# Anatomy is strategy: Skilled reading differences associated with structural connectivity differences in the reading network

CrossMark

William W. Graves [a,*], Jeffrey R. Binder [b], Rutvik H. Desai [c], Colin Humphries [b], Benjamin C. Stengel [b], Mark S. Seidenberg [d]

[a] Department of Psychology, Rutgers, The State University of New Jersey, Newark, NJ, USA
[b] Department of Neurology, Medical College of Wisconsin, Milwaukee, WI, USA
[c] Department of Psychology, University of South Carolina, Columbia, SC, USA
[d] Department of Psychology, University of Wisconsin, Madison, WI, USA

## ARTICLE INFO

## ABSTRACT

Are there multiple ways to be a skilled reader? To address this longstanding, unresolved question, we hypothesized that individual variability in using semantic information in reading aloud would be associated with neuroanatomical variation in pathways linking semantics and phonology. Left-hemisphere regions of interest for diffusion tensor imaging analysis were defined based on fMRI results, including two regions linked with semantic processing – angular gyrus (AG) and inferior temporal sulcus (ITS) – and two linked with phonological processing – posterior superior temporal gyrus (pSTG) and posterior middle temporal gyrus (pMTG). Effects of imageability (a semantic measure) on response times varied widely among individuals and covaried with the volume of pathways through the ITS and pMTG, and through AG and pSTG, partially overlapping the inferior longitudinal fasciculus and the posterior branch of the arcuate fasciculus. These results suggest strategy differences among skilled readers associated with structural variation in the neural reading network.

© 2014 The Authors. Published by Elsevier Inc. This is an open access article under the CC BY-NC-SA license (http://creativecommons.org/licenses/by-nc-sa/3.0/).

## 1. Introduction

Readers acquire extensive knowledge of the spellings, sounds, and meanings of words and the mappings between these codes (Harm & Seidenberg, 2004; Rayner, Foorman, Perfetti, Pesetsky, & Seidenberg, 2001). This knowledge is used in performing tasks such as determining the meaning or pronunciation of a word from print. Reading aloud has been widely studied because of its importance in early reading (Wagner & Torgesen, 1987) and because performance is often impaired in developmental dyslexia and in many types of neuropathology (Coslett, 2000; Gabrieli, 2009; Price & Mechelli, 2005). The types of computations that underlie reading aloud and their neural instantiations have been the focus of extensive research (Schlaggar & McCandliss, 2007).

Writing systems afford two ways to pronounce words from print (Fig. 1A). Pronunciations (phonology) can be computed directly (green arrow in Fig. 1A) from the written code (orthography); however, readers can also compute the meaning of a word

from its spelling, and then use meaning to generate a pronunciation (red arrows in Fig. 1A), as occurs in the related domain of spoken language production (Levelt, Roelofs, & Meyer, 1999). Evidence for these mechanisms derives from several types of research, including developmental studies of learning to read (the orthography–phonology pathway develops more rapidly than the semantic pathway; Harm & Seidenberg, 1999), studies of brain-injured patients for whom one or the other pathway is more impaired (Coslett, 2000), studies in which reliance on a given pathway is changed via manipulations of instructions or stimulus materials (Hino & Lupker, 2000; Kinoshita, Lupker, & Rastle, 2004), and neuroimaging studies (Fiez, Balota, Raichle, & Petersen, 1999; Jobard, Crivello, & Tzourio-Mazoyer, 2003). Whether *skilled* readers differ in the use of these two pathways is uncertain, however. The possibility has been discussed since a classic study by Baron and Strawson (1976) examining "Chinese" (visual) vs. "Phoenician" (phonological) subtypes of readers. However, it has been difficult to obtain clear evidence for the existence of these subtypes among skilled readers of English (Brown, Lupker, & Colombo, 1994; Yap, Balota, Sibley, & Ratcliff, 2012). Many individual differences in reading aloud (e.g., in the magnitude of frequency and spelling-sound consistency effects) may arise from differences in reading proficiency, experience, and speed rather than distinct reading

* Corresponding author. Address: Rutgers University, Department of Psychology, Smith Hall, Room 337, 101 Warren Street, Newark, NJ 07102, USA. Fax: +1 973 353 1171.
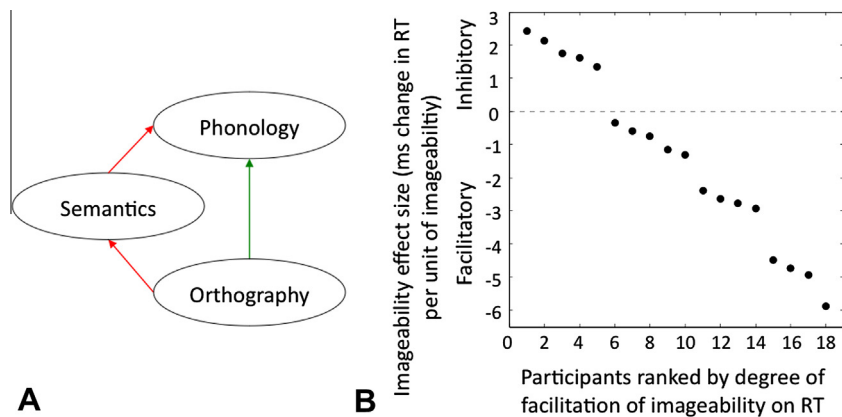E-mail address: william.graves@rutgers.edu (W.W. Graves).

**Fig. 1.** Triangle model and individual effects of imageability. (A) Schematic representation of the triangle model of reading. Red and green arrows indicate different reading pathways. For reading aloud, phonology units are assumed to be phonetic features sufficient to determine speech output. (B) Individual variability in effect of imageability on RT. Increased levels of imageability facilitated reading aloud for most participants, though some showed a weak effect in the opposite direction.

styles or strategies (Seidenberg, 1985). Here we consider potential strategy differences not in terms of overt, deliberative strategy, but rather as implicit differences in reading style that develop over a lifetime of reading.

The present study examined differences among skilled readers by addressing two questions: (1) do skilled readers differ in the extent to which semantic information is used in reading aloud, and (2) are such differences associated with neuroanatomical variability within the reading network? Regarding the first question, reading aloud does not demand access to word meaning, and in dual-route models of the task (Coltheart, Curtis, Atkins, & Haller, 1993; Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001; Perry, Ziegler, & Zorzi, 2007) it plays no role. However, a computation from orthography to semantics and then from semantics to phonology might facilitate processing for some individuals or some words (Plaut, 1997; Plaut, McClelland, Seidenberg, & Patterson, 1996). Findings concerning the use of semantic information in reading aloud are mixed. Many behavioral studies have shown that variables related to semantics, such as number of meanings and rated imageability, modulate reading aloud performance at the group level (Balota, Cortese, Sergent-Marshall, Spieler, & Yap, 2004; Hino & Lupker, 1996; Hino, Lupker, & Pexman, 2002; Rodd, 2004; Shibahara, Zorzi, Hill, Wydell, & Butterworth, 2003; Strain & Herdman, 1999; Strain, Patterson, & Seidenberg, 1995; Woollams, 2005; Yap, Pexman, Wellsby, Hargreaves, & Huff, 2012). However, some of these findings have been challenged (Monaghan & Ellis, 2002), and semantic effects were not observed in other studies (Baayen, Feldman, & Schreuder, 2006; Brown & Watson, 1987; de Groot, 1989).

The triangle model of reading seems most relevant here because it has been used to address the role of semantics in reading aloud (Plaut, 1997; Plaut et al., 1996; Woollams, Lambon Ralph, Plaut, & Patterson, 2007), within a broader theory of lexical processes in reading (Seidenberg, 2012). Learning to read involves learning to compute meanings and pronunciations from print. Skilled readers develop a division of labor between components of the system that allows these codes to be computed quickly and accurately (Harm & Seidenberg, 2004). The contributions from different parts of the system vary depending on factors such as properties of the stimulus (e.g., whether it is a familiar or unfamiliar word, a homophone or homograph, a nonword); properties of the mappings between codes (orthography and phonology are more highly correlated than orthography and semantics); properties of the writing system (its orthographic "depth"), the skill of the reader, and task. Importantly, the Fig. 1 model includes two hypothesized sources of input to phonology: directly from orthography and via the

orthography → semantics → phonology pathway. The orthography → phonology pathway performs functions attributed to the two pathways in the dual-route model. The orth → sem → phon pathway provides additional input during normal reading, unlike the dual-route approach (see Seidenberg & Plaut, 2006 for detailed comparisons between the models). Hence, the triangle framework seems most relevant to the goals of the current study. Before describing specific predictions, we briefly summarize some relevant studies on the neural basis of individual differences in reading.

Although neuroimaging experiments have yielded considerable evidence about components of the reading system (Binder, Medler, Desai, Conant, & Liebenthal, 2005; Fiez et al., 1999; Graves, Desai, Humphries, Seidenberg, & Binder, 2010; Hauk, Davis, & Pulvermüller, 2008; Herbster, Mintun, Nebes, & Becker, 1997; Joubert et al., 2004), and the impact of factors such as reading skill (Hoeft et al., 2007; Jobard, Vigneau, Simon, & Tzourio-Mazoyer, 2011; Kherif, Josse, Seghier, & Price, 2008), socioeconomic status (Seghier, Lee, Schofield, Ellis, & Price, 2008), and type of writing system (e.g., English vs. Chinese; Bolger, Perfetti, & Schneider, 2005), little research has examined variability among skilled readers. The Seghier et al. (2008) and Kherif et al. (2008) research yielded extensive evidence concerning brain activity during reading aloud but did not provide strong tests of the role of semantics. Both studies compared reading aloud to an unfilled rest condition. One concern with this approach is that engagement of semantic processing during rest (Binder, Desai, Graves, & Conant, 2009; Binder et al., 1999) would tend to mask activation of semantics in comparisons to reading aloud.

A study by Jobard et al. (2011) yielded some evidence for individual differences in patterns of brain activity during silent reading rather than overt naming among relatively proficient readers. Participants' performance varied on a test of verbal working memory, a task that correlates with reading and language skills (MacDonald & Christiansen, 2002). This measure negatively correlated with activation in frontal, parietal, temporal, and occipito-temporal regions identified in two meta-analyses of studies comparing reading to rest (Fiez & Petersen, 1998; Turkeltaub, Eden, Jones, & Zeffiro, 2002).

Finally, Welcome and Joanisse (2012) attempted to isolate orthographic, phonological, and semantic components of the reading system by using a series of tasks that vary in the extent to which they engage these types of information, and also examined individual differences among their participants, who showed a range of reading proficiencies. Individual differences in functional magnetic resonance imaging (fMRI) activation related to reading

comprehension were observed in the subgenual anterior cingulate and the dorsal aspect of the posterior superior temporal gyrus, neither of which is strongly implicated in single-word semantic processing (Binder & Desai, 2011; Binder et al., 2009). However, their reading comprehension measure involved discourse-level processing. Correlations of fMRI signal with a single-word reading aloud measure (sight word efficiency from the Test of Word Reading Efficiency; Torgesen, Wagner, & Rashotte, 1999) were found in posterior cingulate and, relevant to the current study, the posterior middle temporal gyrus (Welcome & Joanisse, 2012).

In summary, existing behavioral and neuroimaging studies provide clear evidence for individual differences related to reading skill and other cognitive capacities; however, the evidence concerning variability among skilled readers is limited. We therefore examined whether college-educated proficient readers differ in their use of semantic information in reading aloud, as indexed by the impact of imageability, a measure of the ease with which a word evokes a mental image. Imageability is commonly used to evaluate semantic processing because highly imageable words have richer, more easily computed semantic representations than less imageable words (Paivio, 1991; Plaut & Shallice, 1993; Schwanenflugel, 1991; Shallice, 1988). Below we report large individual differences in the impact of imageability on reading aloud in a sample of 18 skilled readers. This previously undocumented individual variability may explain the variability of findings among previous group studies of imageability effects in reading aloud.

We then addressed the second question, whether differences in the impact of imageability on reading aloud correlated with neuroanatomical differences in brain circuits relating semantics to phonology, using diffusion tensor imaging (DTI). The DTI analysis was conducted using data obtained in an fMRI study by Graves et al. (2010), in which the modulation of brain activation during reading aloud was associated with several commonly-studied lexical properties (frequency, imageability, spelling-sound consistency, and others). That study used a novel design in which stimulus words were selected so as to de-correlate these factors, yielding stimuli that varied independently along each dimension. This design provided a powerful method for examining brain activity associated with each factor decoupled from the others. It also ensured that any spatially overlapping neural effects of the factors would be due to shared neural substrates rather than statistical correlations among the factors. Imageability, the semantic factor, was reliably associated with activation in several regions during reading aloud. These included the angular gyrus (AG) and posterior cingulate/precuneus, regions associated with reading words of high imageability in previous studies (Bedny & Thompson-Schill, 2006; Binder, Medler, et al., 2005; Binder, Westbury, McKiernan, Possing, & Medler, 2005; Sabsevitz, Medler, Seidenberg, & Binder, 2005). The study also identified a novel region centered on the inferior temporal sulcus (ITS) that was activated by words with low spelling-sound consistency.

Whereas there was a strong effect of imageability in the analyses of brain activation, the effect on naming latencies, at the group level, was modest (Graves et al., 2010). Imageability showed a reliable pairwise correlation ($r = -0.097$, $p < 0.05$) with response time (RT) in the expected direction (higher imageability was associated with lower RTs), but it did not account for unique variance in a multivariate regression model. This divergence between fMRI and behavioral effects of imageability might reflect greater sensitivity of the brain measure compared to the behavioral measure. However, it also might be related to variation in participants' reliance on semantics in reading aloud. The DTI analysis in the present study was initiated to determine whether individual differences related to the use of semantics were associated with differences in connectivity within the reading network.

We hypothesized that greater use of semantic information in reading aloud would be correlated specifically with greater structural connectivity between semantic and phonological nodes in the reading network. Because the impact of the current study hinges on selection and interpretation of the regions of interest (ROIs), these are described next in some detail. The two regions hypothesized to be semantic nodes were the AG and ITS. As mentioned above, the AG has been implicated in semantic processing across numerous studies (Binder et al., 2009). This is also true of the ITS (Binder et al., 2009; Cattinelli, Borghese, Gallucci, & Paulesu, 2013). Involvement of the ITS with reading words of low spelling-sound consistency (Graves et al., 2010) also suggests that it may play a role in using semantics to aid the mapping from print to sound. Consistency effects arise from the quasiregular character of the mappings between orthography and phonology in English. In the implemented computational models (e.g., Harm & Seidenberg, 1999; Seidenberg & McClelland, 1989), consistency effects arise from exposure to many words with varying spelling-sound correspondences. In general, the orthography → phonology computation is more difficult for words containing spelling-sound correspondences that are unusual ("strange" words such as *yacht*), atypical (e.g., *pint* vs. *hint*, *lint*, *mint*, *tint* et al.), or highly inconsistent (e.g., *dose-lose-pose*), with such effects modulated by frequency of exposure to the word itself and by reading skill. When the orthography → phonology computation is difficult, the parallel computation from orthography → semantics → phonology provides additional input necessary to converge on the correct phonological code (Plaut et al., 1996). This account is supported by the finding that semantic dementia (SD) patients, for whom use of the orthography → semantics → phonology pathway is impaired, perform poorly in reading inconsistent words aloud, producing regularizations (pronouncing *blown* to rhyme with *crown*) and other errors (Woollams et al., 2007). Although the anterior temporal lobe is the primary area of degeneration in SD, with a relatively focal profile at least in early stages for some cases (Bright, Moss, Stamatakis, & Tyler, 2008), the posterior extent has been shown to include the middle MTG and ITG (Rohrer et al., 2009), spanning the ITS area considered here. The ITS is also associated with the activation of multiple word meanings (Whitney, Jefferies, & Kircher, 2011). The priming of both meanings of homonym targets activated the ITS, whereas priming of only the subordinate meaning activated fronto-temporal areas for semantic control, but not the ITS. Together these findings suggest a key role for the ITS in processing lexical semantics.

If the connectivity of these regions varies with the use of semantic information to help activate phonology, then it is the connections of these regions with areas related to phonological processing, such as the posterior superior temporal gyrus (pSTG; Graves, Grabowski, Mehta, & Gupta, 2008; Indefrey & Levelt, 2004; Vigneau et al., 2006; Wise et al., 2001) and posterior middle temporal gyrus (pMTG; Brambati, Ogar, Neuhaus, Miller, & Gorno-Tempini, 2009; Graves et al., 2010; Indefrey & Levelt, 2004; Richlan, Kronbichler, & Wimmer, 2009), that should vary with the degree to which semantics facilitates reading aloud. The pMTG was linked with phonological retrieval processes in a previous meta-analysis of speech production studies (Indefrey & Levelt, 2004). Activation in this region is consistently compromised in developmental dyslexia, a disorder often attributed to impaired phonological processing or orthography → phonology mapping (Richlan et al., 2009). Damage in this area also leads to acquired impairment in reading pseudowords, a task that depends on orthography → phonology mapping but not semantic processing (Brambati et al., 2009). In our previous fMRI study (Graves et al., 2010), the pMTG ROI used here showed increased BOLD signal for reading words of decreasing bigram frequency (i.e., words with lower orthographic typicality, a variable de-correlated from

biphone frequency in this set). Bigram frequency is necessarily correlated with the frequency with which letter combinations are mapped to phonology, so that the orthography → phonology mapping is less practiced for words with lower bigram frequency, resulting in greater processing difficulty for such words. Taken with evidence above linking pMTG to phonological processing, we interpreted the increased BOLD signal in pMTG with decreasing bigram frequency as indicative of orthography → phonology mapping.

Nearby but spatially distinct from the pMTG is the pSTG. In numerous studies the pSTG has been linked with phonological processing, particularly in studies involving overt speech production (Graves et al., 2008; Indefrey & Levelt, 2004; Vigneau et al., 2006; Wise et al., 2001). Overt reading tasks, however, typically activate the STG diffusely and bilaterally, presumably because the STG supports not only computation of phonological output codes but also general auditory processing and phoneme perception processes. Isolating the pSTG regions specifically involved in phonological output is therefore challenging. Our previous data showed a large effect of RT in the left pSTG, whereby BOLD signal increased with reading RT (Graves et al., 2010). Computational models of reading have demonstrated a correlation between RT observed in behavioral data and the degree to which computed phonological representations deviate from target values (Plaut et al., 1996; Seidenberg & McClelland, 1989), suggesting that RT reflects, in part, the processing associated with converging on accurate phonological representations. Thus, we based the pSTG ROI on the left posterior temporal region modulated by reading RT (Graves et al., 2010), which we propose is a marker for computation of phonological representations relevant to overt naming.

The left posterior occipitotemporal sulcus (pOTS), a region containing the putative "visual word form area" thought to primarily support orthographic processing (Binder, Medler, Westbury, Liebenthal, & Buchanan, 2006; Dehaene, Cohen, Sigman, & Vinckier, 2005; Vinckier et al., 2007), was also identified as an ROI. We defined the pOTS ROI (blue in Fig. 2A) as an area showing increased BOLD signal with decreasing word frequency (Graves et al., 2010; restricted to not extend beyond the atlas definition of the fusiform gyrus), a property of the pOTS reported in previous studies (Bruno, Zumberge, Manis, Lu, & Goldman, 2008; Kronbichler et al., 2004).

Finally, although our hypotheses primarily concern posterior temporo-parietal regions thought to be involved in the computation of orthography, phonology, and semantics leading up to word pronunciation (i.e., the regions in Fig. 4), an ROI located primarily in the pars opercularis and triangularis of the inferior frontal gyrus (IFG) was also included. This ROI was defined based on word-frequency related activation in the IFG from Graves et al. (2010; masked to ensure it did not extend beyond the atlas definition of the IFG). There is ample evidence suggesting a role for this region in aspects of phonological processing (Bookheimer, 2002; Katz et al., 2005; Sandak et al., 2004), although the degree to which activations in this region are distinguishable from effects of working memory or time-on-task is unclear (Binder, Medler, et al., 2005; Cattinelli et al., 2013; Graves et al., 2010; Taylor, Rastle, & Davis, 2013).

## 2. Materials and methods

### 2.1. Participants

The participants considered here are a subset of those involved in a previous fMRI study ($N = 20$; Graves et al., 2010). DTI data were collected on 18 (12 female) healthy, literate adults who spoke English as a first language. Their mean age was 23.1 (SD: 3.6), mean years of education 16.6 (SD: 3.3). All had normal or corrected-
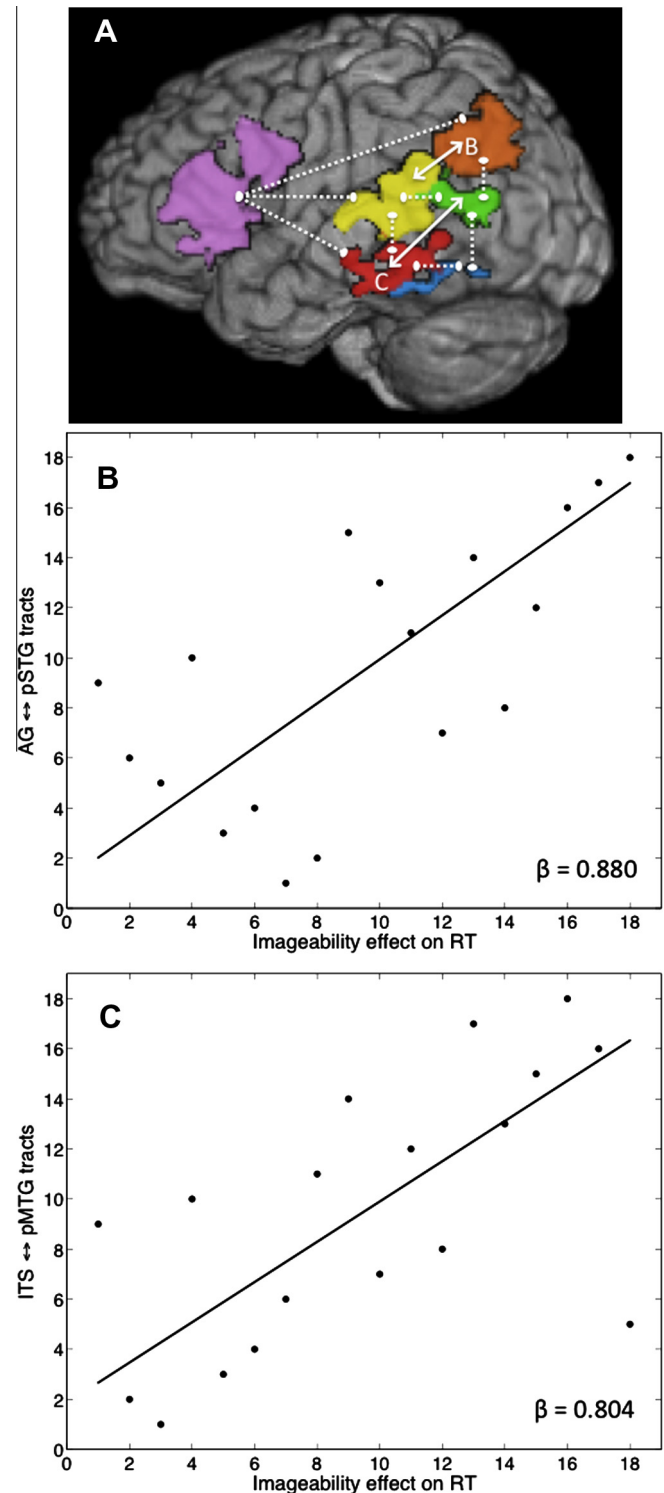


Fig. 2. Regression results. (A) The full set of 6 ROIs is shown, along with the 10 hypothesized pathway connections among them. Pathway volumes that significantly covaried with the behavioral effect of imageability are indicated by solid double-headed arrows, and non-significant connections are indicated with dotted lines. Blue = pOTS, red = ITS, green = pMTG, yellow = pSTG, orange = AG, and violet = IFG. Plots of significant results (corrected $p < 0.05$) for connections through AG and pSTG are shown in (B), and through ITS and pMTG in (C). X-axes are rankings for each participant of the imageability $\beta$-values from the multiple regression analyses on RT. Y-axes are rankings by participant of pathway volumes for the indicated tracts.

to-normal vision and were right-handed on the Edinburgh handedness inventory (Oldfield, 1971). A verbal IQ estimate from the

Wechsler Test of Adult Reading (Wechsler, 2001) showed a mean standard score of 109.3 (SD: 8.4). All participants provided written consent and were paid an hourly stipend according to local Institutional Review Board protocols.

## 2.2. Stimuli and task

Details of the stimuli and task are provided in Graves et al. (2010). The most relevant points to emphasize for the current analysis are that the task was reading aloud, and the stimuli consisted of 465 words for which length in letters, spelling-sound consistency, word frequency, imageability, bigram frequency, and biphone frequency were all uncorrelated. Graves et al. reported that imageability of the stimuli was uncorrelated with word frequencies from a large text-based corpus (Baayen, Piepenbrock, & Gulikers, 1995); it is also uncorrelated with frequencies from a corpus of spoken English (Brysbaert & New, 2009), ($r = 0.08$, $p > 0.05$).

## 2.3. Analysis of behavioral data

To address whether skilled readers differ in the degree to which they use semantic information in reading aloud, we analyzed RTs using multiple linear regression with the following 6 explanatory variables: length in letters, word frequency, consistency, imageability, the multiplicative interaction of word frequency and consistency, and the multiplicative interaction of consistency and imageability. Values for these variables were mean-centered to avoid any multicollinearity that might result from including interaction terms. This analysis was performed separately for each participant, producing effect size estimates in the form of β-weights for each variable. The interaction terms were included because of their theoretical interest involving division of labor during reading aloud (Frost et al., 2005; Plaut et al., 1996; Strain et al., 1995). Bigram and biphone frequency were not included because they did not significantly predict RT in our previous analysis (Graves et al., 2010). Imageability, the main covariate of interest in the current study, showed large variation across individuals in its effect on RT (β-weights from 2.4 to −5.9, Fig. 1B).

## 2.4. Image acquisition and analysis

MRI data were acquired using a 3.0-T GE Excite system with an 8-channel array head radio frequency receive coil. High-resolution, T1-weighted anatomical images were acquired in 134 contiguous axial slices ($0.938 \times 0.938 \times 1.000$ mm) using a spoiled-gradient-echo sequence (SPGR, GE Healthcare, Waukesha, WI). DTI data were acquired using a GE standard single-shot twice-refocused spin-echo pulse sequence (TE: 75.8 ms, TR: 7000 ms, matrix: $128 \times 128$, FOV: 192 mm, slice thickness: 2.5 mm with 0.5 mm gap, 32 axial slices) with 31 diffusion directions defined evenly across a unit sphere with a diffusion weighting of $b = 1000$ s/mm$^2$ and one volume of $b = 0$ s/mm$^2$. A SENSE-based parallel imaging method was used to minimize distortions.

The FSL 4.1 Diffusion Toolbox software was used for probabilistic tractography analysis (Behrens, Johansen Berg, Jbabdi, Rushworth, & Woolrich, 2007; Behrens et al., 2003). This pipeline includes (1) correction for eddy current distortion (using the eddy_correct utility), (2) Bayesian modeling of the posterior probabilities of local diffusion parameters at each voxel using Markov Chain Monte Carlo sampling (implemented in the bedpostx utility), and (3) generation of connectivity distributions from ROIs. ROIs were used as "waypoint" masks for identifying tracts passing through particular points in the brain, as implemented in probtrackx. This program was used in seedmask mode, with one ROI arbitrarily chosen as the seed and the other as the waypoint mask. The use of a waypoint mask ensures that only tracts passing through, but not necessarily ending in, both the seed and waypoint masks are included in calculating the connectivity distribution. Loop checking was performed on tracts to exclude those that looped back on themselves. Other parameters were: curvature threshold = 0.2, samples = 5000, steps per sample = 2000, step length = 0.5 mm.

This analysis produced a dependent measure for each ROI pair that was the number of voxels containing non-zero probability fibers (tracts) passing through the ROIs. Because the ROIs were used as waypoints rather than stopping point masks, the pathways (i.e., set of identified tracts) also extended beyond the ROIs (as evident in Fig. 3). The total volume of each pathway was the dependent variable included in the analyses. This choice was based on the assumption that to enable information flow between regions, it is sufficient for fiber tracts to pass through them. Whether or not the fibers also happen to terminate in either region is a separate issue that should not constrain the information flow between connected regions, as cortical pathways can have collateral projections along their paths (Tanigawa, Wang, & Fujita, 2005).

Each ROI was selected according to criteria described below, and back-projected from group- to individual-space by inverting the transformation matrix used to produce the group-level functional maps. Because this step resulted in somewhat differently
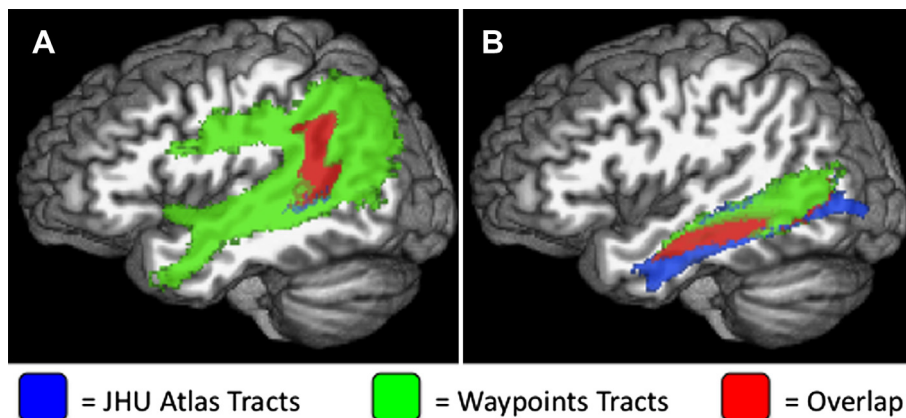


**= JHU Atlas Tracts**  **= Waypoints Tracts**  **= Overlap**

**Fig. 3.** Comparison of results from waypoints analyses with major known tracts. (A) Results from the analysis using AG and pSTG as waypoints are shown in green, compared with the SLF-PT from the JHU atlas shown in blue, and their overlap in red. (B) Results from the analysis using ITS and pMTG as waypoints are shown in green, compared with ILF from the JHU atlas in blue, and their overlap in red. For clarity of display, only tract voxels belonging to clusters of at least 200 mm$^3$ are shown. Note both the extensive amount of overlap as well as the distinct course of the tracts.

sized ROIs for each individual, the pathway volume for each ROI pair in each individual was normalized by dividing it by the total number of voxels contained in the ROIs, then multiplying by 100. We ran all the analyses without this volume normalization step and obtained the same pattern of results.

The resulting normalized volumes were analyzed for association with the β-weights from the regression analyses of individual RT data described above. Specifically, β-weights for effects of the stimulus properties letter length, word frequency, consistency, imageability, the multiplicative interaction of word frequency and consistency, the multiplicative interaction of consistency and imageability, and demographic information on age and level of education (both in years), were used as explanatory variables in a regression analysis for which pathway volume through ROI pairs was the dependent variable. The results are reported in terms of β-weights for a given explanatory variable (Table 1). These β-weights from the regression model are equivalent to standardized regression coefficients.

All values were converted to ranks prior to analysis (Conover & Iman, 1981). Ties were handled such that if, for example, ranks 2 and 3 were based on identical values, each would be assigned the rank of 2.5. Analyses were also performed without converting the data to ranks, and this produced essentially the same results. Although the association of imageability with the pSTG-AG pathway volume in the non-ranked analysis was not quite significant when correcting for all 10 connections ($q = 0.068$), it was significant ($q < 0.05$) when restricted to the 7 core hypothesized connections (the first 7 listed in Table 1, involving the regions in Fig. 4). The association of imageability with the ITS-pMTG pathway volume was significant after correction in both the ranked and un-ranked analyses. As shown in Fig. 2A, we tested all 10 nearest-neighbor connections among the 6 ROIs. Correction for multiple comparisons was performed at a false discovery rate of $q < 0.05$ (Benjamini & Hochberg, 1995).

## 2.5. Definition of ROIs

Six non-overlapping ROIs were defined in the left hemisphere (Fig. 2A). Functional interpretation of these ROIs was based on previously reported fMRI results from these participants (Graves et al., 2010) and on results from previous studies, as described in Section 1. In terms of specific methodological details, ROIs based on Graves et al. (2010) were taken directly from that study using the exact significance and extent criteria described previously. The only modifications made were to limit (mask) the regions so they did not extend beyond relevant anatomical boundaries, as defined in the Talairach atlas (file TT_N27_EZ_ML) included in AFNI (Lancaster et al., 2000). This served to ensure (1) that the functional ROIs did not overlap and (2) that they lay within defined anatomical regions. The ROIs were also restricted to the left hemisphere to help maintain sensitivity to relevant connections while minimizing the number of comparisons. Furthermore, activation during reading aloud in the previous study (Graves et al., 2010) was exclusively left-lateralized in the inferior frontal, inferior temporal, and middle temporal ROIs. The ITS region (red in Fig. 2A) was spatially bounded by the inferior and middle temporal gyri. The AG (orange in Fig. 2A) was spatially bounded by the atlas definition of the AG. The pMTG ROI was masked to be spatially bounded by the atlas definition of the MTG. The pSTG ROI was restricted to not extend beyond the atlas definition of the superior temporal gyrus and sulcus, and similarly for the pOTS (masked to only include areas within left fusiform gyrus) and IFG (masked to only include areas within the left inferior frontal gyrus) ROIs.

Another region, involving temporoparietal cortex in the left posterior Sylvian fissure, also showed an increased BOLD response with decreasing bigram frequency (Graves et al., 2010). We elected

**Table 1**
β-Weights (p-values) for the pathways shown in Fig. 2. Each row represents a connection tested with a separate multiple linear regression model. The models contained an explanatory variable for each of the 8 factor columns. Tests were corrected for multiple comparisons across rows (i.e., each of the 10 connections). Values in bold are significant at a corrected $q < 0.05$.

| | Factors | | | | | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | Length | Frequency | Consistency | Imageability | Frequency × consistency | Imageability × consistency | Age | Education |
| Pathways | | | | | | | | |
| pOTS-ITS | −0.0906 (0.7881) | −0.2846 (0.3164) | 0.6356 (0.0832) | 0.4871 (0.1478) | 0.0203 (0.9416) | −0.3128 (0.2324) | −0.2828 (0.6554) | 0.2470 (0.7075) |
| pOTS-pMTG | −0.2888 (0.4673) | 0.1343 (0.6770) | 0.0429 (0.9421) | 0.3912 (0.3025) | 0.1508 (0.6421) | −0.1172 (0.6896) | −1.3091 (0.0994) | 1.1242 (0.1638) |
| ITS-pMTG | −0.1283 (0.6170) | −0.0273 (0.8960) | 0.1918 (0.4572) | **0.8634 (0.0049)** | −0.0612 (0.7711) | −0.0999 (0.6021) | −1.4777 (0.0111) | 1.1079 (0.0473) |
| ITS-pSTG | −0.1092 (0.7719) | 0.0149 (0.9614) | 0.3644 (0.3432) | 0.7182 (0.0667) | −0.1090 (0.7258) | 0.1912 (0.5011) | −1.0610 (0.1554) | 1.1128 (0.1525) |
| pSTG-pMTG | 0.3425 (0.3575) | −0.2612 (0.3904) | −0.0314 (0.9308) | 0.4056 (0.2528) | −0.3821 (0.2216) | 0.0346 (0.8986) | 0.1753 (0.7969) | −0.3562 (0.6171) |
| pSTG-AG | 0.1004 (0.6983) | −0.3319 (0.1410) | 0.4953 (0.0790) | **0.8339 (0.0064)** | −0.2706 (0.2230) | −0.1823 (0.3558) | −0.3287 (0.5018) | 0.2446 (0.6288) |
| pMTG-AG | 0.0188 (0.9612) | −0.4776 (0.1550) | 0.5861 (0.1516) | 0.2093 (0.5676) | 0.0142 (0.9643) | 0.0636 (0.8254) | 0.0171 (0.9811) | −0.0058 (0.9938) |
| ITS-IFG | 0.3105 (0.4318) | −0.3268 (0.3182) | 0.0959 (0.8044) | 0.0913 (0.8026) | −0.2321 (0.4744) | 0.1615 (0.5803) | 0.0516 (0.9434) | −0.5052 (0.5092) |
| pSTG-IFG | 0.2940 (0.4540) | −0.2986 (0.3576) | 0.0838 (0.8279) | 0.0785 (0.8291) | −0.2283 (0.4796) | 0.1701 (0.5591) | 0.0056 (0.9939) | −0.4936 (0.5170) |
| AG-IFG | 0.3105 (0.4318) | −0.3268 (0.3182) | 0.0959 (0.8044) | 0.0913 (0.8026) | −0.2321 (0.4744) | 0.1615 (0.5803) | 0.0516 (0.9434) | −0.5052 (0.5092) |
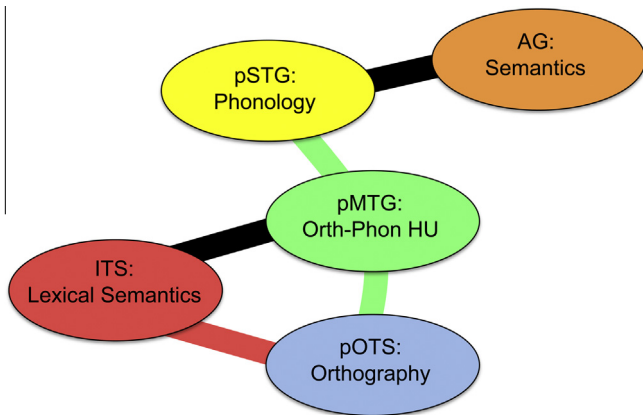
**Fig. 4.** Mapping of the current results (in black) onto a proposed model of the role of temporal and parietal regions in reading aloud. Colors in the ovals correspond to colors of the ROIs in Fig. 2. Connections in green represent the orthography → phonology pathway, while red highlights the semantics branch of the orthography → semantics → phonology pathway. Only the connections between semantic and phonological representations (black) showed an increase in pathway size correlated with facilitatory effects of imageability in reading aloud.

not to include this region as an ROI because it has been linked more conclusively with sensorimotor integration during speech articulation (Buchsbaum et al., 2011; Gow, 2012; Hickok & Poeppel, 2007), a process not of primary interest in this study, and because expanding the number of ROIs would likely offer little benefit while at the same time compounding the multiple comparisons problem.

## 3. Results

The degree to which imageability modulated RT varied widely across individuals, with 11 showing variable amounts of facilitation and 6 showing inhibition, for a range of β-weights between 2.4 and −5.9 (Fig. 1B). This contrasts with the consistency variable, which showed a quite narrow range of effects on RT across participants (β-weights from 1.1 to −1.6). Correlations between the behavioral effect of imageability and DTI pathway volume were examined for each of the ROI pairs of interest in Fig. 2A (and listed in Table 1). Pathways showing significant (corrected $q < 0.05$) correlations with imageability effects are indicated by solid lines with double-headed arrows in Fig. 2A (and bold font in Table 1), while pathways showing non-significant correlations are indicated by dotted lines. The more imageability facilitated reading aloud, the greater the volume of the pathway through ITS-pMTG (Fig. 2C, $\beta = 0.863$, uncorrected $p = 0.005$, $q = 0.032$). The same was true for the AG-pSTG pathway (Fig. 2B, $\beta = 0.834$, uncorrected $p = 0.006$, $q = 0.032$). Although there appears to be an outlier in Fig. 2C (corresponding to the participant ranked 18), its influence was minimized by converting all values to ranks (see Section 2). Pathways through pOTS-ITS, pOTS-pMTG, ITS-pSTG, pMTG-pSTG, and pMTG-AG were not significantly correlated with imageability

effects. No reliable associations were found between pathway volumes and age, level of education, or behavioral effects of word frequency, consistency, letter length, the interaction of word frequency and consistency, or the interaction of consistency and imageability (Table 1). The specificity of the findings to imageability and not the other tested factors makes it unlikely that the findings are due to individual differences in ROI volumes or group differences in pathway volumes. In fact, imageability effects across participants did not significantly correlate with ROI volumes for any of the ROIs. Volumes for both the ROIs and the examined pathways are given for reference in Table 2. Overall, these findings (1) identify novel structural brain correlates underlying individual differences in reading, and (2) reveal functional–anatomical pathways supporting the mapping between semantics and phonology in reading aloud.

To situate these findings within the context of known major white matter pathways, we created an overlap image in Talairach space of the AG-pSTG pathways from each of the individual subjects, and did the same for the ITS-pMTG pathways. These were thresholded so that only tracts co-occurring in at least 9 (50%) of the participants were displayed. Probabilistic maps of major known tracts from the Johns Hopkins University (JHU) white matter atlas were also registered to Talairach space and thresholded at 50% (Hua et al., 2008). As can be seen in Fig. 3A, the AG-pSTG pathway encompassed the parieto-temporal branch of the superior longitudinal fasciculus (SLF-PT), while also extending beyond it. The SLF-PT may correspond to the posterior segment of the arcuate fasciculus as identified by Catani and Jones (2005). One difference between the SLF-PT and the current AG-pSTG pathway, however, is that the latter extends to the AG, while the SFL-PT appears to lie mainly in the posterior peri-Sylvian white matter.

The ITS-pMTG pathway overlapped most closely with the inferior longitudinal fasciculus (ILF), though the course of the ILF had a longer extent in the anterior and posterior directions (Fig. 3B). Defining pathways using spherical ROIs near the ends of these known tracts as waypoints, however, did not yield significant correlations with imageability (for ILF: $\beta = 0.758$; for parieto-temporal branch of arcuate: $\beta = 0.327$; for fronto-temporal branch of arcuate: $\beta = 0.566$; all $q > 0.1$). Thus, while the pathways defined here by functional ROIs partly overlap large fasciculi, there are functionally relevant differences across individuals that are not equivalent to differences in the volumes of these large fasciculi.

## 4. Discussion

This study examined the influence of semantic information on reading aloud, and whether individual differences in the use of this information were related to anatomical differences in relevant parts of the neural circuits for reading. Effects of imageability on RT ranged widely (Fig. 1B), suggesting that skilled readers differ in the extent to which they use semantic information in reading aloud. This variation was associated with the volume of white matter tracts passing through both the ITS, an area that supports lexical semantic processing, and the pMTG, an area implicated in

**Table 2**
Mean ROI (top row) and normalized pathway volumes (with standard errors) for the regions shown in Fig. 2. NT = not tested.

| Mean ROI volumes (in 1.5 × 1.5 × 3 mm voxels) | 135.3 (4.7) | 461.4 (11.5) | 305.8 (8.4) | 1117.7 (29.9) | 822.9 (21.3) | 2058.1 (53.4) |
|---|---|---|---|---|---|---|
|  | pOTS | ITS | pMTG | pSTG | AG | IFG |
| ITS | 831.5 (65.1) | | | | | |
| pMTG | 688.1 (97.3) | 567.8 (62.4) | | | | |
| pSTG | NT | 598.1 (64.6) | 799.5 (57.7) | | | |
| AG | NT | NT | 432.3 (37.5) | 700.5 (55.4) | | |
| IFG | NT | 705.7 (138.7) | NT | 468.3 (110.4) | 615.9 (120.9) | |
|  | Mean normalized pathway volumes | | | | | |

phonological processing. A similar effect was found for the volume of tracts passing through both the AG, an area associated with semantic processing, and the pSTG, an area associated with phonological processing. Variability in how words are read is often attributed to use of different strategies or styles; our results show that one type of individual difference, in the use of semantics in reading aloud, is associated with neuroanatomical differences. Further research will be needed to determine the origins of these individual differences. There may be differences in brain development and structure that cause individuals to vary in how they read aloud. Alternatively, the neuroanatomical differences could result, wholly or in part, from experiential factors including the nature of early language and reading experience, and how reading is taught. The latter alternative is suggested by a study showing white matter changes associated with interventions for reading problems (Keller & Just, 2009). Further studies of this type using other methods in which participants acquire new reading skills (Bailey, Manis, Pedersen, & Seidenberg, 2004; Carreiras et al., 2009; Dehaene et al., 2010) are necessary, however. It may also be possible to track the development of these pathways in longitudinal studies of children who transition from pre-readers to reading (for an example focused on the pOTS see Ben-Shachar, Dougherty, Deutsch, & Wandell, 2011).

## 4.1. Toward an integrated neurocomputational theory

The analyses we conducted were hypothesis-driven, testing whether individual differences in reading aloud would be related to neuroanatomical differences in connectivity between areas thought to be involved in mappings between semantics and phonology, as indicated by other findings. However, the results are novel and require both replication (e.g., with additional subject populations, such as younger readers and adults who vary widely in reading skill) and extension (e.g., addressing individual differences involving other types of information and tasks, and in English and other writing systems). The main result concerning relations between behavioral and neuroanatomical differences is correlational, and the functions of the two semantic-phonological pathways are underdetermined. These are important directions for future research stimulated by interesting results in a promising new area.

Many neuroimaging articles presenting findings of similar scope and interest end here having discussed the limitations of the study and directions for future research. In the remainder of this article, we take the further step of relating the present results to computational models of word reading developed within the "triangle" framework (Plaut et al., 1996; Seidenberg & McClelland, 1989). Such models provide explicit mechanistic accounts of how tasks such as reading aloud are performed, and therefore could be useful in narrowing the interpretation of the present results. There is also considerable interest in developing computational theories of behavioral phenomena such as reading that are closely linked to and constrained by facts about the neurobiological substrate (Barber & Kutas, 2007; Laszlo & Plaut, 2012).

A meta-analytic approach by Taylor et al. (2013) is particularly relevant in that they investigated whether evidence from existing functional neuroimaging studies can adjudicate between dual-route and triangle models of reading. Their study offers a potentially useful framework for how cognitive models and functional neuroimaging can inform each other and advance both approaches. Their results are inconclusive, however, observing that even with their meta-analytic approach it remains difficult to use functional neuroimaging to adjudicate between the models. They note that the implementation of semantic processing in the triangle model distinguishes it from the dual-route model, at least in the domain of reading aloud. However, their analysis of activations for reading spelling-sound inconsistent compared to consistent words was only significant in left inferior frontal cortex, a region that is also associated with domain-general effects such as working memory or time-on-task (Cattinelli et al., 2013; Derrfuss, Brass, Neumann, & Yves von Cramon, 2005; Owen, McMillan, Laird, & Bullmore, 2005). The lack of activation for this condition in areas more typically associated with semantic processing, such as the ITS region considered here, left open the possibility that activation for inconsistent greater than consistent words could reflect either lexical semantic (consistent with the triangle model) or lexical non-semantic (consistent with the dual-route model) processing. That the ITS ROI used in the current study is based on an area that (1) showed increasing activation for words of decreasing consistency, and (2) is located in an area reliably associated with lexical semantic processing across numerous studies (Binder et al., 2009; Cattinelli et al., 2013), suggests it reflects a neural substrate for the involvement of semantics in reading aloud.

The dual-route approaches (Coltheart et al., 2001; Perry et al., 2007) then turn out to be less useful in the present context because they assume that reading aloud normally does not involve semantics. The "dual routes" are procedures for generating phonology from print. The core tenet of these models is that the two pathways are both necessary and sufficient to account for the pronunciation of letter strings (words and non-words) in English. Semantic effects on naming must therefore arise outside the normal naming process. For example, one might credibly ask whether the effects we observed could be "post-lexical", arising not from the computation of the phonological code but from subsequent decision or integration processes. Such post-lexical processes are an important component of reading comprehension, as in the interpretation of multi-word sequences (Desai, Binder, Conant, & Seidenberg, 2010; Humphries, Binder, Medler, & Liebenthal, 2006) and the integration of words with prior linguistic context (Hagoort, 2008). However, the naming task used in the present study makes no demand on decision or integration processes and is notably insensitive to such effects, in contrast to tasks such as lexical decision (Balota, Ferraro, & Connor, 1991; Seidenberg, Waters, Sanders, & Langer, 1984). In addition, although canonical semantic effects such as the N400 occur relatively late in the time course of word recognition, effects of semantic variables such as semantic coherence (the number of contexts in which a word occurs) have been detected 160 ms post word onset (Hauk, Davis, Ford, Pulvermüller, & Marslen-Wilson, 2006; Pulvermüller, Shtyrov, & Hauk, 2009). This timeframe corresponds to early stages of word recognition and reading aloud (Barber & Kutas, 2007), demonstrating that semantic effects are not restricted to later integration or decision-related processes. The cognitive loci of semantic effects are discussed further below. In short, the dual-route framework does not incorporate a role for semantics in the generation of pronunciations. Therefore it provides no explanation of why individuals vary in their use of semantic information during reading aloud, nor any hypotheses for what the neural basis of this variation might be. It is for these reasons that we feel the triangle framework is most useful for interpreting the current results. However, we should be clear that the goal of the current study was not to adjudicate between the triangle and dual-route models, but rather to investigate the neural basis of individual differences in the use of semantics in skilled reading aloud.

The triangle model framework will be used for two purposes: to ground the interpretation of the functions of the areas and pathways seen in the neuroimaging results, and to understand the behavioral and neuroanatomical individual differences associated with the use of semantics in reading aloud. This analysis yields a closer integration of the computational framework and neurobiological data, but also reveals limitations of existing models and

questions concerning factors that determine the "division of labor" between components of the reading system.

## 4.2. Functions of the neuroanatomical pathways

### 4.2.1. The ITS-pMTG pathway

The extent to which imageability affected performance in reading aloud predicted ITS-pMTG pathway volume. Involvement of the ITS region in semantics is suggested by several converging findings (Cattinelli et al., 2013; Rohrer et al., 2009; Whitney et al., 2011; Woollams et al., 2007), as described in Section 1. The ITS ROI was defined in terms of a negative correlation between spelling-sound consistency and BOLD signal in these participants.

Evidence has been cited above for a role of the pMTG in phonological processing (Brambati et al., 2009; Indefrey & Levelt, 2004; Richlan et al., 2009). It is, however, unlikely to be a phonology-specific processing area. In our study, this ROI was defined on the basis of a negative correlation with bigram frequency, which is a property of the orthographic input. In fact, pMTG activation was unrelated to biphone frequency (Graves et al., 2010). Unlike biphone frequency, bigram frequency is necessarily correlated with the frequency with which orthographic combinations are mapped to phonology. The orthography → phonology mapping is less practiced for words with lower bigram frequency, resulting in less efficient orthography → phonology mapping for such words. The pMTG may therefore play a role in orthography → phonology mapping, perhaps as an intermediate representation linking orthographic and phonological codes, analogous to the "hidden unit" representations in triangle models. These models were implemented with pools of units dedicated to different codes (e.g., orthography, phonology, semantics). Because of their computational complexity, the mappings between codes are hypothesized to occur via interlevel units whose characteristics are determined by both input (e.g., orthography) and output (e.g., phonology) codes. The orthographic, phonological, and semantic components are themselves assumed to develop from an initial state based on learning from perceptual-motor experience, and to be shaped by their participation in multiple computations (see Seidenberg, 2012 for discussion).

It should be noted that various areas referred to as pMTG have also been implicated in studies of semantic processing (e.g., Binder, Westbury, et al., 2005; Binder et al., 2003; Noppeney & Price, 2004; Pexman, Hargreaves, Edwards, Henry, & Goodyear, 2007; Souza, Donohue, & Bunge, 2009; Whitney et al., 2011). How can this be reconciled with our interpretation of the pMTG as a component of the orthography → phonology mapping system? One possibility is that a single pMTG site supports both semantic processing and orth–phon mapping. However, the areas referred to as pMTG and linked with semantic processing in these studies may be spatially distinct from the pMTG area that we propose as a part of the orthography → phonology mapping. As suggested by the specificity of the correlations of pathway volume with imageability shown in Fig. 2 (only 2 of the 10 correlations tested were reliable), whether or not such correlations were detected depends a great deal on the morphology and exact location of the ROIs. The pMTG label, however, is both inherently imprecise and not always applied consistently across studies. It is easy to find examples of studies, including some of our own, that attribute a semantic function to pMTG where the area being referred to is either anterior (Noppeney & Price, 2004; Souza et al., 2009; Whitney et al., 2011) or posterior and dorsal (Binder, Westbury, et al., 2005; Binder et al., 2003; Pexman et al., 2007) to the area shown in green in Fig. 2A. In the extensive meta-analysis by Binder et al. (2009), which documented reliable regions of overlap across 87 contrasts between semantic and matched non-semantic tasks, there is a "gap" in the semantic network centered around Talairach

coordinate −50, −50, 5, separating the lateral temporal and inferior parietal components of the network (see Fig. 4 in Binder et al., 2009). This location corresponds almost exactly to the center of the current pMTG ROI (−53, −51, 11), suggesting that semantic regions lie anterior and posterior to the current ROI but are functionally and spatially distinct from it. We propose that the pMTG region identified here, though not part of the semantic system proper, receives semantic information as input for performing other computations in reading aloud. This would also be consistent with the finding from Welcome and Joanisse (2012) that activation in the pMTG correlated with reading aloud of words (which have semantic content) but not non-words (which lack semantic content).

In summary, the behavior of this pMTG region suggests that it functions as a link between orthography and phonology. The fact that pMTG occupies an intermediate anatomical location between orthographic (pOTS) and phonological (pSTG) processing regions is also consistent with this interpretation. Thus the pOTS and pMTG activations correspond to the "front end" of the orthography → phonology computation. Whereas the pMTG appears to support a more abstract, mediational code with mixed characteristics, the pSTG may support a phonological representation more closely related to speech production (see below). The pOTS → pMTG orthography → phonology pathway functions in conjunction with the pOTS → ITS → pMTG circuit, which we interpret as the complementary orthography → semantics → phonology pathway (Fig. 4).

### 4.2.2. The AG-pSTG pathway

The effects of imageability on reading aloud also predicted AG-pSTG pathway volume. Reading aloud involves speech production, and activation in the pSTG has been shown to relate to aspects of speech production that involve phonology but not semantics (Graves et al., 2008; Indefrey, 2011; Vigneau et al., 2006; Wise et al., 2001), as described in Section 1.

Many studies have implicated the AG in semantic processing (see Binder et al., 2009 for relevant meta-analyses; Vigneau et al., 2006). AG activation is observed across a range of conditions contrasting semantically rich vs. impoverished stimuli. For example, the AG activates for meaningful words compared to well-matched but meaningless pseudowords and for concrete or highly imageable words compared to abstract or less imageable words (Binder et al., 2009). There is also some evidence that the semantic processing in AG is not identical to semantic processing in the temporal lobe (Binder & Desai, 2011). Its proximity to dorsal "where" processing streams and the multi-modal nature of this association cortex positions the AG as a convergence region for binding together multiple concepts into a meaningful sentence (Humphries et al., 2006) or overall theme (Schwartz et al., 2011).

The AG may contribute to phonological processing in a manner that is distinct from the inferior temporal region. The dorsal location of the AG suggests that it may not receive direct input from the pOTS, in contrast to the ITS and pMTG. Moreover, the volume of white matter tracts from AG to pMTG did not correlate with imageability effects, suggesting that the AG does not provide input via the pOTS → pMTG → pSTG orth–phon pathway. Instead, we propose that semantic information in the AG is activated concurrently with the phonological representation in pSTG and influences phonological access mainly through feedback to the pSTG. This architecture differs from the standard triangle model, in that there is a second semantic representation (in AG) that influences phonological activation relatively late in processing, independent of orthography. This input may be more critical when reading sentences and connected text, in which phonological retrieval is highly constrained by thematic context, cloze probability, and pragmatic knowledge. It may also be related to the use of phonology in maintaining linguistic information while processing text

(Acheson & MacDonald, 2011). Finally, this circuit can be seen as providing the basis for effects attributed to "post-lexical" processing.

These considerations yield the functional–anatomical model illustrated in Fig. 4. The direct orthography → phonology pathway (green lines) corresponds to pOTS → pMTG → pSTG. In the orthography → semantics → phonology pathway, corresponding to pOTS → ITS → pMTG, the size of the ITS-pMTG pathway is associated with individual variability in the use of semantic information for computing phonology. A second interaction between phonology and semantics occurs in the connectivity between pSTG and AG, again demonstrated by a correlation between pathway volume and individual differences in the use of semantic information. This model represents a step toward integrating functional, structural, and behavioral evidence, within a computational modeling framework. Many issues arising from this tentative account require further investigation, however, particularly the nature of the semantic representation in ITS compared to AG, and the relative timing of these semantic influences on phonological access.

Potential anatomical connections between the ITS and pSTG, however, were not found to correlate with imageability effect sizes across participants. This contrasts with a recent positive finding from an effective connectivity analysis (Boukrina & Graves, 2013) of the same Graves et al. (2010) fMRI dataset, using the same ROIs as those considered here. Specifically, ITS activation was found to drive activation in pSTG for high-imageability words, whereas the opposite pattern (pSTG driving activation in ITS) was found for low-imageability words. Although there may be numerous reasons for discrepancies between anatomical and effective connectivity results, they are consistent in showing modulation by imageability between lexical-semantic and phonology-related regions within the same neural network for reading.

### 4.3. Implications concerning division of labor in the reading system

The final issue concerns the implications of these findings for relations among different components of the reading system. Plaut et al. (1996) proposed that the involvement of the orth → sem → phon pathway in reading aloud depends on characteristics of the orth → phon pathway. For skilled readers, most words and nonwords can be pronounced using knowledge encoded in the orthography → phonology pathway (including both "rule-governed" words and "exceptions"). Based on simulations and a formal analysis of tradeoffs between frequency and spelling-sound consistency, Plaut et al. (1996) predicted that words for which the orth → phon computation is difficult (e.g., relatively uncommon words that have atypical spelling-sound correspondences, such as GAUGE or BROOCH) require greater input from orth → sem → phon. This analysis of the "division of labor" between pathways was consistent with findings from studies of skilled adult readers (Taraban & McClelland, 1987) and reading-impaired patients (e.g., patient MP; Bub, Cancelliere, & Kertesz, 1985).

Division of labor in reading English may also vary across individuals (Plaut, 1997; Plaut et al., 1996). Highly skilled readers pronounce words more rapidly and exhibit smaller consistency effects for lower frequency words (Seidenberg, 1985). In effect, a larger pool of words functions as "high frequency" for these individuals. Given this tuning of the orth → phon pathway, these readers should depend less on input from semantics. Conversely, slower readers show larger consistency effects across a broader frequency range, including some relatively "high frequency" words (Jared, 1997); they may require greater input from semantics. Previous experiments have not examined whether degree of semantic involvement varies in these ways, however.

In the present study, we observed clear individual differences in the use of semantic information associated with specific neuroanatomical differences. There is little evidence, however, that these effects were related to characteristics of the orth → phon system. As Graves et al. (2010) reported, the effect of consistency on response latencies was significant; however, the size of the effect did not differ greatly across participants (see Supplemental figure). Conversely, the effect of imageability on RT was statistically marginal, but there were large individual differences. The correlation between imageability and consistency effects across subjects was also non-significant ($r = -0.014$, $p > 0.95$). Finally, we found no evidence of individual differences in tract density related to the orthography → phonology computation (Table 1).

These results strongly suggest that individual differences in the use of orth → sem → phon can arise from factors other than tuning of the orth → phon pathway, which Plaut et al. had not considered. The experiential and neurodevelopmental factors that underlie these effects need to be addressed in future research. However, the present data do not provide a strong test of the Plaut et al. predictions concerning the impact of variability in the orth → phon pathway on division of labor. Consistency effects varied little among these participants, who are highly educated skilled readers. A stronger test of the division of labor hypothesis will require examining a more heterogeneous group of readers who exhibit greater variability with respect to the magnitude of consistency effects.

### 4.4. Potential limitations

DTI is based on measuring the anisotropic diffusion of water. As such, it is not a direct physiological measure of white matter integrity (Jbabdi & Johansen-Berg, 2011). This, combined with the fact that in this study we are measuring the volume occupied by tracts identified using probabilistic tractography, makes it challenging to assign a direct physiological interpretation to the pathway volume differences. Interpretation of the study results rests on the conventional assumption that larger pathways lead to faster throughput of neuronal impulses that would enable more efficient flow of information between functionally defined areas.

Another methodological choice we made concerned how the ROIs were defined. These were based on group-level results and then back-project them to native space for each participant. The potential unevenness in this mapping process could have resulted in differences in ROI size across participants that was unrelated to performance. We addressed this using normalization procedures, and the results were essentially the same whether normalized by individual ROI size or total amount of white matter. This stability of results points to the validity of our method of defining ROIs. It is also preferred over the alternative of defining the ROIs based on individual activation patterns. The focus of this study is on individual structural neural differences, whereas defining the ROIs based on individual, rather than group, activations would introduce uncertainty about whether any observed differences were due to structural or functional variation.

While the use of ROIs restricted to the left hemisphere was motivated based on results from the previous fMRI study (Graves et al., 2010), the right hemisphere also clearly plays a role in reading, even for single words (Chiarello, 2003). Future studies with, for example, double the number of participants in the current study, will be aimed at exploring structural and functional connectivity for reading in both hemispheres.

The current results also do not allow us to determine the extent to which the relationships identified among the ROIs are specific to reading. For example, the pSTG and ITS regions have also been associated with picture naming (Damasio, Tranel, Grabowski, Adolphs, & Damasio, 2004; Graves, Grabowski, Mehta, & Gordon, 2007).

# 5. Conclusion

Here we examined whether skilled readers differed in their use of semantic information in reading aloud, and whether such individual differences map onto structural neural differences in connectivity of the reading network. We found considerable variation across individuals in the influence of semantics, and this variation corresponded specifically to differences in the degree of structural connectivity between regions connecting areas that process semantic information with areas that process phonological information. These findings have implications for cognitive models of reading, and suggest that there are different ways to be a skilled reader.

# Acknowledgments

# Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.bandl.2014.03.005.

# References

Acheson, D. J., & MacDonald, M. C. (2011). The rhymes that the reader perused confused the meaning: Phonological effects during on-line sentence comprehension. *Journal of Memory and Language, 65*(2), 193–207.

Baayen, R. H., Feldman, L. B., & Schreuder, R. (2006). Morphological influences on the recognition of monosyllabic monomorphemic words. *Journal of Memory and Language, 55*, 290–313.

Baayen, R. H., Piepenbrock, R., & Gulikers, L. (1995). *The CELEX lexical database* (2.5th ed.). Linguistic Data Consortium. University of Pennsylvania.

Bailey, C. E., Manis, F. R., Pedersen, W. C., & Seidenberg, M. S. (2004). Variation among developmental dyslexics: Evidence from a printed-word learning task. *Journal of Experimental Child Psychology, 87*, 125–154.

Balota, D. A., Cortese, M. J., Sergent-Marshall, S. D., Spieler, D. H., & Yap, M. J. (2004). Visual word recognition of single-syllable words. *Journal of Experimental Psychology: General, 133*(2), 283–316.

Balota, D. A., Ferraro, F. R., & Connor, L. T. (1991). On the early influence of meaning in word recognition: A review of the literature. In P. J. Schwanenflugel (Ed.), *The psychology of word meanings* (pp. 187–222). Hillsdale, NJ: Lawrence Erlbaum Associates.

Barber, H. A., & Kutas, M. (2007). Interplay between computational models and cognitive electrophysiology in visual word recognition. *Brain Research Reviews, 53*, 98–123.

Baron, J., & Strawson, C. (1976). Use of orthographic and word-specific knowledge in reading words aloud. *Journal of Experimental Psychology: Human Perception and Performance, 2*(3), 386–393.

Bedny, M., & Thompson-Schill, S. L. (2006). Neuroanatomically separable effects of imageability and grammatical class during single-word comprehension. *Brain and Language, 98*, 127–139.

Behrens, T. E. J., Johansen Berg, H., Jbabdi, S., Rushworth, M. F. S., & Woolrich, M. W. (2007). Probabilistic diffusion tractography with multiple fibre orientations: What can we gain? *NeuroImage, 34*, 144–155.

Behrens, T. E. J., Woolrich, M. W., Jenkinson, M., Johansen-Berg, H., Nunes, R. G., Clare, S., et al. (2003). Characterization and propagation of uncertainty in diffusion-weighted MR imaging. *Magnetic Resonance in Medicine, 50*, 1077–1088.

Ben-Shachar, M., Dougherty, R. F., Deutsch, G. K., & Wandell, B. A. (2011). The development of cortical sensitivity to visual word forms. *Journal of Cognitive Neuroscience, 23*(9), 2387–2399.

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society Series B, 57*(1), 289–3000.

Binder, J. R., & Desai, R. H. (2011). The neurobiology of semantic memory. *Trends in Cognitive Sciences, 15*(11), 527–536.

Binder, J. R., Desai, R. H., Graves, W. W., & Conant, L. L. (2009). Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cerebral Cortex, 19*, 2767–2796.

Binder, J. R., Frost, J. A., Hammeke, T. A., Bellgowan, P. S. F., Rao, S. M., & Cox, R. W. (1999). Conceptual processing during the conscious resting state: A functional MRI study. *Journal of Cognitive Neuroscience, 11*(1), 80–93.

Binder, J. R., McKiernan, K. A., Parsons, M. E., Westbury, C. F., Possing, E. T., Kaufman, J. N., et al. (2003). Neural correlates of lexical access during visual word recognition. *Journal of Cognitive Neuroscience, 15*(3), 372–393.

Binder, J. R., Medler, D. A., Desai, R., Conant, L. L., & Liebenthal, E. (2005). Some neurophysiological constraints on models of word naming. *NeuroImage, 27*, 677–693.

Binder, J. R., Medler, D. A., Westbury, C. F., Liebenthal, E., & Buchanan, L. (2006). Tuning of the human left fusiform gyrus to sublexical orthographic structure. *NeuroImage, 33*, 739–748.

Binder, J. R., Westbury, C. F., McKiernan, K. A., Possing, E. T., & Medler, D. A. (2005). Distinct brain systems for processing concrete and abstract concepts. *Journal of Cognitive Neuroscience, 17*(6), 905–917.

Bolger, D. J., Perfetti, C. A., & Schneider, W. (2005). Cross-cultural effect on the brain revisited: Universal structures plus writing system variation. *Human Brain Mapping, 25*, 92–104.

Bookheimer, S. (2002). Functional MRI of language: New approaches to understanding the cortical organization of semantic processing. *Annual Review of Neuroscience, 25*, 151–188.

Boukrina, O., & Graves, W. W. (2013). Neural networks underlying contributions from semantics in reading aloud. *Frontiers in Human Neuroscience, 7.* Article 518.

Brambati, S. M., Ogar, J., Neuhaus, J., Miller, B. L., & Gorno-Tempini, M. L. (2009). Reading disorders in primary progressive aphasia: A behavioral and neuroimaging study. *Neuropsychologia, 47*, 1893–1900.

Bright, P., Moss, H. E., Stamatakis, E. A., & Tyler, L. K. (2008). Longitudinal studies of semantic dementia: The relationship between structural and functional changes over time. *Neuropsychologia, 46*, 2177–2188.

Brown, G. D., & Watson, F. L. (1987). First in, first out: Word learning age and spoken word frequency as predictors of word familiarity and word naming latency. *Memory and Cognition, 15*, 208–216.

Brown, P., Lupker, S. J., & Colombo, L. (1994). Interacting sources of information in word naming: A study of individual differences. *Journal of Experimental Psychology: Human Perception and Performance, 20*(3), 537–554.

Bruno, J. L., Zumberge, A., Manis, F. R., Lu, Z.-L., & Goldman, J. G. (2008). Sensitivity to orthographic familiarity in the occipito-temporal region. *NeuroImage, 39*, 1988–2001.

Brysbaert, M., & New, B. (2009). Moving beyond Kučera and Francis: A critical evaluation of current word frequency norms and the introduction of a new and improved word frequency measure for American English. *Behavior Research Methods, 41*(4), 977–990.

Bub, D., Cancelliere, A., & Kertesz, A. (1985). Whole-word and analytic translation of spelling to sound in a non-semantic reader. In K. E. Patterson, J. C. Marshall, & M. Coltheart (Eds.), *Surface dyslexia: Neuropsychological and cognitive studies of phonological reading* (pp. 15–34). London: Lawrence Erlbaum Associates.

Buchsbaum, B. R., Baldo, J., Okada, K., Berman, K. F., Dronkers, N., D'Esposito, M., et al. (2011). Conduction aphasia, sensory-motor integration, and phonological short-term memory – An aggregate analysis of lesion and fMRI data. *Brain and Language, 119*, 119–128.

Carreiras, M., Seghier, M. L., Baquero, S., Estévez, A., Lozano, A., Devlin, J. T., et al. (2009). An anatomical signature for literacy. *Nature, 461*, 983–986.

Catani, M., Jones, D. K., & ffytche, D. H. (2005). Perisylvian language networks of the human brain. *Annals of Neurology, 57*, 8–16.

Cattinelli, I., Borghese, N. A., Gallucci, M., & Paulesu, E. (2013). Reading the reading brain: A new meta-analysis of functional imaging data on reading. *Journal of Neurolinguistics, 26*(1), 214–238.

Chiarello, C. (2003). Parallel systems for processing language: Hemispheric complementarity in the normal brain. In M. T. Banich & M. Mack (Eds.), *Mind, brain, and language: Multidisciplinary perspectives* (pp. 229–247). Mahwah, NJ: Lawrence Erlbaum Associates.

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

Coltheart, M., Rastle, K., Perry, C., Langdon, R., & Ziegler, J. (2001). DRC: A dual route cascaded model of visual word recognition and reading aloud. *Psychological Review, 108*(1), 204–256.

Conover, W. J., & Iman, R. L. (1981). Rank transformations as a bridge between parametric and nonparametric statistics. *The American Statistician, 35*(3), 124–129.

Coslett, H. B. (2000). Acquired dyslexia. *Seminars in Neurology, 20*(4), 419–426.

Damasio, H., Tranel, D., Grabowski, T., Adolphs, R., & Damasio, A. (2004). Neural systems behind word and concept retrieval. *Cognition, 92*, 179–229.

de Groot, A. M. B. (1989). Representational aspects of word imageability and word frequency as assessed through word association. *Journal of Experimental Psychology: Learning Memory and Cognition, 15*(5), 824–845.

Dehaene, S., Cohen, L., Sigman, M., & Vinckier, F. (2005). The neural code for written words: A proposal. *Trends in Cognitive Sciences, 9*(7), 335–341.

Dehaene, S., Pegado, F., Braga, L. W., Ventura, P., Filho, G. N., Jobert, A., et al. (2010). How learning to read changes the cortical networks for vision and language. *Science, 330*, 1359–1364.

Derrfuss, J., Brass, M., Neumann, J., & Yves von Cramon, D. (2005). Involvement of the inferior frontal junction in cognitive control: Meta-analyses of switching and stroop studies. *Human Brain Mapping, 25*, 22–34.

Desai, R. H., Binder, J. R., Conant, L. L., & Seidenberg, M. S. (2010). Activation of sensory–motor areas in sentence comprehension. *Cerebral Cortex, 20*(2), 468–478.

Fiez, J. A., Balota, D. A., Raichle, M. E., & Petersen, S. E. (1999). Effects of lexicality, frequency, and spelling-to-sound consistency on the functional anatomy of reading. *Neuron, 24*, 205–218.

Fiez, J. A., & Petersen, S. E. (1998). Neuroimaging studies of word reading. *Proceedings of the National Academy of Sciences of the United States of America, 95*, 914–921.

Frost, S. J., Mencl, W. E., Sandak, R., Moore, D. L., Rueckl, J. G., Katz, L., et al. (2005). A functional magnetic resonance imaging study of the tradeoff between semantics and phonology in reading aloud. *NeuroReport, 16*(6), 621–624.

Gabrieli, J. D. E. (2009). Dyslexia: A new synergy between education and cognitive neuroscience. *Science, 325*, 280–283.

Gow, D. W. (2012). The cortical organization of lexical knowledge: A dual lexicon model of spoken language processing. *Brain and Language, 121*, 273–288.

Graves, W. W., Desai, R., Humphries, C., Seidenberg, M. S., & Binder, J. R. (2010). Neural systems for reading aloud: A multiparametric approach. *Cerebral Cortex, 20*, 1799–1815.

Graves, W. W., Grabowski, T. J., Mehta, S., & Gordon, J. K. (2007). A neural signature of phonological access: Distinguishing the effects of word frequency from familiarity and length in overt picture naming. *Journal of Cognitive Neuroscience, 19*(4), 617–631.

Graves, W. W., Grabowski, T. J., Mehta, S., & Gupta, P. (2008). Left posterior superior temporal gyrus participates specifically in accessing lexical phonology. *Journal of Cognitive Neuroscience, 20*, 1698–1710.

Hagoort, P. (2008). The fractionation of spoken language understanding by measuring electrical and magnetic brain signals. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences, 363*, 1055–1069.

Harm, M. W., & Seidenberg, M. S. (1999). Phonology, reading acquisition, and dyslexia: Insights from connectionist models. *Psychological Review, 106*(3), 491–528.

Harm, M. W., & Seidenberg, M. S. (2004). Computing the meanings of words in reading: Cooperative division of labor between visual and phonological processes. *Psychological Review, 111*(3), 662–720.

Hauk, O., Davis, M. H., Ford, M., Pulvermüller, F., & Marslen-Wilson, W. D. (2006). The time course of visual word recognition as revealed by linear regression analysis of ERP data. *NeuroImage, 30*, 1383–1400.

Hauk, O., Davis, M. H., & Pulvermüller, F. (2008). Modulation of brain activity by multiple lexical and word form variables in visual word recognition: A parametric fMRI study. *NeuroImage, 42*, 1185–1195.

Herbster, A. N., Mintun, M. A., Nebes, R. D., & Becker, J. T. (1997). Regional cerebral blood flow during word and nonword reading. *Human Brain Mapping, 5*, 84–92.

Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience, 8*, 393–402.

Hino, Y., & Lupker, S. J. (1996). Effects of polysemy in lexical decision and naming – An alternative to lexical access accounts. *Journal of Experimental Psychology: Human Perception and Performance, 22*, 1331–1356.

Hino, Y., & Lupker, S. J. (2000). Effects of word frequency and spelling-to-sound regularity in naming with and without preceding lexical decision. *Journal of Experimental Psychology: Human Perception and Performance, 26*(1), 166–183.

Hino, Y., Lupker, S. J., & Pexman, P. M. (2002). Ambiguity and synonymy effects in lexical decision, naming, and semantic categorization tasks: Interactions between orthography, phonology, and semantics. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 28*(4), 686–713.

Hoeft, F., Meyler, A., Hernandez, A., Juel, C., Taylor-Hill, H., Martindale, J. L., et al. (2007). Functional and morphometric brain dissociation between dyslexia and reading ability. *Proceedings of the National Academy of Sciences of the United States of America, 104*(10), 4234–4239.

Hua, K., Zhang, J., Wakana, S., Jiang, H., Li, X., Reich, D. S., et al. (2008). Tract probability maps in stereotaxic spaces: Analyses of white matter anatomy and tract-specific quantification. *NeuroImage, 39*(1), 336–347.

Humphries, C., Binder, J. R., Medler, D. A., & Liebenthal, E. (2006). Syntactic and semantic modulation of neural activity during auditory sentence comprehension. *Journal of Cognitive Neuroscience, 18*(4), 665–679.

Indefrey, P. (2011). The spatial and temporal signatures of word production. *Frontiers in Psychology, 2*. Article 255.

Indefrey, P., & Levelt, W. J. M. (2004). The spatial and temporal signatures of word production components. *Cognition, 92*(1–2), 101–144.

Jared, D. (1997). Spelling-sound consistency affects the naming of high-frequency words. *Journal of Memory and Language, 36*, 505–529.

Jbabdi, S., & Johansen-Berg, H. (2011). Tractography: Where do we go from here? *Brain Connectivity, 1*(3), 169–183.

Jobard, G., Crivello, F., & Tzourio-Mazoyer, N. (2003). Evaluation of the dual route theory of reading: A metanalysis of 35 neuroimaging studies. *NeuroImage, 20*, 693–712.

Jobard, G., Vigneau, M., Simon, G., & Tzourio-Mazoyer, N. (2011). The weight of skill: Interindividual variability of reading related brain activation patterns in fluent readers. *Journal of Neurolinguistics, 24*, 113–132.

Joubert, S., Beauregard, M., Walter, N., Bourgouin, P., Beaudoin, G., Leroux, J.-M., et al. (2004). Neural correlates of lexical and sublexical processes in reading. *Brain and Language, 89*, 9–20.

Katz, L., Lee, C. H., Tabor, W., Frost, S. J., Mencl, W. E., Sandak, R., et al. (2005). Behavioral and neurobiological effects of printed word repetition in lexical decision and naming. *Neuropsychologia, 43*, 2068–2083.

Keller, T. A., & Just, M. A. (2009). Altering cortical connectivity: Remediation-induced changes in the white matter of poor readers. *Neuron, 64*, 624–631.

Kherif, F., Josse, G., Seghier, M. L., & Price, C. J. (2008). The main sources of intersubject variability in neuronal activation for reading aloud. *Journal of Cognitive Neuroscience, 21*(4), 654–668.

Kinoshita, S., Lupker, S. J., & Rastle, K. (2004). Modulation of regularity and lexicality effects in reading aloud. *Memory and Cognition, 32*(8), 1255–1264.

Kronbichler, M., Hutzler, F., Wimmer, H., Mair, A., Staffen, W., & Ladurner, G. (2004). The visual word form area and the frequency with which words are encountered: Evidence from a parametric fMRI study. *NeuroImage, 21*, 946–953.

Lancaster, J. L., Woldorff, M. G., Parsons, L. M., Liotti, M., Freitas, C. S., Rainey, L., et al. (2000). Automated Talairach atlas labels for functional brain mapping. *Human Brain Mapping, 10*, 120–131.

Laszlo, S., & Plaut, D. C. (2012). A neurally plausible parallel distributed processing model of event-related potential word reading data. *Brain and Language, 120*, 271–281.

Levelt, W. J. M., Roelofs, A., & Meyer, A. S. (1999). A theory of lexical access in speech production. *Behavioral and Brain Sciences, 22*, 1–75.

MacDonald, M. C., & Christiansen, M. H. (2002). Reassessing working memory: Comment on Just and Carpenter (1992) and Waters and Caplan (1996). *Psychological Review, 109*(1), 35–54.

Monaghan, J., & Ellis, A. W. (2002). What exactly interacts with spelling-sound consistency in word naming? *Journal of Experimental Psychology: Learning, Memory, and Cognition, 28*(1), 183–206.

Noppeney, U., & Price, C. J. (2004). Retrieval of abstract semantics. *NeuroImage, 22*, 164–170.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*(1), 97–113.

Owen, A. M., McMillan, K. M., Laird, A. R., & Bullmore, E. (2005). N-back working memory paradigm: A meta-analysis of normative functional neuroimaging studies. *Human Brain Mapping, 25*, 46–59.

Paivio, A. (1991). Dual coding theory: Retrospect and current status. *Canadian Journal of Psychology, 45*(3), 255–287.

Perry, C., Ziegler, J., & Zorzi, M. (2007). Nested incremental modeling in the development of computational theories: The CDP+ model of reading aloud. *Psychological Review, 114*(2), 273–315.

Pexman, P. M., Hargreaves, I. S., Edwards, J. D., Henry, L. C., & Goodyear, B. G. (2007). Neural correlates of concreteness in semantic categorization. *Journal of Cognitive Neuroscience, 19*(8), 1407–1419.

Plaut, D. C. (1997). Structure and function in the lexical system: Insights from distributed models of word reading and lexical decision. *Language and Cognitive Processes, 12*(5/6), 765–805.

Plaut, D. C., McClelland, J. L., Seidenberg, M. S., & Patterson, K. (1996). Understanding normal and impaired word reading: Computational principles in quasi-regular domains. *Psychological Review, 103*(1), 56–115.

Plaut, D. C., & Shallice, T. (1993). Deep dyslexia: A case study of connectionist neuropsychology. *Cognitive Neuropsychology, 10*(5), 377–500.

Price, C. J., & Mechelli, A. (2005). Reading and reading disturbance. *Current Opinion in Neurobiology, 15*, 231–238.

Pulvermüller, F., Shtyrov, Y., & Hauk, O. (2009). Understanding in an instant: Neurophysiological evidence for mechanistic language circuits in the brain. *Brain and Language, 110*, 81–94.

Rayner, K., Foorman, B. R., Perfetti, C. A., Pesetsky, D., & Seidenberg, M. S. (2001). How psychological science informs the teaching of reading. *Psychological Science in The Public Interest, 2*(2), 31–74.

Richlan, F., Kronbichler, M., & Wimmer, H. (2009). Functional abnormalities in the dyslexic brain: A quantitative meta-analysis of neuroimaging studies. *Human Brain Mapping, 30*(10), 3299–3308.

Rodd, J. M. (2004). The effect of semantic ambiguity on reading aloud: A twist in the tale. *Psychonomic Bulletin and Review, 11*(3), 440–445.

Rohrer, J. D., Warren, J. D., Modat, M., Ridgway, G. R., Douiri, A., Rossor, M. N., et al. (2009). Patterns of cortical thinning in the language variants of frontotemporal lobar degeneration. *Neurology, 72*, 1562–1569.

Sabsevitz, D. S., Medler, D. A., Seidenberg, M., & Binder, J. R. (2005). Modulation of the semantic system by word imageability. *NeuroImage, 27*, 188–200.

Sandak, R., Mencl, W. E., Frost, S. J., Rueckl, J. G., Katz, L., Moore, D. L., et al. (2004). The neurobiology of adaptive learning in reading: A contrast of different training conditions. *Cognitive, Affective, and Behavioral Neuroscience, 4*(1), 67–88.

Schlaggar, B. L., & McCandliss, B. D. (2007). Development of neural systems for reading. *Annual Review of Neuroscience, 30*, 475–503.

Schwanenflugel, P. J. (1991). Why are abstract concepts hard to understand? In P. J. Schwanenflugel (Ed.), *The psychology of word meanings* (pp. 223–250). Hillsdale, NJ: Erlbaum.

Schwartz, M. F., Kimberg, D. Y., Walker, G. M., Brecher, A., Faseyitan, O. K., Dell, G. S., et al. (2011). Neuroanatomical dissociation for taxonomic and thematic knowledge in the human brain. *Proceedings of the National Academy of Sciences of the United States of America, 108*(20), 8520–8524.

Seghier, M. L., Lee, H. L., Schofield, T., Ellis, C. L., & Price, C. J. (2008). Inter-subject variability in the use of two different neuronal networks for reading aloud familiar words. *NeuroImage, 42*, 1226–1236.

Seidenberg, M. S. (1985). The time course of phonological code activation in two writing systems. *Cognition, 19*, 1–30.

Seidenberg, M. S. (2012). Computational models of reading: Connectionist and dual-route approaches. In M. Spivey, K. McRae, & M. Joanisse (Eds.), *The Cambridge handbook of psycholinguistics* (pp. 186–203). New York: Cambridge University Press.

Seidenberg, M. S., & McClelland, J. L. (1989). A distributed, developmental model of word recognition and naming. *Psychological Review, 96*(4), 523–568.

Seidenberg, M. S., & Plaut, D. C. (2006). Progress in understanding word reading: Data fitting versus theory building. In S. Andrews (Ed.), *From inkmarks to ideas: Current issues in lexical processing* (pp. 25–49). New York: Psychology Press.

Seidenberg, M. S., Waters, G. S., Sanders, M., & Langer, P. (1984). Pre- and postlexical loci of contextual effects on word recognition. *Memory and Cognition, 12*(4), 315–328.

Shallice, T. (1988). *From neuropsychology to mental structure*. New York: Cambridge University Press.

Shibahara, N., Zorzi, M., Hill, M. P., Wydell, T., & Butterworth, B. (2003). Semantic effects in word naming: Evidence from English and Japanese Kanji. *The Quarterly Journal of Experimental Psychology, 56A*(2), 263–286.

Souza, M. J., Donohue, S. E., & Bunge, S. A. (2009). Controlled retrieval and selection of action-relevant knowledge mediated by partially overlapping regions in left ventrolateral prefrontal cortex. *NeuroImage, 46*, 299–307.

Strain, E., & Herdman, C. M. (1999). Imageability effects in word naming: An individual differences analysis. *Canadian Journal of Experimental Psychology, 53*(4), 347–359.

Strain, E., Patterson, K., & Seidenberg, M. S. (1995). Semantic effects in single-word naming. *Journal of Experimental Psychology: Learning Memory and Cognition, 21*, 1140–1154.

Tanigawa, H., Wang, Q., & Fujita, I. (2005). Organization of horizontal axons in the inferior temporal cortex and primary visual cortex of the macaque monkey. *Cerebral Cortex, 15*(12), 1887–1899.

Taraban, R., & McClelland, J. L. (1987). Conspiracy effects in word recognition. *Journal of Memory and Language, 26*, 608–631.

Taylor, J. S. H., Rastle, K., & Davis, M. H. (2013). Can cognitive models explain brain activation during word and pseudoword reading? A meta-analysis of 36 neuroimaging studies. *Psychological Bulletin, 139*(4), 766–791.

Torgesen, J. K., Wagner, R. K., & Rashotte, C. A. (1999). *Test of word reading efficiency*. Austin, Texas: Pro-ed.

Turkeltaub, P. E., Eden, G. F., Jones, K. M., & Zeffiro, T. A. (2002). Meta-analysis of the functional neuroanatomy of single-word reading: Method and validation. *NeuroImage, 16*, 765–780.

Vigneau, M., Beaucousin, V., Hervé, P. Y., Duffau, H., Crivello, F., Houdé, O., et al. (2006). Meta-analyzing left hemisphere language areas: Phonology, semantics, and sentence processing. *NeuroImage, 30*, 1414–1432.

Vinckier, F., Dehaene, S., Jobert, A., Dubus, J. P., Sigman, M., & Cohen, L. (2007). Hierarchical coding of letter strings in the ventral stream: Dissecting the inner organization of the visual word-form system. *Neuron, 55*, 143–156.

Wagner, R. K., & Torgesen, J. K. (1987). The nature of phonological processing and its causal role in the acquisition of reading skills. *Psychological Bulletin, 101*(2), 192–212.

Wechsler, D. (2001). *Wechsler test of adult reading (WTAR)*. San Antonio, TX: The Psychological Corporation.

Welcome, S. E., & Joanisse, M. F. (2012). Individual differences in skilled adult readers reveal dissociable patterns of neural activity associated with component processes of reading. *Brain and Language, 120*, 360–371.

Whitney, C., Jefferies, E., & Kircher, T. (2011). Heterogeneity of the left temporal lobe in semantic representation and control: Priming multiple versus single meanings of ambiguous words. *Cerebral Cortex, 21*, 831–844.

Wise, R. J. S., Scott, S. K., Blank, S. C., Mummery, C. J., Murphy, K., & Warburton, E. A. (2001). Separate neural subsystems within 'Wernicke's area'. *Brain, 124*, 83–95.

Woollams, A. M. (2005). Imageability and ambiguity effects in speeded naming: Convergence and divergence. *Journal of Experimental Psychology: Learning Memory and Cognition, 31*(5), 878–890.

Woollams, A. M., Lambon Ralph, M. A., Plaut, D. C., & Patterson, K. (2007). SD-squared: On the association between semantic dementia and surface dyslexia. *Psychological Review, 114*(2), 316–339.

Yap, M. J., Balota, D. A., Sibley, D. E., & Ratcliff, R. (2012). Individual differences in visual word recognition: Insights from the English lexicon project. *Journal of Experimental Psychology: Human Perception and Performance, 38*(1), 53–79.

Yap, M. J., Pexman, P. M., Wellsby, M., Hargreaves, I. S., & Huff, M. J. (2012). An abundance of riches: Cross-task comparisons of semantic richness effects in visual word recognition. *Frontiers in Human Neuroscience, 6*.