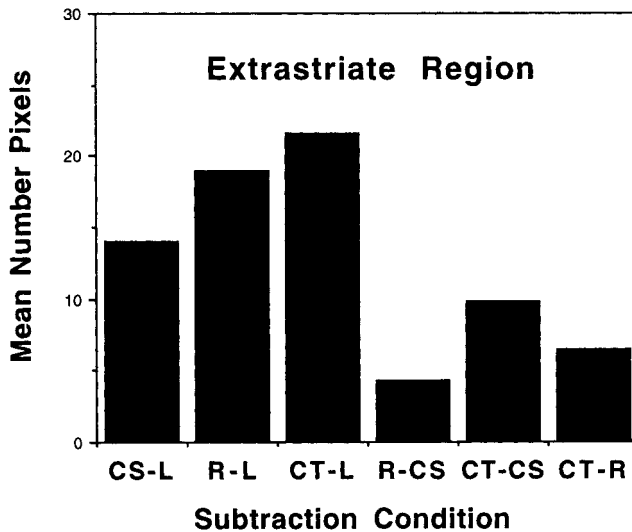
Figure 1. Activation in lateral and medial extrastriate regions across subtraction conditions. CS-L = case minus line; R-L = rhyme minus line; CT-L = category minus line; R-CS = rhyme minus case; CT-CS = category minus case; CT-R = category minus rhyme.

witz, et al. (1995), figures prominently in the behavioral experiment reported in this article.

Semantic processing produced reliable increases in activation relative to phonological or orthographic processing in the superior temporal gyrus (see Figure 3). However, phonological processing also produced greater activation than orthographic processing in this temporal lobe site. Hence, this region appears to be multifunctional. Because Pugh et al. (1996) adhered to the principle of converging operations throughout, a given function was ascribed to a given region only if the activation patterns across all relevant subtractions were consistent and statistically reliable.

Regarding phonological processing, Petersen, Fox, Posner, Mintun, and Raichle (1988) failed to observe temporal lobe activation for printed words in passive word reading relative to a neutral fixation condition, although such activation was observed in processing spoken words. This was taken by Petersen et al. as evidence that phonological processing plays little or no role in visual word identification. Given the emerging behavioral evidence favoring a predominant role for the early involvement of phonological processes in printed word recognition (Lukatela & Turvey, 1991, 1993, 1994; Perfetti & Bell, 1991; Van Orden, 1987), this result is surprising. Furthermore, other investigators have observed both temporal and inferior frontal (i.e., Broca's area) activation in printed word identification (see, e.g., Price et al., 1994), suggesting that the conclusion of Petersen et al. may have been premature. In the current fMRI study, we observed both inferior frontal gyrus and temporal lobe activation in subtractions that isolated phonological processing, and this was true for both pseudoword (e.g., rhyme minus case, rhyme minus line) and real word targets

(e.g., semantic category minus case, semantic category minus line).

The results obtained from the fMRI study (Pugh et al., 1996) show that it is possible, using multiple subtractions, to isolate the cortical regions most strongly associated with orthographic, phonological, and lexical-semantic processing in print perception. The results summarized here reflect statistically significant effects based on group means. The next step was to examine the relation between an individual's cortical profile and his or her performance on standard word identification tasks. Accordingly, in the second phase of this study, the activation scores obtained for each participant were related to his or her performance in a lexical decision task performed out of the magnet. The lexical decision paradigm was chosen because it appears to be sensitive to the contributions of different component processes in word recognition and, particularly for the present purposes, to the relative contributions of orthographic and phonological processing.

The Regularity Effect in Lexical Decision

The vehicle of our efforts to link processes in word identification with brain physiology is the so-called regularity effect in the lexical decision experiment. The presence or absence of regularity effects, defined as longer latencies (or higher error rates) to exception words (PINT) than to regular words (MILL), may indicate whether lexical access is more or less reliant on assembled phonological coding for a given reader or a given reading group (Bruck, 1992; Fletcher et al., 1994; Pugh et al., 1994; Share, 1995; Stanovich & Siegel, 1994; Waters, Seidenberg, & Bruck, 1984).
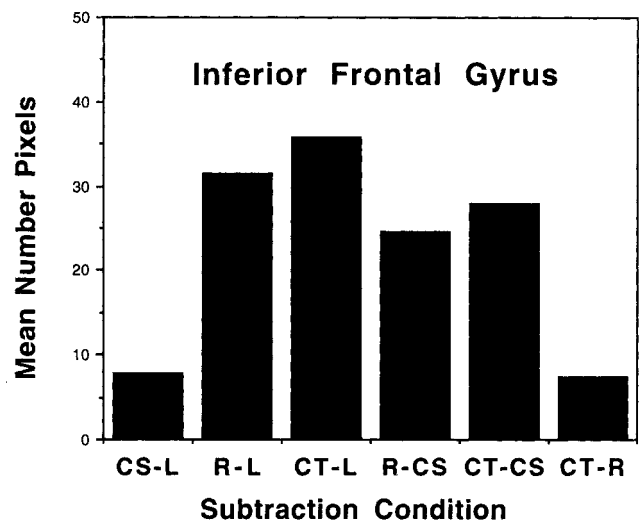

Figure 2. Activation in the inferior frontal gyrus across subtraction conditions. CS-L = case minus line; R-L = rhyme minus line; CT-L = category minus line; R-CS = rhyme minus case; CT-CS = category minus case; CT-R = category minus rhyme.
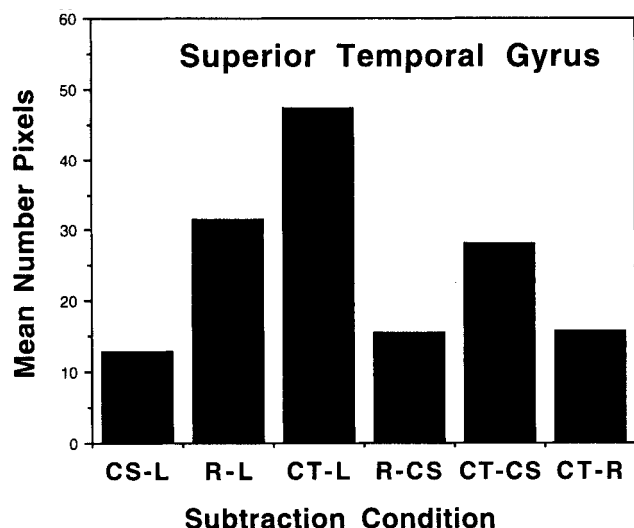
Figure 3. Activation in the superior temporal gyrus across subtraction conditions. CS-L = case minus line; R-L = rhyme minus line; CT-L = category minus line; R-CS = rhyme minus case; CT-CS = category minus case; CT-R = category minus rhyme.

The computational basis of this "reliance" varies depending on the model of word recognition in which the regularity effects are being interpreted. In turn, architectural and operational differences among models lead to varying expectations about patterns of brain activation that might accompany larger or smaller regularity effects. We first discuss the computational models and then extrapolations to brain physiology.

The regularity effect usually is interpreted in the context of dual-coding models of reading. In such models (Coltheart, 1978; Coltheart, Curtis, Atkins, & Haller, 1993; Paap, McDonald, Schvaneveldt, & Noel, 1987; Paap & Noel, 1991), two routes to word identification are posited, a phonologically mediated route and an orthographic, or direct-access, route. The phonological route consists of two stages. The first stage converts orthographic characters into appropriate phonological representations (the output from this mapping is commonly referred to as assembled phonology). In a second stage, these phonological representations are matched to their appropriate entries in the reader's speech lexicon. The alternative direct-access route is, by some accounts (e.g., Share, 1995), thought to develop later as a consequence of extensive exposure to print; it is viewed as involving a more or less direct mapping from orthographic representations to lexical entries. Phonological information becomes available on lexical access, and the lexically derived phonological coding is referred to as addressed phonology.

Thus, a phonological representation of a printed word can come about in at least two ways, and, in the case of some words, those representations can be different. For exception words, the assembled phonological system generates a regularized output (e.g., PINT to rhyme with MINT), whereas

the direct orthographic system is lexically influenced and yields an irregular but correct phonological output (e.g., the correct pronunciation of PINT). Resolution of the conflict between these two competing processes putatively causes delays in responses to exception words relative to regular words, for which no such conflict arises (Paap & Noel, 1991).

The precise manner in which letter strings are processed initially also is thought to differ in the assembled and direct routes. Grapheme-to-phoneme mapping is envisioned as a serial process (Coltheart & Rastle, 1994; Content, 1991; Content & Peereman, 1993; Pugh et al., 1994); hence, a printed word would need to be parsed into its grapheme-sized units (letters and letter clusters). By contrast, the direct route, not constrained by such a mapping strategy, may chunk letter strings at a larger grain size in a parallel manner (Baron & Strawson, 1976). This distinction in coding procedure leads to the prediction that regularity effects, if present, should coincide with word length effects because both would be manifestations of the assembled process. Furthermore, the magnitude of the regularity effect should vary with the position of the irregular segment in the word string. Each of these predicted results has been obtained recently (Coltheart & Rastle, 1994; Pugh et al., 1994).

Within the dual-route perspective, assembled phonological influences are typically predicted to be larger for low- than for high-frequency words. This expectation rests on the assumption that high-frequency words are processed quickly and accurately through the visual orthographic system, thus generating a quick response from addressed phonology before the lagging contribution from assembled routines can compute conflicting representations (Paap & Noel, 1991; Waters & Seidenberg, 1985). Several investigators have obtained the interaction between regularity and frequency that is predicted from this framework (Bruck, 1992; Paap & Noel, 1991; Seidenberg, Waters, Barnes, & Tanenhaus, 1984; Waters et al., 1984). The interaction is obtained more reliably in naming tasks than in lexical decision tasks. Whenever the interaction is not obtained for a particular reader, group of readers, or condition of an experiment, this is taken, in dual-coding accounts, as an indication that lexical access is driven primarily by direct mapping of orthographic information (Paap & Noel, 1991; Pugh et al., 1994).

The dual-coding framework has been challenged. Some theorists have supposed that lexical access is exclusively visual (Brooks & Miller, 1979; Glushko, 1979) or largely phonological (Gough, 1972). Moreover, a growing number of findings have appeared that challenge whether lexical access can ever operate in a purely nonphonological manner, even for high-frequency words; evidence for an early and strong influence from assembled phonology has been obtained in several recent studies (see, e.g., Lukatela & Turvey, 1991, 1993, 1994; Perfetti & Bell, 1991; Van Orden, 1987). Models using distributed representations in parallel-distributed processing (PDP) architectures have become influential of late. In accounts of this kind, simple

distinctions between single and multiple routes often can be blurred. However, even here, the advocates of PDP models make different assumptions about the degree to which orthographic or phonologic information mediates lexical access (Seidenberg & McClelland, 1989; Van Orden, Pennington, & Stone, 1990; see Bernstein & Carr, 1996, for a comprehensive discussion of the various types of architectures that have been proposed).

In single-route accounts of word recognition, the mechanisms assumed to produce the regularity effect (i.e., longer latencies to exception words than to regular words) vary with model-specific assumptions. For instance, in purely orthographic access models, *PINT* words take longer than *MILL* words in overt naming tasks because of a mechanism that synthesizes phonological information from lexical neighbors to yield an articulatory output (Brooks & Miller, 1979; Glushko, 1979). Hence, neighbors such as *MINT, HINT, LINT*, and so on, bias the speech production system toward a regularized pronunciation of *PINT*; accordingly, *PINT* words are named more slowly than *MILL* words (for whom all neighbors yield consistent outputs). This account leads to the idea that neighborhood consistency is the key factor in producing regularity effects, not the degree to which the word follows or does not follow supposed grapheme-to-phoneme correspondence rules. In fact, researchers have tended to confound these variables, essentially comparing regular-consistent with irregular-inconsistent words. Efforts to unconfound regularity and consistency have yielded inconsistent results, however (e.g., Andrews, 1982; Rosson, 1985). In any event, in an account in which access to the lexicon is putatively accomplished without phonological mediation, the occurrence or absence of regularity-consistency effects must depend on differential use of postlexical phonological processing.

Van Orden et al. (1990) put forward a PDP account in which phonological structure plays a central role in word identification. This model assumes massively interconnected orthographic, phonologic, and semantic units, all of which interact in word identification. However, the orthographic-to-phonological and phonological-to-semantic connections are more salient (because they are more consistent) than the orthographic-to-semantic connections, hence the central role of phonological information. Regularity effects, consistency effects, or both emerge as a consequence of weaker orthographic-to-phonological connections for irregular-inconsistent words than for regular-consistent words. No correspondence rules are assumed; statistical regularity is the key. In such an account, both grapheme-to-phoneme correspondence strength and neighborhood consistency contribute to the dynamical properties of the word identification system. The model therefore is neither dual coding nor analogy based; the presence or absence of a regularity effect does not indicate use of different processing systems or routes, as would be assumed in dual-coding accounts. Stone and Van Orden (1993) argued that such variation is produced by changes in parameter settings at the decision level, not in the relative use of

phonological networks. When participants adopt a higher decision threshold (which should be associated with slower reaction times), there is a greater opportunity for both regularity and consistency to influence performance.

In summary, the presence or absence of regularity effects in lexical decision is considered to be diagnostic of phonological involvement in word identification. However, the proposed mechanisms that give rise to those effects vary among theories. Dual-coding accounts explicitly assume that distinct computational systems are associated with the presence or absence of regularity effects, whereas in single-route models in which lexical access is purely orthographic, such variation arises as a consequence of differences in the extent to which postlexical phonological processes are engaged. Finally, in PDP accounts such as Van Orden's (Stone & Van Orden, 1993; Van Orden et al., 1990), the variation is associated with changes in decision threshold settings, not with sublexical pathway dynamics. In the current experiment, we sought correlations between regional brain activation and mode of word identification as a new testing ground for models of the reading process. We begin with a discussion of whether activation associated with phonological processing should be sought in the left or the right cerebral hemisphere.

Role of the RH and LH in Word Identification

Because the Pugh et al. (1996) fMRI study revealed individual differences in patterns of hemispheric activation (e.g., sex-correlated differences in the inferior frontal gyrus), we next consider several lines of evidence that support the possibility that orthographic and phonological processing abilities may differ in their hemispheric bases (Coltheart, 1980; Milner, 1974; Zaidel & Peters, 1981). For example, in studies of split-brain patients, Zaidel and Peters found that the isolated RH showed little capacity for phonological processing; they also found larger effects, relative to the LH, of length, concreteness, and frequency in word reading. Similar findings have been obtained in patients with hemispheric lesions. For example, patients with deep dyslexia (Coltheart, 1980), an acquired dyslexia that is associated with extensive LH lesions, are characterized by extremely poor decoding skill, better performance on concrete than abstract words, and a strong tendency to make semantic substitution errors (e.g., responding *FOOD* to the target *DINNER*). The parallels between the pattern of reading errors in deep dyslexia and the performance of the isolated RH in split-brain patients has suggested to some authors that patients with deep dyslexia rely extensively on RH processes in reading (Coltheart, 1980; Schweiger, Zaidel, Field, & Dobkin, 1989; however, see Patterson & Besner, 1984, for criticisms).

Visual hemifield experiments with neurologically intact individuals provide yet another line of investigation relevant to the cerebral organization of the processes in word identification. To date, results have been equivocal with respect to the hypothesis, derived from split-brain studies, that

phonological processing is associated exclusively with LH function. There certainly is evidence consistent with the expectation that phonological processing is more strongly associated with LH than with RH function. For example, in a word–nonword discrimination task, Cohen and Freeman (1978) found pseudohomophone effects (slowing on nonword decision latencies with nonword targets such as *BRANE* that sound like real words) when stimuli were presented to the right visual field/left hemisphere (RVF/LH), not when they were presented to the left visual field/right hemisphere (LVF/RH). Parkin and West (1985) used briefly displayed regular versus exception words presented to either the RVF/LH or LVF/RH in a naming accuracy task. They found an overall RVF/LH advantage in general as well as regularity effects (lower accuracy on exception words) only in responses to stimuli presented in that visual field.

However, several studies from the neuropsychology group at the University of California, Los Angeles (Zaidel, 1989; Rayman & Zaidel, 1991; Iacoboni & Zaidel, 1996) suggest some degree of RH phonological sensitivity in neurologically normal participants. Iacoboni and Zaidel (1996) obtained regularity effects on lexical decision accuracy (i.e., more errors on exception words than on regular words) of equivalent magnitude for RVF/LH and LVF/RH presentations. Although this finding is inconsistent with that reported by Parkin and West (1985), there are differences between the experiments that may be important. First, Iacoboni and Zaidel found equivalent RVF/LH and LVF/RH effects of regularity using lexical decision. By contrast, the naming task used by Parkin and West, a task requiring explicit articulation, might have amplified LH dominance. Furthermore, in the Parkin and West study, accuracy was extremely low (roughly 3 of 16 items in each cell), and hence performance levels may have been too low to reveal evidence of RH phonological processing in that experiment.

The picture also may be somewhat complicated by sex differences. There are indications that the role of RH in word identification may differ to some degree between men and women (Luh & Levy, 1995; Lukatela, Carello, Savic, & Turvey, 1986). For example, Lukatela et al. (1986) presented data from a lateralized lexical decision task with speakers of Serbo-Croatian. That language is transcribed in two distinct scripts, both of which can be read by educated readers. The study compared latencies and accuracies on words and pseudowords that were either alphabetically and phonologically ambiguous (because they are pronounced differently in the Roman and Cyrillic scripts) or phonologically unambiguous (because pronunciation was the same in both alphabets). Although the pattern of results was complex, phonological ambiguity effects for words (relative slowing on phonologically ambiguous targets) were equivalent for men and women in the RVF/LH but were stronger in women in the LVF/RH. The investigators concluded that the increased sensitivity to a phonological variable in the female participant's RH, in fact, reflects greater phonological representation in that hemisphere for female participants.

Compatibly, Luh and Levy (1995) presented participants with tachistoscopically displayed consonant–vowel–consonant (CVC) displays presented to the LVF/RH, RVF/LH, or bilaterally. Target durations were tailored to produce an overall performance of approximately 50%. Participants were instructed to name each CVC stimulus. In general, a RVF/LH advantage was obtained. However, in two of their experiments, the RVF/LH advantage was different for men and women. Women showed much smaller RVF advantages than men.

The suggestion of greater RH participation in phonological processing for women than for men, in a perceptual identification task, converges with the Lukatela et al. (1986) study, in which a lexical decision task was used. Moreover, each of these findings is consistent with the results of the Pugh et al. (1996) fMRI study; the results from that study also suggest relatively greater involvement of the RH in phonological processing for women than for men. Given the past indication of sex-related variation, we considered whether gender would be related to individual differences in sensitivity to regularity in the current lexical decision experiment.

Other potentially informative differences between RH and LH processing also have been reported in relation to processing letter strings. For example, Iacoboni and Zaidel (1996) observed length effects (i.e., longer latencies for longer letter strings) on latency and accuracy for both words and nonwords in the LVF/RH but for nonwords only in the RVF/LH. Similarly, Ellis, Young, and Anderson (1988) found, in several experiments, that length effects were limited to the LVF/RH. They concluded that LH processing systems are capable of parallel graphemic coding strategies but that the RH is limited to serial processing. Similarly, Bub and Lewine (1988) reported four experiments that revealed greater length effects in the LVF/RH, and, like Ellis et al. (1988), they argued that the RH tends to use serial processing for orthographic strings and the LH appears to process them in a more parallel fashion. In this connection, Brand, Van Bekkum, Stumel, and Kroeze (1983) obtained lateralized same–different judgments of pairs of letter strings and found monotonic increases in latency when the position of the mismatch occurred later in the string for LVF/RH trials but no effect of position in the RVF/LH (Brand et al., 1983). This finding confirms other indications that the RH is more likely to engage serial processing strategies than the LH.

It also has been found repeatedly that the hemispheres give rise to different errors in processing letter strings (Eng & Hellige, 1994; Hellige et al., 1994; Levy, Heller, Banich, & Burton, 1983; Luh & Levy, 1995). For example, in tests of lateralized identification of CVC nonwords, Luh and Levy (1995) found that although a RVF/LH advantage was obtained (and was larger for men than women, as discussed earlier), last-letter-position errors (e.g., X in *GEX*) were proportionately more likely in the LVF/RH than in the RVF/LH. (It also is the case that first-letter errors actually are proportionately less likely in the LVF/RH than in the generally superior RVF/LH.) Hellige and colleagues (Eng

& Hellige, 1994; Hellige et al., 1994) repeatedly have found proportionately higher last-letter errors in the LVF/RH than in RVF/LH. Furthermore, they found that this Hemisphere X Error Type interaction was not restricted to CVCs. They obtained exactly this pattern for both CVC and consonant–consonant–consonant stimuli (Eng & Hellige, 1994). Finding higher error rates on last letters is consistent with a serial (left-to-right) coding strategy; occasional errors are caused by the processor being interrupted before completion. If this is the case, as suggested by all of those authors, then these results, along with the often-obtained Stimulus Length X Visual Field interaction, clearly suggest that the RH is more likely than the LH to engage such serial processing.

Hemispheric differences in processing letter strings, as discussed earlier, are germane to the current investigation of regularity effects in lexical decision. Thus, as we noted, there is evidence that the magnitude of regularity effects covaries with length effects (Pugh et al., 1994); furthermore, there is evidence that the magnitude of regularity effects is correlated inversely with the position of the irregular correspondence in the letter string (Coltheart & Rastle, 1994; Content, 1991; Content & Peereman, 1993). Assembly is thought to begin with parsing of the letter string into grapheme sized units, which then are mapped onto phonological structures. It is plausible that such fine-grained, perhaps serial, parsing of letter strings would make demands on serially oriented RH coding systems. However, as discussed, the evidence also generates the expectation that phonological processing is associated most strongly with LH systems. Taken together, these considerations suggest that readers who exhibit strong regularity effects will show a complex distribution of activation across the two hemispheres within orthographic and phonological subsystems. More specifically, we can speculate that a reader who engages in fine-grained parsing of letter strings in preparation for phonological assembly will make use of serial RH coding systems but that complete phonological assembly will engage primarily LH (phonological) systems. If so, this would lead one to expect a good deal of RH and LH coactivation in regions of the brain associated with orthographic and phonological processing. To test this speculation, it is important to measure the relative activation patterns of LH and RH sites relative to regularity effects in reading. To do this, we computed, for each participant, indexes of the degree of lateralization in orthographic and phonological regions from the Pugh et al. (1996) fMRI data and used these indexes as predictor variables in the current study.

The fMRI results (Pugh et al., 1996) indicated that orthographic processing makes demands on extrastriate sites, whereas assembled phonological processing (isolated most clearly in subtractions in which the rhyme task was examined) makes extensive demands on both the inferior frontal gyrus and the superior temporal gyrus. Furthermore, a sex-correlated pattern of individual differences was observed in the inferior frontal gyrus; women engaged the RH and LH

equivalently, whereas men appeared more left lateralized. Could this discrepancy be related to differences in the way that phonological processing is accomplished? This possibility had to be entertained given the suggestion that participants who accomplish phonological processing bilaterally will show relatively greater regularity effects. If the projected analyses reveal sex-related differences in sensitivity to regularity, this would suggest that lateralization indexes may have value as predictor variables.

Additionally, we sought evidence regarding the generality of conclusions about phonological processing in lexical decision by examining fMRI patterns of activity stemming from the semantic category task. Thus, we could determine whether those participants who were insensitive to regularity in lexical decision (which uses real word stimuli) will be the same ones who showed minimal activation in phonological regions (inferior frontal and superior temporal sites) in the semantic category task (also using real word stimuli) when subtractions that isolated phonology were used (e.g., semantic category minus line; see Table 1 for details). That is, real word reading for these readers might not engage regions implicated as being relevant to assembled phonology in the rhyme task subtractions. By contrast, the readers whose lexical decision performance displayed regularity effects might be expected to have activated these regions strongly in all word reading situations.

Behavioral Experiment: Modes of Word Identification

Method

Participants. Thirty-one right-handed, neurologically normal adults, 13 men (mean age = 28.5 years) and 18 women (mean age = 24 years), participated in the study. (Thirty-one of the 38 participants from the original fMRI experiment [Pugh et al., 1996] were able to return for this subsequent reading experiment.)

Materials and procedure. The stimulus list for the lexical decision task consisted of 96 words and 96 pronounceable nonwords (see the Appendix for the stimulus list). The words were divided into 48 low- (mean Kucera & Francis, 1967, frequency = 7.2) and 48 high-frequency words ($M = 275$). In each group of 48, half were regular with regard to spelling–sound correspondence and half were exception words; these were matched for mean frequency and length. The 96 nonwords were matched for length and were all pronounceable. Participants also were given 40 practice trials before the onset of the experimental trials.

We followed a standard lexical decision procedure. Items were presented in uppercase letters and in a different random order to each participant on a Macintosh SE computer screen. Targets were preceded by a 500-ms fixation point (asterisk) in the middle of the screen, followed by a 500-ms blank screen. Target presentation continued until the participant's response was made or until 1,600 ms had elapsed. Latencies shorter than 150 ms or longer than 1,600 ms were excluded from the analysis. "Word" responses were made with the dominant hand, and "nonword" responses were made with the nondominant hand on two telegraph keys. Reaction time was measured with an accuracy of ±2 ms. The lexical decision procedure lasted approximately 35 min.

Results

An initial ANOVA on the latency data for words included the variables of regularity and frequency as within-subjects variables. Sex was included as a between-subjects variable. A main effect of frequency was found, $F(1, 29) = 62.26$, $p < .001$. The means for low- and high-frequency words were 541 and 507 ms, respectively. The only other significant outcome was an interaction between sex and regularity, $F(1, 29) = 10.53$, $p < .01$ (see Table 2 for relevant means). Analyses conducted separately on the data from the male and female groups revealed a significant effect of regularity only for women, $F(1, 17) = 7.18$, $p < .025$, along with a marginal Regularity × Frequency interaction for this group, $F(1, 17) = 4.31$, $p = .053$. Contrasts revealed that the regularity effect (i.e., longer latencies on exception words than on regular words) for women was reliable only for low-frequency words, $F(1, 17) = 7.61$, $p < .025$ (the mean latency for regular words was 527 ms, and the mean latency for exception words was 550 ms). Hence, the sex difference with regard to regularity was observed primarily on low-frequency words. Overall, there was no difference in average word latencies between men (527 ms) and women (521 ms; $F < 1.0$). Thus, the relative advantage on regular relative to exception words among women was not seen in men; however, the overall mean latencies for both sexes were similar.

fMRI and behavioral analyses. The interaction between sex and regularity in the latency data suggested a possible link with the neuroimaging results. As noted earlier, activation in the inferior frontal gyrus, a site that responded uniquely to phonological subtractions, was lateralized differently for men and women. Men showed activation in this region only in the LH, whereas women, on average, were bilateral (although there was substantial variation among the women). In the current experiment, similar variation oc-

Table 2
Mean Latencies (in Milliseconds) for Low- and High-Frequency Regular and Exception Words

Group	LF		HF	
	Regular	Exception	Regular	Exception
Analysis by sex				
Men	548	539	515	506
Women	527	550	505	503
RH proportion analysis (inferior frontal gyrus)				
Low RH proportion	552	546	520	508
High RH proportion	520	545	499	501
RH proportion analysis (extrastriate region)				
Low RH proportion	538	529	507	500
High RH proportion	533	562	511	509

Note. LF = low frequency; HF = high frequency; RH = right hemisphere.

curred for a behavioral index of phonological processing in printed word recognition (i.e., the regularity effect in lexical decision). Only 3 of 13 men (23%) showed exception word minus regular word differences greater than 10 ms in lexical decision, whereas 10 of 18 women (55%) did; thus, although the effect was correlated with sex, variation within sex was strong.

If it is true that regularity effects indicate the degree of phonological involvement, and if the fine-grained parsing of letter strings thought to be associated with phonological assembly engages RH coding in collaboration with LH coding, then, as discussed in the introduction, it is possible that the key to the observed sex differences was in the relation between reaction time differences on regularity in lexical decision and the degree of cortical lateralization of brain activation in specific regions of interest. Given the substantial variation in both measures that were observed within the female group, we suspected that both measures might be more closely related to each other than each is related to sex. To determine whether this was true, we computed a measure of the relative degree of RH activation in the neuroimaging tasks in all relevant regions of interest: For each participant, we divided the sum of significant voxels in the RH by the sum of RH plus LH in a given region (thus, we were measuring the proportion of RH activation to total activation, and we designated this variable RH proportion). RH proportion was entered as a variable in the analyses of lexical decision latency data.

For the inferior frontal gyrus (the region where the significant Sex × Hemisphere interaction was actually observed), a significant RH Proportion × Regularity interaction was obtained, $F(1, 29) = 16.27$, $p < .001$. To generate means, we also made a median split (low vs. high RH proportion with means of .27 and .52, respectively) on this continuous variable to obtain mean latencies (also see Table 2). This categorical RH proportion variable also showed a significant interaction with regularity, $F(1, 29) = 16.92$, $p < .001$. Contrasts revealed that regularity effects were found only for the high RH proportion participants (those who were essentially bilateral in activation in the inferior frontal gyrus) and were observed only for low-frequency words, $F(1, 15) = 8.65$, $p < .025$ (regular = 520 ms, exception = 545 ms); no other simple effects were significant for either group. Thus, the subset of participants who engaged the right inferior frontal gyrus to a relatively larger extent in the fMRI tasks were more sensitive to spelling-to-sound regularity in the lexical decision task than were the participants who were more left lateralized.

The two individual-differences variables, RH proportion and sex, were correlated: Women had, on average, a higher RH proportion than men. To determine which was a better predictor of the magnitude of regularity effects in lexical decision, we first created an index of each participant's regularity effect; we subtracted his or her average reaction time to regular words from reaction time to exception words, designated the E-R score. To discover which of the predictors (sex or RH proportion) accounted for more of the variance in sensitivity to regularity, we regressed the E-R score on sex and RH proportion. Of central interest in these

regression analyses were the values of R^2 associated with each. For sex, $R^2 = .26, p < .001$. For RH proportion, $R^2 = .36, p < .001$. Thus, the brain activation variable produced a 10% increase in the proportion of variance accounted for relative to sex. Furthermore, when both sex and RH proportion were included in this simultaneous regression model, only RH proportion remained significant, $F(1, 28) = 5.5, p < .05$ (sex produced a nonsignificant 3% increase in variance accounted for above and beyond the brain activation measure alone). In summary, the proportion of RH activation in the inferior frontal gyrus was a better predictor of the magnitude of regularity effects in lexical decision than was gender.

Having found that brain activation data reliably predicted reading differences in lexical decision, we also examined the relation in the reverse direction. We divided participants into two behaviorally defined groups: those who showed E-R reaction time differences of less than 10 ms and those with E-R differences greater than 10 ms. For each group, we created composite cortical activation images. The resulting composites showed clear laterality differences, as illustrated in Figure 4, for two slices in the (phonological) rhyme minus case subtraction condition. Thus, participants who were more sensitive to regularity (and therefore were thought to be relying more on contributions from assembled phonology) showed increased fMRI activation in the right inferior frontal gyrus, a region already implicated (see Figure 2) in deriving phonology from print.

When the RH proportion values in the extrastriate (orthographic) region[3] were computed for each participant and regressed on E-R latency scores, a significant effect was obtained in this region, $F(1, 29) = 10.52, p < .01, R^2 = .27$. The direction of the correlation was positive (i.e., the higher the RH proportion score, the bigger the E-R difference, thus mirroring the effects in the inferior frontal gyrus). A median split was performed and means were computed (also see Table 2). RH proportion and regularity yielded a significant interaction, $F(1, 29) = 14.05, p < .001$. Again, regularity effects were seen only for high RH proportion participants and here only on low-frequency words, $F(1, 15) = 10.35, p < .01$ (regular = 533 ms, exception = 562 ms). Those with stronger fMRI activation in two regions of the RH, the extrastriate and inferior frontal gyrus, were more sensitive to the regularity variable in lexical decision performance.

By contrast, similar analyses of fMRI data from middle temporal, superior temporal, prefrontal dorsolateral, and orbital regions failed to yield significant relations between RH proportion and regularity effects in lexical decision performance. Hence, the relation between RH involvement in fMRI tasks and sensitivity to regularity in reading seemed, based on these analyses, to be associated specifically with differences in activation of posterior (extrastriate) and anterior (inferior frontal) regions of interest. A theoretical account of why lateralization differences in both phonological and orthographic regions predict regularity effects is presented in the *Discussion* section.

Length effects and RH proportion. The literature on laterality effects in visual hemifield experiments indicates

that length effects are more prevalent in the LVF/RH than in the RVF/LH (Bub & Lewine, 1988; Ellis et al., 1988; Iacoboni & Zaidel, 1996). Given this, and given the relation between length effects and regularity effects that has been reported (Pugh et al., 1994), we might anticipate that participants who tend to engage RH sites to a greater extent in fMRI tasks, and consequently show increased sensitivity to regularity, will be more likely to exhibit length effects than those whose fMRI profiles indicate a more left-lateralized pattern. Accordingly, we regressed latency and accuracy on length (three or four letters were considered short, and five or more letters were considered long; only 3 of 96 items were three letters in length) and RH proportion in the inferior frontal gyrus and extrastriate regions. For words, no length or Length × RH Proportion interactions were observed (all $Fs > 1.0$).

By contrast, the nonword latency data (correct rejection reaction time) revealed a striking pattern. A main effect of length was obtained, $F(1, 29) = 62.50, p < .001$, with means of 571 and 600 ms for short and long nonwords, respectively. Although there was no main effect of RH proportion in the inferior frontal gyrus ($F < 1.0$), a reliable RH Proportion × Length interaction was found, $F(1, 29) = 8.05, p < .01, R^2 = .22$. To aid in interpreting this, we again divided participants into low and high RH proportion (by median split). The means (shown in Table 3) revealed that the length effect was larger (37 ms) for high RH proportion participants than for low RH proportion participants (20 ms): This categorical RH proportion measure also significantly interacted with length, $F(1, 29) = 5.12, p < .05$.

Similar results were obtained on nonword reaction time using extrastriate RH proportion. A RH Proportion × Length interaction was obtained, $F(1, 29) = 8.00, p < .01, R^2 = .22$. A median split on RH proportion (see Table 3) revealed that length differences were larger for high RH proportion participants (38 ms) than for low RH proportion participants (19 ms); for this categorical RH proportion index, the interaction with length also was significant, $F(1, 29) = 8.49, p < .01$.

A further analysis was done with sex as a variable instead of RH proportion. No effect of sex on nonword reaction time was obtained, however, and the Sex × Length interaction also failed to obtain significance, $F(1, 29) = 2.16$ $p > .05$, even though the mean length effect was greater for

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[3] As noted in the introduction, certain differences between the lateral and medial aspects of the extrastriate region across subtraction conditions were noted (with medial sites showing somewhat greater sensitivity to real word stimuli than to either consonant strings or pseudowords). However, with reference to the relation between relative left hemisphere and right hemisphere (RH) activation and regularity effects in lexical decision, regression analyses revealed that when the two subregions were entered separately into the model, they showed the same relation (i.e., relatively greater RH activation was associated with increased sensitivity to regularity at both sites). Moreover, when these two small regions were combined, the fit to lexical decision data improved considerably. Hence, in the current study, we combined the lateral and medial aspects of the extrastriate region when using the activation measure as a predictor variable.
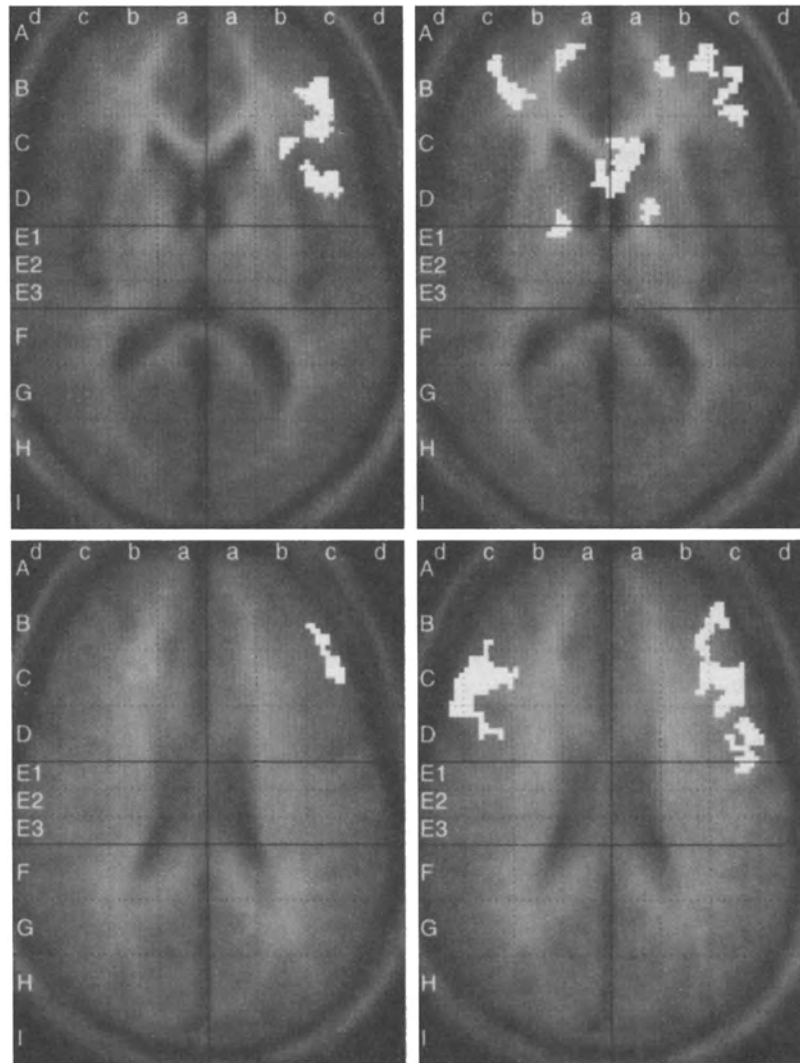
Figure 4. Composite images of the distribution of maximum activation (median *t* value > .80) during the rhyme minus case subtraction comparing 18 phonologically insensitive readers with exception minus regular (E-R) scores < 10 ms (upper and lower images on left) with 13 phonologically sensitive readers with E-R scores > 10 ms (upper and lower images on right). Activations are superimposed on composite anatomical images. The Talairach coordinate system (denoted by uppercase and lowercase letters) is overlaid on images (Talairach & Tornoux, 1988). By convention, brain images are viewed from below so that for each image, the individual's left hemisphere is on the reader's right. For phonologically insensitive readers, unilateral activation at Talairach z level = 8 (upper left image) is centered in the left inferior frontal gyrus (Cb, Cc) and extends into the middle frontal gyrus (Bb, Bc), left precentral cortex (Dc), and anterior insula (Cb). More superiorly at z = 20 (lower left image), activation involves primarily the left inferior frontal gyrus (Cc) and a small part of the left middle frontal gyrus (Bc). In phonologically sensitive readers at z = 8 (upper right image), activity is seen in the bilateral middle frontal gyri (BC, BB) and left inferior frontal gyrus (Cc). At z = 20 (lower right image), activation is centered in inferior frontal gyri bilaterally (Cb, Cc), with involvement of bilateral middle frontal (Bc) and bilateral precentral gyri (Dc) also present.

women. We found no evidence that RH proportion in any other region of the cortex was reliably associated with length effects. In summary, RH proportion was reliably better than sex in predicting reading performance (here, indexed by rejection latency) in the inferior frontal and

extrastriate regions of the cortex. Thus, the more a participant engaged the RH proportionately in two regions, extrastriate and inferior frontal, the more the rejection latencies in the subsequent lexical decision task covaried with nonword length. This pattern of results for nonword length

Table 3

Mean Latencies (in Milliseconds) for Short and Long Nonwords (Correct Rejections)

Group	Short	Long
RH proportion analysis (inferior frontal gyrus)		
Low RH proportion	577	597
High RH proportion	566	603
RH proportion analysis (extrastriate region)		
Low RH proportion	561	580
High RH proportion	581	619

Note. RH = right hemisphere.

effects mirrors closely the pattern observed for word regularity effects; in fact, we found that for these 31 participants, the correlation between the magnitude of regularity effect and the magnitude of the nonword length effect was strong and positive ($r = .54$). We interpreted both effects as expressions of the same mechanism: Participants who tend to engage phonological assembly of print also tend to engage in more fine-grained parsing of letter strings, which in turn is associated with increased sensitivity to length. The implications of this idea are discussed in the Discussion section.

Regression analyses. We considered earlier the hypothesis that participants whose lexical decision performance suggests that they are or are not sensitive to regularity in lexical decision will show differential activation in phonological regions when reading real words in the magnet. To test this hypothesis, we computed the activation (the number of significant voxels) associated with the semantic category minus line subtraction. This particular subtraction was used because (a) the experimental task, performed in the magnet, involved real word reading and so might be more comparable to the lexical decision task, which also used real words, and (b) the experimental and control tasks differed on all three linguistic dimensions—orthographic, phonological, and lexical-semantic—and therefore should provide the best indication of how real word reading distributes activation across cortical regions.

This subtraction did result in the broadest and most intensive cortical activation across regions. As noted earlier, the extrastriate region was shown to be most strongly associated with orthographic processing, the inferior frontal gyrus was most strongly associated with phonological processing, and the superior temporal gyrus appeared to serve both phonological and lexical-semantic processing. Accordingly, we regressed the E-R difference score on activation in these three regions, in both the LH and RH, for each participant. Thus, the initial model had six independent variables. This model was significant, $F(6, 24) = 7.12, p < .001, R^2 = .64$. When two nonsignificant variables were dropped from the model (i.e., the left superior temporal and left inferior frontal), the revised model was still highly significant, $F(4, 26) = 10.55, p < .001$, without an important loss in predictive utility ($R^2 = .62$). All variables in this model were significant, and each variable with its regression coefficient and significance level are shown in Table 4.

The pattern of partial regression coefficients indicates that RH extrastriate and inferior frontal gyrus activation levels were positively correlated with the magnitude of the E-R effect, whereas both the RH superior temporal gyrus and the LH extrastriate were negatively correlated with the effect. Thus, readers who were most sensitive to regularity effects tended to activate extrastriate and inferior frontal sites more strongly in the RH, but they also tended to activate the RH superior temporal gyrus and LH extrastriate regions to a lesser degree than readers whose lexical decision performance was not so influenced by regularity.[4] Recall that we considered the hypothesis that readers not sensitive to regularity in real word reading would minimally activate phonological sites such as the inferior frontal gyrus in regression analyses in which real word reading was measured. However, what we found was that differences in sensitivity to regularity were associated with differences in distributions of RH-LH activation patterns at these sites, not in the presence or absence of activation in general.

The cortical activation pattern for word reading, observed in the magnet, accounted for a considerable proportion of the variance in regularity effects in lexical decision performance out of the magnet. Sex accounted for little variance above and beyond these cortical activation data. When added to this model as a variable, as with the RH proportion analyses just discussed, it made no significant additional contribution. Thus, although women in our sample were, on average, more sensitive to regularity influences, and this variable accounted for 26% of the variance in E-R scores, information about cortical activation in reading tasks had considerably greater predictive utility than did sex (account-

[4] The results from the regression analysis and from the right hemisphere (RH) proportion analysis were consistent for both the extrastriate and the inferior frontal regions. (In the regression model, the absolute values of RH activation were positively correlated with regularity, whereas the left hemisphere [LH] activation values were negatively correlated; accordingly RH proportion, a relative measure, showed an overall positive correlation with regularity.) However, the results from the superior temporal region did not reveal a simple relationship across the two types of analyses. RH proportion in this region was uncorrelated with regularity ($F < 1.0$). Nevertheless, in the regression model, we observed that absolute activation in the RH was strongly and negatively correlated with the magnitude of regularity effects. On first blush, this would lead us to expect that RH proportion would have shown a negative correlation with regularity. Subsequent analyses revealed, however, that RH and LH activation scores in the superior temporal region were highly correlated across participants ($r = .89$). Thus, activation in this region was symmetrical and bilateral (across participants, as LH activation increases so does RH activation). To confirm this, we entered either the RH or LH scores alone into the regression model. Both coefficients were significant, and both were negative when entered alone into the model. However, when both were included in the model, only the RH scores obtained significance, as discussed. Thus, we concluded that the relation with regularity is as follows: Participants whose activation in this region (bilaterally) was stronger were less sensitive to regularity than those whose activation in this region (bilaterally) was weaker.

Table 4

Regression Analysis: Semantic Category Minus Line Activation Data

Variable	β	F	p
Exception word minus regular word difference scores[a]			
Right inferior frontal	.614	22.6	.0001
Right superior temporal	−.278	20.10	.0001
Right extrastriate	.571	5.26	.0302
Left extrastriate	−.537	7.56	.0107
Nonword length effects (long minus short difference scores)[b]			
Right inferior frontal	.198	4.47	.0442
Right superior temporal	−.120	7.17	.0127
Right extrastriate	.428	5.64	.0252
Left extrastriate	−.537	2.48	.1272

[a] $R^2 = .62$. [b] $R^2 = .35$.

ing for 62% of the variance).[5]

The same four-variable regression model was applied to nonword length effect scores (i.e., reaction time difference scores for long vs. short words). As shown in Table 4, the model did a good job of accounting for individual differences in length effects ($R^2 = .35$). Important to our suggestion that the length effect indexed the same underlying process as the regularity effect (i.e., the extent of serial phonological processing), the same pattern of partial correlations was observed. The pattern indicates that right extrastriate and right inferior frontal activation were positively related to the magnitude of the length effects, whereas both the right superior temporal gyrus and the left extrastriate were negatively related. In summary, the patterns of brain activation that result in greater sensitivity to regularity were remarkably similar to those associated with increased magnitude of length effects on nonword rejection latencies, and, as noted, both effects were significantly correlated across participants.

Discussion

Perhaps the most general result from this study is that regional changes in cortical metabolism, observed while participants performed tasks designed to engage specific operations in word identification, covaried with independent measures of behavioral performance believed to reflect those same operations. Thus, we can infer that the cortical activity measured by fMRI is directly associated with the cognitive operations themselves and is not merely an epiphenomenon. Much of the obtained variance reflecting participants' differential sensitivity to phonological structure in lexical decision (as indexed by regularity and nonword length effects) can be accounted for by differences in inter- and intrahemispheric activation in several language and reading-related regions.

Our results strongly suggest that sex differences in the degree of bilateral activation of the inferior frontal gyrus during reading tasks, as reported in Shaywitz, Shaywitz, et al. (1995), are related to component processes in reading.

Women in our sample were more likely than men to activate both hemispheres in the region that was most strongly associated with phonological processing. They also tended to be more influenced by spelling-to-sound regularity on real word reading tasks performed out of the magnet.

The issue of why men and women tend to differ on both the reading performance and the neurobiological profiles is a complex one that will require further study. In this connection, it is important to note that the sex differences observed in our study were differences in the mode of word recognition, not differences in skill. The participants were not selected with the intent to sample a wide range of individual differences; all were fluent readers, and the men and women did not differ in their overall reading speed or accuracy. Nonetheless, the finding that the women were more likely than the men to engage RH processing in the inferior frontal gyrus fits well with the literature. As discussed in the introduction, women in lateralized word processing experiments have, more often than not, shown a smaller RVF advantage than men. This probably reflects a tendency to process words bilaterally (e.g., Luh & Levy, 1995; Bradshaw, Gates, & Nettleton, 1977; Lukatela et al., 1986; Zaidel, Aboitiz, Clarke, Kaiser, & Matteson, 1995). Second, evidence of greater phonological coding for women specifically in the LVF/RH has been suggested in some of these studies (e.g., Luh & Levy, 1995; Lukatela et al., 1986). Differences like these might suggest a tendency for women to dedicate more of the RH to some kinds of language processing than men. If so, this could be expected to lead to an increased role for this hemisphere in women's reading performance. In any event, we emphasize that differences in the degree of lateralization in the inferior frontal gyrus, which are strongly correlated with an individual's gender, are systematically linked to differences in the mode of reading. At minimum, this shows that in the context of

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[5] However, given that there were sex differences in general with respect to localization, we examined men and women separately to determine whether there would be any differences with respect to which predictors would account best for variance in regularity effects. Note that 10 of 18 women had exception minus regular word (E-R) differences greater than 10 ms, whereas only 3 of 13 men showed this pattern. Hence, we were confronted with the fact that men as a group showed far less variability on this dimension. Nonetheless, for women, activation in right extrastriate (positive correlation), right superior temporal (negative correlation), and right inferior frontal (positive correlation) all were significant predictors ($R^2 = .60$). When left extrastriate was added (negative correlation), this variable was marginally significant ($p < .10$) and increased R^2 to .68. Thus, for women who varied more on the regularity effect, the model provided a good account of performance differences. For men, the only significant predictor was right superior temporal, and the correlation was negative (as with women). The R^2 for men was .49. Furthermore, in the other regions, which did not carry significant variance, the pattern of correlations matched the results for women. The relative contributions of each of these regions to E-R variance differed in the two groups; however, the overall pattern of right–left activation in each in relation to phonological sensitivity did not appear to differ systematically between the sexes.

the hierarchical subtraction paradigm, fMRI activation data can be interpreted psychologically.

Having noted the sex differences, we must emphasize that cortical activation profiles predicted better than gender which of the participants would exhibit sensitivity to the phonological structure of test items in reading, as indexed by regularity effects. Not only were activation differences strongly correlated with the magnitude of regularity effects, the neurobiological measures accounted for 10–36% more of the variance in performance than did gender.

Regularity, length, and bilateral activation. The hemispheric distribution of performance-correlated activity observed in the current study requires some comment. At first blush, the finding that increases in proportionate RH activation within the orthographic (extrastriate) and phonological (inferior frontal) regions were associated with greater sensitivity to assembled phonology might appear to be contrary to expectations derived on the basis of some previous investigations (e.g., Coltheart, 1980; Zaidel, 1983). Findings with split-brain participants, for example, have generally been taken to suggest that, in isolation, the LH is able to decode efficiently (i.e., to map from orthography onto phonology) but that the isolated RH is deficient at decoding, although it can recognize some familiar words. This would suggest, on the face of it, that the direct route to the lexicon is associated with RH function, whereas the so-called phonologically mediated route is associated with the LH. However, as discussed earlier, Iacoboni and Zaidel (1996) specifically tested this expectation and failed to find supporting evidence; regularity effects were observed in responses to stimuli presented to both visual fields.

Nevertheless, on the basis of the many indications that phonological processing is chiefly a LH process, we might expect that readers who engaged the RH to a greater degree should in fact be less sensitive to assembled phonology (as indexed by regularity and nonword length effects) than those who did not. In fact, we found the opposite at the inferior frontal and extrastriate sites. Furthermore, remember that the readers who showed regularity effects were not using the RH alone; activation was in fact bilateral. By contrast, readers who were relatively insensitive to regularity were, according to our fMRI measures, left lateralized in the inferior frontal and extrastriate regions and displayed relatively greater RH and LH activation in the superior temporal gyrus.

Why might bilateral activation in both anterior and posterior sites be associated with increased regularity (and increased length) effects? The account we propose is consistent with the bulk of the literature on lateralization of processes in word identification. In the context of dual-coding models, a regularity effect is a consequence of competition between the two processing systems in dealing with exception words. Competition yields two phonological representations, one derived from the assembled routine (i.e., a regularized but incorrect output, such as a short vowel in the word *PINT*) and another derived from the addressed routine (yielding an irregular but correct output, such as a long vowel for *PINT*). As noted in the introduction, several findings converge to suggest that the process-

ing of print that assembles phonemic representations operates in a serial (largely left-to-right) manner (Coltheart & Rastle, 1994; Content, 1991; Content & Peereman, 1993; Pugh et al., 1994). We now may ask how the tendency toward bilateral processing affects the resolution of a coding conflict.

As we noted, two kinds of evidence from visual hemifield studies suggest that the RH processes letter strings in a fine-grained and serial manner: larger length effects in LVF/RH presentations relative to RVF/LH presentations (Bub & Lewine, 1988; Ellis et al., 1988) and more errors on final letters than on initial letters in the LVF/RH (Hellige et al., 1994; Luh & Levy, 1995). The LH, by contrast, may be likely to adopt a parallel mode of letter processing, as evidenced by the absence of length effects and lower proportionate error scores on last letters. Critically, in the current experiment, participants who showed proportionately greater extrastriate and inferior frontal RH activation in the fMRI phase subsequently displayed the following results in the lexical decision phase of the experiment: (a) larger length effects on nonword rejection latencies, which suggests greater reliance on serial coding strategies, and (b) increased sensitivity to regularity, particularly for low-frequency target words.

On the view that regularity effects arise when one computational process yields an incorrectly regularized output for exception words and another yields the (correct) irregular form, we propose that RH serial coding, which is oriented to small phonological units, maps onto phonological representations differently than LH parallel coding, which is oriented to larger units such as onsets or rimes, syllables, morphemes, or whole words (see Koenig, Wetzel, & Caramazza, 1992, for evidence of greater sensitivity to morphological structure in the RVF/LH than in the LVF/RH). A regularized but incorrect output may be the result of a serial coding system, which also has a bias to look for correspondences between letters and phonemes at a small grain size. By contrast, a coding system that is biased to operate on larger sequences of graphemes also can produce a phonological output, but one that is correct even for exception words. Thus, participants who engage the anterior and posterior RH to a greater degree are more likely to display a processing mode dominated by a fine-grained transcoding bias (viz., regularity and nonword length effects).

The claim that regularity effects are based on conflict between a fine-grained assembled phonological code and output from coding at a larger grain size has received empirical support that was reviewed in the introduction. As noted, in previous lexical decision experiments conducted in our laboratory (Pugh et al., 1994), it has been observed that the same experimental conditions that suppressed regularity-consistency effects (conditions in which there were pseudohomophones among the nonword foils) also resulted in diminished effects of word length. Thus, when phonological processing was encouraged by excluding pseudohomophone foils, effects of regularity-consistency occurred and length effects also were observed. We speculate that the relation of bilateral activation to length and

regularity effects in the current study reflects the tendency for fine-grained (serial) mapping strategies to engage the relevant RH structures. When these sites are not engaged, diminished influences of both length and regularity are found.

We now discuss ways in which RH extrastriate and inferior frontal activation might contribute to the increases observed in length and regularity effects. Tables 5 and 6 show the brain activation patterns, along with an overview of the hypothesized roles of specific brain regions in producing relevant differences in reading mode. Note that in the fMRI analyses, across multiple subtractions, the extrastriate region was most strongly activated by orthographic coding (see Figure 1) and that the inferior frontal gyrus was most strongly activated by phonological processing (see Figure 2). We speculate that the output from RH extrastriate processing consists of strings of graphemes. Subsequently, these may be mapped into RH inferior frontal networks, which yield small-grained phonological representations as output. These representations then may be mapped into the richer phonological and lexical systems of the LH, where lexical resolution ultimately occurs. By contrast, the parallel processing tendencies of the LH might yield, for extrastriate output, larger sublexical orthographic units, which in turn map into phonological and lexical networks located at inferior frontal and temporal sites. When both coding strategies are used simultaneously, a reader encounters conflict in the case of exception words such as PINT. Readers disposed to use LH extrastriate and inferior frontal systems exclusively would be less likely to encounter conflict on these words.

Readers who proved insensitive to regularity and length were not in fact completely left lateralized. They tended to engage RH superior temporal sites along with LH superior temporal sites; indeed, they did so more strongly than did readers who were sensitive to regularity (who, in turn, activated the RH extrastriate and RH inferior frontal sites more strongly). Thus, we may suggest that bilaterally organized superior temporal sites are engaged in the processing of larger grain-sized units, possibly collaborating with inferior frontal processing systems in this regard. This possibility provides a coherent account of the obtained relations among length, regularity, and hemispheric activation patterns in the extrastriate, superior temporal, and inferior frontal regions. Furthermore, it incorporates the hypothesis,

for which there is some support, that certain RH processing systems engage in fine-grained (serial) parsing strategies for letter strings.

One need not assume, of course, that the phonological and lexical systems that these RH graphemic and phonemic units map onto are localized in that hemisphere; callosal transfer to the phonologically and linguistically richer LH must be happening. Resolution of the conflict in output that the two codes generate for exception words probably is dependent on LH processing systems. It would be reasonable to assume simply that the fine-grained parsing strategy that maps letters into related phonological units depends to some degree on contributions from RH extrastriate and inferior frontal networks.

Consider the mode of word identification associated with predominant LH extrastriate and inferior frontal activation (along with relatively stronger bilateral superior temporal activation), a mode of lexical processing in which regularity and length effects were weak or absent. As we have suggested, such processing is not necessarily purely visual-orthographic (i.e., processing without any recourse to sublexical phonology). In view of the emerging literature on the dominant role played by phonological coding in word recognition, as, for example, the studies that have isolated early processes by masked priming (Lukatela & Turvey, 1991, 1994; Perfetti & Bell, 1991), we speculate that coding systems in both hemispheres map onto phonological knowledge systems. The key difference between hemispheres would be in the grain size of the mapping (more fine-grained and serially organized for the system associated with RH extrastriate and inferior frontal sites). In short, the lack of regularity effects in a given participant's performance should not be interpreted to mean that access to the lexicon for that individual is necessarily without recourse to phonology. Instead, access may be phonological but at a grain size larger than the phoneme, perhaps to accommodate the exigencies of the morphological influences on the spelling of English words. In fact, Berent and colleagues (Berent & Perfetti, 1995; Berent, Van Orden, & Perfetti, 1995) have shown that regularity effects and more basic subthreshold phonological priming effects are dissociable, with regularity effects displaying more context dependence than phonological priming; priming occurred regardless of whether regularity effects were manifested. Thus, phonological structures may mediate lexical access even when regularity effects are not present. It may be the case that the presence or absence of regularity effects is a signature, not of phonological mediation but of an emphasis on serial and fine-grained-sized mapping routines, which in turn are linked to posterior and anterior RH systems, respectively.

We speculate that LH extrastriate and inferior frontal coding might be biased toward coding orthographic and phonological units of larger sizes, such as syllable rimes and onset clusters, or morphemes. If so, we might anticipate that readers not activating RH extrastriate and inferior frontal regions, despite their preference for course-grained phonological coding, will be sensitive to target word neighborhood consistency (or some other such variable) that can reflect a larger grained relation between a word's orthogra-

Table 5

Summary of Brain Activation Patterns, by Hemisphere, in Readers Sensitive to Regularity and Length and Those Not Sensitive to These Variables

Region	Readers sensitive		Readers not sensitive	
	LH	RH	LH	RH
Extrastriate	Strong	Stronger	Strong	Weak
Inferior frontal	Strong	Strong	Strong	Weak
Superior temporal	Weaker	Weaker	Stronger	Stronger

Note. LH = left hemisphere; RH = right hemisphere.

Table 6
Hypothesized Role in Printed Word Identification

Region	Left hemisphere	Right hemisphere
Extrastriate	Orthographic (parallel/larger units)	Orthographic (serial/smaller units)
Inferior frontal	Phonological (parallel/larger units)	Phonological (serial/smaller units)
Superior temporal	Phonological + semantic (?)	Phonological + semantic (?/larger units)

phy and its morphophonology. In the current lexical decision experiment, however, regularity and consistency were purposefully confounded, so we must await further experiments to sort out the regularity–consistency distinctions (see Bernstein & Carr, 1995, 1996, for a discussion of possible dimensions on which individuals may vary). We also might anticipate that both groups would demonstrate the use of phonology in a further study of word naming.

Why certain readers are more likely to engage the more fine-grained assembled system than others remains to be determined. Whether this is in any way related to some aspect of reading ability remains to be seen. As we found, women were far more likely than men to show this pattern, a finding that could be a consequence either of overall greater RH participation in language functions in women or a consequence of an experience in learning to read that focused them more on the detailed process of grapheme-to-phoneme decoding. If the latter idea has merit, we might speculate that an initial difference between men and women in their approach to reading may itself be a consequence of earlier development by women of relevant linguistic structures and metalinguistic abilities, although this remains to be determined. In any event, it is conceivable that earlier phonological awareness may lead to a focus on smaller grain-sized units, at least in the beginning stages of learning to read, although this hypothesis clearly is in need of testing.

How can we integrate this story with what is known about RH–LH processing differences in general? There is some evidence suggesting a tendency toward more concrete figural coding in the RH and more abstract coding in the LH for several types of behaviors. For instance, Marsolek, Kosslyn, and Squire (1992) found, in an implicit memory task requiring word stem completion, that both within-modality and case-specific visual priming were greater when test stimuli were initially presented to the LVF/RH. They proposed that the RH is more likely to code the specific details of an event in memory and that the LH codes in a somewhat more abstract fashion. Similarly, Metcalfe, Funnell, and Gazzaniga (1995) examined memory performance in a patient who had undergone a complete corpus callosum resection. The RH was superior at rejecting "new" events from similar "old" ones for several types of materials (e.g., visual forms, faces, and categorized word lists). Although such findings do not necessarily force us to predict that more fine-grained letter processing strategies will be engaged in the RH than in the LH for print stimuli, they are consistent with such a notion.

Finally, although a link among laterality differences, regularity, and nonword length effects is a clear outcome of this

study, we must note one apparent inconsistency. On the view that the more bilateral participants used a fine-grained and serial processing strategy, and therefore showed both greater regularity and nonword length effects, we also would expect that length effects on real words would be stronger in this group. However, neither group displayed word length effects; in fact, all participants were actually slightly faster on longer words than on shorter words. Why would this be so? It may be relevant that we are dealing with a small range of length differences (essentially four- vs. five-letter words and nonwords) and length effects usually are more robust for nonwords in general (Ellis et al., 1988). Thus, given the truncated range, influences of this variable might be expected only on nonwords. Furthermore, the four- and five-letter words differed on another potentially relevant dimension, neighborhood size (the five-letter words had fewer neighbors [$M = 4$] than the four-letter words [$M = 14$]), and perhaps this variable worked to obscure length effects in some way (although this difference in neighborhood size also was present for the nonword stimuli). It also has been suggested that words and nonwords differ on the automaticity dimension; nonwords appear to require greater attentional control (Sieroff, Pollatsek, & Posner, 1988; also see Carr, 1992, for a discussion of the relevant neural evidence). Perhaps the attentional variable might override length effects with so limited a range. Regardless of which variables might be interacting with length, we would nevertheless anticipate that a greater range on the length dimension would enable us to detect a group difference even for words, but this conjecture remains to be tested. However this may be, the critical fact remains: There was a strong and positive correlation between sensitivity to regularity for words and length effects (at least for nonwords) across participants, and each of these effects was strongly associated with individual differences in brain activation. All of this strongly implies that the bilateral participants were processing in a different mode, and, in our view, the most likely difference concerns the grain size of orthographic and phonological coding processes.

Theoretical implications. Our findings suggest that the cortical systems that are associated with different types of orthographic and phonological coding in printed word identification are located chiefly in different brain regions. Perhaps it is less important that they differ in laterality than that they simply differ (Milner, 1974). The variation in functional localization that we observed would appear to be broadly consistent with dual- or multiple-coding models of reading (but, as we explained, we need not necessarily assume that any system codes without recourse to phonol-

ogy). The basic finding is that participants whose lexical decision performance showed regularity effects (and greater length effects) used different cortical sites than did those who were relatively insensitive to these variables. These results appear to challenge alternative conceptualizations to which we referred in the introduction. For example, in purely orthographic, single-route models (Brooks & Miller, 1979; Glushko, 1979), the presence or absence of regularity effects would have to reflect postlexical processing differences. To explain the individual differences uncovered in our study, one would have to suppose that certain individuals use postlexical phonological coding to aid in making lexical decisions but that others do not. However, prelexical orthographic processing should be invariant across groups. Thus, those engaging postlexical phonology should activate phonological regions (inferior frontal and superior temporal) and the other should not. However, the finding of variation in the orthographically relevant extrastriate region would be unexpected in the single-route account.

In the PDP model proposed by Van Orden et al. (1990), phonological processing dominates the process of lexical access. Individual differences in sensitivity to regularity are explained by assuming differences in decision threshold setting, not in pathway selection (Stone & Van Orden, 1993). Higher threshold settings at the decision stage are assumed to be responsible for the increased magnitude of regularity-consistency effects. However, in the current study, participants who showed regularity effects were neither slower nor faster than those who did not. Instead, the two types of readers activated cortical regions in distinct ways. When performance in lexical decision contains signature effects of phonological assembly, different neural systems appear to be activated than when it does not. Such a result would not be anticipated on the threshold setting account. Hence, although these results do not rule out alternative conceptualizations, they appear most compatible with dual- or multiple-coding accounts.

In this connection, we should point out that a good deal of behavioral evidence suggests that skilled adult readers can modulate their word recognition processes to rely more or less on assembled phonological coding. Depending on task demands, the experimental context, or both, regularity effects can be made to appear or disappear in lexical decision performance (see Pugh et al., 1994, for a demonstration). Other evidence of context-induced shifts in the relative contributions of assembled phonology has been reported by several investigators (McQuade, 1981; Monsell, Patterson, Graham, Hughes, & Milroy, 1992; Paap & Noel, 1991; Pugh et al., 1994; Shulman, Hornak, & Sanders, 1978). It will be important to discover whether these experimentally induced shifts in the magnitude of regularity effects are associated with differential use of RH extrastriate and inferior frontal systems as assessed by fMRI.

To conclude, one implication of our findings is that it is possible to derive candidate cognitive models of the reading process from neuroimaging results. Perhaps, though, the most important lesson from this study is that the brain activation data obtained by fMRI do indeed pass a test of predictive utility on psychological performance and, in do-

ing so, promise to inform substantially research on the reading process.

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(Appendix follows on next page)

Appendix

Word Stimuli

Low-frequency regular words

wade, dock, pest, hike, math, greed, chore, grill, flag, junk, tile, rust, float, peel, wing, curl, sage, goat, dish, heel, doom, cart, flop, sail

High-frequency regular words

still, feel, thin, corn, nine, race, least, face, wake, these, beach, shell, came, fat, place, real, part, main, road, game, land, heat, desk, flat

Low-frequency exception words

deaf, worm, wool, warp, tomb, hood, wand, sew, sown, comb, steak, gross, flood, pint, doll, crow, hoof, cough, warn, vase, wasp, glove, bury, pour

High-frequency exception words

give, says, break, touch, lose, choose, watch, heard, both, some, phase, wash, come, foot, put, love, word, head, move, dead, live, pass, post, gone

Nonwords

afe, kun, koe, boaf, brak, boup, fote, lort, deek, delf, dort, goam, doke, droe, feeb, doan, fime, frem, sroe, gorl, herg, soam, klow, vole, larn, lige, luma, geel, nule, neek, nime, poan, boul, roce, rafe, rupe, soin, slok, skoe, mupe, thip, tirt, tove, goom, wike, werg, wyra, pung, blik, tive, coyd, nayt, dewt, voar, nyre, frue, kalp, kive, klum, korb, soaf, gaek, tals, deze, jile, rauk, tane, sume, sebe, sike, byne, woag, yura, woid, toin, sloar, moyce, brone, chape, shroe, chube, sitch, clane, goask, theel, grome, nownd, krame, moash, mulny, teece, ratch, skear, sloab, smook, stroat