

6 Computational Modeling and the Neural Bases of Reading and Reading Disorders

Jay G. Rueckl and Mark S. Seidenberg

As the content of this volume reveals, considerable progress has been made in understanding basic reading processes through extensive behavioral and neuroimaging studies of normal and impaired reading. This research has led to the development of detailed models of word reading, reading acquisition, and the bases of reading impairments. As many researchers have noted, writing systems afford two ways of determining the meanings of words: by mapping from spelling to meaning (the “direct” route) or by mapping from spelling to an intermediate phonological code and then to meaning (phonologically mediated access). The origin of the term *dual-route model* is obscure, but the concept of visual and phonological procedures was discussed as early as Baron and Strawson (1976; cf. Carr & Pollatsek, 1985; Seidenberg, 1985). Research within this framework has focused on the properties of these routes, and how their use differs as a function of factors such as type of word (e.g., high or low frequency), type of writing system (deep or shallow), and reader skill (see Seidenberg, 1995, for review).¹

One of the major theoretical approaches that has emerged from this research is a theory of normal and disordered reading based on principles of the connectionist or parallel distributed processing (PDP) framework (Harm & Seidenberg, 1999, 2004; Plaut, McClelland, Seidenberg, & Patterson, 1996; Seidenberg & McClelland, 1989). This theory has been implemented as a series of computational models that simulate different aspects of reading; they are collectively referred to as the “triangle” model. Specific principles on which the model is based (e.g., statistical learning of mappings between orthographic, phonological, and semantic codes; cooperative division of labor between components) are relevant to interpreting evidence concerning brain mechanisms. The modeling framework can be used to generate behavioral and neuroimaging predictions about different types of words, individual differences among readers, how properties of orthographies influence reading, the bases of developmental and acquired reading impairments,

AU: Check year for Seidenberg.

AU: Correct way to spell out PDP?

and other central questions. Specific predictions aside, the model provides a way of thinking about how the brain solves the computational problem of reading efficiently and for interpreting neuroimaging data.

The purpose of this chapter is to explain this approach and to discuss its implications for future research. Along the way, we describe how computational models are implemented, review key insights that have emerged from simulations of the triangle model, and demonstrate how these insights can be used to interpret the results of neuroimaging studies.

CONNECTIONISM AND COMPUTATIONAL MODELING

AD: Check heading levels throughout chapter.

Connectionist models are sometimes called neurally inspired because they incorporate structures and processes that are meant to mirror—at a quite abstract level—those found in the brain.² Thus, a connectionist network is composed of many simple, neuron-like processing units called *nodes* that communicate by sending excitatory and inhibitory signals to one another. Each signal is weighted by the strength of the connection that it is sent across, and the state of each node (its *activation*) is a nonlinear function of the sum of these weighted signals. Like neural synapses, the connections in a network are plastic, and a learning algorithm is used to adjust their strengths (or *weights*) such that, over the course of learning, the flow of activation becomes tailored to the structure and task demands of the environment in which the network is embedded (for overviews, see Elman et al., 1996; Rumelhart, Hinton, & Williams, 1986).

To model a specific cognitive process, this general theoretical framework must be augmented by domain-specific facts and conditions. In the case of reading, the essential facts concern the relationships between the spellings, sounds, and meanings of words (orthography, phonology, and semantics). As is clear from the triangle representation, each code can be computed directly from another code or indirectly via the remaining code. The semantic code, for example, can be computed directly from orthography or indirectly via phonology (spelling–sound–meaning). The phonological code can be computed directly from orthography or indirectly via semantics (spelling–meaning–sound). These facts follow from the nature of spoken language (mappings between sound and meaning) and the nature of writing systems (written symbols are associated with both sounds and meanings).³ These facts have been widely noted and incorporated in many reading models. Disagreements have focused on issues such as how these codes are represented (e.g., word-specific vs. distributed representations) and the extent to which the different pathways are involved in determining the meaning or pronunciation of a word.

In the triangle model, the relations among the codes are embodied by the architecture of the model. As depicted in Figure 6.1, the model includes distinct layers of nodes responsible for representing the orthographic, semantic, and phonological properties of written words. In each layer, the patterns of activation that represent different words are chosen so that words that are similar on the relevant linguistic dimension are represented by similar patterns of activation.

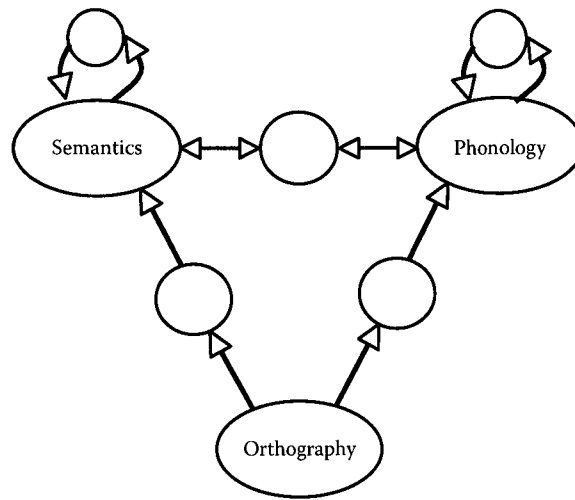


FIGURE 6.1 The triangle model (adapted from Harm & Seidenberg, 2004).

Thus, similarly spelled words are represented by similar patterns of activation over the orthographic layer, semantically similar words are represented by similar patterns of activation over the semantic layer, and so on. The nodes in these layers communicate with one another via the sets of connections (and “hidden units,” which will be discussed in more detail later) depicted in the figure. Seeing a word causes its corresponding pattern of activation to be instated over the orthographic layer. Activation then propagates to the phonological and semantic layers via the connections and hidden units (which are discussed in more detail later) depicted in Figure 6.1. Note that the inclusion of the phon↔sem pathway entails that the computation of word meaning is, in part, mediated by phonological knowledge and, conversely, that the computation of a word’s pronunciation is, in part, mediated by semantic knowledge.

An important tool for connectionists in general, and for proponents of the triangle model in particular, is computational modeling. The term *computational modeling* refers to the implementation of cognitive theories as computer simulations. There are a number of motivations for implementing theories in this way. First, simulations require a far more explicit theoretical description than is typically provided by traditional box-and-arrow models. Second, the behavior of a connectionist network is a consequence of complex, nonlinear interactions among a large number of components. Simulations provide a means of verifying that the model works as advertised; they can also lead to new insights about the nature of the underlying mechanism. Finally, simulations are a form of experimentation, allowing the modeler to investigate the effects of various sorts of manipulations. In the case of dyslexia, simulations have explored both hypotheses about possible underlying causes for the deficit and the effectiveness of various remediation strategies (Harm, McCandliss, & Seidenberg, 2003).

Simulations of connectionist models involve three steps: the initial specification of the model, training, and testing and analysis. During the first step the modeler specifies the network's architecture, and activation and learning functions; the structure of the its task environment; and the representational scheme for the network's input and outputs (i.e., the relationship between patterns of activation within the network and properties of its environment, including the actions it can take). The purpose of a simulation is to determine how these factors jointly determine the network's behavior. Thus, during the training phase the network is presented with a series of inputs, responds to each in turn, and adjusts its pattern of connectivity in accordance with its learning rule. At any point during the course of training, the modeler can employ a variety of behavioral and analytic tools to ask how the network is behaving and why it is behaving in the way that it is.

Over the last two decades a number of simulations of the triangle model have been conducted. Often these simulations focus on a single leg of the triangle (either orth \Rightarrow phon, e.g., Plaut et al., 1996; Seidenberg & McClelland, 1989; or orth \Rightarrow sem, e.g., Plaut & Gonnerman, 2000; Plaut & Shallice, 1993; Rueckl & Raveh, 1999), but recently several simulations of the full model have been reported (Harm & Seidenberg, 2004; Kello & Plaut, 2003). In many cases the network was trained on a set of real English words (Harm & Seidenberg, 2004; Plaut et al., 1996; Seidenberg & McClelland, 1989), but simulations involving Chinese (Yang, Zevin, Shu, McCandliss, & Li, 2006) and artificial vocabularies (Plaut & Gonnerman, 2000; Rueckl & Raveh, 1999) have also been conducted. Collectively, these simulations have been used to study a wide variety of tasks and phenomena, including word and nonword naming (Kello & Plaut, 2003; Plaut et al., 1996; Seidenberg & McClelland, 1989), reading for meaning (Harm & Seidenberg, 2004), the role of morphology in reading (Plaut & Gonnerman, 2000; Rueckl & Raveh, 1999), the effects of brain damage on reading (Plaut, 1995; Plaut & Shallice, 1993), developmental dyslexia (Harm & Seidenberg, 1999), and the effects of educational and remedial practices (Harm et al., 2003).⁴

Given the number and range of these simulations, we have chosen not to provide a comprehensive review (for this, the reader is referred to Harm & Seidenberg, 2004, and Seidenberg, 2005). Instead, our intention is to use some of the simulation results to illustrate how the network's behavior embodies the consequences of several critical computational principles. We then discuss the insights these principles provide about recent behavioral and neuroimaging results, as well as the implications of these principles for the direction of future research.

COMPUTATIONAL PRINCIPLES

THE IMPORTANCE OF STATISTICAL STRUCTURE

Learning attunes a connectionist network to the structure of its environment. In the case of reading, this structure involves the frequency and consistency of the correspondence between the orthographic, phonological, and semantic properties

of written words. Simulations of the triangle model have demonstrated the close relationship between the network's behavior and the statistical structure of the task environment and highlighted the differences between the triangle model and other conceptions of the word identification process.

Many of the simulations have focused on the mapping between orthography and phonology. This mapping is "quasiregular" in the sense that correspondences between the components of written and spoken words vary in the degree to which they are correlated, and the correlations are rarely perfect. For example, -ILL is always pronounced /il/ (as in PILL), and -INT is usually pronounced /int/ (as in MINT)—except that in the context of P- it is pronounced /Int/ (PINT)—but OUGH is pronounced differently in the contexts R-, C-, D-, PL-, THR-, and coda -T. Simulations have shown that the behavior of the triangle model reflects this fact: The speed with which a word can be named depends on whether the pronunciation of its body is consistent with the pronunciation of other words containing the same body. As is the case for human readers, the effects of orth⇒phon consistency are inversely related to word frequency, decrease as reading skill increases, and occur in both word and nonword naming (see Plaut et al., 1996, and Seidenberg & McClelland, 1989, for relevant simulation results and discussions of related behavioral findings).

The mapping from orthography to semantics is less systematic than the one from orthography to phonology, but even in this mapping statistical structure exists, particularly in the form of morphological regularities. That is, while in general there is no correlation between orthographic and semantic similarity, morphologically related words tend to both look alike and overlap in meaning (contrast BAKE, TAKE, and LAKE with BAKE, BAKER, and BAKERY). Simulations (e.g., Plaut & Gonnerman, 2000; Rueckl & Raveh, 1999) have shown that the triangle model can take advantage of these regularities, sometimes in rather subtle ways. For example, Plaut and Gonnerman (2000) showed that in their model morphological priming (the influence of seeing one word on the recognition of a subsequently presented morphological relative) depends not only on the joint orthographic–semantic similarity of the prime and target, but also on the "morphological richness" of the language. Priming was more robust if the network was trained on a language that contains a great deal of morphological structure (like Hebrew) than on a language in which morphological regularities are less frequent (like English).

THE DIVISION OF LABOR

In dual-route models a central issue concerns relations between the proposed pathways. The architecture of these models entailed that the visual and phonological pathways to meaning operated independently and in parallel. However, there were different views about which pathway would dominate in normal skilled reading. Some researchers (e.g., Coltheart, 1978, and subsequently) assumed that the visual pathway was faster in virtue of being more direct; moreover, the phonological pathway was thought to be unreliable given the irregularities in English

spelling–sound correspondences. Other researchers concluded that each pathway would tend to succeed for some types of words (e.g., direct: high frequency words, words with irregular pronunciations; phonologically mediated: words with “rule-governed” pronunciations).

In Coltheart, Rastle, Perry, Langdon, & Ziegler (2001) dual-route cascade (DRC) model, the two pathways mapping between orthography and phonology are not independent. Both pathways contribute to the activation of phonemes that are used in pronouncing a word or nonword. The routes involve different types of knowledge and processes (rules vs. an interactive-activation model). These built-in differences between the routes determine the division of labor between them, with exceptions handled lexically and nonwords nonlexically. As the 2001 model was implemented, the two routes interact very little in processing words, because the nonlexical route finishes much more slowly than the lexical route.

The triangle model incorporates a different idea: There is a cooperative division of labor such that input from all parts of the system jointly determines both what a word means and how it is pronounced. In the Harm and Seidenberg (2004) model, for example, the meaning of a word is activated by input from both orth \Rightarrow sem and orth \Rightarrow phon \Rightarrow sem parts of the triangle. This cooperative computation is possible because the same types of representations (distributed) and processing mechanisms (spread of activation) are used in all parts of the model. Thus, both orthographic and phonological units can activate semantic units. Harm and Seidenberg (2004) term this property *representational homogeneity*. The division of labor between the pathways emerges as the model learns to compute from orthography to meaning quickly and efficiently.

Harm and Seidenberg (2004) reported an extensive series of simulations exploring the division of labor in the triangle model, focusing primarily on the computation of word meaning. Using a variety of measures (including direct measures of the input the semantic units receive from other parts of the network, as well as the behavioral effects of lesions removing one or the other pathway), they confirmed that semantic activation depends on the cooperative interactions of the orth \Rightarrow sem and orth \Rightarrow phon \Rightarrow sem pathways. Their findings demonstrated that the semantic units receive significant input from both orth \Rightarrow sem and orth \Rightarrow phon \Rightarrow sem for almost all words, and that the model with both pathways intact computes meanings more efficiently than the paths do independently. Their results also revealed that the division of labor is affected by lexical properties such as frequency and spelling–sound consistency. On average, the isolated orth \Rightarrow sem and orth \Rightarrow phon \Rightarrow sem pathways were equally likely to compute the correct meaning of a low-frequency consistent word. In contrast, the orth \Rightarrow sem pathway was more accurate for high-frequency words and for low-frequency inconsistent words.

Two other findings that emerged from the Harm and Seidenberg (2004) simulations are particularly important. First, the division of labor changed over the course of learning. Early on, the model’s behavior was controlled by the orth \Rightarrow phon \Rightarrow sem pathway; as learning progressed and the orth \Rightarrow sem pathway became more efficient, the model moved toward a more cooperative division of

labor. Second, even at the end of training, the computation of phonology enjoys certain advantages over the computation of meaning: It occurs more rapidly, is less sensitive to visual masking, and so forth. These characteristics of the network's behavior relate well to findings concerning both the primacy of phonological codes in reading acquisition (Jorm & Share, 1983; Liberman & Shankweiler, 1985), the central role of phonology in skilled reading (Frost, 1995; Van Orden, Pennington, & Stone, 1990), and the close link between phonological deficits and impairments in reading acquisition (Fletcher et al., 1994; Snowling, 1991; Stanovich & Siegel, 1994).

The prominent role of phonology in both skilled reading and reading acquisition is a reflection of the fact that spelling and pronunciation are more highly correlated than spelling and meaning (Van Orden et al., 1990). However, with sufficient practice, the model picks up on mappings between spelling and meaning. The resulting division of labor therefore reflects characteristics of all of the mappings between codes, which vary from less predictable (orth \Rightarrow sem, phon \Rightarrow sem) to more predictable (orth \Rightarrow phon). These aspects of the model's performance highlight the important role of statistical structure in determining its behavior, but statistics are not the whole story. Another crucial factor is that the triangle model employs a *compensatory learning* procedure.

COMPENSATORY LEARNING

In the triangle model, learning is error driven, that is, changes in the strengths of the connections are based on the difference between the actual response of the model to an input and the ideal response given that input. Error (the difference between the actual and ideal responses) is generated whenever the network cannot produce the correct response or does so too slowly. In a system where input converges from several sources, the response of the network depends on the joint influence of those inputs, and thus the learning that occurs in one component of the network depends on the successes and failures of other components. In the triangle model, for example, the learning that occurs within the orth \Rightarrow sem pathway will depend on how quickly and accurately the orth \Rightarrow phon \Rightarrow sem pathway can activate the meaning of a written word. If the correct meaning can be generated rapidly by the orth \Rightarrow phon \Rightarrow sem pathway alone, little learning will take place within the orth \Rightarrow sem pathway. In contrast, if the orth \Rightarrow phon \Rightarrow sem pathway is not up to the job, the orth \Rightarrow sem pathway can learn to compensate for this deficiency. This type of learning contrasts with mechanisms that are correlative rather than driven by error, the classic example being Hebbian learning (Hebb, 1949). In such systems, learning of an item by one component (e.g., orth \Rightarrow sem) would be independent of the success or failure of other components (e.g., orth \Rightarrow phon \Rightarrow sem).

Compensatory learning is what allows the triangle model to maximize the cooperative interactions among its components. To illustrate this point, consider how the model learns to compute the meaning of a homophone. Under normal presentation conditions, homophones are disambiguated through the use of both orth \Rightarrow sem and orth \Rightarrow phon \Rightarrow sem. The isolated orth \Rightarrow phon \Rightarrow sem pathway can

produce correct patterns for higher frequency, dominant homophones. In the intact model, however, $\text{orth} \Rightarrow \text{sem}$ also delivers relevant activation quickly, particularly for higher frequency words. The role of $\text{orth} \Rightarrow \text{sem}$ is shaped by the fact that the $\text{orth} \Rightarrow \text{phon} \Rightarrow \text{sem}$ pathway cannot accurately compute both meanings of a homophone pair. The latter pathway eventually becomes more tuned to the higher frequency member of a pair because it is trained more often; however, $\text{orth} \Rightarrow \text{sem}$ also processes these words effectively and so contributes significantly

LEARNED HIDDEN REPRESENTATIONS

The triangle model employs two kinds of representations: The representations over the visible layers (i.e., the orthographic, phonological, and semantic layers) are stipulated by the modeler and (as noted earlier) are designed to capture certain kinds of similarity. In contrast, the modeler makes no a priori assumptions about the patterns of activation over the hidden layers; instead, the organization of these representations emerges from the learning process that adjusts the pattern of connectivity to improve the network's performance. The choice of stipulated representations is nontrivial, and significant advances have been made by considering the consequences of different representational schemes (see, for example, Plaut et al.'s, 1996, discussion of the implications of different means of representing the serial position of the letters or phonemes in a word). That being said, we believe that in the long run the properties of the learned hidden representations will be of greater theoretical significance. For example, as we discuss later, these properties suggest certain hypotheses about the function of the cortical circuits that underlie skilled (and disordered) word recognition. More broadly, the principles that determine how hidden representations are organized provide a means for paying back the "loan on intelligence" that is taken out when a theory stipulates what a person knows and how that knowledge is represented (Rueckl, 2002).

Hidden representations are necessary for the computation of some input–output mappings (the exclusive-OR task being the most well known, see Rumelhart et al., 1986), but in principle hidden units can play a role in the computation of any mapping. In particular, hidden units mediate the mapping computed by each leg ($\text{orth} \Rightarrow \text{phon}$, $\text{orth} \Rightarrow \text{sem}$, and $\text{phon} \Rightarrow \text{sem}$) of the triangle model, and simulations of the triangle model (and other connectionist models) have begun to yield insights about characteristics of learned hidden representations. One important insight is that the hidden representations are as *componential* as the prevailing conditions allow. That is, if there are statistical regularities involving components of an input (e.g., letters, word bodies, morphemes), the patterns of activation over the hidden units representing that input will contain (more or less) subpatterns corresponding to these components. Another key insight is that the hidden representations are organized to capture both similarities among the input patterns and similarities among the responses to which these inputs must be mapped. Thus, for example, the hidden units mediating the $\text{orth} \Rightarrow \text{phon}$ mapping are organized such that words that are similar in spelling (LAKE, TAKE) have relatively similar hidden representations, but so too do words that are similar in pronunciation (BEAR,

AU: Add Rueckl 2002
to refs.

BARE). Taken together, these characteristics provide the network with an efficient means for dealing with quasiregularity. For example, by positioning the representation of PINT somewhere near—but not too near—the representations of MINT and HINT, the network can take advantage of the similarities among these words (namely, that NT is pronounced /nt/) while also ensuring that PINT isn't pronounced as a rhyme of MINT. Similarly, learned hidden representations also provide a means for the network to generalize its knowledge to novel situations—for example, generating a plausible pronunciation of the nonword ZINT.

A number of simulations of the triangle model have explored how factors such as phonological consistency (Plaut et al., 1996; Seidenberg & McClelland, 1989) and morphological structure (Rueckl & Raveh, 1999) influence the organization of its hidden units. One noteworthy finding was reported by Harm et al. (2003) in a simulation exploring hypotheses concerning the effectiveness of various intervention methods designed to overcome developmental reading disorders. The simulation implemented the orth⇒phon leg of the triangle model and the model was trained to pronounce English words. To instantiate the hypothesis that dyslexia is an anomaly related to the representation of phonology, half of the connections among the phonological nodes were eliminated before training began. This manipulation renders the phonological system less able to clean up noisy input, and thus puts more pressure on the orth⇒phon connections to deliver precise input to the phonological layer. A comparison of this model's behavior to that of an intact network revealed that both networks correctly pronounced a high percentage of the words from their training set, but the impaired network was much worse at reading nonwords. Analysis of the hidden representations showed why: The impaired network's hidden representations were more holistic and less clustered by phonological similarity. As a consequence, the mapping from the hidden layer to the phonological representations was more idiosyncratic in the impaired model, and although experience with familiar words allowed the network to associate the hidden patterns for these words with their correct pronunciations, this knowledge could not be effectively generalized when the network was confronted with an unfamiliar input.

One surprising aspect of these results concerns the specificity of the input the phonological units receive from the hidden layer. One might suppose that the problems associated with dyslexia arise because the orthographic processes provide relatively noisy input to the phonological system, and that the nonword reading is more impaired than word reading because top-down knowledge can compensate somewhat for this degraded bottom-up input. However, the Harm et al. (2003) simulations suggest the opposite conclusion. Harm et al. compared the pattern of hidden-layer input to the phonological layer to the pattern of activation representing the pronunciation of each word. They found that these patterns were more similar in the impaired network than in the intact model. Thus, at least in this case, the deficit in reading skill was associated with hyperspecific inputs to the phonological level, not the sort of degraded inputs one might have expected. This finding not only points to the subtle properties of the learned hidden representations, but also to the importance of the compensatory nature of the learning

mechanism. The reason that the bottom-up input needed to be more exact is that the impaired network had fewer resources available (in the form of connections among the clean-up units) to compensate for any imprecision in the input to the phonological system. This result could also help explain the inconsistent evidence concerning the relationship between phonological processing and dyslexia—mild impairments in phonological processing that may be difficult to observe in commonly used tests of phonological processing could still have significant consequences on the reading acquisition process (see Harm & Seidenberg, 1999, as well as the following discussion).

THE TRIANGLE MODEL AND THE NEURAL BASES OF WRITTEN WORD RECOGNITION

The development of the triangle model has centered primarily on behavioral studies of skilled adult readers. That is, for the most part, simulation studies have examined how closely the behavior of the model mirrors that of participants in experiments studying skilled word recognition, and to a large extent the experiments that have been conducted to test the predictions of the model have focused on the behavior of skilled readers. In contrast, although there have been some simulations addressing findings concerning the neural bases of reading (e.g., Plaut et al., 1996; Plaut & Shallice, 1993), there has not yet been a serious attempt to ground the model in the wealth of recent findings concerning the brain mechanisms that support reading, nor is there a large number of brain-based experiments directly inspired by the triangle model.

In this section we discuss the relationship between the triangle model and evidence concerning the neural underpinnings of word recognition. In the last several decades, the development of neuroimaging techniques—in particular, functional magnetic resonance imaging (fMRI) and positron emission tomography (PET)—led to a rapid growth in our understanding of the neural underpinnings of reading. The neuroimaging evidence points towards three major left hemisphere (LH) components, each of which contains functionally dissociable subregions: a *posterior ventral* circuit including lateral extrastriate areas and a left inferior occipitotemporal (OT) area; a *posterior dorsal* circuit including the angular gyrus and supramarginal gyrus (SMG) in the inferior parietal lobule and the posterior aspect of the superior temporal gyrus (Wernicke's area); and an *anterior* circuit centered in and around Broca's area in the inferior frontal gyrus (IFG; see S. Frost et al., this volume.)

Inferences concerning the computational role of each region are based on evidence concerning the effects of factors such as lexical status (word–pseudoword), word frequency, and task (e.g., reading aloud vs. reading for meaning). This evidence suggests that the dorsal and anterior systems support phonological processes such as spelling-to-sound decoding and overt naming. These regions are strongly activated during phonologically oriented tasks (e.g., rhyme judgments) and in beginning readers (who are thought to be strongly reliant on phonological

recoding). In addition, activation in the anterior region is inversely correlated with phonological consistency (Fiez, Balota, Raichle, & Petersen, 1999; Frost et al., 2005; Herbster, Mintun, Nebes, & Becker, 1997), as would be expected of circuits underlying phonological processes in reading. Within the ventral system, the more anterior (middle temporal gyrus [MTG] and ITG) components appear to be semantically tuned: These regions tend to be strongly activated by tasks that recruit semantic processes (Price, Moore, Humphreys, & Wise, 1997; Rossell, Price, & Nobre, 2003); similarly, activation in these regions is correlated with semantic variables such as imageability (Frost et al., 2005; Sandak et al., 2004). In contrast, activation of OT is relatively unaffected by semantic variables, but is influenced by orthographic factors (Cornelissen, Tarkiainen, Helenius, & Salmelin, 2003; Dehaene, Cohen, Sigman, & Vinckier, 2005; Devlin, Jamison, Gonnerman, & Matthews, 2006; Vinckier et al., 2007) as well as variables such as frequency and lexicality (Fiebach, Friederici, Muller, & von Cramon, 1999; Kronbichler et al., 2004). Hence, this region is often described as the visual word form area (VWFA; Dehaene, Le Clec'H, Poline, Bihan, & Cohen, 2002; McCandliss, Cohen, & Dehaene, 2003).

At a broad level, then, the neuroimaging evidence suggests that the cortical reading system involves two major subsystems: a dorsal-anterior circuit that maps written words onto their phonological forms and a ventral circuit that computes the meanings of written words directly (that is, without phonological mediation). This is a comforting result in that it comports with a large body of behavioral findings and computational considerations that lead to the same conclusion. It is also suggestive of a mapping between the components of the triangle model and subcircuits of the cortical reading system. Specifically, we hypothesize that the role of the orthographic input units in the model is subserved by the occipito-temporal juncture (OT), that the O→S pathway in the model is embodied by the cortical pathway including the OT and the more anterior regions of the ventral system (MTG and ITG), and that the O→P leg of the model is instantiated by a cortical circuit that includes the OT and components of the dorsal and anterior subsystems (SMG and IFG, respectively). In light of this hypothesis, it is interesting to note that like the O→P subsystem in the triangle model, the dorsal-anterior pathway develops earlier in reading acquisition, is more strongly implicated in phonological processing, and operates less efficiently in less skilled readers (Pugh et al., 2000; Turkeltaub et al., 2003). Similarly, like O→S in the model, the ventral system develops more slowly but is more strongly implicated in skilled performance.

Thus, the hypothesized mapping between the triangle model and the cortical reading system seems like a reasonable first approximation. However, it should also be noted that others (e.g., Fiebach et al., 2002; Jobard, Crivello, Tzourio-Mazoyer, 2003) have interpreted the neuroimaging evidence in terms of more traditional dual-route models—models that are based on different computational principles, hold that the direct and phonological routes operate largely or completely independently of one another, and assume that the phonological route plays a relatively minor role in skilled word recognition, particularly when reading for meaning (e.g.,

AD: Same as orth-*sem* and orth-*phon*? If so, use one style throughout chapter.

Coltheart, 1978; Coltheart et al., 2001). To a certain extent, adjudicating between these views will be a question for future research. However, a consideration of the available evidence provides support for the triangle-model interpretation. Next, we consider evidence related to three issues: interactions between phonology and semantics in skilled word recognition, learning-related changes in brain activation, and the organization of representations in the OT/VWFA.

INTERACTIONS BETWEEN PHONOLOGY AND SEMANTICS

According to the triangle model, word recognition is achieved through cooperative interactions among the components of the reading system. These interactions are shaped by a compensatory learning mechanism that allows the contribution of one pathway to make up for deficiencies in the other. For example, the orth \Rightarrow sem pathway plays an especially important role in computing the meaning of a low-frequency homophone (e.g., EWE) because the connectivity of the orth \Rightarrow phon \Rightarrow sem pathway is tuned to compute the meaning of its higher frequency partner (YOU).

Thus, one signature of the cooperative division of labor is that the contribution of one pathway is stronger when the contribution of the other pathways is deficient. Given the fairly large number of neuroimaging studies of reading that have now been conducted, it is noteworthy that very few have attempted to look for such a signature—perhaps because the strategy has most often been to gather evidence that might isolate the specific contribution of various key cortical regions rather than focusing on the coordination among these regions. One exception is a study by Frost et al. (2005) that used fMRI to investigate the neural underpinnings of the Strain effect—a behavioral phenomenon first reported by Strain, Patterson, and Seidenberg (1995).

Strain et al. (1995) conducted a behavioral study examining the interaction between semantic and phonological influences on spoken word naming. To do so, they varied imageability (a semantic variable associated with the richness of a word's meaning), spelling-to-sound consistency (a phonological variable), and word frequency. Strain et al. found that the effect of consistency (consistent words named faster and more accurately than inconsistent words) was largest for words that are low in both frequency and imageability, and that the effect of imageability (high-imageable words named faster and more accurately than low-imageable words) occurred for low-frequency inconsistent words but not for low-frequency consistent words. This pattern of results suggests that word naming relies on both the orth \Rightarrow phon and orth \Rightarrow sem \Rightarrow phon pathways and that the influence of each pathway is most pronounced when the other pathway is slowest and most error prone. Thus, this pattern is a manifestation of the cooperative interactions between the phonological and semantic pathways posited by the triangle model. (It is worth noting that simulations of the triangle model confirmed that its behavior exhibits this same pattern; Harm & Seidenberg, 2004.)

Frost et al. (2005) used fMRI to identify the neurobiological correlates of the Strain et al. (1995) findings. The stimuli included low-frequency words that

varied in imageability and spelling-to-sound consistency. These critical words were presented in a sequence that also included nonword fillers, and participants were instructed to read aloud the words but not the nonwords. The behavioral results revealed the Consistency \times Imageability interaction found by Strain et al. In the fMRI analyses, higher activation for high-imageable words was found in the middle temporal gyrus (MTG) and the angular gyrus (AG)—regions that are often associated with semantic effects in reading (e.g., Price et al., 1997; Rossell et al., 2003). In contrast, as had previously been reported by Fiez et al. (1999) and Herbster et al. (1997), higher activation for inconsistent relative to consistent words was found in the IFG. Critically, this consistency effect was modulated by imageability: Imageability was associated with reduced consistency-related activation in IFG. This interaction appears to be the principal neural signature of the behavioral trade-off between semantics and phonology revealed by Strain and colleagues.

In addition to illuminating the division of labor among the cortical subsystems that underlie skilled reading, the Strain effect has also proven to be a useful tool for shedding light on reading disability. In a recent study, Pugh et al. (in press) observed that compared to nonimpaired controls, reading disabled adolescents exhibited an exaggerated Strain effect: Both groups benefited from high frequency and high imageability when reading difficult-to-decode inconsistent words, but these benefits were more pronounced for the disabled readers. The neurobiological underpinnings of this difference were examined by an analysis contrasting hemodynamic responses to the easiest (high frequency/high imageable/inconsistent) and hardest (low frequency/low imageable/inconsistent words) words. For nonimpaired readers, the easier words were associated with relatively reduced activation in most of the critical cortical reading circuits. In contrast, for reading-disabled individuals, easier words were associated primarily with heightened activation at key LH reading-related regions. An analogous pattern was observed in a second experiment, in which stimulus repetition was used to manipulate ease of processing. Whereas easier (i.e., repeated) words resulted in less activation of reading-related regions in nonimpaired readers, they evoked more activation in these regions for disabled readers.

One speculative interpretation of these results is that both disabled and nonimpaired readers rely on the cooperative interaction of the orth \Rightarrow phon and orth \Rightarrow sem \Rightarrow phon pathways, but the division of labor between these components of the reading system differs in the two groups. In particular, a greater reliance on the orth \Rightarrow sem \Rightarrow phon pathway (perhaps compensating for deficiencies in the orth \Rightarrow phon system) would yield the more pronounced benefits of imageability and frequency exhibited by the reading disabled. What would remain an open question is why the manipulations that are associated with a decrease in activation in the nonimpaired readers are associated with an increase in activation in the reading disabled. One possibility is that there is an inverted-U-shaped relationship between learning and neural activation, and that reading-disabled and nonimpaired readers are at qualitatively different points on this learning curve (see Pugh et al., in press, and the following discussion). Although this specific

interpretation is clearly speculative and requires additional experimental support, the fact that the hemodynamic responses of impaired and nonimpaired readers differ in this way will surely prove telling about the neurobiological basis of both skilled and disordered reading.

LEARNING-RELATED CHANGES IN THE DIVISION OF LABOR

A variety of findings indicate that in normally developing readers, increasing proficiency is associated with a shift in the relative contributions of the ventral and dorsal-anterior pathways. For example, in a cross-sectional study of young (7- to 17-year-old) normally developing readers, Shaywitz et al. (2002) found that during reading tasks, younger children exhibited strong engagement of the dorsal and anterior systems but showed limited engagement of the ventral system. In contrast, older children tended to show increased engagement of the ventral system, particularly the LH OT region. Importantly, this shift was related to reading proficiency and not merely chronological age: Activation in the OT was positively correlated with reading skill, such that greater activation was associated with higher reading scores. These results indicate that early in the acquisition process (when most written words are relatively unfamiliar), beginning readers rely on a more distributed system with greater right hemisphere involvement. As reading skill increases, a many of these regions play relatively diminished roles, whereas LH ventral regions (especially OT) become more critical (see Booth et al., 2001, and Turkeltaub, Gareau, Flowers, Zeffiro, & Eden, 2003, for additional support for this conclusion).

The dorsal-to-ventral shift that occurs as reading skill increases is also evident in the effects of word familiarity on the brain activation in skilled adult readers. Thus, compared to familiar words, unfamiliar pseudowords tend to result in more activation in the dorsal and anterior sites associated with phonological processing, but less activation in the more anterior sites in the temporal lobe associated with word meaning (Mechelli et al., 2005; Pugh et al., 1996; Rumsey et al., 1997). Experimental manipulations of familiarity yield similar results (Katz et al., 2005; Poldrack & Gabrieli, 2001). For example, Katz et al. (2005) found that multiple repetitions of a word resulted in reduced activation in a number of regions, including, in particular, the dorsal (SMG) and anterior (IFG) phonological circuits. This pattern was found in both lexical decision and naming, and was more pronounced in the lexical decision task, presumably reflecting the greater phonological demands of the naming task. (There was somewhat weak evidence of an increase in activation in anterior ventral sites—more so in lexical decision than overt naming.)

Learning-related changes in the neurobiology of reading are accompanied by behavioral changes that also suggest a shift in the division of labor between semantic and phonological processes. For example, beginning readers exhibit strong effects of spelling-to-sound consistency on both low- and high-frequency words (Waters, Seidenberg, & Bruck, 1984). In contrast, in skilled adult readers the effects of spelling-to-sound consistency are generally limited to the processing of

relatively unfamiliar low-frequency words. Experimentally increasing familiarity through repetition also diminishes or eliminates the consistency effect (Katz et al., 2005; Visser & Besner, 2001).

These learning-related changes in the magnitude of the consistency effect have often been taken as evidence the phonological route plays a secondary role—its primary contribution in skilled reading confined to the processing of relatively unfamiliar words and nonwords. According to this sort of account, the consistency effect comes about because the lexical and phonological routes yield conflicting information about the pronunciation of inconsistent words, with the phonological route assumed to operate via rules that “regularize” an inconsistent word (for example, reading PINT as a rhyme for HINT.) However, this conflict only has behavioral consequences if the lexical and sublexical processes have similar time courses. Repeated encounters with a word have the effect of speeding the lexical route, and thus as a word becomes more familiar the slower sublexical route becomes increasingly irrelevant to the recognition of that word. On this view, the dorsal-to-ventral shift in brain activation reflects this learning-related marginalization of the phonological route: Increased familiarity with a word results in a reduction in dorsal and anterior activation and/or an increase in the activation of an anterior ventral area (MTG), as would be expected if learning results in both the progressive engagement of the ventral (lexical) system and a corresponding disengagement of the dorsal and anterior (sublexical/phonological) subsystems.

The triangle model offers a different interpretation of both the behavioral and the neurobiological evidence. With regard to the behavioral evidence, the triangle model shares with the independent-routes account the assumption that the interaction of consistency and familiarity (measured by frequency, repetition, or skill level) is due, in part, to the greater influence of the orth \Rightarrow sem system on the recognition of high-frequency words. In contrast, the models differ in their assumptions about the characteristics of the phonological path. Due to the kind of computations it implements, in the triangle model the orth \Rightarrow phon pathway can compute the correct pronunciation of both consistent and inconsistent words. Inconsistent words are more difficult due to their statistical properties, but with sufficient training this difference is minimized. Indeed, simulations have shown that the widely observed interaction of frequency and consistency occurs even when the orth \Rightarrow phon pathway operates in isolation (i.e., when the orth \Rightarrow sem \Rightarrow phon pathway isn’t implemented). Thus, in contrast to a common interpretation of behavioral findings, the fact that under certain circumstances consistent words are read no faster than inconsistent words does not necessarily entail that the phonological pathway played an insignificant role in the reading of those words. This conclusion only follows given certain assumptions about the nature of the phonological recoding process—incorrect assumptions from our perspective.

A similar argument applies to the neurobiological evidence. Neuroimaging studies of perceptual and motor skill learning have demonstrated that although initial skill acquisition (unskilled performance) is associated with increased activation in task-specific cortical areas, continued practice of an acquired skill tends to be associated with task-specific *decreases* in activation in the same cortical

regions (e.g., Poldrack & Gabrieli, 2001; Ungerleider, Doyon, & Karni, 2002; Wang, Sereno, Jongman, & Hirsch, 2003). Thus, while one interpretation of the reduction in the activation of the dorsal-anterior circuit that occurs as a word becomes more familiar is that it reflects the disengagement of phonological recoding as the direct route (subserved by the ventral system) takes over, another explanation is that this reduction reflects the increasing efficiency of the phonological circuit that occurs over the course of learning (and that is revealed behaviorally in phenomena such as the Frequency \times Consistency interaction discussed earlier).

In light of this contrast, the results of an fMRI experiment by Sandak et al. (2004) are particularly interesting. In the initial phase of that experiment participants completed a behavioral session in which they performed tasks that were designed to focus their attention on different properties of three sets of pronounceable pseudowords. Specifically, the participants made orthographic (consonant-vowel pattern) judgments about one set of pseudowords, phonological (rhyme) judgments about another set, and semantic (category) judgments about a third. (In the semantic condition, participants learned a novel semantic association for each pseudoword; these associations formed the basis for the category judgments.) Over the course of the training session, each pseudoword was presented eight times (and in the same training condition across repetitions). Following training, participants completed an event-related fMRI session in which they overtly named trained pseudowords, untrained pseudowords, and real words. The experiment yielded a wealth of results, of which the ones involving the contrast between phonological and semantic training are especially relevant here.

Behaviorally, phonological and semantic training produced comparable benefits, as indexed by faster naming times compared to the orthographic condition. Neurobiologically, however, the effects of phonological and semantic training were remarkably different. Compared to the other training conditions, phonological training resulted in a reduction in the activation of dorsal (SMG) and anterior (IFG) sites that are thought to subserve phonological recoding. In contrast, semantic training was associated with increased activation in MTG, an anterior ventral site that has been implicated in semantic processing. Note, then, that these results include both elements of the dorsal-to-ventral shift—a reduction in dorsal/anterior activation and an increase in ventral activation. However, given the strong link between the activation changes and the nature of the training tasks that gave rise to them, these results do not suggest that the behavioral consequences of semantic and phonological training were due to the same underlying mechanism (a shift from phonological to lexical processes). Rather, they reveal that semantic and phonological training differentially affected the computations performed by the ventral and dorsal-anterior pathways. Semantic training involved the establishment of new semantic representations in MTG, resulting in more activation in this region and speeding overt naming by strengthening the contribution of the orth \rightarrow sem \rightarrow phon mapping. Phonological training improved the efficiency of the dorsal/anterior circuit (by strengthening the pre-existing knowledge that allows readers to generate a plausible pronunciation for an unfamiliar pseudoword), resulting in faster naming times and less activation in these regions.

One other aspect of the Sandak et al. (2004) results is of particular importance here. Phonological training was not only associated with an activation reduction in SMG and IFG, but also with a reduction in the activation of the ventral OT region (the VWFA). This pattern was also observed in the Katz et al. (2005) study discussed earlier: Repetition of real words (in both lexical decision and naming) led to an activation reduction in the SMG, IFG, *and* OT. Interpreting the reduced activation in the SMG and IFG as reflecting disengagement of these systems with learning creates a paradox if the same logic is applied to the reduced activation observed in the OT, given its crucial role in skilled reading. A more plausible interpretation is that the activation reduction in the OT, like the concurrent reductions in the SMG and IFG, is a reflection of an item-specific improvement in processing efficiency.

ROLE OF OT/VWFA

Given the critical role of the ventral OT region in skilled reading and reading acquisition, considerable effort has been dedicated to understanding its precise role. Several kinds of hypotheses have emerged from these efforts. According to some accounts (Cohen & Dehaene, 2004; Dehaene et al., 2002, 2005), the role of the OT is to store prelexical visual word forms—representations of letters and letter combinations. Other accounts (e.g., Kronbichler et al., 2004) suggest that the OT stores lexical (rather than prelexical) representations. Critically, by either account the representations stored in this region are orthographic in nature. That is, they capture information about how a word (and by the first account, a pseudo-word) is spelled (in a way that abstracts over variations in font, case, and so on) independently of the word's phonological and semantic properties. An alternative account is that the OT acts as an interface between information about visual form and higher order properties such as what a word means and how it is pronounced (Devlin et al., 2006).

Earlier we posited that the OT region in the brain is the analog of the orthographic input units in the triangle model. Given the nature of the orthographic representations used in extant simulations, this mapping would seem to suggest that the triangle model embodies the prelexical/orthographic account of the role of the OT. However, it is important to distinguish between the theory and its implementation. Implementations of the model have employed stipulated orthographic representations to investigate the properties of the downstream processes that map visual inputs onto semantic and phonological representations. However, this simplification overlooks important properties of the human reading system, which are relevant to the debate about the OT. First, we assume that all representations in the reading system are learned. Orthographic representations, for example, are learned primarily by seeing (comprehending) and writing (producing) letters and letter strings. Thus the units labeled “orthographic” in the simplified models are more like hidden-layer representations that mediate between perception and production. We assume the same is true for phonology (units

mediate comprehension and production of speech) and semantics (units mediate comprehending and producing messages).

Second, the properties of the orthographic units will be shaped by their participation in various mappings. Orthography is both the input to the mapping between O and P and the output of the mapping from P to O. Since the same hidden units are used in both directions, the properties of the orthographic representations will be shaped by their participation in both mappings. More generally, the “orthographic” representations can be thought of as hidden-unit representations that mediate many mappings. There is considerable evidence that phonological representations are shaped by orthographic knowledge; phonemic representations are closely tied to exposure to an alphabet (Bertelson & de Gelder, 1989). Harm and Seidenberg’s (1999) simulation showed this developmental tendency. Phonology is likely to have a similar effect in shaping orthographic representations. These properties of the computational model are consistent with the idea that OT employs componential representations that are organized to capture both input (visual/orthographic) and output (phonological and semantic) similarity. In this respect, our account is similar to the interface hypothesis proposed by Devlin et al. (2006).²

AD: Same as orth-
phon and phon-orth?
If so, use one style
throughout chapter.

Like other theories about the role of the OT in reading (Dehaene et al., 2005; Devlin et al., 2006; McCandliss et al., 2003), our account assumes that the visual system is organized such that at the time that a child begins to learn to read, printed words activate the OT and are represented in a manner that is relatively invariant over visual properties such as size and retinal position. Attempts to name these words or understand what they mean can generate error signals that pressure the OT to construct representations that are better suited to these tasks. Thus, while bottom-up input from the earlier parts of the visual system will tend to force the OT to represent visually similar words with similar codes, top-down feedback from phonological and semantic regions will tend to force the OT to organize its representations to capture phonological and semantic similarity.

Recent neuroimaging studies provide evidence that representations in the OT are phonologically and semantically “tuned” in this way. For example, in an fMRI study by Mencl et al. (2005), readers made lexical decisions about words that were preceded by primes that were either (a) both orthographically and phonologically similar to the targets (bribe–TRIBE), (b) orthographically similar but phonologically dissimilar (couch–TOUCH), or (c) unrelated (lunch–SCREEN). The phonologically dissimilar pairs (couch–TOUCH) evoked more activation than the phonologically similar pairs (bribe–TRIBE) in several LH cortical areas hypothesized to underlie phonological processing, including IFG, Wernicke’s area, and SMG. Notably, this phonological priming effect was also obtained within the LH OT (VWFA), as would be expected if the organization of the OT is influenced by phonological similarity and not purely orthographic similarity, as other accounts (Dehaene et al., 2005; Kronbichler et al., 2004) would suggest.

Other results provide evidence that the OT is semantically tuned as well. For example, Devlin et al. (2006) contrasted the activation of this region when readers were presented with prime-target pairs such as teacher–TEACH and

corner-CORN. These pairs are matched in terms of orthographic similarity, but differ in their semantic (and morphological) relatedness. Devlin et al. observed differential priming effects on the activation of the OT, again suggesting that orthographic similarity is not the sole determinant of how words are represented in this region.

It is important to note that while the triangle model predicts that the OT is both phonologically and semantically tuned, it also suggests that the influence of phonology will be more pronounced (for readers of English in particular). One reason for this difference is that the mapping between spelling and phonology is far more systematic than the mapping between spelling and meaning, and thus phonological feedback will provide a more coherent influence on the organization of the OT representations. Another relevant factor is the developmental trajectory of the reading system. As discussed earlier, the orth \Rightarrow phon \Rightarrow sem path dominates performance early in the acquisition process, and thus phonological feedback will be especially influential in the initial stages of learning (when the representations in the OT are most open to reorganization).

The differential influence of phonological feedback on the OT provides an explanation for a variety of findings. For example, we noted earlier that activation in this region during reading tasks is correlated with reading skill in children and adolescents (Paulesu et al., 2001; Shaywitz et al., 2002, 2004), and, critically, that dyslexics do not engage this region during reading (Paulesu et al., 2001; Shaywitz et al., 1998, 2002). This would be expected if the phonological system serves as a teacher that helps the OT develop representations that are appropriate for reading and if the underlying cause of dyslexia is a phonological deficit. If the phonological system fails to provide an appropriate teaching signal, the OT would not be able to learn properly and the reader would have to rely on other (less well-suited) processes.

The differential influence of phonological feedback on the OT is also relevant to the results of experiments investigating learning-related changes in skilled readers. Recall that in both the Katz et al. (2005) and Sandak et al. (2004) experiments discussed earlier, activation in the OT tracked activation in dorsal (SMG) and anterior (IFG) phonological sites. That is, manipulations that yielded activation reductions in other phonological sites (repetition in lexical decision and naming in Katz et al., phonological training in Sandak et al.) also produced activation reductions in the OT, whereas the manipulation that did not affect the phonological regions (semantic training in Sandak et al.) also failed to affect activation in OT. From our perspective, the strong coupling of OT with SMG and IFG reflects the systematic structure of the mapping from spelling to meaning and, as a consequence, the coherence of phonological feedback to OT. Given the arbitrary relation of spelling and meaning, semantic feedback will generally be less coherent, and thus more difficult to detect. (Morphological regularities provide an exception to this rule, as morphologically related words are typically similar in both form and meaning. Thus, we predict that when learning involves regularities of this sort there will be a measurable effect on activation in the OT.)

Aut: Check years for
Shaywitz et al. 1998
not in refs.

IMPLICATIONS AND FUTURE DIRECTIONS

In the preceding sections, we identified the computational principles embodied by the triangle model, described the results of simulations that illustrate how the model accounts for a wide variety of behavioral findings, and considered how the model might provide insights about the neural mechanisms that underlie reading. In this final section we look to the future, identifying some of the research questions that seem to us to be most pressing.

THE ARCHITECTURE OF THE READING SYSTEM

As indicated by both the earlier discussion and several of the other chapters in this volume, a great deal is now known about the network of cortical regions that subserve printed word recognition. That being said, there is surely much yet to be learned.

One critical issue concerns the further differentiation of the major cortical reading systems. As we noted earlier, although early neuroimaging results suggested that the reading system is comprised of three major subsystems (Pugh et al., 2000), this partitioning is rather coarse-grained and the accumulating evidence indicates that each of these regions includes several functionally distinct sites. For example, we have emphasized the contrast between the posterior and anterior components of the ventral system: The former includes the OT (the VWFA) and functions as an interface between the visual input and phonological and semantic subsystems; the latter includes areas responsible for processing word meaning, including the MTG and ITG. One important question is whether a more fine-grained differentiation of these ventral regions is needed (as suggested, for example, by the model of progressive abstraction within the fusiform region described by Dehaene et al., 2005, and Vinckier et al., 2007). Of particular interest given our hypothesis about the process that results in the specialization of the OT for reading is whether phonological and semantic feedback tunes the same region, or if instead they influence anatomically distinct sites. Similarly, within both the anterior and dorsal systems, functionally distinct sites have been identified based on their differential contribution to phonological or semantic processing (Devlin, Matthews, & Rushworth, 2003; McDermott, Petersen, Watson, & Ojemann, 2003; Roskies, Fiez, Balota, Raichle, & Petersen, 2001).

For us, getting better fine-grained characterization of these systems is a pressing concern for several reasons. One is that many of the sites in question are involved in speech perception and production as well as reading. Thus, there is the opportunity to connect reading research to the large body of findings concerning the neurobiology of speech (Hickok & Poeppel, 2004; Indefrey & Levelt, 2004; Scott & Johnsrude, 2003) and constrain our theories accordingly. Second, and relatedly, the relation between the processes involved in speech and reading is a relatively undeveloped aspect of the triangle model. It is not implausible that there are a number of “phonological” representations involved in speech perception and production, and these representations could differ in both their function and their

organization (e.g., whether they better capture acoustic similarity, articulatory similarity, or more abstract phonological properties).⁵ The triangle model does not differentiate among these possibilities and quite likely falls short because of this. For example, in the triangle model the phonological layer functions as the primary phonological subsystem in both “speech perception” (mapping phonology to semantics) and “speech production” (mapping semantics to phonology). Arguably, in the brain these functions are subserved by different regions (STG and IFG, respectively).

It is worth noting that the preceding discussion illustrates that the relationship between the model and brain data is a two-way street. On the one hand, we believe the model provides a useful theoretical framework for interpreting neurobiological evidence and generating hypotheses that can be tested using neurobiological methods. On the other hand, we expect that the results of neurobiological studies will motivate revisions of the computational theory, which is clearly oversimplified at present.

THE ROLE OF MORPHOLOGICAL STRUCTURE

Readers are influenced by the morphological structure of the words they read. Morphological effects on word recognition have been studied extensively using behavioral paradigms (for review, see Henderson, 1985; Rueckl, Mikolinski, Raveh, Miner, & Mars, 1997; Seidenberg & Gonnerman, 2000). In contrast, relatively little is known about the relationship between morphological structure and the cortical subsystems that support word reading, and only recently has research on this topic begun to emerge (e.g., Bick, Goelman, & Frost, 2008; Bozic, Marslen-Wilson, Stamatakis, Davis, & Tyler, 2007; Devlin et al., 2006). For a number of reasons, we believe there is a pressing need for this to change.

First, with the exception of morphological relatives, words that are similar in spelling or pronunciation are generally not similar in meaning. In other words, morphological regularities are a major source of statistical structure in the otherwise arbitrary mapping from form to meaning. From our perspective, statistical structure organizes the recognition process, and thus morphological regularities are as central to the operation of the orth \Rightarrow sem pathway as spelling-to-sound regularities are to the operation of the orth \Rightarrow phon pathway. In this light, it is interesting to note that many of the empirical and theoretical debates related to phonological recoding have parallels in the literature concerning the role of morphology in reading.

Second, and relatedly, manipulations of morphological variables could prove valuable in studying the division of labor between the phonological and semantic subsystems. It is striking that although there are many parallels between the literatures on the roles of phonology and morphology in reading, and, indeed, although many of the same scientists contribute to both literatures, relatively few studies have investigated whether morphological effects are modulated by phonological variables or vice versa, or, more generally, how the morphological and phonological properties of printed words jointly determine the process by which those words are recognized.

AU: Add Seidenberg & Gonnerman to refs.

Finally, understanding the effects of morphological structure on word recognition will be a critical aspect of research that compares word recognition processes across languages and writings systems (e.g., see R. Frost, this volume).

CROSS-LANGUAGE RESEARCH

Our working hypotheses are that the same neural systems are implicated cross-linguistically and that the computational principles that establish the division of labor in English also apply to other writing systems. These principles imply that because languages and writing systems differ in their statistical properties (e.g., orthographic depth—the degree to which an orthographic unit is consistently mapped to the same phonological unit), learning to read in different languages will give rise to somewhat different outcomes. However, these differences will not involve qualitatively distinct organizations, but rather different weightings in the division of labor between the phonological and semantic pathways. Cross-language comparisons, therefore, provide critical tests of the neurobiological and computational generality of our theory.

There is now an extensive body of behavioral research on word recognition in numerous languages. The results of this research are generally consistent with the claim that word recognition in skilled adult readers does not differ in any fundamental manner across writing systems. That is, although there may be differences in, for example, the types of phonological units that drive word recognition (Paulesu et al., 2000; Ziegler & Goswami, 2005; Ziegler, Perry, Jacobs, & Braun, 2001), there is ample evidence that readers of all writing systems employ both direct and phonologically mediated routes, that phonology plays an early and critical role in word recognition, and so forth (R. Frost, 1998; Perfetti, 1985). Similarly, studies of the neuroanatomy of word recognition (e.g., Chee, O'Craven, Bergida, Rosen, & Savoy, 1999; Fiebach et al., 2002; Kuo et al., 2003; Paulesu et al., 2000; Salmelin, Service, Kiesilä, Uutela, & Salonen, 1996) suggest that a common set of left hemisphere cortical regions, including occipitotemporal, temporoparietal, and inferior frontal networks, are almost always engaged in reading irrespective of the specific writing system under investigation. Also consistent with behavioral evidence, the neurobiological findings suggest that language-specific differences are a matter of degree, not of kind (Kuo et al., 2003; Paulesu et al., 2000).

Two positions that contrast with the conclusions of the previous paragraph should be noted. First, R. Frost (this volume) has compiled a variety of behavioral results indicating that readers of English and Hebrew differ in their responses to a range of experimental manipulations. He attributes these differences to the greater morphological richness of the Hebrew language and questions whether these differences can be accounted for by a “universal” theory that assumes that the set of computational principles underlies word recognition in any language. Our response is twofold. First, the simulations reported by Plaut and Gonnerman (2000) (discussed earlier in the section “Computational Principles”) provides some evidence that at least one finding of the sort reported by Frost falls out of the

dynamics of the triangle model when it is trained on writing systems that differ in their statistical properties. Second, although we expect that the other sorts of results discussed by Frost can be understood in the same way, we agree that simulations exploring this question would be illuminating regardless of how they turned out. In our view, though, both a deep understanding of the behavioral results and the ability to conduct truly compelling simulations will require a more thorough characterization of the Hebrew language and writing system than is currently available. Differences in the morphological structure of Hebrew and English words occur against the backdrop of variation along a number of potentially relevant dimensions, including the orthographic depth of the writing systems, the number and frequency of the root morphemes in each language, the relationship between morphological structure and syllabic structure, and the size of the orthographic and phonological neighborhoods of the words in each language, to name a few. In addition to simulations that would serve to test the triangle model, corpus analyses to better characterize the languages and behavioral studies that examine the effects of these and other variables are also needed.

A second challenge to the universalist account of word recognition, this time at the neurobiological level, comes from some neuroimaging studies of reading in Chinese. In general, reading Chinese words activates many of the same cortical regions that are activated during the reading of words in English and other alphabetic languages (Kuo et al., 2003, 2004; Tan et al., 2000). However, there is some evidence that certain regions are uniquely activated by Chinese words, including both superior parietal (Kuo et al., 2003) and left middle frontal regions (Tan et al., 2000). These results, should they hold up, most likely point toward an underdeveloped aspect of our account. Namely, the theory assumes that the development of the reading system reflects the interaction of several factors: general computational principles, facts concerning the structure of the language and writing system, and initial conditions (the state of the cognitive and neural system at the time that a child begins to learn to read). At this point we have not developed a detailed account of the initial conditions (especially with regard to the properties of relevant cortical regions), nor have we developed an account of the computational processes that underlie neural specialization. These issues are not in principle problematic for our approach, but the Chinese neuroimaging results may suggest that they will need to be addressed sooner rather than later.

DYSLEXIA

A unique property of computational models is that they provide a way to test causal hypotheses about normal and atypical development, and the effects of brain injury. One can configure or train the models in different ways and determine if they lead to identifiable variations in behavior. For example, Harm and Seidenberg (2004) showed that a model trained with feedback on both phonology and semantics learned more rapidly than one trained with regular feedback about semantics and only occasional feedback about phonology. These results are causal: Changing the model in specific ways has specific effects. They also run

counter to claims that children should learn to read visually, avoiding phonological mediation, because it is more efficient (e.g., Smith, 1978). Other experiments of this type could be conducted to determine whether there are benefits to ordering words in specific ways or teaching children about particular subword units (such as rhymes).

The models can also be used to study developmental impairments in learning to read words. A developmental disorder is simulated by introducing an anomaly in the architecture of the model, how processing occurs within the model, or in the experience the model is providing. In an early example of this type, Seidenberg and McClelland (1989) varied the number of hidden units in their model, which mapped from orthography to phonology. A model with too few hidden units could encode strong regularities between spelling and sound, but had difficulty learning irregular correspondences (as in AISLE and DONE). This pattern is seen in some dyslexic children; the pattern is sometimes termed developmental surface dyslexics (Castles & Coltheart, 1993; Manis, Seidenberg, Doi, McBride-Chang, & Peterson, 1996). However, it should be noted that most beginning readers are surface dyslexic in the sense that they perform better on words with consistent spelling-sound patterns and worse on exceptions.

The models provide tools for testing hypotheses about the causes of dyslexia, and they suggest some novel hypotheses (such as the architectural anomaly studied by Seidenberg & McClelland, 1989), but they do not make strong predictions about which anomalies actually occur in children. Most of the behavioral evidence points to the role of phonological information in developmental dyslexia. The basic hypothesis is that failures to development segmental phonological representations (i.e., differentiate BAT into three components) interfere with learning spelling-sound correspondences, which slows the child's entry into reading and has cascading effects on comprehension, spelling, and other aspects of school performance. This deficit has little effect on spoken language because speech does not require segmental representations. Humans were using spoken language long before writing systems were invented, and the speech of illiterates is normal. Segmental representations assume importance in the context of alphabetic writing systems, which represent phonemes. Similarly, other types of writing systems require other phonological representations, for example, subsyllabic (onset-rhyme) or syllabic (Ziegler & Goswami, 2005). Thus, the impairment in dyslexia is thought to be an anomaly related to the representation of phonology that has little effect on speech but greatly interferes with learning to read.

Harm and Seidenberg (1999) reported a simulation of this pattern. There are several ways to introduce phonological anomalies in the triangle model: for example, the representations themselves can be degraded (e.g., by deleting units), or the representations can be intact but the passing of activation along the pathway can be made imprecise (e.g., by deleting connections or adding noise to the activation function). Harm and Seidenberg examined the effects of mild and strong phonological impairments on two aspects of model performance: the acquisition of spelling-sound knowledge and an analogue of a common speech-perception task—the categorical perception of phonemes. A mild impairment interfered with

learning spelling–sound correspondences, producing a particularly strong deficit in nonword generalization, consistent with observations about dyslexic children. Performance on the speech-perception task remained normal, however. With a stronger phonological impairment, both reading and speech tasks were affected. Thus, the simulation results are consistent with the idea that a mild impairment could affect learning to read while having no discernable effect on spoken language processing. The results were also consistent with the observation that children with impairments in the use of spoken language (often termed *specific language impairment*) are both dyslexic and exhibit impaired speech perception (Bishop, North, & Donlan, 1996; Joanisse, Manis, Keating, & Seidenberg, 2000).

There is a strong consensus that dyslexia is associated with a phonological deficit; dyslexics consistently perform poorly on tests that require knowledge of phonemic structure. However, the basis for this impairment, and whether it is a cause or an effect of poor reading, is still unclear. Many researchers have examined whether dyslexics exhibit subtle impairments in auditory or speech processing. The literature here is highly inconsistent. Deficits have been observed in some studies (e.g., Ziegler, Pech-Georgel, George, Alario, & Lorenzi, 2005), but in others the effects have been limited to a subset of dyslexics who are also more broadly language impaired (Manis et al., 1996). There are also reports of failures to observe speech or auditory deficits in dyslexics who are not language impaired (e.g., Ramus & Szenkovits, this volume). Other failures to observe such effects may have occurred but would not be published because they are negative results. It is also possible that differences between dyslexics and nondyslexics are more prominent when they are young; such differences may resolve by the time the children reach ages at which they are identified as dyslexic. At this point, the hypothesis that dyslexia derives from a milder form of the speech-related processing impairment that is observed in children with specific language impairment (SLI) remains a viable hypothesis. Further studies, coupled with modeling of the sort described earlier, will be critical in addressing this debate and the related question of whether dyslexia is best viewed as a single phenotype or a condition comprised of several subtypes.

AD: Correct way to spell out SLI?

CONCLUSION

From the connectionist perspective, a reader's behavior is the manifestation of the interaction of a number of neural subsystems that cooperate to map a word's written form onto representations of its phonological and semantic properties. The division of labor among these subsystems is determined by a number of factors, including fundamental computational principles, neural constraints, and initial conditions related to the knowledge available to the beginning reader. Critically, the division of labor is also shaped by a learning process that attunes the reader to the statistical structure of the mappings among orthography, phonology, and semantics. Through the learning process, regularities in the task environment shape the reading network's pattern of connectivity, which in turn organizes the flow of activation that gives rise to behavior.

One purpose of this book (and the meeting from which it stems) is to identify the most promising directions for future research that would help us understand and address reading disability. Given the perspective articulated in this chapter, these directions might be organized around (a) identifying the environmental regularities that shape the reading process (for better or worse), (b) understanding the learning process that attunes a reader to the task environment (and that, perhaps, goes astray in dyslexia), and (c) characterizing the division of labor among the components of the reading system and identifying the forces that constrain the solution the reading system settles on.

Differences among languages and writing systems provide excellent opportunities for investigating how the reading system is shaped by environmental regularities, although we would note that cross-language comparisons would benefit from a more detailed and sophisticated characterization of the relevant regularities than is currently available. (This is especially the case when one considers the interplay of phonological and morphological regularities, which are generally investigated independently of one another.) An emphasis on statistical regularities would also benefit more applied research focusing on the causes and treatment of dyslexia. For example, reading disabled and nonimpaired children likely differ in the amount and variety of their reading experiences. If so, to what extent might differences in outcome be causally related to these differences in experience?

Environmental regularities can also be manipulated experimentally in “artificial lexicon” studies (e.g., Bailey, Manis, Pedersen, & Seidenberg, 2004; Sandak et al., 2004), which also provide a means for investigating the learning process that attunes the reader to the mappings among orthography, phonology, and semantics. It is noteworthy that learning has typically not been seriously addressed by theories of skilled word recognition, which stipulate complex mental structures and processes but generally fail to consider how these hypothesized entities come into being. From our perspective this is a mistaken approach in that it leaves such theories underconstrained and limits their utility as frameworks for addressing theoretically important questions, including, in particular, the nature of the developmental trajectory (or trajectories) associated with reading disability. This is especially problematic given intriguing new results concerning the neurobiological correlates of learning in dyslexic readers (e.g., Pugh et al., in press).

Our account stresses that behavior reflects both environmental regularities and the learning process that attunes readers to these regularities, but in the end, behavior is most directly the consequence of the cooperative interactions among the neural subsystems that subserve reading. Although the research directions highlighted in the preceding paragraphs would shed light on the division of labor among these subsystems, other lines of research should also be directed toward this goal. In part this would involve developing experiments that, like the Strain paradigm, are explicitly designed with this goal in mind. One possibility would be to explore the interactions of phonological and morphological variables, which presumably differ in the degree to which they reflect the operation of the orth-phon and orth-sem pathways. Another important advance, especially in light of

the growing importance of neuroimaging, would be the development of analytic techniques that are intended to characterize the interactions among regions rather than the activation of particular regions. Mencl, Frost, and Pugh (this volume) discuss some of the possibilities now on the horizon.

ACKNOWLEDGMENTS

This research was supported by National Institute for Child Health and Development grant HD-01994 to Haskins Laboratories. We would like to thank Ken Pugh, Einar Mencl, Stephen Frost, Len Katz, Nicole Landi, Rebecca Sandak, Laurie Feldman, and other members of the Haskins community for their contributions to the ideas presented here.

NOTES

1. The term *dual-route model* is ambiguous because it also refers to models in which there are two procedures for mapping from spelling to phonology (e.g., Coltheart, Curtis, Atkins, & Haller, 1993; Newcombe & Marshall, 1973). These models have focused on normal and disordered reading aloud and said little about access of meaning. See Coltheart (2000) and Harm and Seidenberg (2004) for discussion.
2. Although there are models where the units in a network (at either the single-unit or collective level) are meant to correspond to specific neural circuits, in general this is not the case. For example, the structure of the triangle model is not based on any particular assumptions about the organization of the cortical regions underlying reading. (However, questions about the relationship between the organization of the model and the organization of the cortical reading system are not uninteresting and are likely to drive future research.)
3. This statement is true independent of the fact that some writing systems encode phonological information more directly than others (see discussion of orthographic depth). Even arbitrary symbols such as & and / are associated with both pronunciations and meanings.
4. There are other connectionist models of word reading that have employed so-called localist networks (e.g., Grainger & Jacob, 1996; McClelland & Rumelhart, 1981). This research, much of which focuses on orthographic phenomena, is not reviewed here because it incorporates very different assumptions about knowledge representation and processing.
5. See Plaut and Kello (1999) for a connectionist model of a multilevel speech perception/production system that learns to represent phonological structure based on acoustic and articulatory constraints.

AU: Add Newcombe & Marshall to refs.

REFERENCES

- Bailey, C. E., Manis, F. R., Pedersen, W. C., & Seidenberg, M. S. (2004). Variation among developmental dyslexics: Evidence from a printed-word-learning task. *Journal of Experimental Child Psychology*, 87, 125–154.
- Baron, J., & Strawson, C. (1976). Use of orthographic and word specific knowledge in reading words aloud. *Journal of Experimental Psychology: Human Perception and Performance*, 2, 386–393.
- Bertelson, P., & de Gelder, B. (1989). Learning about reading from illiterates. In A. M. Galaburda (Ed.), *From reading to neurons* (pp. 1–23). Cambridge, MA: MIT Press.
- Bick, A., Goelman, G., & Frost, R. (2008). Neural correlates of morphological processes in Hebrew. *Journal of Cognitive Neuroscience*, 20, 406–420.
- Bishop, D. V. M., North, T., & Donlan, C. (1996). Nonword repetition as a behavioural marker for inherited language impairment: Evidence from a twin study. *Journal of Child Psychology and Psychiatry*, 37, 391–403.
- Booth, J. R., Burman, D. D., Van Santen, F. W., Harasaki, Y., Gitelman, D. R., Parrish, T. B., & Mesulam, M. M. (2001). The development of specialized brain systems in reading and oral language. *Child Neuropsychology*, 7, 119–141.
- Bozic, M., Marslen-Wilson, W. D., Stamatakis, E. A., Davis, M. H., & Tyler, L. K. (2007). Differentiating morphology, form, and meaning: Neural correlates of morphological complexity. *Journal of Cognitive Neuroscience*, 19, 1464–1475.
- Carr, T. H., & Pollatsek, A. (1985). Recognizing printed words: A look at current models. In D. Besner, T. G. Waller, & G. E. MacKinnon (Eds.), *Reading research: Advances in theory and practice* (Vol. 5, pp. 1–82). Orlando, FL: Academic Press.
- Castles, A., & Coltheart, M. (1993). Varieties of developmental dyslexia. *Cognition*, 47, 149–180.
- Chee, M. W. L., O'Craven, K. M., Bergida, R., Rosen, B. R., & Savoy, R. L. (1999). Auditory and visual word processing studied with fMRI. *Human Brain Mapping*, 7, 15–28.
- Cohen, L., & Dehaene, S. (2004). Specialization within the ventral stream: The case for the visual word form area. *NeuroImage*, 22, 466–476.
- Coltheart, M. (1978). Lexical access in simple reading tasks. In G. Underwood (Ed.), *Strategies of information processing* (pp. 151–216). London: Academic Press.
- Coltheart, M. (2000). Dual routes from print to speech and dual routes from print to meaning: Some theoretical issues. In A. Kennedy, R. Radach, J. Pynte, & D. Heller (Eds.), *Reading as a perceptual process*. Oxford, UK: Elsevier.
- Coltheart, M., Curtis, B., Atkins, P., & Haller, M. (1993). Models of reading aloud: Dual-route and parallel-distributed-processing approaches. *Psychological Review*, 100(4), 589–608.
- Coltheart, M., Rastle, K., Perry, C., Langdon, R., & Ziegler, J. (2001). DRC: A dual route cascaded model of visual word recognition and reading aloud. *Psychological Review*, 108, 204–256.
- Cornelissen, P., Tarkiainen, A., Helenius, P., & Salmelin, R. (2003). Cortical effects of shifting letter position in letter strings of varying length. *Journal of Cognitive Neuroscience*, 15, 731–746.
- Dehaene, S., Cohen, L., Sigman, M., & Vinckier, F. (2005). The neural code for written words: A proposal. *Trends in Cognitive Sciences*, 9, 335–341.
- Dehaene, S., Le Clec'H, G., Poline, J. B., Bihan, D. L., & Cohen, L. (2002). The visual word form area: A prelexical representation of visual words in the left fusiform gyrus. *NeuroReport*, 13, 321–325.

Alt: Add chapter page numbers

- Devlin, J. T., Jamison, H. L., Gonnerman, L. M., & Matthews, P. M. (2006). The role of the posterior fusiform gyrus in reading. *Journal of Cognitive Neuroscience*, 18, 911–922.
- Devlin, J. T., Matthews, P. M., & Rushworth, M. F. S. (2003). Semantic processing in the left inferior prefrontal cortex: A combined functional magnetic resonance imaging and transcranial magnetic stimulation study. *Journal of Cognitive Neuroscience*, 15, 71–84.
- Elman, J. L., Bates, E. A., Johnson, M., Karmiloff-Smith, A., Parisi, D., & Plunkett, K. (1996). *Rethinking innateness: A connectionist perspective on development*. Cambridge, MA: MIT Press.
- Fiebach, C. J., Friederici, A. D., Muller, K., & von Cramon, D. Y. (2002). fMRI evidence for dual routes to the mental lexicon in visual word recognition. *Journal of Cognitive Neuroscience*, 14, 11–23.
- Fiez, J. A., Balota, D. A., Raichle, M. E., & Petersen, S. E. (1999). Effects of lexicality, frequency, and spelling-to-sound consistency on the functional anatomy of reading. *Neuron*, 24, 205–218.
- Fletcher, J. M., Shaywitz, S. E., Shankweiler, D. P., Katz, L., Liberman, I. Y., & Stuebing, K. K. (1994). Cognitive profiles of reading disability: Comparisons of discrepancy and low achievement definitions. *Journal of Educational Psychology*, 86, 6–23.
- Frost, R. (1995). Phonological computation and missing vowels: Mapping lexical involvement in reading. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 21, 398–408.
- Frost, R. (1998). Toward a strong phonological theory of visual word recognition: True issues and false trails. *Psychological Bulletin*, 123, 71–99.
- Frost, S. J., Mencl, W. E., Sandak, R., Moore, D. L., Rueckl, J., Katz, L., et al. (2005). An fMRI study of the trade-off between semantics and phonology in reading aloud. *NeuroReport*, 16, 621–624.
- Grainger, J., & Jacobs, A. M. (1996). Orthographic processing in visual word recognition: A multiple read-out model. *Psychological Review*, 103, 518–565.
- Harm, M., McCandliss, B. D., & Seidenberg, M. S. (2003). Modeling the successes and failures of interventions for disabled readers. *Scientific Studies of Reading*, 7, 155–182.
- Harm, M. W., & Seidenberg, M. S. (1999). Phonology, reading acquisition, and dyslexia: Insights from connectionist models. *Psychological Review*, 106, 491–528.
- Harm, M. W., & Seidenberg, M. S. (2004). Computing the meanings of words in reading: Cooperative division of labor between visual and phonological processes. *Psychological Review*, 111, 662–720.
- Hebb, D. O. (1949). *The organization of behavior*. New York: Wiley.
- Henderson, L. (1985). Towards a Psychology of morphemes. In A. W. Ellis (Ed.), *Progress in the psychology of language* (Vol. 1, pp. 15–72). London: Erlbaum.
- Herbster, A., Mintun, M., Nebes, R., & Becker, J. (1997). Regional cerebral blood flow during word and pseudoword reading. *Human Brain Mapping*, 5, 84–92.
- Hickok, G., & Poeppel, D. (2004). Dorsal and ventral streams: A framework for understanding aspects of the functional anatomy of language. *Cognition*, 92, 67–99.
- Indefrey, P., & Levelt, W. J. M. (2004). The spatial and temporal properties of word production components. *Cognition*, 92, 101–144.
- Joanisse, M. F., Manis, F. R., Keating, P., & Seidenberg, M. S. (2000). Language deficits in dyslexic children: Speech perception, phonology, and morphology. *Journal of Experimental Child Psychology*, 77, 30–60.

- Jobard, G., Crivello, F., & Tzourio-Mazoyer, N. (2003). Evaluation of the dual route theory of reading: A meta-analysis of 35 neuroimaging studies. *NeuroImage*, 20, 693–712.
- Jorm, A. F., & Share, D. L. (1983). Phonological recoding and reading acquisition. *Applied Psycholinguistics*, 4, 103–147.
- Katz, L., Lee, C. H., Frost, S. J., Mencl, W. E., Rueckl, J., Sandak, R., et al. (2005). Effects of printed word repetition in lexical decision and naming on behavior and brain activation. *Neuropsychologia*, 43, 2068–2083.
- Kello, C. T., & Plaut, D. C. (2003). Strategic control over rate of processing in word reading: A computational investigation. *Journal of Memory and Language*, 48, 207–232.
- Kronbichler, M., Hutzler, F., Wimmer, H., Mair, A., Staffen, W., & Ladurner, G. (2004). The visual word form area and the frequency with which words are encountered: Evidence from a parametric fMRI study. *NeuroImage*, 21, 946–953.
- Kuo, W. J., Yeh, T. C., Lee, C. Y., Wu, Y. T., Chou, C. C., Ho, L. T., et al. (2003). Frequency effects of Chinese character processing in the brain: an event-related fMRI study. *NeuroImage*, 18, 720–730.
- Kuo, W. J., Yeh, T. C., Lee, J. R., Chen, L. F., Lee, P. L., Chen, S. S., et al. (2004). Orthographic and phonological processing of Chinese characters: An fMRI study. *NeuroImage*, 21, 1721–1731.
- Liberman, I. Y., & Shankweiler, D. (1985). Phonology and the problems of learning to read and write. *Remedial and Special Education*, 6, 8–17.
- Manis, F., Seidenberg, M., Doi, L., McBride-Chang, C., & Peterson, A. (1996). On the basis of two subtypes of developmental dyslexia. *Cognition*, 58, 157–195.
- McCandliss, B. D., Cohen, L., & Dehaene, S. (2003). The visual word form area: Expertise for reading in the fusiform gyrus. *Trends in Cognitive Sciences*, 7, 293–299.
- McClelland, J. L., & Rumelhart, D. E. (1981). An interactive activation model of context effects in letter perception: I. An account of basic findings. *Psychological Review*, 88, 375–407.
- McCusker, L., Hillinger, M., & Bias, R. (1981). Phonological recoding and reading. *Psychological Bulletin*, 89, 217–245. AU: Cite McCusker or delete from refs.
- McDermott, K. B., Petersen, S. E., Watson, J. M., & Ojemann, J. G. (2003). A procedure for identifying regions preferentially activated by attention to semantic and phonological relations using functional magnetic resonance imaging. *Neuropsychologia*, 41, 293–303.
- Mechelli, A., Crinion, J. T., Long, S., Friston, K. J., Lambon-Ralph, M. A., Patterson, K., et al. (2005). Dissociating reading processes on the basis of neuronal interactions. *Journal of Cognitive Neuroscience*, 17, 1753–1765.
- Mencl, W. E., Frost, S. J., Sandak, R., Lee, J. R., Jenner, A. R., Mason, S., et al. (2005). Effects of orthographic and phonological priming in printed word identification: An fMRI study. Manuscript submitted for publication.
- Paap, K. R., & Noel, R. W. (1991). Dual route models of print to sound: Still a good horse race. *Psychological Research*, 53, 13–24. AU: Update available? AU: Cite Paap or delete from refs.
- Paulesu, E., Démonet, J.-F., Fazio, F., McCrory, E., Chanoine, V., Brunswick, N., et al. (2001). Dyslexia: Cultural diversity and biological unity. *Science*, 291, 2165–2167.
- Paulesu, E., McCrory, E., Fazio, F., Menoncello, L., Brunswick, N., Cappa, S., et al. (2000). A cultural effect on brain function. *Nature Neuroscience*, 3, 91–96.
- Perfetti, C. A. (1985). *Reading ability*. New York: Oxford University Press.
- Plaut, D. (1995). Double dissociation without modularity: Evidence from connectionist neuropsychology. *Journal of Clinical and Experimental Neuropsychology*, 17, 291–321.
- Plaut, D. C., & Gonnerman, L. M. (2000). Are non-semantic morphological effects incompatible with a distributed connectionist approach to lexical processing? *Language and Cognitive Processes*, 15, 445–485.

- Plaut, D. C., & Kello, C. T. (1999). The emergence of phonology from the interplay of speech comprehension and production: A distributed connectionist approach. In B. MacWhinney (Ed.), *The emergence of language* (pp. 381–415). Mahwah, NJ: Lawrence Erlbaum Associates.
- Plaut, D. C., McClelland, J. L., Seidenberg, M., & Patterson, K. E. (1996). Understanding normal and impaired word reading: Computational principles in quasi-regular domains. *Psychological Review*, 103, 56–115.
- Plaut, D. C., & Shallice, T. (1993). Deep dyslexia: A case study of connectionist neuropsychology. *Cognitive Neuropsychology*, 10, 377–500.
- Poldrack, R. A., & Gabrieli, J. D. E. (2001). Characterizing the neural mechanisms of skill learning and repetition priming: Evidence from mirror reading. *Brain*, 124, 67–82.
- Price, C. J., Moore, C. J., Humphreys, G. W., & Wise, R. J. S. (1997). Segregating semantic from phonological processes during reading. *Journal of Cognitive Neuroscience*, 9, 727–733.
- Pugh, K. R., Frost, S. J., Sandak, R., Rueckl, J. G., Constable, R. T., Della Porta, G., et al. (in press). An fMRI study of the effects of stimulus difficulty on printed word identification: A comparison of non-impaired and reading disabled adolescent cohorts. *Journal of Cognitive Neuroscience*
- Pugh, K. R., Mencl, W. E., Jenner, A. J., Katz, L., Frost, S. J., Lee, J. R., et al. (2000). Functional neuroimaging studies of reading and reading disability (developmental dyslexia). *Mental Retardation and Developmental Disabilities Review*, 6, 207–213.
- Pugh, K. R., Shaywitz, B. A., Shaywitz, S. A., Constable, R. T., Skudlarski, P., Fulbright, R. K., et al. (1996). Cerebral organization of component processes in reading. *Brain*, 119, 1221–1238.
- Roskies, A. L., Fiez, J. A., Balota, D. A., Raichle, M. E., & Petersen, S. E. (2001). Task-dependent modulation of regions in the left inferior frontal cortex during semantic processing. *Journal of Cognitive Neuroscience*, 13, 829–843.
- Rossell, S. L., Price, C. J., & Nobre, C. (2003). The anatomy and time course of semantic priming investigated by fMRI and ERPs. *Neuropsychologia*, 41, 550–564.
- Rueckl, J. G., Mikolinski, M., Raveh, M., Miner, C., & Mars, F. (1997). Morphological priming, fragment completion, and connectionist networks. *Journal of Memory and Language*, 36, 382–405.
- Rueckl, J. G., & Raveh, M. (1999). The influence of morphological regularities on the dynamics of a connectionist network. *Brain and Language*, 68, 110–117.
- Rumelhart, D. E., Hinton, G., & Williams, R. (1986). Learning internal representations by error propagation. In D. E. Rumelhart, J. McClelland, & the PDP Research Group (Eds.), *Parallel distributed processing: Explorations in the microstructure of cognition. Vol. 1: Foundation* (pp. 318–362). Cambridge, MA: MIT Press.
- Rumsey, J. M., Horwitz, B., Donohue, B. C., Nace, K., Maisog, J. M., & Andreason, P. (1997). Phonological and orthographic components of word recognition: A PET-rCBF study. *Brain*, 120, 739–759.
- Salmelin, R., Service, E., Kiesilä, P., Uutela, K., & Salonen, O. (1996). Impaired visual word processing in dyslexia revealed with magnetoencephalography. *Annals of Neurology*, 40, 157–162.
- Sandak, R., Mencl, W. E., Frost, S. J., Rueckl, J. G., Katz, L., Moore, D., et al. (2004). The neurobiology of adaptive learning in reading: A contrast of different training conditions. *Cognitive, Affective, & Behavioral Neuroscience*, 4, 67–88.
- Scott, S. K., & Johnsrude, I. S. (2003). The neuroanatomical and functional organization of speech perception. *Trends in Neurosciences*, 26, 100–107.

AU: Update available?

- Seidenberg, M. S. (1995). Visual word recognition: An overview. In P. Eimas & J. L. Miller (Eds.), *Handbook of perception and cognition: Language* (pp. 137–179). New York: Academic Press.
- Seidenberg, M. S. (2005). Connectionist models of word reading. *Current Directions in Psychological Science*, 14(5), 238–242.
- Seidenberg, M. S., & McClelland, J. L. (1989). A distributed, developmental model of visual word recognition. *Psychological Review*, 96, 523–568.
- Shaywitz, B., Shaywitz, S., Blachman, B., Pugh, K. R., Fulbright, R., Skudlarski, P., et al. (2004). Development of left occipitotemporal systems for skilled reading following a phonologically based intervention in children. *Biological Psychiatry*, 55, 926–933.
- Shaywitz, B. A., Shaywitz, S. E., Pugh, K. R., Mencl, W. E., Fullbright, R. K., Constable, R. T., et al. (2002). Disruption of posterior brain systems for reading in children with developmental dyslexia. *Biological Psychology*, 52, 101–110.
- Smith, F. (1978). *Understanding reading*. New York: Holt, Rinehart, & Winston.
- Snowling, M. J. (1991). Developmental reading disorders. *Journal of Child Psychology and Psychiatry*, 32, 49–77.
- Stanovich, K. E., & Siegel, L. S. (1994). Phenotypic performance profile of children with reading disabilities: A regression-based test of the phonological-core variable-difference model. *Journal of Educational Psychology*, 86, 24–53.
- Strain, E., Patterson, K., & Seidenberg, M. S. (1995). Semantic effects in single word naming. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 21, 1140–1154.
- Tan, L. H., Spinks, J. A., Gao, J. H., Liu, H. L., Perfetti, C. A., Xiong, J., et al. (2000). Brain activation in the processing of Chinese characters and words: A functional MRI study. *Human Brain Mapping*, 10, 16–27.
- Turkeltaub, P. E., Gareau, L., Flowers, D. L., Zeffiro, T. A., & Eden, G. F. (2003). Development of neural mechanisms for reading. *Nature Neuroscience*, 6, 767–773.
- Ungerleider, L. G., Doyon, J., & Karni, A. (2002). Imaging brain plasticity during motor skill learning. *Neurobiology of Learning and Memory*, 78, 553–564.
- Van Orden, G. C., Pennington, B. F., & Stone, G. O. (1990). Word identification in reading and the promise of subsymbolic psycholinguistics. *Psychological Review*, 97(4), 488–522.
- Vinckier, F., Dehaene, S., Jobert, A., Dubus, J. P., Sigmna, M., & Cohen, L. (2007). Hierarchical coding of letter strings in the ventral stream: Dissecting the inner organization of the visual word-form system. *Neuron*, 55, 143–156.
- Visser, T., & Besner, D. (2001). On the dominance of whole-word knowledge in reading aloud. *Psychonomic Bulletin and Review*, 8, 560–567.
- Wang, Y., Sereno, J. A., Jongman, A., & Hirsch, J. (2003). fMRI evidence for cortical modification during learning of Mandarin lexical tone. *Journal of Cognitive Neuroscience*, 15, 1019–1027.
- Waters, G. S., Seidenberg, M. S., & Bruck, M. (1984). Children's and adults' use of spelling-sound information in three reading tasks. *Memory and Cognition*, 12, 293–305.
- Yang, J., Zevin, J. D., Shu, H., McCandliss, B. D., & Li, P. (2006). A triangle model of Chinese reading. Proceedings of the Twenty-Eighth Annual Conference of the Cognitive Science Society. Mahwah, NJ: Lawrence Erlbaum.
- Ziegler, J. C., & Goswami, U. (2005). Reading acquisition, developmental dyslexia, and skilled reading across languages: A psycholinguistic grain size theory. *Psychological Bulletin*, 131, 3–29.

- Ziegler, J. C., Pech-Georgel, C., George, F., Alario, F. X., & Lorenzi, C. (2005). Deficits in speech perception predict language learning impairment. *Proceedings of the National Academy of Sciences*, *102*, 14110–14115.
- Ziegler, J. C., Perry, C., Jacobs, A. M., & Braun, M. (2001). Identical words are read differently in different languages. *Psychological Science*, *12*, 379–384.