Triangulation of the neurocomputational architecture underpinning reading aloud

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The goal of cognitive neuroscience is to integrate cognitive models with knowledge about underlying neural machinery. This significant challenge was explored in relation to word reading, where sophisticated computational-cognitive models exist but have made limited contact with neural data. Using distortion-corrected functional MRI and dynamic causal modeling, we investigated the interactions between brain regions dedicated to orthographic, semantic, and phonological processing while participants read words aloud. We found that the lateral anterior temporal lobe exhibited increased activation when participants read words with irregular spellings. This area is implicated in semantic processing but has not previously been considered part of the reading network. We also found meaningful individual differences in the activation of this region: Activity was predicted by an independent measure of the degree to which participants use semantic knowledge to read. These characteristics are predicted by the connectionist Triangle Model of reading and indicate a key role for semantic knowledge in reading aloud. Premotor regions associated with phonological processing displayed the reverse characteristics. Changes in the functional connectivity of the reading network during irregular word reading also were consistent with semantic recruitment. These data support the view that reading aloud is underpinned by the joint operation of two neural pathways. They reveal that (*i*) the ATL is an important element of the ventral semantic pathway and (*ii*) the division of labor between the two routes varies according to both the properties of the words being read and individual differences in the degree to which participants rely on each route.

triangle model | anterior temporal lobe | semantic reliance | reading | surface dyslexia

Cognitive neuroscience offers the exciting prospect of understanding the neural basis of cognitive behaviors, a goal which requires integration of sophisticated cognitive models with knowledge about the underlying neural machinery. As a key cognitive skill, reading provides an advanced test case. Computationally implemented theories present detailed accounts of how reading is accomplished at a cognitive level (1–4). To achieve a full understanding of reading and its impairment in neurological disorders, these cognitive theories must be integrated with information about the neural basis of the reading system. However, although various studies have explored the neural basis of reading (5), the level of integration between cognitive and neural models remains limited. In the present study, we used an improved functional MRI (fMRI) protocol to test the specific predictions of an influential computational model of word reading: the connectionist "Triangle Model" (2). We were able to map specific elements of this cognitive model onto different cortical regions, thereby providing a direct link between cognitive theorizing and neural implementation. Specifically, we provide insights into the division of labor between semantic and phonological processes in supporting reading aloud, which has been a long-standing source of controversy among cognitive models (6, 7). Moreover, we demonstrate that this division of labor is jointly influenced by variation in the properties of words being read and by individual differences in the neurocognitive architecture across participants and that these individual differences can be predicted using an independent behavioral measure of reading style.

Cognitive and neural models of single-word reading agree that multiple pathways contribute to reading aloud (1, 2, 8–10). These pathways consist of a route that maps directly from orthographic forms to phonological representations (allowing us, for example, to pronounce novel letter strings such as "FLUMPT") and an indirect route mediated by word-level lexical or semantic knowledge. The exact function of these pathways remains a source of active debate, much of it focused on the role of semantic (word meaning) knowledge in reading aloud. Dual-route models hold that all words can be read either via grapheme-to-phoneme rules or through access to orthographic and phonological lexica that are distinct from knowledge of word meaning (1, 10). In contrast, the Triangle Model proposes that semantic knowledge plays an integral part in pronouncing words correctly (2, 6, 11). The cornerstone of this second approach is the view that, because reading is, in evolutionary terms, a recently developed skill, it is unlikely to be served by a dedicated neural architecture. Instead, it is underpinned by the phylogenetically more mature primary systems of vision, phonology, and semantics (9). This idea has been instantiated in several connectionist computational models known as Triangle Models because they comprise a direct pathway from visual (or orthographic) to phonological representations (here termed the "O→P pathway") and an indirect pathway in which the translation from orthography to phonology is mediated through access to semantic knowledge (2–4, 12). In such models, the direct O→P pathway becomes sensitive to the statistical

Significance

Reading is a critical linguistic skill, but understanding of its cognitive and neural bases is incomplete. Using functional MRI, we found reading-related activation in two areas of anterior temporal cortex, an area not previously associated with reading. Activation profiles of these sites were consistent with the predictions of computational reading models that ascribe a key role to semantic knowledge in reading words with irregular spellings. We also found individual differences in the reading neural network that were predicted by an independent measure of semantic reliance in reading. Such individual differences have been hypothesized on theoretical grounds to explain variation in reading abilities among neurodegenerative patients. Here we provide the first direct evidence, to our knowledge, for their existence in the healthy brain.

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regularities in the mapping from spelling to sound. It therefore is efficient in computing the pronunciations of words with typical spelling-to-sound mappings (e.g., "MINT") but is less successful for words with exceptional spelling-to-sound correspondences, such as "PINT" (2, 13). The indirect, semantically mediated pathway (O→S→P) provides additional support for reading, which is especially important for exception words that are poorly served by the O→P pathway.

The Triangle Model assumes that each of the primary systems of vision, phonology, and semantics makes distinct contributions to reading. This position is supported by neuropsychological investigations of patients with acquired dyslexias, in which damage to visual, phonological, and semantic systems are associated with distinct patterns of reading deficit. The visually based reading deficit sometimes termed "pure alexia" is associated with damage to the left ventral occipitotemporal cortex (14, 15), an area that is ubiquitously activated for tasks involving orthographic processing (8, 16). Critically, such patients also have visual deficits for nonorthographic stimuli such as checkerboards and faces (15, 17, 18), supporting the primary systems view that this brain region is a more general visual-processing area. In a similar vein, patients with phonological dyslexia have concomitant phonological deficits in tasks that do not involve written words (19–21). Lesion–symptom mapping studies indicate that these patients' reading deficits are associated with damage to frontal and temporal perisylvian cortex (22). The involvement of premotor cortex in such patients is of particular interest, because this region is robustly activated when healthy individuals read aloud in the scanner (23). This area is strongly associated with phonological processing and in the computation of phonological output representations (24, 25). These findings reinforce the notion that reading aloud draws on a core phonological system that also is recruited by nonreading tasks.

Involvement of the semantic system in reading aloud has proved the most controversial element of the Triangle Model. Semantic involvement is supported by the study of surface dyslexia, a reading disorder characterized by poor reading of exception words. This pattern is strongly associated with semantic dementia (SD), a disorder in which patients suffer from a progressive, selective deterioration in semantic knowledge (26). Both reading deficits and semantic deficits in this group have been linked to atrophy centered on the left anterior temporal lobe (22, 27, 28), suggesting that this area makes a critical contribution both to semantic knowledge and to the reading of exception words. However, although these studies provide persuasive evidence for the co-occurrence of semantic impairment and exception word reading deficits, they provide limited data regarding the exact neuroanatomical locus of such effects. A number of recent neuroimaging studies have highlighted the involvement of the ventral anterior temporal lobe (ATL), i.e., the inferior temporal and fusiform gyri, in semantic processing of verbal and nonverbal stimuli (29–31) in an area that coincides with the peak neural correlate of semantic impairment in patients with SD (32). The ATL is rarely activated in studies of word reading. One intriguing exception is a study in which participants were trained to associate pseudowords with particular meanings (33). Following this training, activation in the lateral ATL was observed when participants read the pseudowords aloud, suggesting that linking of novel pseudowords with meanings triggered engagement of the ATL. In general, however, there is scant neuroimaging evidence for the involvement of the ATL in the reading of familiar words, as various authors have noted (8, 34–36). As a consequence, the ATL is rarely included in models of the neural basis of reading (5, 36).

There are two possible interpretations of these results. The first is that the ATL and, by extension, the semantic representations supported by this region, are not involved in the process of converting print to sound. Indeed, some have claimed that exception-word reading deficits in patients with SD are caused instead by mild atrophy in the posterior temporal lobe (7, 37). [There are, however, cases of surface dyslexia in SD without evidence of disruption to posterior temporal regions; see Woollams et al. (38).] The alternative argument, which we propose and test in this paper, is that the ATL does make a critical contribution to reading aloud and that the paucity of neuroimaging evidence for this contribution is the result of a number of technical and methodological factors. When these factors are addressed, we demonstrate that ATL activation is present and that it conforms to the predictions of the Triangle Model.

It is well known that various methodological factors can reduce the probability of ATL activations being observed in neuroimaging studies. These include use of a restricted field of view that excludes the inferior parts of the temporal lobe from image acquisition and the use of low-level baselines that do not adequately control for automatic activation of the semantic system during passive conditions (39). In addition, gradient-echo fMRI is susceptible to magnetic field inhomogeneities that cause signal dropout and distortion in the orbitofrontal and ventral temporal cortices, including the ATL (40). One technique that combats this problem involves spin-echo (SE) imaging combined with processing that corrects for the spatial distortion incurred in problem areas (41). A number of studies using this distortion-corrected fMRI have found activation in the ventral and lateral ATLs for semantic decisions made in response to written and spoken words, pictures, and environmental sounds (29, 30, 42). To our knowledge, the present study is the first to use this technique to investigate reading aloud.

In addition to general challenges in imaging the ATL, there are two issues that are specific to reading studies. The first is that it is not straightforward to predict which words should elicit the greatest activation in regions dedicated to semantic processing. Based on the Triangle Model and the poor exception word reading of patients with SD, one might expect the semantically mediated reading route to be more active when participants read exception words (6). In contrast, other authors have argued that reading any word elicits automatic activation of its meaning and that this activation occurs independently of any functional role in accessing the appropriate phonological form (36). This view predicts similar levels of activation for regular and exception words, with activation influenced instead by psycholinguistic variables such as frequency and imageability that index the strength of semantic representation.

The second issue concerns individual differences in the degree to which people require semantic activation to compute the pronunciations of exception words. It has been observed that similar levels of semantic impairment in SD can result in varying degrees of impairment in exception word reading (6). In a few cases, patients even may present initially with normal exception word reading despite having measurable semantic impairment. Based on these findings, it has been proposed that individuals vary in their reliance on the semantic pathway, with Triangle Model simulations used to demonstrate that this variation in semantic reliance theoretically could account for the variability observed in SD (4, 6, 11). Individuals with an efficient and flexible direct pathway need little semantic support, whereas those with a less efficient direct pathway will need to fall back on semantic activation for harder words with atypical spelling–sound correspondences. The Triangle Model therefore predicts that the size of an individual's consistency effect (i.e., the difference in reading performance between words with consistent versus inconsistent mappings) indexes the degree to which they use semantic knowledge when reading aloud. We refer to this quantity as a reader's level of semantic reliance (SR). One important prediction arising from this research is that the level of ATL activation during reading varies systematically across individuals as a function of the individual's SR. This between-subject

Table 1. Mean accuracy and RT in each condition

	HF regular	HF exception	LF regular	LF exception	Baseline
Accuracy, %	99.9 (4.4)	99.2 (1.4)	99.3 (1.5)	91.1 (6.3)	100 (0)
RT, ms	695 (85)	698 (85)	733 (96)	777 (112)	815 (126)

Standard deviations in parentheses.

variability may be an additional factor contributing to the failure to find ATL activations in previous studies. In this study, we used a behavioral measure of SR to model this variation explicitly, for the first time to our knowledge.

In summary, the Triangle Model predicts that reading aloud should engage regions of the ATL involved in semantic processing but the existing neuroimaging literature provides little support for this claim, hampering efforts to integrate the cognitive model with neural data. Importantly, the absence of evidence for ATL involvement in word reading may be a result of (*i*) factors in imaging protocols that reduce the likelihood of observing activation in the ATL and (*ii*) failure to take into account the degree to which ATL activation in reading may be modulated by both word-level and subject-level variability. To maximize sensitivity to ATL activation in the present study, we used a distortion-corrected SE fMRI protocol with full brain field-of-view and an active baseline (see Fig. S1 for signal-to-noise map). We also tested for the effects of word-level factors as well as subject-level variation in SR. Although word-level variation is commonly investigated in reading studies, this is the first study to our knowledge to test for changes in activation relating to individual differences in SR. Our investigation proceeded in two stages. First, we investigated the effects of frequency and spelling-to-sound regularity on activation in regions involved in orthographic, phonological, and semantic processing. Dynamic causal modeling was used to explore the interactions between these areas. In the second part of the study, we tested the hypothesis that individual differences in SR could explain variation in ATL activation. We adopted a triangulation technique for identifying areas involved in the semantic reading pathway. The Triangle Model predicts that activation associated with semantically mediated reading is influenced by the type of word being read (exception > regular) and by the degree to which individual participants make use of this pathway (high SR > low SR). We therefore sought regions that exhibited a conjunction of these independent word-based and subject-based effects.

Results

Behavioral Results. During scanning, participants read aloud single words that varied in frequency and spelling-to-sound regularity. Accuracy and response times (RTs) are reported in Table 1. Accuracy of word responses was analyzed in 2 × 2 ANOVA, which confirmed the expected main effects of frequency [$F(1,25) = 59.8$, $P < 0.001$] and regularity [$F(1,25) = 39.1$, $P < 0.001$] and an interaction [$F(1,25) = 44.3$, $P < 0.001$]. Similar effects were found when RTs were analyzed [frequency: $F(1,25) = 70.6$, $P < 0.001$; regularity: $F(1,25) = 10.4$, $P = 0.003$; interaction: $F(1,25) = 15.7$, $P = 0.001$]. Hence, the participants as a group exhibited the well-established pattern of performance in single-word reading, in which exception words are read less efficiently than regular words, particularly if they are low in frequency.

Whole-Brain Analysis of Reading vs. Baseline. We performed a whole-brain analysis to identify areas involved in word reading.

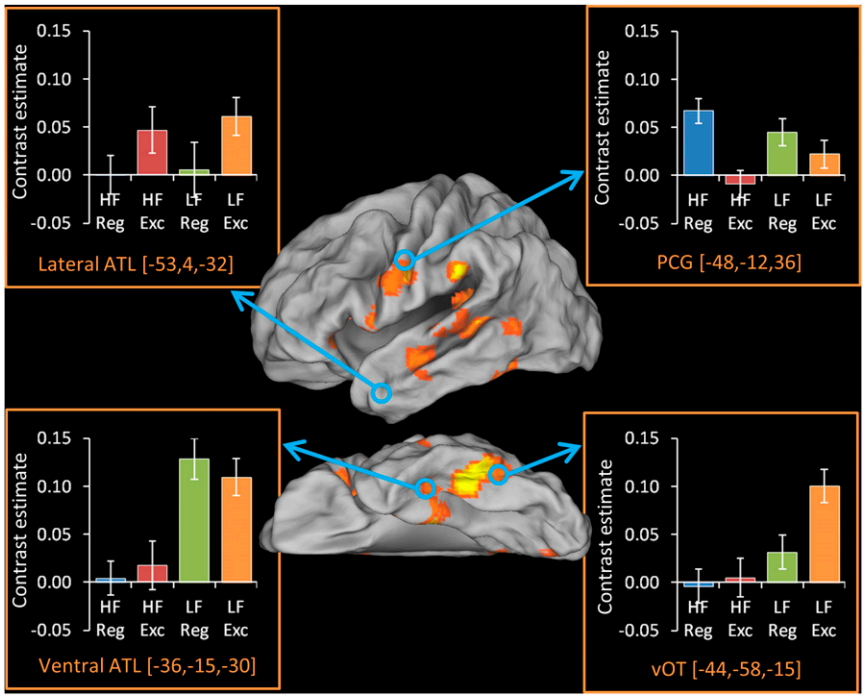

Fig. 1. Activations for each word type in ROIs. The activation map indicates areas activated for contrast of all word types over baseline, for 26 participants, thresholded at a cluster-corrected level of $P < 0.05$ (see *Methods* for details). Bar charts indicate the contrast estimate for each word type over baseline within four a priori ROIs. Error bars indicate one SEM. Exc, exception; Reg, regular.

Table 2. Effects of frequency and regularity in ROIs

ROI	Effect of frequency	Effect of regularity
vOT	**$F(1,25) = 13.0$, $P = 0.001$**	$F(1,25) = 2.77$, $P = 0.11$
PCG	$F(1,25) = 0.14$, $P = 0.71$	**$F(1,25) = 12.4$, $P = 0.002$**
vATL	**$F(1,25) = 13.6$, $P = 0.001$**	$F(1,25) = 0.02$, $P = 0.91$
Lateral ATL	$F(1,25) = 0.16$, $P = 0.69$	$F(1,25) = 2.88$, $P = 0.10$

Significant effects are shown in bold. No regions displayed a significant frequency × regularity interaction.

This analysis revealed a network of regions commonly identified in reading studies, including posterior temporal, inferior parietal, and premotor regions (Fig. 1; peak coordinates are reported in Table S1). Importantly, we also observed activation on the ventral surface of the ATL (anterior fusiform/inferior temporal gyrus). Signal in this area typically is heavily attenuated by dropout; however, as in the present investigation, recent studies using distortion-corrected fMRI have implicated this region in a range of semantic tasks (29, 30), providing initial support for the involvement of ATL semantic regions in reading aloud.

Effects of Word-Level Factors. We next examined sensitivity to word-level factors in four a priori regions of interest (ROIs) selected based on their involvement in orthographic, phonological, and semantic processes (Fig. 1). Effects of frequency and regularity in each region were assessed with a series of 2 × 2 ANOVAs (Table 2). The ventral occipitotemporal cortex (vOT) responded more strongly to low-frequency (LF) than to high-frequency (HF) words and to exception words than to regular words. In the precentral gyrus (PCG), activation was greater for regular words than for exception words. In the lateral ATL, the opposite pattern was observed, although this difference fell short of statistical significance ($P = 0.1$) for the group as a whole. [The nonsignificance of this result stems from the fact that, as described later, participants with low SR did not activate this area at all and therefore were unlikely to show an effect of word type. When the four participants with the least SR were excluded from the analysis, the effect of regularity became significant in this region ($P = 0.03$).] The ventral ATL (vATL) displayed a different pattern, activating to an equal extent for regular and exception words but displaying greater activation for LF than for HF words. Further analysis confirmed that the two ATL regions displayed divergent profiles: When the two sites were compared directly in 2 × 2 × 2 ANOVA, there was a significant interaction between frequency and site [$F(1,25) = 11.9$, $P = 0.002$] and a marginal interaction between regularity and site [$F(1,25) = 3.78$, $P = 0.06$]. This result suggests a dissociation in function between these different ATL subregions, which we consider further in *Discussion*.

We also examined four additional regions linked to semantic processing outside the ATL: the inferior frontal gyrus, angular gyrus, posterior middle temporal gyrus, and inferior temporal sulcus. Results from these ROI analyses are presented in Fig. S2. None of these regions showed a significant effect of spelling–sound regularity (Table S2).

Dynamic Causal Modeling. We next explored functional interactions between orthographic, semantic, and phonological regions. The Triangle Model predicts greater direct interaction between orthographic and phonological areas for regular words and greater functional connectivity via the semantic pathway for exception words. These predictions were tested in dynamic causal modeling (DCM) that modeled connections between the vOT, PCG, and lateral ATL. Endogenous connections between these regions, in the absence of experimental manipulation, were all positive (Fig. 2*A*). Importantly, we assessed changes in functional connectivity when participants read regular and exception words. Modulation of the functional connectivity in response to each word type is presented in Fig. 2. When participants read regular words, there was a significant increase in functional connection strength from the vOT to the ATL and PCG and from the ATL to the PCG. The pattern of connectivity was different during exception word reading. vOT→ATL and ATL→PCG connections again were significantly modulated, and additional feedback connections to the ATL and vOT were observed. Crucially, there was no modulation of the direct vOT→PCG functional connection when participants read exception words. The modulation of the vOT→PCG parameter was compared directly between word types using a paired-samples t test, which confirmed that the functional connection was modulated more strongly by regular words than by exception words [$t(25) = 3.16$, $P = 0.004$]. This functional connectivity analysis therefore supports the Triangle Model's prediction that direct interaction between orthographic and phonological processing regions is strongest when participants read regular words.

Effect of Subject-Level Variation in SR. Twenty-four participants completed a behavioral test outside the scanner that provided an index of the degree to which they rely on semantic knowledge to read exception words (based on the difference in reading performance for reading low-imageability words with consistent vs. inconsistent spelling–sound mappings). Fig. 3 shows the correlation across participants between the SR index and contrast estimates in each of our ROIs. We found a strong positive correlation between activation in the lateral ATL and SR ($P = 0.01$), supporting the idea that this area supports semantically mediated reading. In fact, participants with the lowest SR did not activate this area at all. Activation in vATL was not correlated with SR. There also was a weak negative correlation between SR and activation in the PCG (one-tailed $P = 0.05$). Individuals with high SR activated this area to a lesser extent, indicating that the greater involvement of semantic processing regions was offset by reduced activation in phonological regions.

We also examined correlations in our additional regions associated with semantic processing outside the ATL. As shown in Fig. S2, activity in these regions was not correlated with SR.

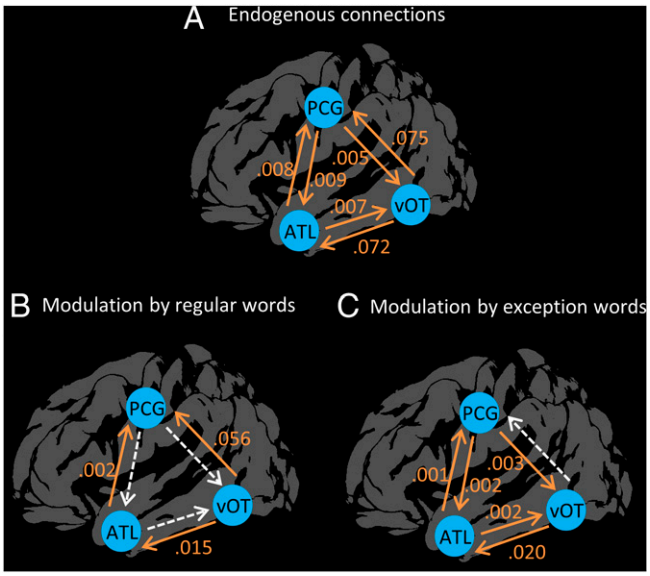

Fig. 2. Functional interactions between regions and their modulation by regular and exception word, as revealed by DCM. (*A*) Endogenous connections between regions in the absence of stimuli. (*B* and *C*) Changes in functional connectivity during word reading. Positive values indicate increases in connectivity upon stimulus presentation. Statistically significant modulations are shown in orange.

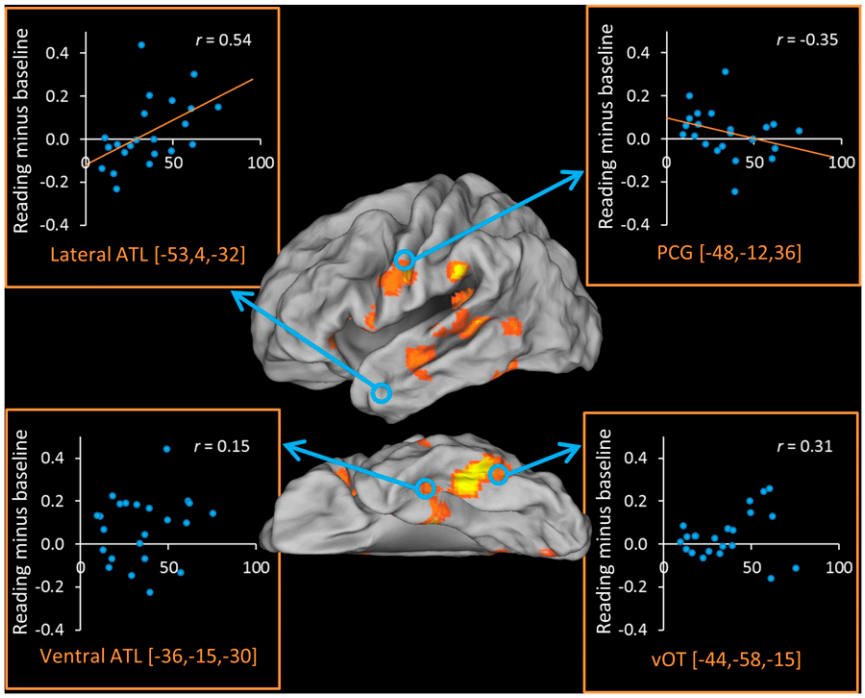

Fig. 3. Correlations between reading activation and semantic reliance in each ROI. Reading activation in each ROI is plotted against the behavioral measure of SR. Data were available for 24 participants.

Whole-Brain Triangulation of the Semantic Contribution. Finally, we performed whole-brain conjunction analyses to test whether any regions outside our ROIs showed the combination of an exception > regular effect and a positive correlation between reading activation and SR, as identified in the lateral ATL ROI. We also tested for the reverse conjunction. The results of the individual tests and their conjunctions are shown in Fig. 4. Peak coordinates for the conjunctions are reported in Table 3 (coordinates for individual contrasts are given in Tables S3 and S4). The semantic conjunction identified two clusters in the lateral ATL, with no effects elsewhere in the brain. The reverse conjunction identified two clusters in the PCG, the larger of which extended into postcentral gyrus. Again, no effects were found elsewhere. This triangulation analysis supports our earlier ROI-based approach in two ways. First, it indicates that the a priori ROIs for semantic and phonological regions were close to the key centers of activity in our data. Second, it confirms that the conjunction of word- and subject-level effects was specific to these regions.

Discussion

Reading is a critical skill that has been studied from both cognitive and neural perspectives. Here, we integrated these two approaches by using fMRI to investigate the neural basis of an implemented computational model of word reading: the Triangle Model (2). We focused particularly on the role of the ATL, a key site for the representation of semantic knowledge, in reading. The potential contribution of this area has been overlooked in the neuroimaging literature; however, the Triangle Model predicts that the semantic representations supported by this area are critically involved in reading, particularly (*i*) for words with exceptional spelling-to-sound mappings and (*ii*) in individuals who rely heavily on semantic information to read these words. We identified a site in the lateral ATL that uniquely demonstrated both these characteristics. Furthermore, areas of premotor cortex involved in phonological processing demonstrated the reverse pattern, indicating a division of labor between direct and semantically mediated pathways for converting written

Table 3. MNI coordinates for conjunction analyses of regularity and SR

Analysis	Location	Extent in voxels	Z	MNI coordinates *x*	*y*	*z*
Exc > reg ∩ positive semantic reliance	Anterior MTG and temporal pole	96	2.21	−48	14	−34
			2.16	−40	10	−42
			1.80	−34	18	−42
	Anterior ITG	52	2.16	−52	−6	−32
			1.71	−42	−8	−32
Reg > exc ∩ negative semantic reliance	Precentral and postcentral gyri	95	2.54	−50	−6	32
			2.28	−60	−22	34
	Precentral gyrus	70	2.66	−58	−6	20
			2.12	−50	−2	20

Exc, exception; ITG, inferior temporal gyrus; MTG, middle temporal gyrus; Reg, regular.

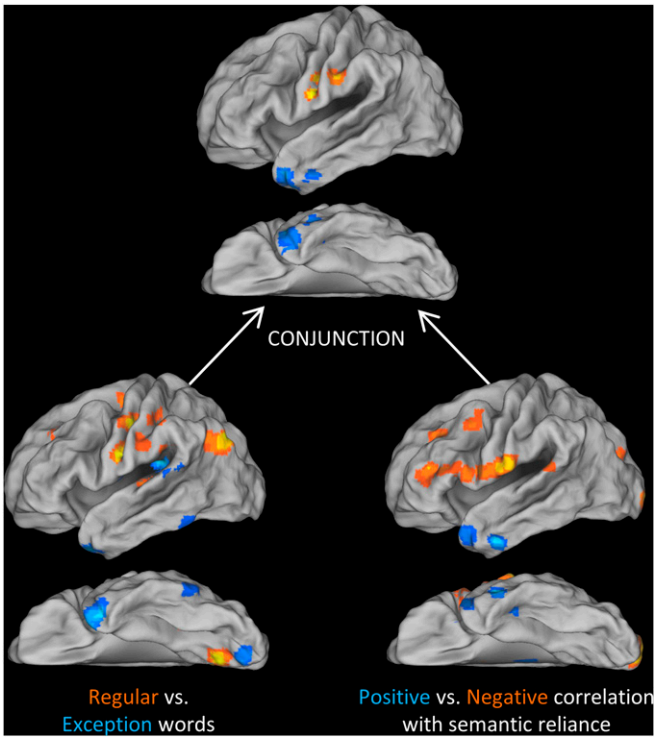

Fig. 4. Whole-brain conjunction analysis of word-level and subject-level effects.

words to speech sounds. These findings necessitate a reconsideration of the neural network for reading aloud and indicate that individual differences in reading style can have major and theoretically meaningful effects on the configuration of this network.

Fig. 5 illustrates how elements of the Triangle Model of reading aloud might map onto the neural regions investigated in this study. The network outlined here is broadly consistent with the established notion of distinct dorsal and ventral pathways for reading (5, 8, 43, 44). The vOT cortex is strongly implicated in the visual analysis of words and letters (8, 16) and therefore is linked to the orthographic processing units of the Triangle Model. This region displayed less activation for higher-frequency words, as is consistent with reduced processing demands for words with highly familiar orthographic forms. In addition (and consistent with the DCM results), some researchers have suggested that this region summates feedback from semantic and phonological regions, and this function is why its activation mirrors the behavioral RT pattern (45). PCG is critically involved in phonological processing (24) and has been linked specifically with articulatory-motor phonological codes required for speech production (25, 46). This area therefore maps to the phonological component of the Triangle Model. According to the model, the "direct" pathway between these regions is sensitive to statistical regularities in the mapping between spelling and sound and is well-suited to reading words that conform to these patterns. In line with this view, our DCM analysis revealed strong functional connectivity between the vOT and PCG when participants read words with regular spelling-to-sound mappings but not when they read exception words. However, this functional connection does not rule out the involvement of other regions; in particular, regions of the inferior parietal cortex also may be involved in the direct mapping from orthography to phonology (5, 35, 36). Like the PCG, these regions exhibited greater activation for regular words.

Our main focus was on the potential role of the ATL in semantically mediated reading. We identified two distinct ATL regions that have not hitherto been considered parts of the reading network. These regions had distinct activation profiles, consistent with different elements of the Triangle Model. First, we found robust activation of the vATL during reading of both regular and exception words. Activations for written words are commonly found in the mid-fusiform gyrus (typically between $y = -35$ and $y = -50$) (36, 43). Although we did observe activation in this area, the vATL activation we refer to here was more anterior still, at $y = -18$. This region is severely affected by signal dropout in standard fMRI, perhaps explaining why most previous studies have not observed activation here. However, PET studies and recent distortion-corrected fMRI studies indicate that this is a key site for the representation of conceptual knowledge (30, 31). Because the great majority of experience with written words involves reading for meaning (3), it is likely that this core semantic knowledge is activated automatically whenever written words are processed (36).

The vATL displayed uniform activation for regular and exception words, and its activation was not predicted by the individual's level of SR in reading, supporting the idea that its activation reflects automatic retrieval of word meaning, irrespective of whether this information plays a functional role in access to phonology. We therefore have linked the vATL with the semantic representations in the Triangle Model. These representations develop as the ATL learns to map between the various sources of information (e.g., visual, auditory, verbal) that contribute to understanding of a concept (4, 47). As a consequence, they are able to capture supramodal semantic structure that extends beyond a single modality (48).

The second ATL region lay on the lateral surface of the temporal lobe. Wilson et al. (49) recently found that this region was activated when participants read exception words but not when they read pseudowords. The present study reveals that it responds more strongly to exception words than to regular words and is activated more strongly by individuals with high SR. The considerable between-subject variability in this area may explain why lateral ATL activation has not been observed in most previous studies of reading aloud. The activation profile of this region suggests that it plays an intermediary role in mapping between word meaning and speech sounds (50). According to the Triangle Model, semantic knowledge makes a critical contribution to the reading of exception words, whose irregular pronunciations are poorly served by the direct O→P pathway. As a consequence, although semantic representations in the vATL are activated whenever written words are processed, the interaction between these and phonological regions, mediated by the lateral ATL, is increased for exception words. In addition, the intermediary

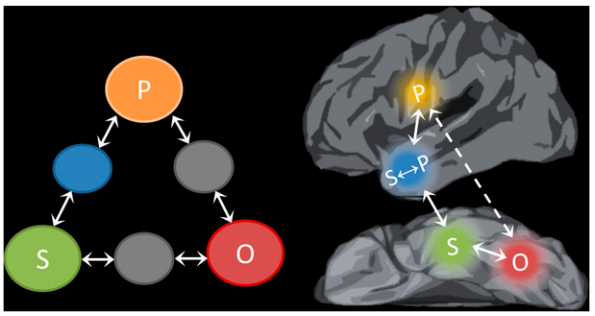

Fig. 5. Schematic of the Triangle Model (*Left*) and its possible mapping onto the neural regions investigated in this study (*Right*). Highlighted neural regions are those investigated in the present study. Other regions also may contribute to reading aloud. The O→P pathway is shown as a dashed line because the exact white-matter connections that support this functional connection are currently unknown. O, orthography; *P*, phonology; S, semantics.

function of the lateral ATL is up-regulated in individuals who rely heavily on semantic activation to support exception word reading.

The structural connectivity of the lateral ATL is well-suited to an intermediary role between semantic and phonological representation. In addition to reciprocal connections with the vATL (51), the lateral ATL is connected directly to prefrontal and premotor cortices via the extreme capsule complex and with phonological processing areas in the posterior superior temporal gyrus via the middle longitudinal fasciculus (51, 52). Neuropsychological studies and neuroanatomically constrained computational models also implicate the lateral ATL in semantically mediated speech production (50, 53). This role is consistent with the view that (*i*) as a result of the convergence of multiple white-matter tracts and connections, the ATL region as a whole acts as a representational system and (*ii*) there are graded specializations in different parts of this system, as a consequence of systematic variations in structural connectivity across the region (54, 55).

These findings have important implications for models of the neural basis of reading. Functional neuroimaging studies have long distinguished between a dorsal reading pathway, typically assumed to include the posterior vOT, supramarginal gyrus, PCG, and posterior inferior prefrontal cortex, and a ventral reading pathway, comprising the anterior portion of vOT and the ventral and anterior parts of inferior prefrontal cortex (5, 8, 36, 43, 44). The present results indicate that the ATL contains important and hitherto unrecognized elements of the ventral pathway and also begin to reconcile the neuroimaging literature on reading aloud with the striking deficits in exception word reading observed in patients with SD (6, 35). The ventrolateral ATL region is the centerpoint of atrophy in SD (27), suggesting that this region is implicated in exception word reading. However, the lack of corroboratory evidence from neuroimaging studies has led to speculation that more subtle damage to posterior temporal cortex is the cause of these patients' reading deficits (7, 37). In contrast to these claims, the lateral ATL region we have identified falls squarely within the typical region of atrophy in SD, providing converging evidence that this anterior region plays an important role in computing the pronunciations of exception words.

A second major contribution is the finding that individual differences in SR predicted the degree to which individuals activated both semantic and phonological regions when reading aloud. A growing literature indicates substantial variability in the functional architecture of the reading network across individuals (56, 57). This conclusion is perhaps not surprising, given that reading is a relatively late-acquired skill and individuals vary greatly in their level of reading ability, in their exposure to print (58), and in the nature of the reading instruction they receive. A number of studies have reported structural and functional correlations with reading skill (59–62). For example, Welcome and Joanisse (59) asked participants to make orthographic, phonological, and semantic judgments to pairs of written words. In line with our findings, the left PCG was selectively activated by phonological judgments. The semantic task activated the posterior temporal, inferior parietal, and prefrontal regions. No ATL activation was observed, perhaps reflecting the technical challenges of measuring activity in this region (see the Introduction). These authors also investigated how reading-related activation (collapsed over orthographic, phonological, and semantic judgments) was predicted by measures of reading ability, revealing a complex pattern of increases and decreases in activity as a function of reading skill.

Our approach differs from these in that the SR measure used here is not an index of general reading skill; rather, it is a measure of the degree to which semantic knowledge contributes to exception word reading. According to the Triangle Model, this measure indexes the division of labor between the direct and semantic reading routes (6, 11). Readers with high SR are assumed to activate the semantic pathway strongly when reading exception words, whereas those with lower SR are thought to favor the direct pathway. In line with this view, we found that greater SR was associated with both increases and decreases in activation in different parts of the reading network. Readers with high SR tended to activate the lateral ATL more than those with low SR, but the reverse was true for activation in the PCG. Thus, our study indicates a division of labor between the anterior temporal semantic regions and the prefrontal phonological regions that varies across subjects.

Another recent fMRI study suggests that similar divisions of labor exist across other brain areas. Seghier et al. (56) identified two networks whose activation during reading varied across individuals. They found that subjects with slow exception word reading were more likely to activate a network comprising the anterior vOT, left inferior frontal cortex, medial frontal gyrus, and supramarginal gyrus. ATL activation was not observed by Seghier et al. perhaps for the technical reasons described above; however, this area has strong anatomical connections with the inferior prefrontal and occipitotemporal cortex and thus is likely to form part of this ventral network.

Although the present study was concerned with the functional reading network, these functional effects are likely to be underpinned by differences in structural connectivity between reading-related regions. Graves et al. (63) investigated how individual differences in reading style relate to the volumes of key white-matter tracts in the left hemisphere. Their individual difference measure (the size of the imageability effect computed over words varying along a number of other dimensions, including spelling–sound consistency) was used to index semantic involvement in reading aloud. This measure was positively related to the volume of two white-matter tracts, corresponding to the inferior and middle longitudinal fasciculi (ILF and MLF), which course through the temporal lobe and converge in the anterior temporal region (64). Participants showing greater semantic involvement tended to have greater volume in both tracts. The fascinating implication linking cognitive function and white-matter neuroanatomy (hodology) is that these tracts play an important functional role in semantically mediated reading by connecting distinct processing regions within the semantic reading route. Each tract projects to large but primarily non-overlapping swathes of temporal, parietal, and occipital cortex. The only shared gray-matter terminations of the ILF and MLF are those found at their convergence within the ATL.

The critical next step is to establish which of these connected regions is functionally responsible for the individual differences in semantic reliance. Graves et al. (63) hypothesized that connections between the posterior temporal and inferior parietal sites were critical. Our functional neuroimaging data are consistent with Graves et al.'s hodological findings but support a different interpretation, namely that the ATL, and not the posterior regions, provides the semantic contribution to reading aloud. Our results suggest that the ILF and MLF are implicated in semantically mediated reading because they connect posterior regions with the anterior temporal cortex. This alternative hypothesis is, of course, consistent with the convergent evidence for the importance of the ATL in semantic representation and the fact that patients with SD, with semantic impairment contingent on ATL-centered atrophy, exhibit acquired surface dyslexia.

Finally, we briefly consider why individuals differ in the degree to which they use the semantic vs. direct routes in reading aloud. Dilkina et al. (4) proposed two factors that may influence this difference: the amount of the individual's reading experience and the relative capacity of the two routes (11). In their connectionist simulations, greater reading experience resulted in the development of a more efficient O→P pathway, so that most words could be read with minimal contribution from semantic knowledge. Similarly, when the capacity of the direct pathway

was increased by providing it with more processing units, the contribution of the semantic route was reduced. One possibility, therefore, is that highly semantic readers adopt greater reliance on semantic representations to compensate for poorer orthographic or phonological processing skills. This account is consistent with our individual difference effects, whereby readers with high SR demonstrate greater activation in an ATL semantic site but less activity in the PCG phonological area. Future research will need to adopt a developmental perspective to reveal the origins of these individual variations in the neurocognitive reading system.

Methods

Participants. Twenty-seven healthy, right-handed participants took part (11 male; mean age, 25y; range, 20–39 y). Data from one participant were discarded because of image artifacts. All participants were native English speakers with no history of neurological or psychiatric disorders and with normal or corrected-to-normal vision. None reported any difficulty with reading. The study was approved by the UK National Research Ethics Service Greater Manchester West research ethics committee and informed consent was obtained from all participants.

In-Scanner Task. Participants read aloud 180 words taken from the Cambridge surface reading list (65). We selected these stimuli because they have proven highly reliable in identifying surface dyslexia in patients with SD (6). The words in the surface list are divided into four conditions based on an orthogonal manipulation of frequency and regularity. Further details of the stimulus characteristics are provided in *SI Details of the In-Scanner Reading Task*.

All words were presented individually for reading aloud. Each trial began with a fixation cross, presented in the center of the screen for 500 ms and followed by a single word presented in black text (Arial font) on a white background. Each word was presented for a total of 2,200 ms. Participants were instructed to read the words aloud as quickly and accurately as possible. As a baseline task, participants were presented with strings of Greek letters of between three and five characters in length. They were instructed to say "ok" upon seeing each string.

Stimuli were presented in a blocked design using Eprime software. Each block consisted of five trials (duration, 13.5 s) taken from one of the four word conditions or from the baseline condition. Blocks were presented in a fixed, pseudorandom order. After every five blocks of task, there was 13.5-s rest block during which the screen remained blank.

Verbal responses were captured using an MRI-compatible microphone manufactured by Optoacoustics and were digitally recorded for later analysis. To minimize head movement, participants were asked to speak without moving their jaw (i.e., with teeth together) and practiced this speaking before entering the scanner.

Imaging Acquisition and Preprocessing. We used an SE imaging sequence combined with a postacquisition distortion correction, which greatly improves signal quality in the ventral temporal lobes (41). Standard preprocessing steps and statistical analyses were performed in SPM8. Full details of the imaging protocol and temporal signal-to-noise maps are provided in *SI Image Acquisition and Preprocessing*.

Following preprocessing, data were treated with a high-pass filter with a cutoff of 160 s, and images were masked to restrict analysis to cerebral gray-matter voxels and were analyzed using a general linear model. At the individual subject level, each of the five stimulus conditions was modeled with a separate regressor (HF regular, HF exception, LF regular, LF exception, and Greek character baseline). Blocks were modeled with a boxcar function convolved with the canonical hemodynamic response function. Motion parameters were entered into the model as covariates of no interest.

Whole-Brain Analysis of Reading vs. Baseline. To identify regions making a general contribution to reading across word types, we contrasted all word reading with the baseline task. A voxel-height threshold of $P < 0.01$ was adopted for all whole-brain analyses. To control for multiple comparisons, a minimum cluster size was determined using a Monte Carlo analysis (66). This modeled the entire smoothed image volume, assumed an individual voxel type-1 error rate of 0.01, and ran 1,000 simulations to determine the minimum cluster size associated with a corrected $P < 0.05$. The cluster threshold obtained using this method was 57 voxels.

Effects of Word-Level Factors. We next investigated effects of stimulus type in left-hemisphere ROIs associated with orthographic, phonological, and semantic processes. For each region, we created a sphere with a 10-mm radius centered on coordinates obtained from previous studies. Orthographic and phonological regions were identified using published meta-analyses of reading studies. The vOT is strongly associated with orthographic processing. We used the mean MNI vOT coordinates (−44, −58, −15) from a meta-analysis of 35 reading studies (8). Phonological processes, both in word reading and in language tasks more generally, are strongly associated with the PCG. This region was not included in the Jobard et al. meta-analysis (8), so we selected peak MNI coordinates (−48, −12, 36) from Turkeltaub et al.'s (23) meta-analysis of 11 reading studies.

Semantic processing depends critically on the ATL, but this region has rarely been identified in studies of single-word reading. To investigate this region, we therefore obtained two sets of coordinates from previous neuroimaging and neurostimulation studies of semantic processing. PET and distortion-corrected fMRI studies have consistently identified activation in the vATL for meaningful stimuli across multiple modalities (30, 31, 67). We took coordinates on the border of the anterior fusiform and inferior temporal gyri (MNI coordinates −36, −15, −30) from an fMRI study in which participants made synonym judgments to written words (29). In parallel, transcranial magnetic stimulation has been used to probe the functions of the lateral ATL (68, 69). To investigate this area, we selected coordinates in the anterior middle temporal gyrus (MNI coordinates −53, 4, −32) that were the stimulation target in the aforementioned studies.

Our main focus in this study was on the ATL, because evidence from patients with SD suggests that this region supports the semantic contribution to reading aloud. In a secondary analysis, however, we investigated four other regions associated with semantic processing: the inferior frontal gyrus, angular gyrus, posterior middle temporal gyrus, and inferior temporal sulcus. Full details of these sites are provided in *SI Additional Semantic ROIs Outside the ATL*.

In each ROI, the Marsbar toolbox (70) was used to obtain contrast estimates for each participant for each of the reading conditions relative to baseline. Condition effects within and between ROIs then were assessed using ANOVA.

DCM. DCM is a method for assessing the neuronal interactions between specified brain regions and the modulation of these interactions under different experimental conditions (71). We used this technique to assess interactions between neural regions associated with orthographic, semantic, and phonological processes, as defined above. We selected the lateral ATL site as our semantic region because this site showed the expected pattern of greater activation for exception words than for regular words. For each participant, we estimated parameters for a single DCM model with the following properties:

i) Orthographic (vOT), semantic (ATL), and phonological (PCG) regions were assumed to have bidirectional endogenous (fixed) connections with one another.

ii) The strength of each of these endogenous connections was allowed to vary upon presentation of regular and exception words. This design yielded two modulation parameters for each connection: its change in strength (relative to rest) when regular words were presented and its change when exception words were presented.

iii) External input to the model was applied at the vOT region, because this region is strongly connected with the primary visual cortex. Input corresponded to presentation of words or baseline character strings, because both elicited activation in vOT.

Further details of the DCM are provided in *SI Further Details of DCM Analyses*.

Effect of Subject-Level Variation in SR. To investigate individual differences in SR, on a separate day to the imaging 24 of the 26 participants completed a short word reading test (see *SI Outside-Scanner Test of SR During Reading* and Table S5 for full details). The measure of SR was based on the difference in reading performance for reading low-imageability words with consistent vs. inconsistent spelling–sound mappings. Low-imageability words have intrinsically weak semantic representations (72), so individuals who rely heavily on semantic activation in reading find it difficult to read these words, particularly when they have exceptional pronunciations that are not well served by the direct O→P pathway. In contrast, people who rely on the O→P pathway to read all words show small effects of consistency. In other words, the size of the consistency effect is taken as a measure of the degree to which an individual relies on semantic activation to read words with atypical mappings. This conclusion

is in line with connectionist triangle models, which show increasing consistency effects as the division of labor in reading is shifted toward the semantic (O→S→P) pathway and away from the direct (O→P) pathway (4, 11). We assessed whether the SR measure was correlated with activation (for reading all words vs. baseline) in our four a priori ROIs and included this variable in a whole-brain analysis as detailed below.

Triangulation of the Semantic Contribution in the Whole Brain. Connectionist models predict that regions involved in the semantic reading pathway should be influenced both by the spelling-to-sound regularity of the word and by the reader's degree of SR. We therefore used a triangulation approach, seeking voxels that displayed a conjunction of these effects. A contrast of reading vs. baseline was computed for each participant, and the resulting maps were entered into a second-level model that included the SR measure as a between-subjects covariate. This method allowed us to identify voxels in which reading activation was correlated with SR. To ensure that reading speed could not influence these results, we included each participant's mean in-scanner reading RT as a second covariate in the model. In a separate model, we contrasted activation elicited by regular vs. exception words (with no covariates).

A conjunction analysis was performed to identify voxels that were more active for exception words than for regular words and whose activity was positively correlated with SR across subjects. We performed a second conjunction to test for the reverse pattern. Each conjunction was assessed against the conjunction null hypothesis (73) to identify voxels that were significantly active in both contrasts. Because the conjunction test is inherently conservative (74), a voxel threshold of $P < 0.05$ was adopted for these analyses, with a minimum cluster size of 50 voxels.

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