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Can Cognitive Models Explain Brain Activation During Word and Pseudoword Reading? A Meta-Analysis of 36 Neuroimaging Studies

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Reading in many alphabetic writing systems depends on both item-specific knowledge used to read irregular words (*sew*, *yacht*) and generative spelling–sound knowledge used to read pseudowords (*tew*, *yash*). Research into the neural basis of these abilities has been directed largely by cognitive accounts proposed by the dual-route cascaded and triangle models of reading. We develop a framework that enables predictions for neural activity to be derived from cognitive models of reading using 2 principles: (a) the extent to which a model component or brain region is engaged by a stimulus and (b) how much effort is exerted in processing that stimulus. To evaluate the derived predictions, we conducted a meta-analysis of 36 neuroimaging studies of reading using the quantitative activation likelihood estimation technique. Reliable clusters of activity are localized during word versus pseudoword and irregular versus regular word reading and demonstrate a great deal of convergence between the functional organization of the reading system put forward by cognitive models and the neural systems activated during reading tasks. Specifically, left-hemisphere activation clusters are revealed reflecting orthographic analysis (occipitotemporal cortex), lexical and/or semantic processing (anterior fusiform, middle temporal gyrus), spelling–sound conversion (inferior parietal cortex), and phonological output resolution (inferior frontal gyrus). Our framework and results establish that cognitive models of reading are relevant for interpreting neuroimaging studies and that neuroscientific studies can provide data relevant for advancing cognitive models. This article thus provides a firm empirical foundation from which to improve integration between cognitive and neural accounts of the reading process.

Keywords: dual-route cascaded model, triangle model, fMRI, PET, activation likelihood estimation

One major aim of neuroimaging research on language processing is to understand the brain mechanisms that underpin our ability to read both familiar words and pronounceable nonwords (pseudowords). This is an interesting problem because, at least in languages like English characterized by ‘deep’ orthography (Katz

& Frost, 1992), it requires both item-specific and generative knowledge. Most adults are able to read words with both regular and consistent spelling–sound mappings (such as *few*, *new*, or *stew*) and irregular and inconsistent mappings (such as *sew*, which is pronounced like *so*, not *sue*), and they are able to generalize this knowledge to pseudowords (such as *tew*). In this meta-analysis, we propose a unified framework that enables us to relate cognitive accounts of our ability to read these three kinds of stimuli to neural activity as revealed by functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) studies.

Until now, integration of cognitive and neural accounts has proved extremely difficult because cognitive models, such as the dual-route cascaded (DRC) model (Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001), triangle model (Harm & Seidenberg, 2004; Plaut, McClelland, Seidenberg, & Patterson, 1996), and connectionist dual-process (CDP+) model (Perry, Ziegler, & Zorzi, 2007, 2010), are not intended to simulate neural computations directly or to make explicit claims regarding the magnitude or location of neural activity. However, by focusing on (a) the degree to which a model component or brain region is *engaged* by a stimulus, driven by whether or not it represents that stimulus, and (b) how *effortful* a stimulus is to process if it is represented by a component or region, we are able to derive clear predictions about the expected hemodynamic response when people read words versus pseudo-

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words and irregular words versus regular words. These predictions are then tested against a quantitative meta-analysis of 36 neuroimaging studies. By delineating the convergence between the current state of the cognitive and neuroscientific literature, we demonstrate that cognitive models provide an appropriate foundation for guiding investigations of the brain bases of reading and that neuroscientific studies can provide data relevant for advancing cognitive models.

This meta-analysis uses activation likelihood estimation (ALE)—a technique that provides a means to quantify whether the clustering of activation peaks reported across studies reflects consistent functional organization. We derive meta-analytic statistical maps that provide anatomically precise hypotheses for future functional imaging studies and for other methods that rely on the spatial precision provided by functional imaging, such as electroencephalography (EEG and MEG) and transcranial magnetic stimulation (TMS). Turkeltaub, Eden, Jones, and Zeffiro (2002) originally developed the ALE method to quantify activation for word reading versus rest, and a similar technique was used to assess activation for word reading relative to rest across writing systems (Bolger, Perfetti, & Schneider, 2005). However, we are the first to use this technique to evaluate the predictions of reading models for neural responses to different classes of items (regular and irregular words and pseudowords), and to show that despite the variation in methods (PET, fMRI) and tasks (e.g., reading, lexical decision), the results from different studies converge and concord with existing knowledge of brain function.

In the sections that follow, we first describe the DRC, CDP+, and triangle models of reading. Next, we describe the principles by which we relate the processing conducted by model components to brain activation. We then outline predictions for brain activation during reading derived using these principles, giving concrete examples to illustrate how our approach differs to approaches taken in previous neuroimaging studies. Finally, we briefly introduce the ALE technique employed in the current meta-analysis.

Cognitive Models of Reading

In the DRC model (Coltheart et al., 2001; presented in Figure 1) there are two implemented routes for translating orthography to phonology. The nonlexical route contains rules for converting graphemes (letters or combinations of letters) into phonemes (single sounds) and is essential for reading pseudowords. The lexical route maps the orthographic form of known whole words to their corresponding phonological form and is essential for reading irregular words. The application of the nonlexical route to irregular words results in regularization errors (e.g., pronouncing *pint* as if it rhymed with *mint*). Likewise, though pseudowords are able to activate representations for visually similar words in the lexical route, the application of the lexical route to pseudowords results in omission errors (i.e., no response) or lexical captures (e.g., pronouncing *starn* as *start*). Regular words are pronounced correctly by both routes. Although it has been implemented only in very rudimentary form (Coltheart, Woollams, Kinoshita, & Perry, 1999), the DRC model also includes a semantic system that provides an alternative route by which whole-word phonological forms can be accessed from whole-word orthographic forms.

In contrast to the DRC model, the triangle model (presented in Figure 2) does not separate whole- and subword spelling-sound

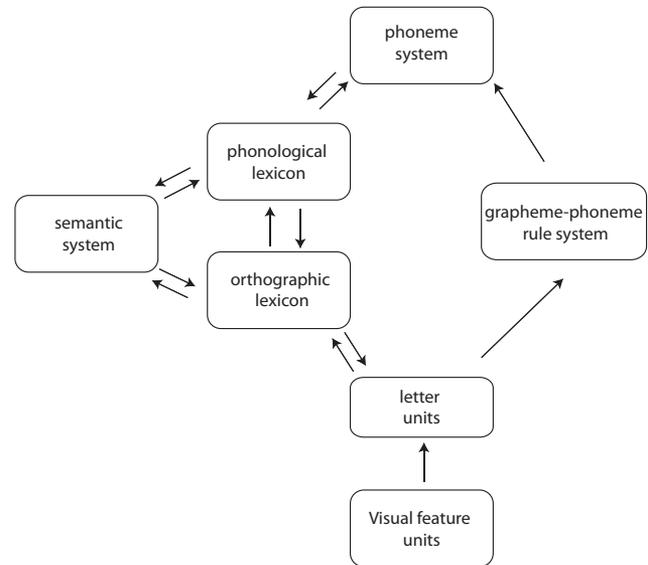


Figure 1. The dual-route cascaded model of reading aloud (Coltheart et al., 2001).

mappings. Instead, words and pseudowords are read with a more graded “division of labor” (Plaut et al., 1996, p. 56) between two pathways: one that maps orthography to phonology directly and another that maps orthography to phonology via semantic representations. The model does not have any built-in knowledge of how words are pronounced. Instead, it learns the relationship between orthography and phonology by being presented with the orthographic form of a word, attempting a pronunciation, and receiving the correct pronunciation as feedback. This feedback then modifies the strength of the connections between units, thereby increasing the probability of generating correct pronunciations in future.

Plaut et al. (1996) conducted computational simulations of such a system that focused on the generation of phonology from orthography. In these simulations, the semantic route to reading was not fully implemented. Instead, semantic support provided additional input to the phoneme units that pushed them toward their correct activations. Plaut et al. showed that this semantic support was particularly important for reading low-frequency inconsistent words whose spelling-sound mappings were difficult for the direct orthography-phonology route to learn. In contrast, the direct pathway captured statistical regularities in spelling-sound patterns and was particularly important for reading pseudowords because they do not have semantic representations. More recent work (Harm & Seidenberg, 2004), using a version of the triangle model with implemented semantic representations, has focused on the generation of semantics (rather than phonology) from orthography.

A point that needs explicit discussion here concerns the distinction between spelling-sound regularity and consistency. The regular grapheme-phoneme conversion (GPC) rules that govern the nonlexical route of the DRC model were selected on the basis of frequency in the language, with the most common pronunciation of a grapheme being considered its phoneme correspondence. Each GPC maps a grapheme to a single phoneme and is largely insensitive to context (i.e., what the other letters in a word are; see

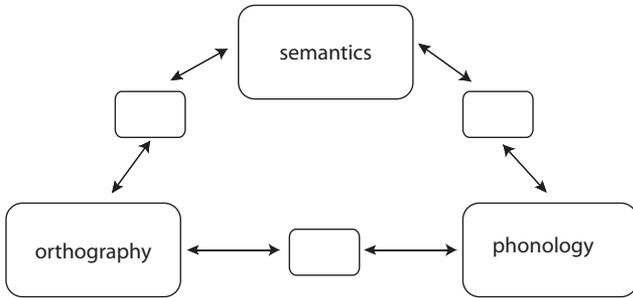


Figure 2. The triangle model of reading aloud (Harm & Seidenberg, 2004; Plaut et al., 1996).

Rastle & Coltheart, 1999). In contrast, the orthography–phonology mappings in the triangle model are sensitive to context; they encode how often a letter is pronounced a particular way given the other letters that surround it. The important variable governing pronunciation in this model is how consistent a word’s pronunciation is with other words that have similar spellings. Consistency is most commonly quantified on the basis of a word’s body (vowel plus following consonants) because the consonants following a vowel exert a strong influence on the pronunciation of English monosyllables (Treiman, Mullenix, Bijeljac-Babic, & Richmond-Welty, 1995). However, implementations of the triangle model have been shown to capture consistency at multiple levels (Harm & Seidenberg, 1999; for a fuller discussion of the distinction between regularity and consistency, see Zevin & Seidenberg, 2006). In addition, because the orthography–phonology connections in the triangle model are mediated by hidden units, this pathway is capable of encoding nonlinear spelling–sound mappings (e.g., that *have* is pronounced one way and *gave, pave, and wave* are pronounced another).

The CDP+ model (presented in Figure 3) contains a lexical route that is identical to that of the DRC model. However, unlike in the DRC model, the nonlexical route (or sublexical network) is not restricted to single grapheme–phoneme correspondences, but instead is a two-layer network that learns the most common spelling–sound correspondences at multiple levels. Similarly to the triangle model, the sublexical network of the CDP+ model can thus be said to be governed by spelling–sound consistency and could learn, for example, that *a* is most commonly pronounced as in *hat, mat, and cat* and that *a* followed by *ll* is pronounced as in *tall, wall, and ball*. This also means that multiple phonemes may be activated for each grapheme in a word or pseudoword. However, because it has only two layers, the CDP+ model sublexical network is much more limited than the triangle model in its ability to learn a consistent and an inconsistent spelling–sound mapping for the same combination of letters. For example, it would have considerable difficulty learning that *ave* is pronounced one way in *have* but another way in *gave, pave, and wave*. Both routes of the CDP+ model are activated in parallel for all item types. The lexical route is essential for correct reading of inconsistent words, and the nonlexical route is essential for correct reading of pseudowords. Any conflict between the two routes is resolved in the phonological output buffer via a settling process in which different pronunciations inhibit each other.

Some of the neuroimaging studies included in this meta-analysis manipulated spelling–sound regularity and others spelling–sound

consistency; often studies used a combination of the two variables. It was therefore not possible to control the regularity contrast as carefully as we might have liked, for example, by only including or comparing studies that defined words by regularity, or consistency, or at different grain sizes of consistency. Throughout this meta-analysis we use the term *regularity* when referring to the DRC model and *consistency* when referring to the triangle and CDP+ models. When discussing a particular experiment, we use the authors’ terminology.

The Relationship Between Processing in Model Components and Brain Activation

In considering the relationship between model components and brain activity, we must first acknowledge that none of the cognitive models discussed can be falsified by neuroimaging data concerning where in the brain a particular process is implemented (Coltheart, 2006b; Seidenberg & Plaut, 2006). However, all three models make claims about the computational processes that are important for reading words versus pseudowords, and irregular and inconsistent words versus regular and consistent words. They therefore make predictions about the *functional overlap* and/or *functional separation* of systems used to read these different word types. If we make the critical assumption that computational processes that are functionally separated in the two models can be mapped onto separate brain processes (Henson, 2005; Henson, 2006a, 2006b), then (a) these cognitive models become relevant for making predictions about the neural bases of reading processes, and (b) neuroimaging data become relevant for assessing these cognitive models. Our aim is not to adjudicate between the models but rather to highlight how well they explain and predict the neural instantiation of different aspects of the reading process. Our quantitative meta-analysis will therefore assess the *neural overlap* and *neural separation* of systems activated when reading different word types.

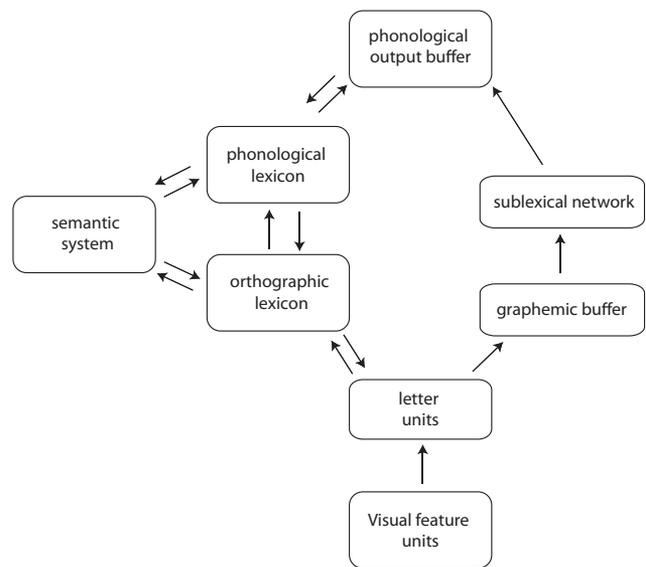


Figure 3. The connectionist dual-process model of reading aloud (Perry et al., 2007).

The blood-oxygenation-level-dependent (BOLD) signal measured by fMRI reflects the amount of input and intracortical processing performed by a specific brain region when processing a stimulus (Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001). We argue that two factors are relevant for assessing how processing in model components relates to BOLD signal: (a) the extent to which a model component or brain region is engaged by a stimulus, and (b) once a model component or brain region is engaged, how much effort is exerted in processing that stimulus. Considering first engagement, we propose that stimuli that are represented by a model component or brain region will engage it more, and thus elicit greater activity, than stimuli that are not represented by that component or region. With regard to effort, we suggest that within a set of stimuli that are represented by a region, some will fit the representations extremely well, thus requiring minimal effort to process and eliciting a relatively small amount of activity, and others will fit less well and thus require more effort to process and elicit a relatively large amount of activity. We further assume that BOLD signal reflects the summed activation in a model component over time and units. This results in the proposed inverted U-shaped function (depicted in Figure 4) that relates processing in a model component to BOLD signal. The large increasing section of the function is driven by strong versus minimal engagement of a component or brain region, and the somewhat smaller decreasing section is driven by engagement with maximal effort versus engagement with minimal effort.

The principles of engagement and effort are implicit in the two most common designs for brain imaging studies. The standard subtraction design is based on the principle of engagement; for example, brain activity during viewing of houses is subtracted from activity during viewing of faces to localize the fusiform face area because it is assumed that faces engage representations in this region more than houses (Kanwisher, McDermott, & Chun, 1997). A second common design is based on the effort principle; for example, unique versus repeated (or novel vs. familiar) presentations of faces are contrasted on the assumption that both engage the fusiform face area, but repeated or familiar faces are processed with less effort than unique or novel faces and thus elicit reduced neural activity in this region (Andrews & Ewbank, 2004; Grill-Spector, Henson, & Martin, 2006; Henson, Shallice, & Dolan,

2000; Rotshtein, Henson, Treves, Driver, & Dolan, 2005). Our novel contribution is to explicitly delineate the principles of engagement and effort and to characterize them in a way that makes them directly applicable to cognitive models. In the Discussion section we consider how our framework relates to a similar inverted U-shaped function proposed by Price and Devlin (2011) to explain activity in left ventral occipitotemporal cortex (vOT) at different stages of reading development and for different types of written stimuli. We also suggest ways in which our framework may help to forge the gap between cognitive neuroscience and developmental reading research.

Using Effort and Engagement to Derive Predictions for Neuroimaging Data

This section outlines how the principles described above are used to derive predictions from the DRC, CDP+, and triangle models for neural activity during word > pseudoword, pseudoword > word, irregular > regular word, and regular > irregular word reading. Figure 5 summarizes the predictions derived from each model. In each section we discuss which portion of the inverted U-shaped function is tapped by the contrast: strong versus minimal engagement of a model component or brain region for which a large difference in activity is expected, or effortful versus less effortful processing in a component or region, for which a somewhat smaller difference in activity is expected. We also suggest additional contrasts that could be used to examine the portion not tapped by our contrasts. For the contrast words > pseudowords, we conduct a novel simulation to examine activity for pseudowords, low-frequency words, and high-frequency words in the orthographic lexicon of the DRC model. This provides an example of how the influence of engagement and effort on processing can be directly derived from cognitive models. In most other cases, predictions are derived from quantitative data published in cognitive modeling articles. In a few cases, these data were not available, and we had to use qualitative judgments to derive predictions, on the basis of information such as the type of information represented by a component, or the how the model performed with different types of stimuli.

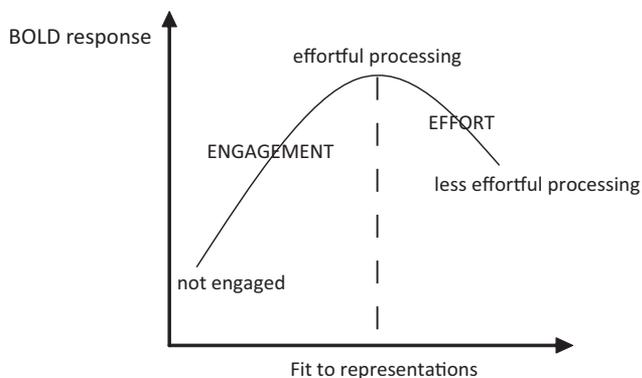


Figure 4. Inverted U-shaped function showing how engagement and processing effort in a model component relate to blood oxygenation level dependent (BOLD) signal.

Words > Pseudowords

In the DRC model, pseudowords have no lexical representations and can be pronounced accurately only via the GPC rules represented in the nonlexical route. This idea is supported by the existence of brain-damaged patients with acquired phonological dyslexia who have impaired pseudoword reading but retain the ability to read known regular and irregular words, reflecting isolated damage to a part of the brain corresponding to the nonlexical route (Coltheart, 1982, 2006a; Funnell, 1983; Henry, Beeson, Stark, & Rapcsak, 2007; Marshall & Newcombe, 1973; Roeltgen & Heilman, 1984). Lesion analysis of progressive aphasic patients with impaired pseudoword reading has linked this deficit to neural atrophy in the inferior parietal lobe, posterior middle and superior temporal gyri, and posterior fusiform gyrus (Brambati, Ogar, Neuhaus, Miller, & Gorno-Tempini, 2009). Some neuroimaging studies have taken these neuropsychological demonstrations to imply that “nonwords cannot activate word units in the orthographic and

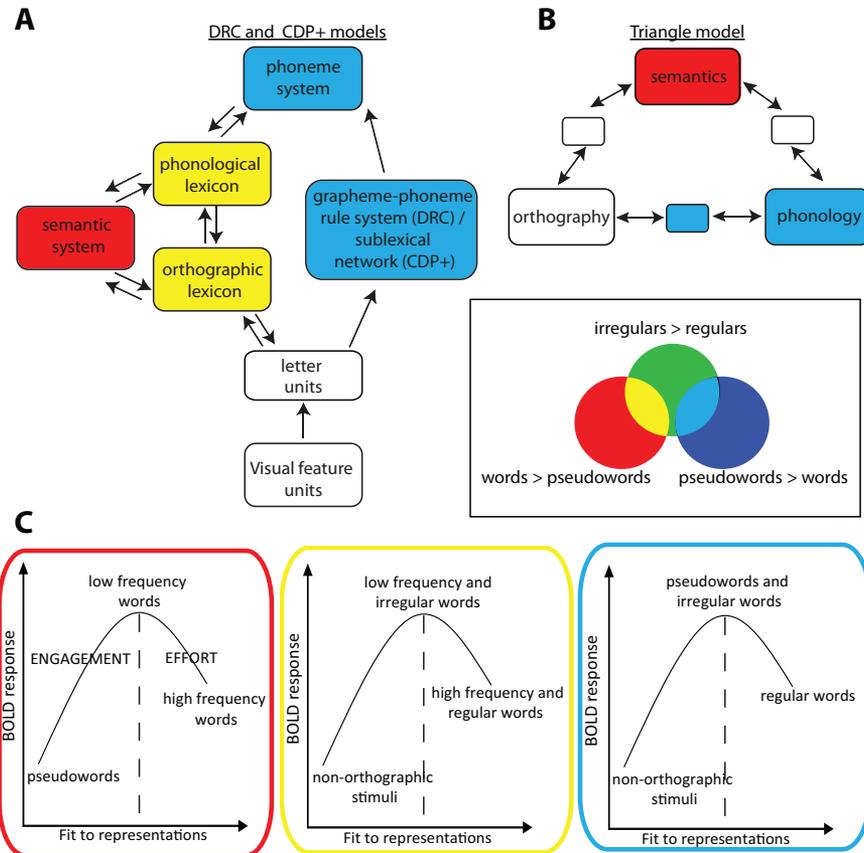


Figure 5. Predictions for activity in components of cognitive models during contrasts of interest, derived using the principles of engagement and effort. Each contrast is represented by a different color (blue, green, red), and overlaps between these colors (blue-green = cyan, green-red = yellow) represent cases where two contrasts are predicted to activate the same component. Note that the orthographic system of the triangle model is not predicted to be activated by any of the contrasts included in this meta-analysis because activity in this component should vary according to orthographic typicality, rather than lexicality or regularity. (A) Dual-route cascaded (DRC) and connectionist dual-process (CDP+) models. (B) Triangle model. (C) Schematics to show how each contrast was derived from the principles of engagement and effort. BOLD = blood oxygenation level dependent.

phonological lexicons” (Binder, Medler, Desai, Conant, & Liebenthal, 2005, p. 678), that is, that pseudowords do not engage representations in the lexical route. However, others have proposed instead that

in models based on localist word codes, the main determinant of the summed word node activation level for any given item is its neighborhood size. Because this factor was matched for words and nonwords, summed word node activation level should not have differed greatly for words and nonwords. (Binder et al., 2003, p. 383)

These examples illustrate confusion in the literature as to whether the DRC model predicts differences in lexical route activation for words relative to pseudowords.

To resolve this confusion, we use the principles of engagement and effort to translate the processing conducted by the lexical route of the DRC model to predictions for neural activity. The orthographic lexicon is a generalization of an interactive activation and competition model (Grainger & Jacobs, 1996; McClelland & Ru-

melhart, 1981) in which word units are activated by any item containing the right letters in the right position. Thus, pseudowords do activate word units of which they are neighbors (e.g., *starn* activates *stark*, *stern*, etc.). This activation cascades to the phonological lexicon and ultimately to the phoneme system (Coltheart et al., 2001, p. 224). However, whereas words fully activate their corresponding unit (as they contain all the right letters in the correct position), pseudowords only partially activate these units. Thus, because words but not pseudowords are represented by the orthographic lexicon, the prediction follows that words should engage and therefore activate a brain region corresponding to this system to a greater extent than pseudowords. Because the phonological lexicon receives activity from the orthographic lexicon and operates in the same manner (Rastle & Brysbaert, 2006), we also predict that reading and recognizing the visual forms of words relative to pseudowords should elicit greater activity in a brain region encoding whole-word phonological representations.

If words engage the lexicons more than pseudowords, which contrast might highlight effortful versus less effortful processing in such brain regions? Both low- and high-frequency words engage the orthographic and phonological lexicons, but activity rises slower and peaks later for low-frequency words. Summed activity over time is therefore higher for low-frequency than high-frequency words, reflecting the fact that low-frequency words require more effortful processing. Predictions derived from the DRC model thus fit the proposed inverted U-shaped function: pseudowords < low-frequency words and low-frequency words > high-frequency words.

Support for the above predictions is provided by the results of a novel simulation using Coltheart et al.'s (2001) implementation of the DRC model. The model was presented with 768 monosyllabic words under two conditions: when the words were assigned a frequency of less than one per million in the model's lexicon (low frequency) and when they were assigned a frequency of 1,000 times per million in the model's lexicon (high frequency). These were compared to 768 pseudowords, pairwise matched to the 768 words for length and neighborhood size using the ARC Nonword Database (Rastle, Harrington, & Coltheart, 2002). The task simulated was lexical decision, and thus processing terminated when the model had sufficient information to make a "word" or "pseudoword" decision according to the criteria delineated in Coltheart et al. (2001, pp. 228–229). Figure 6 shows total orthographic lexicon activity (sum of all units) at each cycle and summed-over cycles, for the item in each group with the median amount of activity. It is clear that activity is lower at both each cycle and summed-over cycles for pseudowords than words, reflecting the fact that they engage the orthographic lexicon to a lesser extent than words. Furthermore, processing is completed later and rises to a higher peak, resulting in higher summed activity over cycles, for low-frequency than high-frequency words. This result demonstrates that although both these word types engage the orthographic lexicon, low-frequency words are more effortful to process than high-frequency words.

On the basis of this simulation then, the DRC model predicts that the contrast words > pseudowords will tap engagement versus minimal engagement of brain regions corresponding to the orthographic and phonological lexicons and that contrasting high- and low-frequency words would tap the amount of effort exerted by these same brain regions during reading. The CDP+ model makes the same predictions (pseudowords < low-frequency words and low-frequency words > high-frequency words), as its lexical route is identical to that of the DRC model. The orthographic lexicon contains context- and form-independent representations of the appearance of the letter sequences comprising familiar words, and both the DRC and CDP+ models therefore predict word > pseudoword activity in brain regions involved in processing higher level visual information, such as occipitotemporal cortex. Both models also predict word > pseudoword activity reflecting the downstream engagement of the phonological lexicon. This activity may be observed in left supramarginal gyrus as this region has been suggested to represent the phonological forms of spoken words (Davis & Gaskell, 2009; Gow, 2012).

In contrast to the DRC and CDP+ models, the triangle model does not possess whole-word representations. Instead, the visual and spoken forms of words and pseudowords are represented as distributed patterns over a common set of orthographic and phonological units. In Plaut et al.'s (1996) and Harm and Seidenberg's (1999, 2004) implementations of the model, orthographic units were simply turned on or off to represent input patterns and thus would be equivalently engaged by words and pseudowords. However, Plaut et al. postulated that an orthographic system should be sensitive to how often letters occur in particular combinations and therefore that, "in the limit, the orthographic representation might contain all the letter combinations that occur in the language" (p. 67). This statement implies that a fully implemented orthographic component of the triangle model should develop representations of commonly occurring bigrams, trigrams, and perhaps even whole words.

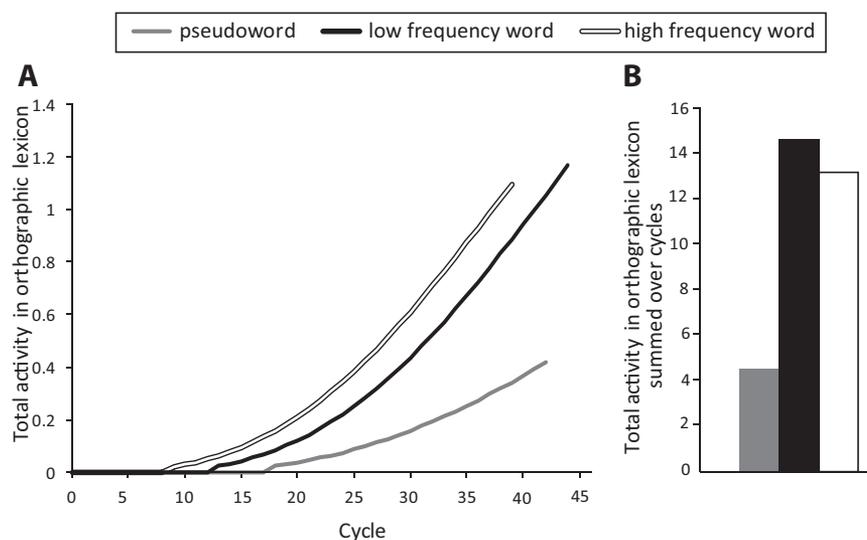


Figure 6. Total dual-route cascaded model orthographic lexicon activity (sum of all units) for the pseudoword, low frequency word, and high frequency word with the median amount of activity during a lexical decision task. (A) Activity at each cycle. (B) Activity summed over cycles.

One proposal for how this might come about is presented in simulations of orthographic learning by Sibley, Kello, Plaut, and Elman (2008), which were then incorporated into a version of the triangle model by Sibley, Kello, and Seidenberg (2010). Sibley et al. (2008) trained a sequence encoder to take variable-length inputs such as *cake*, *carrot*, or *caterpillar*, encode them as a compact fixed-width parallel code, and reproduce the input sequence at output. In Simulation 2b they showed that the model could learn to do this for 75,000 orthographic word forms and that performance then generalized to untrained pseudowords that followed the same orthographic structure, but not to untrained scrambled pseudowords. This suggests that the orthographic system developed representations of letter combinations that occur in words (i.e., have greater than zero n -gram frequency) but did not develop representations of letter combinations that do not occur in words (i.e., have zero n -gram frequency). We can therefore infer that this version of the triangle model predicts that pseudowords with zero n -gram frequency should engage brain regions representing orthographic form to a lesser extent than words and pseudowords with greater than zero n -gram frequency. In a further experiment, Sibley et al. (2008, Figure 4) varied the word likeness of pseudowords in a graded manner, showing that generalization performance was better (i.e., error was smaller) the more word-like participants rated an item to be. We therefore suggest that brain regions encoding higher level visual form should also exert greater processing effort, and thus be more active, for words and pseudowords with low relative to high n -gram frequency. These predictions fit with the proposed inverted U-shaped function relating engagement and effort of processing to brain activity: zero n -gram frequency pseudowords $<$ low n -gram frequency pseudowords and words, and low n -gram frequency pseudowords and words $>$ high n -gram frequency pseudowords and words. Note, however, that unlike in the DRC and CDP+ models, the triangle model predicts that activity in higher level visual processing regions should vary as a function of orthographic typicality rather than lexicality.

Considering semantic rather than orthographic factors, words clearly possess meaning, whereas pseudowords typically do not. In the DRC and CDP+ models, pseudowords weakly activate word neighbors in the orthographic and phonological lexicons and should therefore engage the semantic system to a minimal extent. These models therefore predict that pseudowords should activate brain regions representing semantics to a lesser extent than words. As neither the DRC nor the CDP+ model has a fully implemented semantic system, we are not able to make precise predictions on the basis of these models about the types of words that would be more or less effortful to process for brain regions representing semantics.

For the triangle model, explicit simulations with an implemented semantic system combine with the principles of engagement and effort to allow more precise predictions. Harm and Seidenberg (2004, Simulation 17) showed that within dense orthographic neighborhoods (e.g., *cat*, *bat*, *mat*), orthographically similar pseudowords (e.g., *dat*) did not activate and engage the semantic representations of existing words because the model learned a very precise mapping between orthography and semantics. In contrast, within more sparse neighborhoods (e.g., *yacht* cannot be changed into another word by transposing, substituting, or deleting a single letter), the model developed less precise orthography–semantic mappings because it did not need to dis-

criminate between similar-looking words. Thus, orthographically similar pseudowords (e.g., *yasht*) had the potential to activate and engage the source word’s semantic representation. Overall, words always engage the semantic system, whereas the extent to which this is the case for pseudowords depends on the properties of the words to which pseudowords are similar. Harm and Seidenberg (p. 690, Simulation 10) also showed that low-frequency relative to high-frequency words generated more error in the orthography–semantic pathway and took longer to settle on a semantic representation. Thus, semantic processing is more effortful, and brain activity in regions that represent semantics should be relatively greater, for low- than high-frequency words. The predictions from the triangle model for regions that process semantics once more fit the inverted U-shaped function: pseudowords $<$ low-frequency words and low-frequency words $>$ high-frequency words. We note that this prediction is identical to that derived from the orthographic and phonological lexicons of the DRC and CDP+ models.

A recent meta-analysis by Binder, Desai, Graves, and Conant (2009) suggested that semantic processing is distributed over a network of brain regions encompassing the angular gyrus, middle temporal gyrus, fusiform and parahippocampal gyri, dorsomedial prefrontal cortex, inferior frontal gyrus (IFG), ventromedial prefrontal cortex, and posterior cingulate gyrus. Thus, we expect the contrast words $>$ pseudowords to elicit activity in a number of these regions—a result that would be compatible with both the DRC and CDP+ models and the triangle model.

Pseudowords $>$ Words

In deriving predictions for this contrast, two components of the DRC model are relevant, both of which are engaged equivalently, but exhibit differences in processing effort, for words and pseudowords. The phoneme system of the DRC model is engaged by all items processed by the lexical and nonlexical routes. However, because the lexical route does not usually generate a phonological output for pseudowords and the nonlexical route typically operates more slowly than the lexical route, phoneme system processing continues for longer, and thus effort should be greater, for pseudowords than words. Similarly, the nonlexical route of the DRC model is equivalently engaged for words and pseudowords, as they both contain familiar graphemes. However, for words, the lexical route usually drives output before nonlexical route processing is complete. This is not the case for pseudowords; thus nonlexical route processing on average continues for longer, and effort is greater, for pseudowords than words. The DRC model therefore predicts that the contrast pseudowords $>$ words will highlight brain regions concerned with grapheme-phoneme conversion and phonological output.

In line with our prediction, many neuroimaging studies framed within the DRC model have suggested that pseudowords should activate brain regions that represent spelling–sound mappings more than words. However, some studies have implied that this is because the nonlexical route is not engaged by words. For example, Fiebach, Friederici, Muller, and von Cramon (2002, p. 19) claimed, “Grapheme to phoneme conversion rules assemble the phonological form of the orthographic stimulus in the case that the correct lexical entry is not rapidly identified on the basis of visual word form information.” Similarly, Fiez, Balota, Raichle, and Petersen (1999, p. 205) suggested, “In the absence of prior experience, pronunciation may involve slower alternative or additional

processes, such as a rule-based system that transforms sublexical orthographic to sublexical phonological units.” This is not the case. As outlined earlier, and as Fiebach et al. (p. 12) also stated, “both routes will be activated in parallel” by all stimuli containing familiar graphemes. We thus predict activation differences in brain regions representing spelling–sound mappings not because pseudowords should engage them more than words, but because effortful processing should continue for longer for pseudowords than words. To capture activity related to engagement versus nonengagement of the DRC model’s nonlexical route, a contrast between words and pseudowords and false fonts or unfamiliar alphabetic stimuli (as used by Price, Wise, & Frackowiak, 1996, for example) would be necessary. Such a contrast would also be necessary to capture engagement-related activity in the sublexical route in the CDP+ model and the orthography–phonology pathway in the triangle model. The contrast words and pseudowords > false fonts was not included in the meta-analysis, as it would have highlighted all brain areas involved in reading and would therefore have been uninformative with regard to evaluating the correspondence between cognitive model components and neural activity.

For the triangle model, although all stimuli written in a familiar orthography will engage the orthography–phonology route and phoneme system, pseudowords may still be more effortful to process than words. Triangle model simulations have not directly investigated this; however, in Plaut et al. (1996, Simulation 3) and Harm and Seidenberg (2004, Simulation 3), low-frequency words took longer to settle on a phonological output and generated more error across time steps in the orthography–phonology mappings than high-frequency words. As pseudowords will engage the orthography–phonology route but effectively have zero frequency, we can predict that the model would generate more error in the orthography–phonology pathway and take longer to settle on a phonological output for pseudowords relative to words. This prediction also applies to the CDP+ model because its sublexical network will not have experienced the precise spelling–sound patterns present in any particular pseudoword, and will thus generate more error and engage in a longer settling process in both the sublexical network and the phonological output buffer for pseudowords relative to words. We can therefore derive the predictions from the triangle and CDP+ models that pseudowords relative to words require more effortful processing, and thus should elicit greater activity, in areas of the brain involved in converting spelling to sound and in assembling phonological output.

Irregular Words > Regular Words

As described earlier, the DRC, CDP+, and triangle models differ in their treatment of spelling–sound regularity. The DRC model treats words as either regular (nonlexical route outputs the correct pronunciation) or irregular (correct pronunciation depends on the lexical route overcoming the incorrect regularized pronunciation). In contrast the orthography–phonology mappings in the triangle model and the sublexical network in the CDP+ model encode spelling–sound consistency as a graded variable. Furthermore, although all three models suggest that correct pronunciation of irregular and inconsistent spelling–sound correspondences depends on some degree of item-specific knowledge (to ensure that *sew* is not read to rhyme with *few*, for example), they differ with regard to whether this item-specific knowledge is primarily form-

based (DRC and CDP+ models) or associated with word meaning (triangle model). In the paragraphs that follow, we use these distinctions and the principles of engagement and effort to derive predictions for brain activity during irregular relative to regular word reading.

The existence of patients with surface dyslexia, who have impaired irregular word reading but relatively intact pseudoword reading (Patterson, Coltheart, & Marshall, 1985), has been taken as support for the dependence of irregular word reading on the lexical route. This has led a number of authors to postulate that in neuroimaging studies with healthy adults, irregular words will engage a brain region that corresponds to the orthographic lexicon to a greater extent than regular words. For example Jobard, Crivello, and Tzourio-Mazoyer (2003, p. 697) stated that “irregular words such as ‘yacht’ cannot be properly pronounced following the application of GPC rules and therefore need to engage the direct route” (the direct route corresponds to the lexical route of the DRC model). However, in the DRC model, only the outcome of the full reading process yields information about whether a word is regular (i.e., whether the pronunciations computed via the lexical and nonlexical routes are the same). This position is supported by the overwhelming body of evidence demonstrating that typical adults do not have control over their use of lexical versus nonlexical reading strategies (Chateau & Lupker, 2003; Kinoshita & Lupker, 2007; Kinoshita, Lupker, & Rastle, 2004) and that there are alternative explanations for the so-called route emphasis effect of a reaction time cost associated with switching between irregular and pseudoword reading (Reynolds & Besner, 2008). In summary, it does not follow from the DRC model’s proposal that specific processes or brain regions are necessary for reading particular word types that such processes or brain regions are more engaged by these word types.

Although engagement of the components of the DRC model does not differ for irregular versus regular words, irregular words may still require more effortful processing. The lexical and nonlexical routes generate different outputs for irregular words, and this generates conflict in the phoneme system that has to be resolved before a pronunciation can be generated. The DRC model therefore predicts that irregular relative to regular words are more effortful to process and should thus elicit greater activity, in a brain region involved in computing phonological output. Because phoneme system resolution takes longer for irregular words, lexical and nonlexical route activity also continues for longer. This means that effort, and hence activity, should be greater, for irregular than regular words in neural systems that correspond to the orthographic and phonological lexicons, and that perform nonlexical spelling–sound conversion.

For the triangle model, Binder et al. (2005, p. 686) argued that resolving phonological output would be more effortful for inconsistent words “because of conflicting input to the phonological system from semantic and orthographic systems.” This seems to imply that the triangle model encodes a regular pronunciation in the orthography–phonology connections (akin to the DRC model’s nonlexical route) and an irregular pronunciation in the orthography–semantics–phonology connections (akin to the DRC model’s lexical route). This is not the case. The triangle model develops distributed mappings between orthography, semantics, and phonology that enable it to pronounce all words correctly by using the two routes in conjunction; the phoneme units simply sum

their inputs from the two pathways (Plaut, 1997, p. 773). However, there is another sense in which inconsistent words may generate conflict; multiple mappings may be represented within the orthography–phonology pathway, and these need to be resolved before the phoneme units can settle on a response. This was demonstrated by Plaut et al. (1996, Simulation 3) and Harm and Seidenberg (2004, Simulation 3) in which low-frequency inconsistent words generated more error than high-frequency and/or consistent words in the orthography–phonology pathway, resulting in a longer settling time in the phonological attractor network. The triangle model therefore predicts that inconsistent relative to consistent words require more effortful processing, and should elicit greater activity, in brain regions that represent orthography–phonology mappings and that are involved in computing phonological output. However, it should be remembered that in this model differences in activation patterns between consistent and inconsistent words will always be graded, depending on overall error rate and latency rather than stimulus class.

The CDP+ model also predicts brain activation differences for inconsistent relative to consistent words for three reasons. First, inconsistent words generate conflict in the phonological output buffer between the correct lexical route output and the potentially incorrect sublexical route output, as in the DRC model. Inconsistent words should therefore be more effortful and elicit greater activity than consistent words in brain regions that compute phonological output. Second, and again as in the DRC model, consistent and inconsistent words equivalently engage the lexical route, but because generating an output in the phoneme system takes longer for inconsistent words, lexical route processing also continues longer than for consistent words. Inconsistent words should thus elicit greater activity than consistent words in brain regions representing whole-word orthography and phonology. Third, as in the triangle model, the CDP+ model proposes that inconsistent words may activate multiple mappings within the sublexical network (e.g., *spook* might activate a pronunciation for *oo* as in *book* and as in *spoon*). Inconsistent words therefore require more effortful processing than consistent words, and should generate greater activity, in brain regions that map spelling to sound.

Finally, we discuss whether semantic activation should differ for irregular versus regular words. As neither the DRC nor the CDP+ model has a fully implemented semantic system, we are only able to make predictions about the impact of regularity on brain regions involved in semantic processing on the basis of the triangle model. Plaut et al. (1996) showed that removal of semantic support (lesioning the semantic pathway) was more detrimental to phonological output accuracy for low-frequency inconsistent words than high-frequency and/or consistent words. Reports of poor irregular relative to pseudoword reading (i.e., surface dyslexia) in patients with semantic dementia support this idea (Patterson et al., 2006; Woollams, Lambon Ralph, Plaut, & Patterson, 2007). In a model with more fully implemented semantic representations, Harm and Seidenberg (2004) then showed that accuracy at generating phonology from orthography was influenced by imageability (a semantic variable) for low-frequency inconsistent words but not high-frequency or consistent words, mirroring data from adult readers (Strain, Patterson, & Seidenberg, 1995, 2002). These findings led Graves, Desai, Humphries, Seidenberg, and Binder (2010, p. 1800) to argue that the brain regions representing semantics will

be more engaged by low-frequency, low-consistency words than high-frequency, high-consistency words.

Why should this be the case? In a model trained only to generate phonology, the orthography–semantics–phonology route might experience less pressure to learn the mappings for consistent words, because the orthography–phonology route learns these quickly and easily. In which case stronger orthography–semantic connections might develop, leading to greater engagement of the semantic system, for irregular than regular words. However, the primary goal of reading is to access meaning, and developing strong connections between orthography and semantics would optimize reading speed for all items. Accordingly, Harm and Seidenberg (2004, Simulation 11) showed that the orthography–semantic route generated meanings for consistent words as accurately as for inconsistent words, with better performance for high- than low-frequency items. Behavioral experiments showing that semantic decisions are unaffected by a word’s regularity (Taft & van Graan, 1998) also support the idea that engagement of semantic representations is not modulated by regularity. Thus, when learning to generate meaning as well as pronunciation, the triangle model predicts that consistent and inconsistent words should equivalently engage and activate brain regions that represent semantics, with greater processing effort and activity for low- than high-frequency words.

Regular Words > Irregular Words

In the DRC model, regular words can be read correctly by the nonlexical route, whereas irregular words cannot, leading some to propose that regular words should produce more activity than irregular words in brain regions concerned with grapheme–phoneme conversion. For example, Jobard et al. (2003) included the contrast regular words > irregular words in their set of subtractions intended to highlight the nonlexical route to reading. Binder et al. (2005) made the same claim when they proposed that, according to one interpretation of the DRC model (which they termed the exclusive dual-route model), “regular words (especially low-frequency regular words) are expected to produce more activation of the GPC route than irregular words” (p. 678).

If we use the principles of engagement and effort, it is clear that this prediction does not fall out of the DRC model. The model does not have advance knowledge of the regularity of a stimulus. The nonlexical route therefore converts graphemes to phonemes, and the lexical route transforms whole-word orthography to phonology, for all items irrespective of their regularity. Thus, neither nonlexical nor lexical route engagement is modulated by regularity. Furthermore, regular words do not generate conflict in the phoneme system and are therefore less effortful for phonological output regions than irregular words. This also means that regular words are processed for less time in the lexical and nonlexical routes than irregular words and are thus less effortful for brain regions corresponding to these regions. Overall, regular words engage both routes to the same extent and are less effortful to process than irregular words. The prediction therefore follows from the DRC model that the contrast regular > irregular words will not highlight activity in any brain regions.

For this contrast, the CDP+ and triangle models make the same prediction. Consistent words engage the lexical and sublexical routes of the CDP+ model to the same extent as inconsistent

words. They are also less effortful to process in the sublexical route and do not generate conflict in the phonological output buffer and thus are processed for less time in the lexical route. Similarly, consistent words engage all components of the triangle model to the same extent as inconsistent words and require less effortful processing in the orthography–phonology route and phonological output system, and equivalent effort in the semantic system.

Summary of Predictions (Illustrated in Figure 5)

The orthographic and phonological lexicons of the DRC and CDP+ model should be engaged more by words than pseudowords and exert more effort for irregular relative to regular words because processing should continue for longer. In contrast, the orthographic system in the triangle model is sensitive to orthographic typicality, not lexicality or regularity. The semantic systems of all three models should be engaged more by words than pseudowords. Resolving phonological output should be more effortful for pseudowords than words and irregular than regular words in all three models. The nonlexical route of the DRC model should continue processing for longer, and thus exert more processing effort, for pseudowords relative to words, and irregular relative to regular words, because resolving phonological output takes longer for these item types. In the sublexical network of the CDP+ model and the orthography–phonology pathway of the triangle model, both pseudowords relative to words and irregular words relative to regular words should require more effortful spelling–sound conversion.

Meta-Analysis Approach

Neuroimaging studies have used a multitude of different tasks, stimuli, methods, participants, and analysis techniques, reflecting their different research aims. Jobard et al.'s (2003) meta-analysis of 35 neuroimaging studies of reading, framed within the DRC model, was a first and influential attempt to gain some consensus. Jobard et al. obtained clusters of activation peaks in left superior and middle temporal and supramarginal gyri from contrasts that they expected to highlight nonlexical route processing. They therefore proposed that these regions play some role in the conversion of letters to sounds. However, somewhat unexpectedly, most of the other clusters they identified contained activation peaks corresponding to contrasts that they expected to highlight both lexical and nonlexical route processing. If taken at face value, their meta-analysis therefore suggests that there are no processes that are either engaged to a greater extent or more effortful when reading words relative to pseudowords.

Our meta-analysis differs from that of Jobard et al. (2003) in two important ways. First, we included only stimulus-driven contrasts in which the same task was performed on words and pseudowords and/or irregular and regular words, and excluded studies that used task-driven contrasts, such as semantic versus phonological decision. As outlined, models of reading make clear predictions about the processes engaged and effort required when participants perform the same task on different word types but make few (if any) predictions for how activity should change as a function of externally imposed task demands. The included contrasts were obtained from studies in which participants performed overt or silent reading, lexical decision, visual feature detection (e.g., presence of a

gap or ascending component), phonological lexical decision (does this item sound like a real word?), one-back matching requiring detection of consecutive item repetition, and phonological (rhyme) judgments.

Second, we used the ALE technique developed by Turkeltaub et al. (2002) and extended by Laird et al. (2005) and Eickhoff et al. (2009). This approach enabled us to quantify whether the overlap between activation peaks reported across studies was greater than would be expected if the results from different studies were randomly distributed. Furthermore, Eickhoff et al.'s extension of the ALE method means that it now assesses where there is above-chance clustering between experiments as opposed to between individual foci. This is important because in some studies several different foci within the same local activation maxima may be reported. Cluster analysis of coordinates as performed by Jobard et al. (2003) points to regions consistently seen in multiple studies but need not indicate functional convergence between different experiments, which is what meta-analysis should be concerned with. Further details on the ALE technique are provided in the Method section.

As outlined earlier, the DRC, CDP+, and triangle models of reading make predictions regarding the involvement of semantics in reading words versus pseudowords. To aid us in evaluating these predictions, we compared our activation maps with those from a meta-analysis of semantic processing by Binder et al. (2009), which also used the ALE technique.

Method

Study identification

A search was conducted on titles, abstracts, and keywords using the Scopus bibliographic database on June, 29, 2012, with the following Boolean operation: “*brain mapping* or *functional magnetic resonance imaging* or *fMRI* or *positron emission tomography* or *PET* or *neuroimaging* and *visual word* or *reading* or *word naming* or *word recognition* or *orthograph**.” This search yielded 4,299 articles. Titles, abstracts, and, where necessary, full texts were then screened with the following inclusion criteria (an example of a study that was excluded is given for each):

1. Functional MRI or PET involving healthy adult participants (Simos et al., 2002; MEG, not fMRI or PET);
2. Visual presentation of single words in an alphabetic language (Sakurai et al., 2000; Japanese words);
3. Same task on words and pseudowords and/or irregular words and regular words with a direct contrast between the two (Pugh et al., 1996; different tasks for words and pseudowords);
4. Whole-brain analysis (S. M. Wilson et al., 2009; regions of interest, not whole-brain analysis);
5. Availability of peak activation coordinates from a group activation map (Pugh et al., 2008; dyslexics vs. nondyslexics, no individual group data).

We chose PET and fMRI studies that performed whole-brain analyses and required that they reported peak activation coordinates from a group activation map for healthy, unimpaired adult readers. We only included studies using single words written in an alphabetic script because nonalphabetic scripts inherently constrain the extent to which people can use nonlexical versus lexical and semantic representations to read and recognize words and pseudowords. We did not exclude experiments in which contrasts between words and pseudowords were not compared with a baseline such as viewing false fonts and/or saying “OK” to fixation. Using such control tasks enables one to determine whether stimuli elicit activation or deactivation relative to baseline. However, as there is disagreement over how to interpret stimulus-driven differences in deactivation (Binder et al., 2005; Mechelli, Gorno-Tempini, & Price, 2003), it did not seem justified to include only those studies reporting greater than baseline activity.

Our decision to include multiple tasks, as opposed to just reading aloud, which has been the primary focus of cognitive modeling investigations, was in part motivated by a study by Carreiras, Mechelli, Estevez, and Price (2007). This found that activations in brain areas associated with reading (as opposed to making decisions or overt motor responses) were very similar in lexical decision and reading aloud, the tasks used by the majority of studies included in this meta-analysis. Furthermore, by subtracting one stimulus type from another during the same task, task-related activity is constant and will not contribute to differential activity for different word types. We included silent (as well as overt) reading largely because this tends to vary by research group. For example, Mechelli, Price, and colleagues (Mechelli et al., 2005; Mechelli, Friston, & Price, 2000; Mechelli et al., 2003) used silent reading to minimize “task induced effects and avoid the activation of temporal regions caused by subjects processing their own voice” (Mechelli et al., 2003, p. 269). It could have biased our findings if we had excluded all the experiments conducted by a particular research group. We would also have suffered from a lack of power if including only the 12 studies that used reading aloud.

Of further consideration is an argument made by Binder et al. (2005), that activity that increases with reaction time (RT) within any particular word type (regular, irregular, pseudoword) reflects general executive processing rather than processing corresponding to any particular model component. Binder et al. (p. 679) stated that

by using multiple regression analyses in which normalized RT values were coded separately for each stimulus condition ... this analysis thus identified candidate brain regions that are likely to be modulated by non-specific differences in task difficulty, such as working memory, attention, decision, and response selection systems.

Response time differences are without doubt associated with increased neural activity and may reflect general executive processes. However, the inverted U-shaped curve depicted in Figure 4 shows that differences in task difficulty, as measured by increasing RT, also reflect the effort involved in performing computations of interest (e.g., spelling–sound mapping or phonological conflict resolution). If response time differences were only associated with generic or executive processes, then they would not be an informative measure in behavioral studies. We thus elected to include the coordinates of all peak activations elicited by our contrasts of interest and did not discount those that also correlated with response time within conditions.¹

The result of our inclusion and exclusion criteria was 36 articles, 34 of which included a word versus pseudoword contrast and eight of which contrasted irregular and regular words. Twenty-eight of the studies used fMRI, and eight used PET. There were 165 foci included in the word > pseudoword contrast and 283 in the pseudoword > word contrast. There were 46 foci that responded more strongly to irregular than regular words and only two that showed the reverse pattern, one from Cummine et al. (2012) and one from Osipowicz et al. (2011). We therefore did not include the contrast regular > irregular words in our analyses. Neuroimaging data from 546 participants contributed to the contrast between words and pseudowords, and data from 137 participants contributed to the contrast between irregular words and regular words. A list of the articles along with critical methodological details is provided in Table 1.

Data Analysis

Twenty-two studies reported contrasts in the standard space of Talairach and Tournoux (1988), and 14 reported contrasts in Montreal Neurological Institute (MNI) space (Evans et al., 1993). Although these are both nominally Talairach coordinate systems, there are known differences between the standard brains used in normalization that create problems for localizing activity in certain regions such as the inferior temporal lobe (Brett, Johnsrude, & Owen, 2002). We therefore converted all coordinates from contrasts of interest (words vs. pseudowords, irregular vs. regular words) to MNI space using the tal2icbm transform (Lancaster et al., 2007), which reduces the bias associated with reference frame and scale in Talairach–MNI conversion. We chose to use the MNI space, since this is representative of the brains of the healthy adult participants used in standard neuroimaging studies.

The ALE technique, implemented in the GingerALE software (Laird et al., 2005; <http://www.brainmap.org>), was then used to determine where there was significantly greater overlap between the peak coordinates reported across experiments than would be expected if their results were randomly distributed. The methods employed in the current ALE analysis are described in full in Eickhoff et al. (2009) but can be summarized as follows. For each experiment, three-dimensional Gaussian probability distributions are computed around each of the peak coordinates. The width of these Gaussian distributions takes into account the spatial uncertainty of each active location using Eickhoff et al.’s estimate of the intersubject and interlaboratory variability observed in neuroimaging experiments. The sum of these Gaussian probability distributions yields a modeled activation (MA) map for each experiment. These MA maps contain for each voxel the probability of an activation being located at that position. ALE scores are then calculated on a voxel-by-voxel basis (largely confined to gray matter) by taking the union of the MA maps for each experiment. This results in an image containing ALE scores for each voxel, representing the convergence of the reported foci at that position.

These ALE scores are then compared to a null distribution in order to assess their statistical significance. This null distribution is

¹ Note that most articles did not provide the item-wise data necessary to determine whether activations were correlated with response time.

Table 1
Details of Articles Included in Meta-Analysis

Study	Imaging method	No. of subjects	Task	Design	Statistical threshold	Number of foci		
						Words > pseudowords	Pseudowords > words	Irregulars > regulars
Abutalebi et al. (2007) ^a	fMRI	12	Silent reading (German)	Blocked	$p < .001$, FWE corrected	0	27	
Binder et al. (2003) ^{a,b}	fMRI	24	LDT	Event related	$p < .01$, voxel-wise uncorrected	26	9	
Binder et al. (2005) ^{a,b}	fMRI	24	Read aloud	Event related	$p < .001$, voxel-wise uncorrected	48	73	31
Bruno et al. (2008) ^{a,b}	fMRI	28	Phonological LDT	Event related	$p < .05$, FDR corrected	0	9	
Carreiras et al. (2007) ^b	fMRI	36	LDT and read aloud (Spanish)	Event related	$p < .05$, voxel-wise corrected	5	7	
Cummine et al. (2012) ^a	fMRI	20	Read aloud	Event related	$p < .01$, cluster-level corrected			1
Dietz et al. (2005) ^a	fMRI	16	Read aloud and silently	Blocked	$p < .001$, voxel-wise uncorrected	0	3	
Fiebach et al. (2002) ^a	fMRI	12	LDT (German)	Event related	$p < .05$, cluster-level corrected	13	4	
Fiebach et al. (2005) ^a	fMRI	14	LDT (German)	Event related	$p < .0005$, uncorrected, cluster corrected $p < .05$	0	3	
Fiebach et al. (2007) ^{a,b}	fMRI	16	LDT (German)	Event related	$p < .05$, cluster-level corrected	2	3	
Fiez et al. (1999) ^a	PET	11	Read aloud	Blocked	$p < .05$, voxel-wise uncorrected	0	3	2
Graves et al. (2010) ^a	fMRI	20	Read aloud	Event related	$p < .05$, voxel-wise corrected			3
Hagoort et al. (1999) ^{a,b}	PET	11	Read aloud and silently (German)	Blocked	$p < .01$, voxel-wise uncorrected	8	9	
Henson et al. (2002) ^a	fMRI	12	LDT	Event related	$p < .01$, when > 10 contiguous voxels	8	7	
Herbster et al. (1997) ^a	PET	10	Read aloud	Blocked	$p < .001$, voxel-wise uncorrected	2	1	1
Jensen et al. (2011) ^a	fMRI	12	LDT	Event related	$p < .05$, FDR corrected	12	0	
Joubert et al. (2004) ^a	fMRI	10	Passive viewing (French)	Blocked	$p < .0005$, voxel-wise uncorrected	6	13	
Kronbichler et al. (2004)	fMRI	24	Phonological LDT (German)	Event related	$p < .01$ FDR corrected	0	6	
Kuchinke et al. (2005) ^b	fMRI	20	LDT (German)	Event related	$p < .001$, uncorrected	14	8	
Mayall et al. (2001)	PET	12	Detect gap in letter	Blocked	$p < .05$, voxel-wise corrected	0	1	
Mechelli et al. (2000) ^{a,b}	fMRI	6	Silent reading	Blocked	$p < .05$, voxel-wise corrected	1	7	
Mechelli et al. (2003) ^b	fMRI	20	Silent reading	Blocked	$p < .05$, voxel-wise corrected	4	3	
Mechelli et al. (2005) ^b	fMRI	22	Silent reading	Blocked	$p < .05$, voxel-wise corrected	1 (irregular > pseudoword)	2 (pseudoword > irregular, pseudoword > regular)	1
Nosarti et al. (2010)	fMRI	30 pseudowords > words, 12 irregulars > regulars	Silent reading (English and Italian collapsed)	Blocked	$p < .001$, uncorrected	0	3	4
Osipowicz et al. (2011) ^{a,b}	fMRI	17	Silent reading	Blocked	$p < .01$, FWE corrected	1 (irregular > pseudoword)	1 (pseudoword > irregular)	3
Paulesu et al. (2000)	PET	12	Read aloud (Italian/English)	Blocked	$p < .001$, corrected for spatial extent	0	9	
Price et al. (1996) ^a	PET	6	Visual feature detection	Blocked	$p < .001$, voxel-wise uncorrected	2	7	
Rumsey et al. (1997) ^a	PET	14	Read aloud	Blocked	$p < .01$, when > 8 contiguous voxels	1	4	
Sachs et al. (2008)	fMRI	16	LDT (German)	Event related	$p < .05$, when > 12 contiguous voxels	5	0	
Tagamets et al. (2000)	fMRI	11	One-back matching	Blocked	$p < .001$, uncorrected	0	3	
Thompson et al. (2007) ^a	fMRI	17	LDT	Event related	$p < .05$, FDR corrected	0	25	
Vartiainen et al. (2011) ^a	fMRI	15	Silent reading (Finnish)	Blocked	$p < .05$, FDR corrected	0	3	
Vigneau et al. (2005)	fMRI	13	Read aloud (French)	Blocked	$p < .001$, voxel-wise uncorrected	3	14	
M. A. Wilson et al. (2012)	fMRI	16	Read aloud, say "yes" to false fonts (French)	Blocked	$p < .05$, FWE corrected	3 (irregular > pseudoword)	0	
Woollams et al. (2011) ^b	fMRI	15	LDT	Event related	$p < .001$, uncorrected	0	10	
Xu et al. (2001)	PET	12	Rhyme judgment	Blocked	$p < .001$, voxel-wise uncorrected	0	6	

Note. fMRI = functional magnetic resonance imaging; PET = positron emission tomography; LDT = lexical decision task; FWE = family-wise error; FDR = false discovery rate. ^aCoordinates reported in Talarach and Tourmoux (1988) space. ^bStudies that matched words and pseudowords on sublexical orthographic variables.

constructed by an iterative procedure that takes a random voxel and its activation probability from each MA map and computes the union of these activation probabilities in the same manner as for the meta-analysis itself. This produces an ALE score under the null hypothesis of spatial independence. This procedure is then repeated 10^{11} times to construct a sufficient sample of the null distribution against which to compare the empirical data.

Results were thresholded at $p < .05$, false discovery rate corrected, and only clusters greater than 100 mm^3 are reported. Anatomical labels were generated by MRICron (Rorden, Karnath, & Bonilha, 2007), which uses the automated anatomical labeling template provided by the MNI. In order to compare the results of our meta-analysis with those from Binder et al. (2009), it was necessary to convert their activation maps from Talairach and Tournoux to MNI space with a version of the tal2icbm transform.²

Results

Words > Pseudowords

Activations that were greater for words than pseudowords were almost entirely left lateralized. Table 2 and Figure 7 give details of all clusters. The largest cluster and that which encompassed peak coordinates from the greatest number of studies ($n = 5$) was identified in middle temporal gyrus and angular gyrus. There were also two smaller clusters in left and right middle temporal gyrus that contained peaks from three and four studies, respectively. Further large clusters were located in parahippocampal and fusiform gyri (peaks from two studies), posterior cingulum and precuneus (four studies), and medial orbitofrontal cortex and gyrus rectus (two studies). Several smaller clusters containing peaks from between two and four studies were identified in the left middle and superior frontal gyri. The remaining clusters less than 500 mm^3 were found in the cingulate, precuneus, left medial orbitofrontal cortex, left fusiform gyrus, left IFG, and left superior temporal and superior frontal gyri.

We compared the ALE maps resulting from our word > pseudoword comparison with those from Binder et al.'s (2009) meta-analysis of neuroimaging studies of semantic processing. Figure 7 shows that there was extensive overlap between these two activation probability maps; specifically within the left middle temporal and angular gyri, left parahippocampal and fusiform gyrus, left superior frontal gyrus, and precuneus and posterior cingulum. However, the clusters in left middle temporal and angular gyri had a more posterior and dorsal extent than those obtained by Binder et al. in these regions. There were also relatively large clusters in medial orbitofrontal cortex and gyrus rectus and right middle temporal gyrus that did not overlap with Binder et al.'s semantic activation.

Pseudowords > Words

Activations that were greater for pseudowords than words were also largely left lateralized (see Table 3 and Figure 7). The largest cluster with the most contributing studies ($n = 22$) extended through left inferior frontal and precentral gyri and superior temporal pole. The second largest (16 studies) was located in left posterior fusiform gyrus and occipitotemporal cortex, and the third, with six studies contributing, extended through left and right

supplementary motor area. Relatively large clusters were also obtained in left insula (eight studies), right IFG (four studies), left parietal cortex (two clusters with four and three studies), and right inferior parietal cortex (three studies). Smaller clusters less than 500 mm^3 and with three or fewer contributing studies were obtained in right superior occipital cortex, left superior temporal gyrus, left and right superior parietal cortex, right inferior frontal and temporal gyri, left middle temporal gyrus, left middle occipital cortex, and right middle frontal gyrus. The clusters that showed greater activity for pseudowords than words did not overlap with the semantic processing regions identified by Binder et al. (2009) except in the opercularis and triangularis regions of the left IFG.

Irregular Words > Regular Words

Greater activity for irregular words than regular words was found in only one left hemisphere cluster, which included peaks from five studies (see Table 4 and Figure 7). This cluster included regions of the IFG, insula, and underlying white matter. Figure 7 shows that the left IFG activation we obtained for the irregular > regular word contrast did partially overlap with the left IFG cluster identified by Binder et al., most notably in the triangularis region. However, it is also clear that irregular > regular word activation extended more laterally than semantic activation and overlapped almost entirely with activity that was shown to be greater for pseudowords than words.

Discussion

This meta-analysis has provided evidence of substantial cross-study convergence in the neural systems involved in word and pseudoword reading. Such cross-study consistency is reassuring; despite the many different languages, tasks, stimuli, and imaging methods, neuroimaging studies produce replicable spatial patterns of differential activity to written stimuli. This discussion will examine how consistent this evidence is with the DRC, CDP+, and triangle models of reading and will outline where more research is needed to improve convergence between neural and cognitive accounts of the reading process. We argue that the components in these cognitive models fit well with the functional anatomy revealed by our contrasts between words and pseudowords and regular and irregular words, and therefore organize the Discussion according to these contrasts. Following this, we consider clusters obtained in this meta-analysis that do not appear to correspond to components of cognitive models of reading and conclude by considering how our framework relates to other areas of cognitive neuroscience and theories of reading development.

Relationship Between Meta-Analysis Results and Cognitive Model Components

Figure 8 summarizes the relationship between anatomical structures, their putative functions, and model components. The contrasts that revealed these correspondences are now discussed in turn.

² We would like to thank Jeff Binder for providing his ALE maps and Matthew Brett and Jonathan Peelle for their help with the transformation of these maps into MNI space.

Table 2

Activation Likelihood Estimation Results for Studies Reporting Greater Neural Responses to Words Than Pseudowords

Cluster	MRICron label	Volume (mm ³)	No. of studies	<i>p</i> (uncorrected)	MNI coordinates		
					<i>x</i>	<i>y</i>	<i>z</i>
1	Left middle temporal gyrus	4,296	5	.003	-50	-66	18
	Left middle occipital cortex			.003	-46	-72	38
	Left angular gyrus			.002	-52	-58	30
2	Left parahippocampal gyrus	1,512	2	.003	-32	-36	-12
	Left fusiform gyrus			.002	-22	-34	-14
3	Left posterior cingulum	1,064	4	.002	-6	-48	32
	Right precuneus			.002	2	-56	24
4	Left medial orbitofrontal cortex	824	2	.002	-8	28	-10
	Left rectus			.002	-4	26	-18
5	Left middle temporal gyrus	824	3	.002	-64	-54	-10
6	Right middle temporal gyrus	720	4	.002	54	-64	20
7	Left superior frontal gyrus	712	4	.002	-18	38	44
8	Left middle frontal gyrus	704	2	.002	-38	18	44
9	Left middle frontal gyrus	504	3	.002	-24	24	52
10	Left posterior cingulum	464	4	.002	-4	-34	34
	Right middle cingulum			.001	2	-36	38
11	Left precuneus	456	2	.002	-10	-54	18
12	Left medial orbitofrontal cortex	376	1	.002	-12	46	-8
13	Left precuneus	232	2	.002	-4	-56	44
14	Left fusiform gyrus	176	1	.002	-30	-22	-26
15	Left inferior frontal gyrus	152	2	.001	-52	34	6
16	Left superior temporal gyrus	152	2	.002	-54	-36	16
17	Left medial superior frontal gyrus	144	2	.001	-2	56	4

Note. Results are thresholded at $p < .05$, false discovery rate corrected. Clusters > 100 mm³ reported. MNI = Montreal Neurological Institute.

Words > pseudowords. Our meta-analysis identified a cluster in left anterior fusiform gyrus ($-22, -34, -14$), part of the occipitotemporal visual processing stream, that responded more strongly to words than pseudowords.³ Both the DRC and CDP+ models predict such an effect in a brain region that processes higher level visual information, if this brain region corresponds to the orthographic lexicon. In contrast, this pattern of activity is only predicted by the triangle model if the pseudowords were constructed from letter combinations that do not occur in words (Sibley et al., 2008, 2010), as such stimuli should engage the orthographic system to a lesser extent than words. Although many of the studies included in this meta-analysis did not adequately match words and pseudowords on orthographic variables, only Henson, Price, Rugg, Turner, and Friston (2002) created their nonword stimuli by permuting the letters in the word stimuli (thereby creating orthographically illegal sequences); all other studies used pronounceable pseudowords. It is therefore unlikely that word > pseudoword activity in anterior fusiform was driven by differences in orthographic typicality, and thus the orthographic system of triangle model does not offer an explanation for this effect.

However, there is an alternative explanation, which is that activity in anterior fusiform reflects semantic processing. This proposal is supported by previous research showing that this region is sensitive to semantic variables such as imageability (Hauk, Davis, Kherif, & Pulvermüller, 2008; Wise et al., 2000) and by the overlap between our anterior fusiform word > pseudoword cluster and a cluster that Binder et al. (2009) identified as being involved in semantic processing. If word > pseudoword activity in anterior fusiform is a result of processing meaning, this can be accommodated by all three cognitive models, as their semantic systems are engaged to a greater extent by words than pseudowords.

Future research should establish whether word > pseudoword activity in anterior fusiform reflects that fact that this region represents whole-word orthographic forms or because it is influenced by semantics. Pattern analysis fMRI (Haynes & Rees, 2006; Kriegeskorte et al., 2008) might be one way to achieve this; it could potentially establish whether the information encoded by fine-grained patterns of activity reflects the orthographic or semantic similarity between words (see Braet, Wagemans, & Op de Beeck, 2012, for evidence of orthographic coding in a more posterior fusiform region). Another informative method is repetition suppression, which can be used to examine whether brain regions are sensitive to the similarity between consecutively presented events (e.g., word pairs similar in meaning vs. orthographic form; for relevant examples, see Devlin, Jamison, Matthews, & Gonnerman, 2004; Glezer, Jiang, & Riesenhuber, 2009). Evidence that a region of the brain represents whole-word orthographic forms would constitute support for the DRC and CDP+ models and go against a central concept of the triangle model, that words and orthographically typical pseudowords can only be discriminated on the basis of semantics.

A second word > pseudoword cluster was identified in left angular and middle temporal gyri ($-50, -66, 18$). Due to its overlap with a cluster revealed by a contrast of spoken words > pseudowords in a meta-analysis by Davis and Gaskell (2009), this could reflect engagement (via the orthographic lexicon) of the DRC and CDP+ models' phonological lexicon. However, words differ from pseudowords not only because they are phonologically

³ Although only two studies had peaks within this anterior fusiform cluster, other studies are likely to have contributed to its location and size.

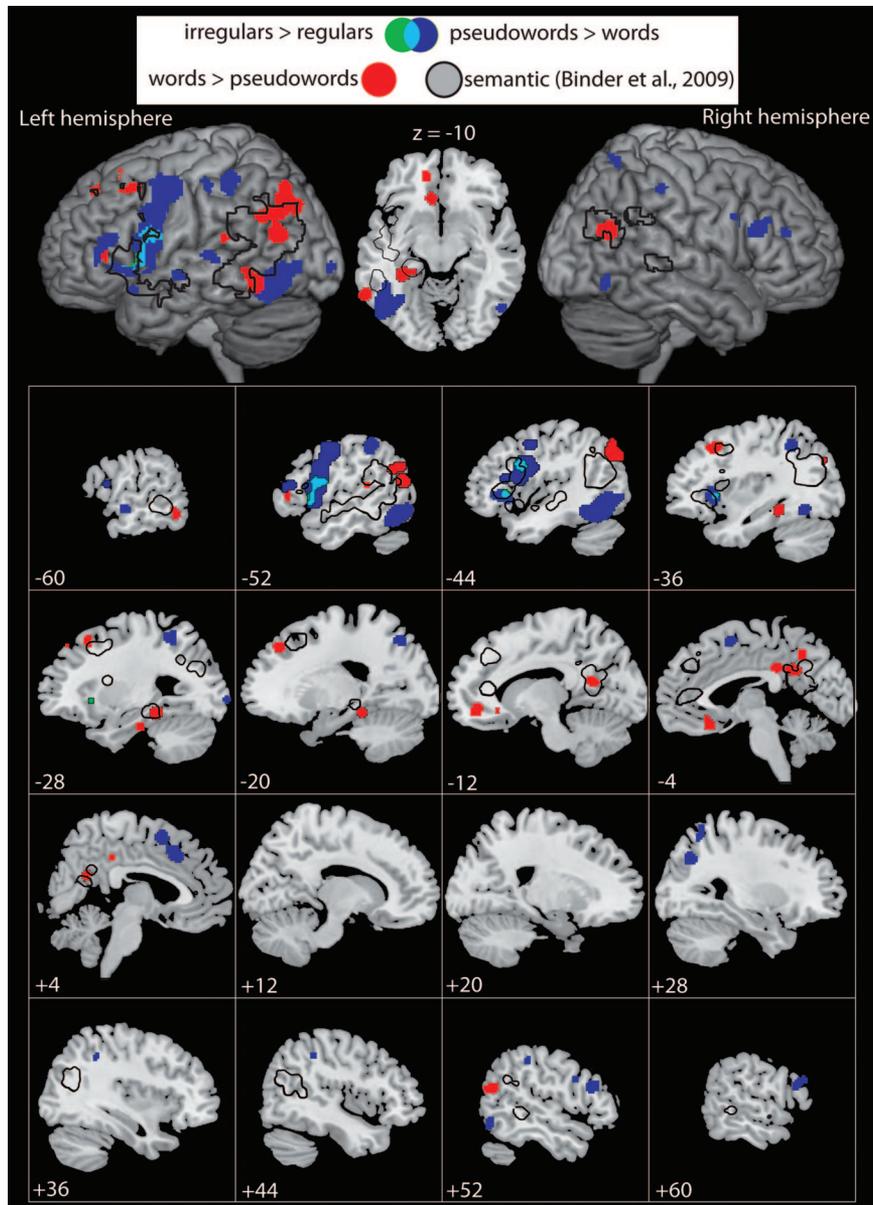


Figure 7. Activation likelihood estimation map of foci from all contrasts (red = words > pseudowords, blue = pseudowords > words, green = irregular > regular words, cyan = overlap between blue and green maps), together with those from Binder et al.'s (2009) meta-analysis (black outline). Thresholded at $p < .05$, false discovery rate corrected. Activations are displayed as left and right hemisphere renderings and on serial sagittal sections through stereotaxic Montreal Neurological Institute space at 8-mm intervals with slice locations in the lower left of each image. A coronal section at $z = -10$ is also displayed to show occipitotemporal activations more clearly.

familiar but also because they have meaning; thus, this activity could equally reflect semantic processing. This latter interpretation is supported by the overlap between our word > pseudoword cluster and a cluster that Binder et al. (2009) found to be involved in semantic processing. Both Binder et al. and Price (2010) argued that the angular gyrus is involved in semantic and conceptual processing rather than in the recognition of familiar phonological forms. Thus, it seems more likely that word > pseudoword activity in this region reflects greater engagement of the semantic system as predicted by all three cognitive models.

A smaller word > pseudoword cluster, that again overlapped with a semantic processing cluster obtained by Binder et al. (2009), was also found in a somewhat more ventral region of left middle temporal gyrus. Neuropsychological data support the idea that this region of middle temporal gyrus also plays a role in semantic processing. For example, Bates et al. (2003) used lesion-symptom mapping to show that spoken language comprehension was affected by lesions to middle temporal gyrus. Furthermore, impaired comprehension of spoken language can be induced by cortical stimulation of this region (Boatman et al., 2000). Word > pseudoword clusters obtained in left

Table 3

Activation Likelihood Estimation Results for Studies Reporting Greater Neural Responses to Pseudowords Than Words

Cluster	MRICron label	Volume (mm ³)	No. of studies	<i>p</i> (uncorrected)	MNI coordinates		
					<i>x</i>	<i>y</i>	<i>z</i>
1	Left inferior frontal gyrus opercularis	12,616	22	.007	-46	6	26
	Left precentral gyrus			.005	-52	8	16
	Left precentral gyrus			.004	-52	-4	46
	Left superior temporal pole			.003	-54	12	-2
	Left inferior frontal gyrus triangularis			.002	-50	32	16
2	Left inferior frontal gyrus triangularis	7,272	16	.002	-44	22	16
	Left inferior occipital			.004	-48	-62	-12
	Left inferior temporal gyrus			.003	-46	-50	-16
	Left inferior occipital			.002	-42	-76	-2
3	Left fusiform	2,464	6	.002	-36	-60	-12
	Right middle cingulum			.003	4	20	44
	Right supplementary motor area			.003	2	10	56
4	Left insula	1,720	8	.002	-6	4	58
	Right supplementary motor area			.003	-40	22	0
5	Right inferior frontal gyrus triangularis	1,280	4	.003	50	24	22
	Right inferior frontal gyrus triangularis			.002	60	24	24
6	Left inferior parietal lobe	952	4	.002	-36	-48	46
	Left inferior parietal lobe			.002	-26	-48	54
7	Left inferior parietal lobe	904	3	.003	-50	-40	50
8	Right inferior parietal lobe	560	3	.002	40	-44	42
	Right supramarginal gyrus			.002	48	-34	44
9	Right superior occipital	488	2	.002	28	-68	36
10	Left superior temporal gyrus	328	3	.002	-64	-26	6
11	Left superior parietal lobe	304	1	.002	-22	-68	50
12	Right inferior frontal gyrus opercularis	296	2	.002	48	8	28
13	Right inferior temporal gyrus	256	2	.002	52	-66	-10
14	Left superior parietal lobe	248	1	.002	-24	-58	48
15	Right superior parietal lobe	248	1	.002	30	-60	54
16	Left inferior parietal lobe	240	1	.002	-48	-24	48
17	Left middle temporal gyrus	224	2	.002	-60	-8	-6
18	Left middle occipital	176	1	.002	-26	-98	-2
19	Right middle frontal gyrus	128	2	.002	48	40	20
20	Left superior temporal pole	120	2	.002	-48	18	-14
22	Right superior parietal lobe	112	1	.002	32	-64	64

Note. Results are thresholded at $p < .05$, false discovery rate corrected. Clusters $> 100 \text{ mm}^3$ reported. MNI = Montreal Neurological Institute.

middle frontal gyrus and precuneus are also likely to reflect semantic processing due to their overlap with semantic processing regions identified by Binder et al. Increased engagement of brain regions that process semantics is predicted by all three cognitive models, although we acknowledge that they have single semantic systems, whereas the

results of this meta-analysis suggest that multiple regions contribute to processing of word meaning.

Future research should clarify whether activity in angular and middle temporal gyri during reading primarily reflects processing of lexical phonology or semantics. Once more, pattern analysis fMRI and repetition suppression techniques provide useful methods for interpreting activity in these regions, as for anterior fusiform. It is also imperative that research establishes whether activation of semantic representations is necessary for correct reading aloud, as this remains a key point of contention between the DRC and CDP+ models and the triangle model. The position of DRC and CDP+ model proponents is exemplified by Coltheart, Tree, and Saunders's (2010, p. 259) discussion of semantic dementia in which they stated, "The disorder begins with just the semantic system compromised. Because, in the DRC model, reading aloud accuracy is perfect without the use of the semantic system, at this stage in the disorder, reading accuracy is intact." Thus, this model proposes that semantic information, although routinely activated, is not crucial to correct reading aloud. In contrast, in the triangle model, semantic representations are necessary for accurate reading of irregular words and lesions to the semantic system cause deficits in reading-aloud accuracy (Plaut et

Table 4

Activation Likelihood Estimation Results for Studies Reporting Greater Neural Responses to Irregular Than Regular Words, Single Cluster, Volume = 2,160 mm³, Five Contributing Studies

MRICron label	<i>p</i> (uncorrected)	MNI coordinates		
		<i>x</i>	<i>y</i>	<i>z</i>
Left inferior frontal gyrus opercularis	.002	-44	10	28
Left inferior frontal gyrus opercularis	.001	-52	10	18
Left inferior frontal gyrus opercularis	.001	-50	14	0
Left insula	.001	-30	20	-2
Left inferior frontal gyrus triangularis	.001	-44	22	2
Left white matter	.001	-32	14	6

Note. Results are thresholded at $p < .05$, false discovery rate corrected. Cluster $> 100 \text{ mm}^3$ reported. MNI = Montreal Neurological Institute.

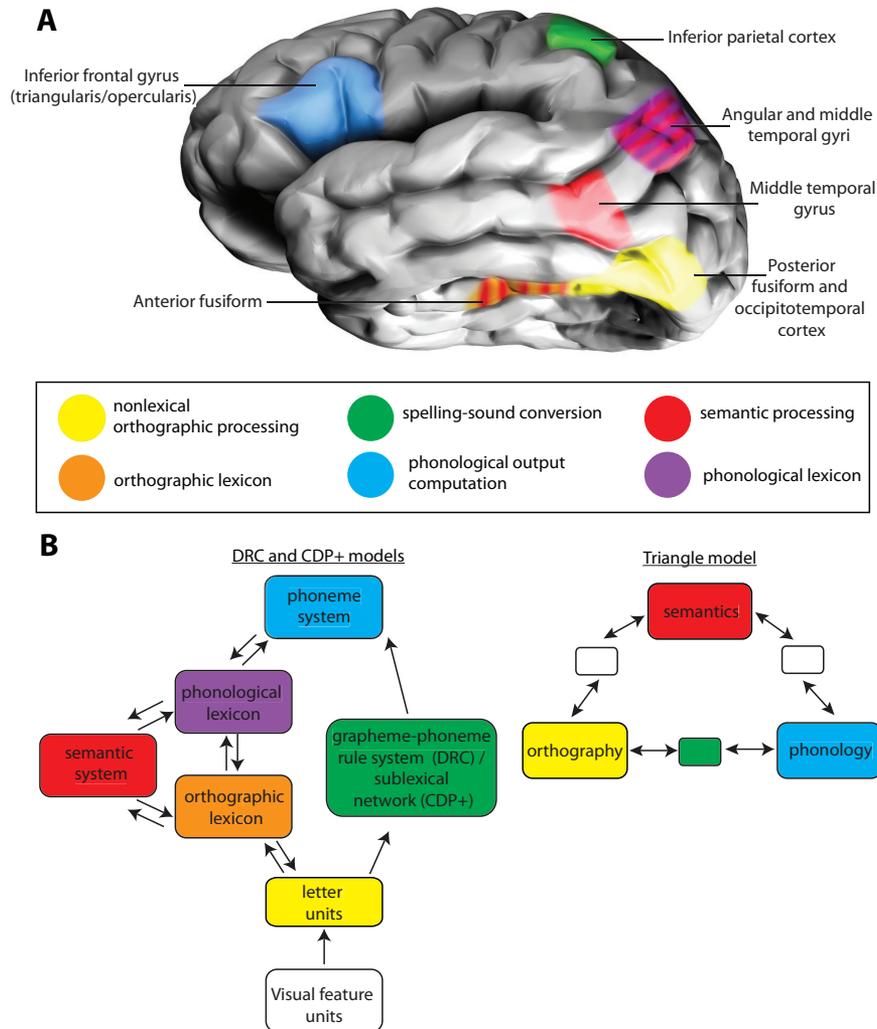


Figure 8. Illustration of the relationship between processes involved in word and pseudoword reading, cognitive model components, and anatomical structures. (A) Brain schematic rotated to show underside of temporal lobe. Striped colors indicate that a brain region could perform two processes. (B) Corresponding components in cognitive models. Note that although nonlexical orthographic processing is clearly the function of model components colored in yellow, none of the cognitive models predicted the pseudoword > word activity we obtained in left posterior fusiform and occipitotemporal cortex. DRC = dual-route cascaded; CDP+ = connectionist dual-process.

al., 1996), thus explaining the co-occurrence of semantic dementia and surface dyslexia (Patterson et al., 2006; Woollams et al., 2007). The correlational nature of fMRI methods means that we cannot draw conclusions about the causal role of these activated regions from this meta-analysis. Methods such as TMS could be used to disrupt processing in brain regions putatively associated with semantic processing and test whether this causes word reading impairments (see, e.g., Pobric, Jefferies, & Lambon Ralph, 2007). This demonstrates a way in which neuroimaging combined with brain stimulation techniques might enable one to distinguish between the accounts proposed by the two models.

Pseudowords > words. Our pseudoword > word contrast revealed a cluster of activity that extended through left posterior fusiform gyrus and occipitotemporal cortex ($-48, -62, -12$), a region that encompasses the putative visual word form area, pos-

tulated to represent sublexical orthographic form by Dehaene et al. (2005). This pattern of activity (reflecting increased processing effort) is predicted by Sibley et al.'s (2008) triangle model orthographic system, if the pseudowords were constructed from letter combinations that are less commonly occurring than those in the words. However, we reanalyzed our pseudoword > word data including only the studies that had carefully matched on sublexical orthographic variables⁴ and obtained the same activation cluster in posterior fusiform and occipitotemporal cortex, although it did not extend so far into inferior occipital cortex. Although we acknowledge that it is extremely difficult to match words and pseudowords

⁴ Studies that matched words and pseudowords on sublexical orthographic variables and were entered into this analysis are noted in Table 1.

for all sublexical orthographic variables (Keuleers & Brysbaert, 2011), it seems that the pattern of activity we observed in this region was not entirely driven by differences in orthographic typicality.

Price and Devlin (2011) proposed that pseudowords elicit greater left vOT activity than words because they elicit greater top-down feedback from higher level language regions, a proposal that is considered in greater detail in the conclusion section. Such top-down feedback should be greater in the active tasks used by the majority of the studies included in this meta-analysis (e.g., reading aloud, lexical decision) that necessitate processing in multiple brain regions, than in passive viewing tasks. Greater top-down feedback for pseudowords during active than passive tasks may therefore explain why we obtained pseudoword > word activity in this region, whereas Dehaene and colleagues (Cohen et al., 2002; Szwed et al., 2011; Vinckier et al., 2007), who typically use passive tasks, have reported equivalent activity for pseudowords and words. If pseudoword > word activity in visual cortex was driven by feedback from other language regions, it is poorly explained by all three cognitive models. Although they all include bidirectional connections between many or all components, there has been no investigation of whether greater activity for pseudowords than words in other model components might feedback and influence orthographic processing.

It is critical that future research establishes whether a large sample of pseudowords produces greater activity in left occipitotemporal cortex than words that are well matched for sublexical variables. If this effect turns out to be reliable, cognitive neuroscience and computational modeling research should explore the interplay between enhanced engagement, because a familiar orthographic pattern fits representations, and enhanced processing effort due to feedback from higher levels of representation. Such endeavors will benefit from integrating the body of work conducted by Dehaene, Price, and colleagues. MEG and EEG are key tools for examining the time course of linguistic processing and have been used to investigate similar questions about task-induced effects in the domain of spoken language. Garagnani, Shrtsov, and Pulvermüller (2009) showed that when stimuli were attended, the mismatch negativity effect was greater for pseudowords than words, whereas when stimuli were unattended the reverse pattern emerged. If active versus passive tasks also modulate left occipitotemporal activity to written words and pseudowords, and if this is driven by top-down feedback, occipitotemporal activity modulation should be observed later than, and correlate with, differential patterns of activity in downstream regions processing phonology and/or semantics. An example of how MEG and EEG can be used to explore feed-forward and feedback influences on response profiles in sensory cortices, again in the domain of spoken language, is provided by Sohoglu, Peelle, Carlyon, and Davis (2012).

Our pseudoword > word contrast also highlighted activity in left inferior parietal cortex. Neuroimaging research has proposed many functions for the parietal cortex, including verbal working memory (Honey, Bullmore, & Sharma, 2000; Jonides et al., 1998), spatial attention (Cohen, Dehaene, Vinckier, Jobert, & Montavont, 2008), and more general executive processes (Binder et al., 2005). In the context of single-word and pseudoword reading, however, we suggest a more specific role for this region in spelling–sound conversion. This is supported by S. M. Wilson et al. (2009), who found that patients with semantic dyslexia and surface dyslexia,

who pronounce low-frequency irregular words incorrectly (e.g., *pint* read to rhyme with *mint*) due to overreliance on spelling–sound rules, activated left parietal cortex more than control participants when reading words. Booth et al. (2003) also advocated the idea that this region is involved in processing nonlexical spelling–sound knowledge, finding that left parietal cortex activity correlated with performance on cross-modal, but not intramodal, spelling and rhyming tasks. Further evidence comes from Hashimoto and Sakai (2004), who observed increased responses in left inferior parietal cortex following training on novel symbol–phoneme associations, relative to training on novel symbol–non-speech associations, implicating it in learning visual–verbal associations. If pseudoword > word activity in left inferior parietal cortex reflects effortful spelling–sound conversion, it is predicted by all three models. In the DRC model, nonlexical route processing continues for longer, and is thus more effortful, for pseudowords than words. In the triangle and CDP+ models, pseudowords generate more error and take longer to process in the orthography–phonology/sublexical route than words, leading to greater processing effort, and therefore activity, in brain regions performing spelling–sound conversion should be greater.

Finally, we discuss activity in left IFG (opercularis and triangularis), insula cortex, and precentral gyrus that was also greater for pseudowords than words. Previous research has implicated these regions in phonological processing. For example, Poldrack et al. (1999) obtained left IFG opercularis activity in tasks involving phonological relative to semantic manipulations (e.g., rhyme vs. synonym judgment), and Mechelli, Josephs, Lambon Ralph, McClelland, and Price (2007) found that the left insula was more active when naming phonologically (e.g., *bell–belt*) relative to semantically related (e.g., *robin–nest*) words and objects. Mechelli et al. suggested that left insula contributes to discriminating competing phonological and articulatory codes, whereas the opercularis region of the left IFG is involved in phonological short-term memory. A role for left IFG opercularis in phonological short-term memory is also supported by a meta-analysis by Owen, McMillan, Laird, and Bullmore (2005), and a particular role for this region in resolving conflict is proposed by Thompson-Schill and colleagues (Novick, Kan, Trueswell, & Thompson-Schill, 2009; Schnur et al., 2009). In contrast, Binder et al. (2005) argued that because activity in this region correlates with response time when reading all word types (regular, irregular, pseudoword), it reflects general executive demands that are nonspecific to reading. However, all word types can have varying phonological output demands, due to length, familiarity, articulatory factors, etc.; thus, given the substantial literature implicating left IFG in phonological processing, we adhere to our argument that activity in this region (during reading) reflects the difficulty of resolving phonological output.

We therefore suggest that in the context of reading tasks, the left IFG and insula correspond to the phoneme system of the DRC model, phonological output buffer of the CDP+ model, and phoneme units of the triangle model. In all three models this component engages in more effortful processing for pseudowords than words, taking longer to settle on a phonological output in the DRC model, and additionally generating more error in the CDP+ and triangle models.

Irregular > regular words. Relative to regular words, irregular words consistently enhanced activity in just two clusters, in left frontal regions encompassing the orbitalis, triangularis, and

opercularis regions of the IFG and insula. This activation almost entirely overlapped with our prefrontal pseudoword > word cluster and did not overlap with any of our word > pseudoword clusters. Although irregular > regular word activity did overlap somewhat with an IFG cluster that Binder et al. (2009) implicated in semantic processing, there was also three-way overlap in this region with pseudoword > word activity. The results of this meta-analysis therefore provide no evidence that irregular words engage the semantic system more than regular words, and instead suggest that both pseudowords and irregular words require more effortful phonological output resolution.

Our results stand in contrast to those of Jobard et al. (2003), who implicated left IFG triangularis in semantic processing, and those of Graves et al. (2010, p. 1809), who argued that this region is “involved specifically in top-down attentional modulation of semantic networks in the [middle temporal gyrus/inferior temporal sulcus].” Other researchers have advocated similar views, suggesting that anterior and posterior left IFG play a role in controlled semantic and phonological processing, respectively (Devlin, Matthews, & Rushworth, 2003; Gough, Nobre, & Devlin, 2005; Pol-drack et al., 1999). The contrasts that contributed to Jobard et al.’s IFG cluster included semantic decision > viewing pseudowords and phonological decision > lexical decision. Their findings are therefore entirely compatible with another view that argues against posterior–anterior distinctions in left IFG, instead suggesting that left IFG plays a more general role in controlled linguistic processing (Gold, Balota, Kirchhoff, & Buckner, 2005). In the context of the tasks included in this meta-analysis, namely, word and pseudoword reading and recognition, we therefore stand by our suggestion that the most likely role for the left IFG is in controlled processing related to resolving phonological output.

Our results are in line with the DRC and CDP+ models, which suggest that irregular words enhance activity in the phoneme system and phonological output buffer relative to regular words, due to the effort needed to resolve the conflict between pronunciations produced by the lexical and nonlexical routes. They are also predicted by the triangle model, in which resolving pronunciation in the phoneme units is more effortful for inconsistent than consistent words. Finally, as outlined in the introduction, the triangle model predicts that engagement of semantic representations and semantic processing effort should be equivalent for consistent and inconsistent words, as this facilitates fast and efficient access to meaning from orthography.

One consideration for future research is that Graves et al. (2010) suggested that binary contrasts (employed by most neuroimaging studies included in this meta-analysis) may be less sensitive to activity modulated by regularity or consistency than the continuous manipulation employed in their multiparametric investigation. Unlike this meta-analysis, Graves et al. obtained inconsistent > consistent word activity in left temporal cortex (as well as left IFG), a region that Binder et al. (2009) found to be involved in semantic processing. In support of their argument, Graves et al. cited two studies by Bolger and colleagues (Bolger, Hornickel, Cone, Burman, & Booth, 2008; Bolger, Minas, Burman, & Booth, 2008) that also treated consistency as a continuous variable and found greater activation of left inferior temporal and fusiform gyri by inconsistent than consistent words. If more studies follow the method of Graves et al. and Bolger and colleagues, and manipulate variables of interest continuously, then a future meta-analysis

might obtain evidence for involvement of inferior temporal and fusiform regions in irregular word reading.

A more general goal for future computational modeling, behavioral, and neuroscientific investigations should be to investigate how learning environment and test task influence the extent to which semantic representations are recruited during irregular and regular word processing. As proposed in the introduction, the triangle model predicts that sole emphasis on the generation of phonology during learning may lead to greater semantic activation for inconsistent than consistent words, whereas environments that also emphasize the generation of meaning should not. Learning environment should also interact with task; tasks that focus on phonological output minimize the recruitment of the semantic system, whereas those that require lexical and semantic access maximize semantic involvement (as shown by the greater impact of semantic variables in lexical decision versus reading aloud; Balota, Cortese, Sergent-Marshall, Spieler, & Yap, 2004). One way forward in resolving these issues may be to capitalize on recent advances in word learning methodologies (e.g., Bowers, Davis, & Hanley, 2005; Gaskell & Dumay, 2003; McKay, Davis, Savage, & Castles, 2008; Merkx, Rastle, & Davis, 2011; Taylor, Plunkett, & Nation, 2011) to test these predictions explicitly.

Summary of Correspondence Between Model Components and Neuroimaging Data (Illustrated in Figure 8)

This meta-analysis demonstrated that words (relative to pseudowords) activated left anterior fusiform gyrus, a region that may correspond to the orthographic lexicon of the DRC and CDP+ models, and a region in middle temporal and angular gyri, which could correspond to the phonological lexicon in these models. However, given overlap with Binder et al.’s (2009) meta-analysis, word > pseudoword activity in both of these regions may instead reflect semantic processing, consistent with the DRC, CDP+, and triangle models. Pseudoword (relative to word) activity was obtained in a more posterior portion of left fusiform gyrus and occipitotemporal cortex. Thus, left occipitotemporal regions show hierarchical organization with word > pseudoword responses found in brain regions further along the visual processing pathway and pseudoword > word responses found closer to primary visual cortex. We note with interest that analogous hierarchical organization was found in a meta-analysis of lexicality effects for spoken words (Davis & Gaskell, 2009). Pseudoword > word activity in brain region that processes visual form is not currently well explained by the DRC, CDP+, or triangle model of reading, and it may be that top-down feedback from subsequent processing levels is necessary to account for such data (Price & Devlin, 2011). Investigation of top-down processing, in line with work in the visual domain by Kherif, Josse, and Price (2011) and Devlin et al. (2004) and in the spoken domain by Garagnani et al. (2009) and Sohoglu et al. (2012), using both neuroimaging and modeling techniques, could increase our understanding of visual word processing in left occipitotemporal cortex. Consistent with all three models, the contrast pseudowords > words also activated left inferior parietal cortex and left IFG, likely involved in spelling–sound conversion and computing phonological output, respectively. The only brain area that showed enhanced activity for irregular relative to regular words was in an overlapping region of

left inferior frontal cortex and was proposed to reflect the effort involved in resolving phonological output for these words, a process embodied in all three models.

Clusters That Did Not Correspond to Cognitive Model Components

Although cognitive models cannot be expected to account for every process that might occur when performing a particular task, processes that fall outside the scope of the models are considered here, as they are important when relating cognitive theory to neuroimaging data. The contrast words > pseudowords revealed clusters in left superior frontal gyrus, precuneus and posterior cingulum, medial orbitofrontal cortex and gyrus rectus, and right middle temporal gyrus. Activity in orbitofrontal cortex may be related to decision making and expectation (Kringelbach & Rolls, 2004), processes that were likely engaged by the lexical and phonological decision and visual feature detection tasks included in this meta-analysis and are outside the scope of the models. Binder et al. (2009) also obtained activation in left superior frontal gyrus, attributing this to processing of the emotional content of stimuli, and precuneus and posterior cingulum, which was suggested to reflect recall of episodic memories. These distributed activations, which, in conjunction with word > pseudoword clusters in middle temporal gyrus and middle frontal gyrus and are related to processing the meaningful content of words, are not captured by the single semantic system included in cognitive models of reading. Reading research might therefore benefit from considering debates about the modality-specific versus amodal nature of semantic representations (Barsalou, 2008; Patterson, Nestor, & Rogers, 2007).

A small word > pseudoword cluster (<200 mm³) was also obtained in left IFG triangularis, one voxel of which overlapped with the large pseudoword > word activation we obtained in left IFG. Although none of the models predict greater engagement or processing effort for words than pseudowords in this region, the two studies that contributed to this cluster in fact used the contrast irregular words > pseudowords. It therefore seems likely that this activity reflects phonological processing effort that may not have been equated for the irregular word and pseudoword stimuli included in these studies.

Several right hemisphere clusters were revealed by the contrast pseudowords > words, the largest of which were in inferior frontal and inferior parietal cortices. These form part of the multiple demand network described by Duncan (2010) and may reflect the fact that pseudowords are generally more difficult to process than words. One issue with this interpretation is that it raises the possibility that activation in the left hemisphere homologues of these regions might be explained in the same way. However, in the context of a reading task, we have presented good evidence to support a more specific role for the left IFG in resolving phonological output and for the left inferior parietal cortex in mapping between spelling and sound, both of which are more effortful for pseudowords than words. The two further pseudoword > word clusters we obtained in left and right supplementary motor cortex are attributed to the motoric processes of preparing articulatory patterns for speech output (Indefrey & Levelt, 2004; Papoutsis et al., 2009) following phonological processing. These articulatory functions are not explicitly incorporated into any of the models.

Jobard et al.'s (2003) meta-analysis identified a cluster in left anterior middle temporal gyrus that they suggested played a role in spelling-sounds conversion. This meta-analysis obtained a small pseudoword > word cluster in an overlapping region. As these clusters also overlap with activity obtained from a contrast of listening to pseudowords versus words in Davis and Gaskell's (2009) meta-analysis, we instead advocate their suggestion that this region is involved in auditory and phonetic processing. In the context of reading tasks, this may result from listening to one's own voice or "inner speech," a process that is not incorporated in cognitive models of reading.

A further point that should be acknowledged is that none of our contrasts revealed activation clusters in anterior temporal lobe, a region implicated in semantic processing by both neuropsychological data (Patterson et al., 2007) and Binder et al.'s (2009) meta-analysis. This may be because the single-word reading studies included in this meta-analysis do not make great enough demands on the semantic system and may have been exacerbated by the fact that the anterior temporal lobe is difficult to image using conventional methods (Devlin et al., 2000; Visser, Jefferies, & Lambon Ralph, 2010).

The Validity and Utility of the Engagement and Effort Framework

This meta-analysis of neuroimaging studies of single-word reading used the principles of engagement and effort to outline a way to relate processing in cognitive models to neural activity. We have argued that stimuli that a model component or brain region represents should engage and therefore activate it more than stimuli that it does not represent. However, within a set of stimuli that a region does represent, lower activity should be seen for stimuli that fit the representations well and require minimal processing effort, than for stimuli that fit less well and require greater processing effort. Neither of these principles in isolation is sufficient to explain how brain activity relates to cognitive processing. Effort without engagement suggests that the areas most activated by a stimulus would be those least able to process that stimulus; for example, white noise would activate all brain regions more than any other stimulus, as it is the most effortful thing to process. More than 2 decades of brain imaging research shows this to be clearly false. Conversely, engagement without effort suggests that the more familiar a stimulus is, that is, the better it fits the representations in a brain region, the greater neural activity should be. In fact the opposite is true, as shown by numerous demonstrations of repetition suppression—presenting a stimulus multiple times results in a reduction of neural activity. Thus, nonlinearity is a necessity in any framework purporting to relate brain activity to cognitive processing.

It is therefore unsurprising that Price and Devlin (2011) also adopted an inverted U-shaped function to explain how stimulus type and expertise modulate activity in left vOT. They argued that left vOT activity is driven by both sensory input and top-down feedback from brain regions processing higher order information (e.g., phonology and semantics), which conveys information about the extent to which the sensory input was predicted. Before learning to read, or if presented with an unfamiliar orthography, orthographic forms are not associated with spoken form or meaning, and thus vOT activity to written text will be

relatively low because it will process the sensory input but will not receive top-down predictions. Driving the upward slope of the inverted U-shaped function, vOT activity to written text will be higher once an individual has learned to read a particular orthography because it will process the sensory input and receive top-down predictions from phonology and/or semantics. However, once top-down feedback connections are established, some stimuli will be easier to predict than others, either because an individual has a high level of experience or because the stimulus is highly familiar. This difference in predictability drives the downward slope of the function: Highly predictable sensory inputs generate lower prediction error, and lower activity in left vOT, than less predictable sensory inputs.

Price and Devlin's (2011) proposal is similar to our framework in that it suggests that contrasts between different stimulus types (or between individuals with differing levels of expertise) can elicit activity in a particular brain region for two reasons: differences in engagement of processes, with greater engagement leading to greater activity, and differences in effort of processing, with lower effort leading to lower activity. The similarity between the two approaches supports the utility of our framework for subsequent research aiming to relate cognitive theories to neuroimaging data. However, Price and Devlin's central claim is that neural activity reflects both processing of the sensory input and the influence of top-down predictions from other brain regions. In contrast, our framework showed that the majority of the activation clusters obtained in this meta-analysis could be explained by differences in the extent to which a stimulus fits the representations *within* a particular brain region. Where this was not the case, we suggested that investigating the extent to which activity within a component of the reading system is influenced by its connections with other components should be a key effort for reading research. This is a clear area in which cognitive neuroscience and computational models can guide and inform each other (for an example of such a research effort in the domain of spoken language, see Gaggepain, Henson, & Davis, 2012). To forge links between cognitive neuroscience and cognitive modeling more generally, researchers in both fields should also consider how their data could be used to make predictions and evaluate existing findings in the other field. For example, computational modelers could more explicitly investigate the degree of unit activation over time, with a view to making predictions for brain imaging studies, and cognitive neuroscientists could more often consider how imaging designs based on the principles of engagement and effort relate to activation in cognitive model components. This meta-analysis illustrates how the existing neuroimaging literature provides a firm empirical foundation on which to base such investigations and forge such links.

We now make some suggestions for how the principles of engagement and effort relate to developmental reading research, focusing on the influence of both developmental stage and item type on processing during learning to read. We argued that written words that do not fit the representations in an individual's reading system will not engage that system. This could be the case for individuals at the earliest stages of learning and for letters or letter combinations that have been infrequently encountered. Share (1995) proposed the self-teaching hypothesis that suggests that the process of (laborious) decoding, which involves nonlexical

spelling-sound conversion and should occur in both of these situations, facilitates the acquisition of word-specific orthographic information. The earliest stages of learning (on both an individual and item level) are therefore about developing letter-sound knowledge, and it may be helpful to think of this skill acquisition as enabling decoding mechanisms to be engaged. In characterizing the later stages of learning, Perfetti and Hart (2001) argued in their lexical-quality hypothesis that learning to read involves acquiring well-specified orthographic representations but also well-specified phonological and semantic representations and the links between these three domains. It is this process that creates the effort section of the inverted U-shaped curve. Written words with well-specified representations will require less effortful processing than words with poorly specified representations. This can be the case for individuals at later (relative to earlier) stages of learning and for items that have been frequently (relative to infrequently) encountered.

Our meta-analysis supports Perfetti and Hart's (2001) proposal that the quality of representations in multiple domains (orthographic, phonological, semantic and/or lexical, sublexical) is important for successful word reading. Developmental research provides substantial evidence for this position. For example, although phoneme awareness and knowledge of spelling-sound correspondences are clearly crucial for reading (Muter, Hulme, Snowling, & Stevenson, 2004), Ricketts, Nation, and Bishop (2007) showed that vocabulary is important for exception word reading in English, and Nation and Cocksey (2009) found that young children's word reading was predicted by their ability to recognize a word's auditory form (i.e., lexical phonological representations). We therefore advocate the view, articulated by Nation (2009), that more research is needed on how rather than just if mappings between orthographic (lexical or sublexical) and semantic representations (as well as between orthographic and phonological representations) develop and are activated during reading. Investigating such processes may in itself bridge the gap between adult psycholinguistic and cognitive neuroscientific research and developmental research, as forging efficient links between all aspects of the reading system is surely what enables one to move from being a novice to a skilled reader. Furthermore, our framework is applicable to other domains than reading. For example, in regions involved in face processing, we suggested that typical adults should show a profile of nonface stimuli < novel and unique face stimuli, and novel and unique face stimuli > familiar and repeated face stimuli. One could determine a child's proficiency and developmental progression in face processing, or identify difficulties in face processing, by observing deviations from this profile. We hope that future research efforts will benefit from the firm empirical foundation provided by the framework, results, and interpretation set out in this meta-analysis.

Conclusions and Future Directions

The principles of engagement and effort enabled us to derive clear predictions from the DRC, CDP+, and triangle models of reading for how neural activity should be modulated by lexicality and spelling-sound regularity. We then demonstrated that there is an impressive degree of convergence between the functional organization of the reading system embodied in these cognitive models and the neural organization of brain areas activated during reading tasks. Our results

are thus consistent with the idea that word pronunciations can be accessed from their written forms in more than one way (i.e., using spelling–sound mappings or lexical–semantic representations). Several ongoing questions for the cognitive neuroscience of reading were suggested by our results and interpretation including: (a) Do whole-word orthographic representations develop over the course of reading development, or does whole-word knowledge only emerge through interactions between orthography, phonology, and semantics? (b) How are early stages of orthographic processing influenced by feedback from subsequent levels of representation (lexical, semantic, phonological)? (c) Are semantic representations necessary for accurate reading aloud, and does this vary with spelling–sound regularity, learning environment, and output demands? We note that these are also some of the most intriguing questions for cognitive psychologists concerned with understanding word reading. However, by providing a principled way to ground these cognitive questions in specific neural systems consistently activated in functional brain imaging studies, our meta-analysis allows us to recast these cognitive questions in terms of functional neuroanatomy. Thus, we can ask, (a) Does activation of left fusiform gyrus for written words relative to pseudowords reflect engagement of whole-word orthographic or semantic representations, or feedback from other language processing regions? (b) How might processing in posterior fusiform and occipitotemporal regions be influenced by top-down processes? (c) How is irregular relative to regular word reading influenced by lesioning or stimulating left temporal cortex, thus impairing engagement of semantic representations, and does the impact of such manipulations vary with stimulus type, task, and/or individual differences? In this way, our meta-analysis has shown that cognitive models are relevant for interpreting neuroimaging data and that neuroscientific studies can provide answers that are relevant for cognitive models.

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