Part III

Neural Correlates of Language Production and Comprehension

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Neural Correlates of Semantic Processing in Reading Aloud

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For over a century, beginning at least as early as Cattell (1886), experimental psychologists have investigated the mental processes involved in reading single words aloud. For writing systems such as English, the task is challenging because of the many inconsistencies in the correspondences between spelling and sound. Early investigations into the neural systems supporting this task relied on autopsy studies, which established some of the critical brain regions responsible for acquired alexia (Déjerine, 1892). Integration of experimental and anatomical data, on the other hand, began comparatively recently, spurred in particular by the advent of noninvasive functional brain imaging. Reading aloud is thought to involve a combination of orthographic (visual word form), phonological (word sound), and perhaps semantic (word meaning) information processing. Although the necessity for orthographic and phonological processing is undisputed, the degree to which semantic information is recruited to aid in reading aloud is a matter of debate. One possibility is that, for example, words with unusual correspondences between spelling and sound (e.g., YACHT, COLONEL) might benefit more from the collateral recruitment of semantic codes than words with more regular spelling–sound correspondences (Plaut, McClelland, Seidenberg, & Patterson, 1996).

Although there is agreement that semantic information is not always necessary for single-word reading aloud, two major cognitive and computational models posit very different roles for semantic processing in this task. Dual-route models, such as the dual-route cascaded (DRC) model, propose two separate pathways, one that implements a set of grapheme–phoneme correspondence (GPC) rules for mapping letter combinations to sound combinations (Coltheart, Curtis, Atkins, & Haller, 1993; Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001; see also Coltheart &

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Kohnen, Volume 2, Chapter 43). Words with mappings that do not follow such rules are processed through a "lexical" route, in which the word's orthographic and phonological forms are matched with corresponding whole-word structural (i.e., nonsemantic) representations in a lexicon. Output from both pathways is passed to a response buffer for overt speech. Although a role for semantic processing is sketched as an offshoot of the lexical pathway, any such role is considered incidental, and no dual-route model has attempted to model the influence of semantics on reading aloud (Coltheart et al., 2001; Perry, Ziegler, & Zorzi, 2007).

Parallel distributed processing (PDP) models (e.g., Harm & Seidenberg, 2004; Plaut et al., 1996; Seidenberg & McClelland, 1989; see also Watson, Armstrong, & Plaut, Volume 1, Chapter 6), on the other hand, propose a single mechanism for processing all words, which involves multiple constraint satisfaction in a neural network composed of simple neuron-like units. In this system, distributed representations of orthographic, phonological, and semantic information are recruited to varying degrees depending on the properties of the individual word. For example, reading aloud words with highly consistent spelling–sound mappings is determined primarily by mappings between orthography and phonology. This is particularly true for high-consistency words that appear often in the language (i.e., high-frequency words). For well-sampled training corpora, such words would be presented more often during training, leading to a strengthening of associations (connection weights) between orthographic and phonological information for higher-frequency words. This leads to the prediction, borne out in the experimental data, that high-frequency, high-consistency words are processed more efficiently (in terms of faster response times and lower error rates) than words of lower frequency and consistency (Seidenberg, Waters, Barnes, & Tanenhaus, 1984).

Conversely, low-frequency, low-consistency words have relatively weak connections between orthography and phonology. However, the connections between orthographic and semantic information, on the one hand, and semantic and phonological information, on the other, should not be affected by spelling–sound consistency. This leads to the prediction that low-consistency words, for which orthography–phonology mappings are less robust, rely more on activation of semantic information than do high-consistency words. Thus, the PDP framework specifies a role for semantic information in reading aloud, and predicts stimulus conditions for which that role will be more or less prominent. A specific experimental prediction is that reading aloud words for which semantic information is expected to play a role should be modulated by semantic variables such as imageability. Support for this prediction is provided by behavioral studies in which low-consistency, low-frequency words are read aloud faster if they are of high compared to low imageability (Shibahara, Zorzi, Hill, Wydell, & Butterworth, 2003; Strain & Herdman, 1999; Strain, Patterson, & Seidenberg, 1995; Woollams, 2005).

In discussing the neurobiological basis of semantic processing in reading aloud, relevant behavioral and hemodynamic neuroimaging studies will be presented in terms of three variables thought to influence the degree of semantic processing in reading aloud: imageability, spelling–sound consistency, and word frequency. In

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addition to the neural localization results provided by such studies, the question of when semantic processing occurs in reading aloud is addressed in the section on chronometry. In the final section we attempt to clarify the different contributions of neural systems supporting semantic processing in reading aloud with reference to patterns of symptoms and pathology in several neurological disorders.

Hemodynamic Functional Neuroimaging Studies

Imageability

A word's imageability is the degree to which it evokes a mental image, as judged by subjective ratings averaged across a group of participants (Bird, Franklin, & Howard, 2001; Clark & Paivio, 2004; Cortese & Fugett, 2004; Gilhooly & Logie, 1980; Paivio, Yuille, & Madigan, 1968; Toglia & Battig, 1978). Semantic representations for highly imageable words are thought to be richer or more easily accessed (Paivio, 1991; Schwanenflugel, 1991; Shallice, 1988). As with the demonstrated effects of imageability on behavioral performance in reading aloud, functional imaging studies showing effects of imageability on brain activation can provide evidence for the use of semantics in helping to compute phonological output from orthographic input. Two recent functional magnetic resonance imaging (fMRI) studies from our lab investigated imageability effects on blood oxygen level dependent (BOLD) signal during reading aloud (Binder, Medler, Desai, Conant, & Liebenthal, 2005; Graves, Desai, Humphries, Seidenberg, & Binder, 2010). Using separate datasets, both studies found reading aloud of higher-imageability words to be associated with increased neural activity in bilateral angular gyrus (AG) and posterior cingulate/precuneus (PC). These were among the areas found to be reliably activated when comparing semantically rich to semantically impoverished conditions across more than 100 studies in a recent meta-analysis (Binder, Desai, Graves, & Conant, 2009). Thus, it appears that imageability effects can be used both as a behavioral indicator of semantic involvement in reading aloud and as a means of revealing neural systems that support this semantic access.

Additional insight into the interpretation and consistency of such findings can be gained by comparison with results from other reading-related studies. Interpreting divergent findings across studies using different tasks, however, is potentially problematic, as task demands can differ in multiple ways, the import of which is not always clear. For example, in one fMRI study that examined imageability effects (Hauk, Davis, Kherif, & Pulvermüller, 2008), participants read single words silently and no performance measures were collected. Positive correlations between imageability and BOLD signal were reported in the fusiform gyrus bilaterally but not in AG or PC regions. The divergence of these results from those discussed previously could be due, for example, to the shorter display time used by Hauk et al. (100 ms) compared to that of Binder et al. (2000 ms) and Graves et al. (1000 ms), or to a lesser degree of task engagement during passive reading compared to reading aloud.

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Convergent findings for imageability, on the other hand, come from studies using tasks that emphasize comprehension, such as lexical decision or semantic decision (e.g., similarity matching). Four such studies found activation in AG and PC for highly imageable compared to less imageable words (Bedny & Thompson-Schill, 2006; Binder, Westbury, McKiernan, Possing, & Medler, 2005; Jessen et al., 2000; Sabsevitz, Medler, Seidenberg, & Binder, 2005). Although divergent findings have also been reported (Fiebach & Friederici, 2003; Pexman, Hargreaves, Edwards, Henry, & Goodyear, 2007), the more general convergence of activation in these areas across a large number of lexical-semantic processing studies (Binder et al., 2009), and specifically in studies investigating effects of imageability, points to a highly reliable association of the AG and PC regions with semantic processing.

Consistency

Spelling–sound consistency relates to the computation of phonology from orthography, and can be defined in terms of a word's "friends" and "enemies." Friends of a word share the spelling and pronunciation of its rime (vowel nucleus and coda), whereas enemies share the same rime spelling but differ in pronunciation. Words with low spelling–sound consistency (e.g., PINT has many enemies such as LINT, HINT, and MINT, but no friends) generally elicit longer response times (RTs) than high-consistency words (Andrews, 1982; Baron & Strawson, 1976; Glushko, 1979; Jared, 1997, 2002; Taraban & McClelland, 1987). Other types of overlap (e.g., BAT, BAG) also affect processing to a much lesser degree (Kessler & Treiman, 2001) and so tend to be excluded from neighborhood calculations.

Functional brain imaging studies investigating the effects of spelling–sound consistency during single-word reading (either silently or aloud) typically report activation for low- compared to high-consistency words in left lateral prefrontal and medial premotor areas such as the inferior frontal gyrus (IFG) and anterior insula (Binder, Medler, et al., 2005; Fiez, Balota, Raichle, & Petersen, 1999; Graves et al., 2010; Herbster, Mintun, Nebes, & Becker, 1997; Mechelli et al., 2005). In studies of reading aloud, additional activations for low- compared to high-consistency words were found at the junction of the inferior and precentral sulci (inferior frontal junction, IFJ), and the supplementary motor area (SMA; Binder, Medler, et al., 2005; Fiez et al., 1999; Graves et al., 2010). Positive correlations between RT and BOLD signal are found in these areas during both reading aloud (Binder, Medler, et al., 2005; Graves et al., 2010) and lexical decision (Binder, Westbury, et al., 2005). These areas also show activation under conditions of high compared to low demands on working memory (Owen, McMillan, Laird, & Bullmore, 2005) and cognitive control (Derrfuss, Brass, Neumann, & Yves von Cramon, 2005). The co-occurrence of activation for low-consistency words with activations related to increased demands on working memory and cognitive control raises the possibility that activation in these areas may not be due specifically to lexical processing.

An increased reliance on semantic processing for reading low-consistency words is predicted by PDP models, but findings of a reliable association between reading low-consistency words and activation in temporal or parietal areas typically associated with lexical semantics, rather than more general processes such as those related to working memory, have been scarce. Initial evidence that such a pattern might obtain in the left middle temporal gyrus (MTG) was reported by Frost et al. (2005), who manipulated consistency along with word frequency and imageability in reading aloud. Using a region-of-interest (ROI) approach restricted to left IFG, MTG, and angular gyrus, they found activation for low-consistency, high-imageability words in the MTG. ROI-based approaches are advantageous in that they increase the power to detect subtle effects in hypothesized areas. They are also disadvantageous in that they de-emphasize strict control over false positives and are silent regarding contributions from neural areas outside the ROI. Using a whole-brain analysis, we recently found activation for reading aloud low- compared to high-consistency words in an area similar to the MTG ROI used by Frost et al. (2005), spanning the middle part of the MTG and inferior temporal gyrus (ITG; Graves et al., 2010). Together these findings point to a role for the MTG/ITG in accessing semantic information to aid in mapping orthographic input to phonological output. This is in contrast to the pattern of activation found in AG and PC, which showed positive correlations of BOLD signal with imageability, but no correlation with spelling–sound consistency (Graves et al., 2010). Such a pattern suggests a distinction between the processing that occurs in MTG/ITG and AG/PC during reading aloud.

Word frequency

Effects of word frequency tend to be quite robust in both behavioral and functional neuroimaging studies. Words of lower frequency elicit longer RTs compared to those of higher frequency, with other factors equated. Most functional imaging studies report neural effects of word frequency in the direction of activation for reading low- compared to high-frequency words (Fiez et al., 1999; Hauk, Davis, & Pulvermüller, 2008; Joubert et al., 2004; Kronbichler et al., 2004). Similar frequency effects are reported in studies using picture naming tasks (Graves, Grabowski, Mehta, & Gordon, 2007; S. M. Wilson, Isenberg, & Hickok, 2009). For reading, these activations tend to occur in left IFG/anterior insula, IFJ, and SMA – areas similar to those activated for low- compared to high-consistency words (Binder, Medler, et al., 2005; Fiez et al., 1999; Herbster et al., 1997; Mechelli et al., 2005) – and in areas showing activation for increasing demands on working memory (Owen et al., 2005) and cognitive control (Derrfuss et al., 2005).

We recently investigated the degree and location of this overlap in a study of reading aloud in which word frequency, consistency, imageability, bigram frequency, biphone frequency, and number of letters were orthogonally manipulated (Graves et al., 2010). Positive correlations between BOLD signal and RT, and negative correlations between BOLD signal and imageability, consistency, and word frequency all overlapped in the left IFJ, a region strongly associated with cognitive control processes (Derrfuss et al., 2005). Positive correlations of RT and negative correlations of consistency and word frequency with BOLD signal were also found in the left IFG and anterior insula. The consistent pattern of overlap for these disparate effects in left inferior frontal areas across multiple studies and within the same study suggests that these regions may be responding to more general processing demands rather than demands specifically related to lexical processing.

Effects of word frequency in the opposite direction (activation for high- compared to low-frequency words) are relatively rare and, with the exception of our recent study (Graves et al., 2010), have only been reported in neuroimaging studies using silent reading (Yarkoni, Speer, Balota, McAvoy, & Zacks, 2008) or lexical decision (Carreiras, Riba, Vergara, Heldmann, & Münte, 2009; Prabhakaran, Blumstein, Myers, Hutchison, & Britton, 2006). That this pattern of activation has primarily been reported for lexical decision is notable because semantic variables such as imageability and lexical variables such as word frequency tend to show greater effect sizes with lexical decision compared to reading aloud (Balota, Cortese, Sergent-Marshall, Spieler, & Yap, 2004; Balota, Ferraro, & Connor, 1991; Forster & Chambers, 1973; Schilling, Rayner, & Chumbley, 1998). Evidence that word frequency could modulate semantic processing comes from findings that high-frequency words elicit retrieval of more features (McRae, Cree, Seidenberg, & McNorgan, 2005) and more associations with other words compared to low-frequency words (Nelson & McEvoy, 2000), and are found in more numerous and diverse contexts (Adelman, Brown, & Quesada, 2006). Thus, while word frequency effects can arise at multiple levels of the lexical system (for a review see Monsell, 1991), activations for high- compared to low-frequency words could in part reflect a more extensive and rapid access to semantic information in the case of high-frequency words. This component should be distinguishable from other aspects of lexical processing to the extent that it spatially overlaps effects of variables such as imageability that are thought to be more specifically related to lexical semantics. In our recent study of reading aloud (Graves et al., 2010), such an overlap was found in bilateral PC and AG. These areas were also found in a large-scale meta-analysis (Binder et al., 2009) to be reliably associated with lexical semantic processing. Thus, the overall pattern of overlapping positive correlations of word frequency and imageability with BOLD signal in areas implicated in lexical semantic processing suggests that the PC and AG support semantic processing in reading aloud. Unlike the MTG/ITG, however, the AG/PC was not found to be modulated by spelling–sound consistency. Together with the finding that activation in the AG/PC region was positively associated with imageability and frequency, this pattern suggests that the MTG/ITG activation may reflect recruitment of semantic information during computation of a pronunciation, whereas activation in the AG/PC may reflect another process such as word comprehension.

Chronometry

Information on the time course of activation within the lexical system should help determine whether semantic information is accessed alongside orthographic and phonological information, as predicted by PDP models, or whether its access is incidental, perhaps following both orthographic and phonological access, as compatible with DRC models. Two widely used methods for time course investigations with resolution on the order of milliseconds are electroencephalography studies analyzed in terms of event-related potentials (ERP), and magnetoencephalography (MEG).

MEG is a particularly promising technique in that it combines exquisite temporal resolution with spatial resolution that, while not as fine-grained as fMRI, can detect locations of distinct cortical activity. Compared to fMRI, there are relatively few research groups using MEG, and although the number of MEG centers is expanding, so far there have been few MEG studies of reading aloud. An exception is a study by Simos et al. (2002), in which an area of the MTG was shown to be more active for low-consistency words than pronounceable nonwords. This result is very close to the area showing a negative correlation between BOLD signal and consistency for reading words aloud in fMRI (Graves et al., 2010). Although this convergence of findings across MEG and fMRI experiments is encouraging, temporal specificity was sacrificed by merging the data into two large time bins (150–300 and 300–1000 ms), and it is not clear that the MEG result is specific to low-consistency words. One line of study that would be useful in clarifying the role of semantic processing in reading aloud would be to examine the neural effects of factors such as word frequency and imageability as they unfold in time and space. Although we are aware of no such study of reading aloud, there are several relevant studies of word recognition (also discussed in Lee & Federmeier, Volume 1, Chapter 10).

ERP and MEG studies report lexical and semantic effects occurring in both relatively early (~150 ms) and late (~400 ms) time-frames. As summarized in two recent reviews, effects of word frequency and lexicality (differences between words and nonwords) are present by 150 ms post-stimulus-onset (Dien, 2009; Pulvermüller, Shtyrov, & Hauk, 2009). A recent lexical decision ERP study replicated the finding of early effects of word frequency and further showed that they subside over about 100 ms then re-emerge as a sustained difference lasting up to 500 ms post-stimulus (Hauk, Davis, Ford, Pulvermüller, & Marslen-Wilson, 2006). This study also investigated a variable called "semantic coherence," a measure of the number of contexts in which a word occurs, which was significantly correlated with word frequency. Effects of this variable occurred by 160 ms post-stimulus, subsided, then re-emerged at 425 ms, suggesting the presence of separate early and late stages of semantic processing. If words and word-like nonwords differ primarily in degree of meaningfulness, and high-frequency words have more associations with other words in

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the language, then it seems plausible that early temporally overlapping effects of word frequency, lexicality, and semantic coherence reflect initial activation of semantic features.

Regarding effects of imageability, a study using a concrete/abstract judgment task compared differences in MEG activity to abstract and concrete words and found differences peaking around 400 ms post-stimulus-onset (Dhond, Witzel, Dale, & Halgren, 2007). Cortical sources of effects arising in this time-frame were identified that showed greater activity for concrete compared to abstract words in right AG and bilateral PC. Activations in these regions for concrete compared to abstract words have also been found in fMRI studies using similar tasks (Bedny & Thompson-Schill, 2006; Binder, Westbury, et al., 2005; Sabsevitz et al., 2005). Although imageability effects peaked at around 400 ms, they began to diverge in the PC as early as 330 ms. Considering that the abstract words, while significantly less imageable than the concrete ones, were still quite imageable (the mean imageability was 401 for their abstract words and 576 for concrete words, on a scale from 100 to 700), it may be the case that differences across levels of imageability would have arisen even earlier had the levels been more clearly separated.

Imageability effects have also been investigated using ERP. For example, Holcomb and colleagues compared the time courses for concrete (highly imageable) and abstract (less imageable) words both in isolation and in sentence contexts. During lexical and semantic decisions to individual words, differences between word types emerged by 300 ms but not within the earlier 150–300 ms time window (Kounios & Holcomb, 1994). Similar results were found for making semantic or imagery decisions to sentence-final words. That is, differences between word types emerged by around 300 ms but not earlier (West & Holcomb, 2000). Another study by the same group, however, did find differences between concrete and abstract sentence-final words during a meaningfulness judgment task that emerged within an early 150–300 ms window (Holcomb, Kounios, Anderson, & West, 1999). Thus, evidence for imageability effects occurring early during lexical access is somewhat equivocal. Additionally, none of the specific studies discussed here examined the time course of imageability effects during reading aloud, leaving open the question of whether or not semantic processing occurs in parallel with early orthographic and phonological processing.

Distinct Neural Substrates

Before proposing a set of neural regions supporting semantic processing in reading aloud, it is important to note that several regions are good candidates for supporting direct mapping from orthography to phonology, including the left posterior superior temporal sulcus, supramarginal gyrus, and midfusiform gyrus. A discussion of the possible roles of these regions in reading aloud is beyond the scope of this chapter, and we refer the interested reader to other studies that address this topic (Binder, Medler, et al., 2005; Graves et al., 2010; Richlan, Kronbichler, & Wimmer, 2009).

The pattern of results described above points to two spatially and possibly functionally distinct regions supporting semantic processing during reading aloud. One involves the angular gyrus and posterior cingulate/precuneus, for which overlapping effects in the direction of greater activity for higher values of imageability and word frequency have been found. The other involves a more anterior region in the middle part of the MTG/ITG, for which increasing activity was found for reading words of decreasing spelling–sound consistency (Graves et al., 2010). We propose that this MTG/ITG area, compared to the AG and PC, plays a more central role in mapping from semantics to phonology for the purpose of generating a phonological code. Consistent with this interpretation are results from a meta-analysis of word production studies (Indefrey & Levelt, 2004), in which the mapping from lexical-semantic to phonological codes is suggested to occur along the MTG.

Activation in the AG and PC regions, on the other hand, may reflect integration or activation of conceptual/semantic information, perhaps in a manner similar to that described in accounts of convergence zones. According to relevant aspects of the Damasio (1989) account, first-order convergence zones integrate information from adjacent early sensory cortex. This somewhat abstracted but still modality-dependent information is further abstracted by higher-order convergence zones located in multimodal association cortex. Due to their anatomical locations and patterns of connectivity, as summarized in more detail elsewhere (Binder et al., 2009), the AG and PC regions may be considered higher-order convergence zones for integration of multimodal information relevant to lexical semantics. Such representations contribute to word comprehension but may play a smaller role in computation of phonology. A schematic diagram of the proposed posterior left hemisphere pathways for reading aloud is provided in Figure 9.1.

The AG and PC are prominent components of the "default-mode" network (Gusnard & Raichle, 2001). As discussed in more detail elsewhere (Binder et al., 2009), these areas are part of a larger semantic system that appears to be active during resting and other passive states. One implication of this is that studies comparing conditions of interest to a resting baseline are likely to miss activations in these regions. In fact, several functional neuroimaging studies that examined effects of word frequency restricted their analyses to areas that were more active for words compared to a resting baseline (Carreiras, Mechelli, & Price, 2006; Fiez et al., 1999; Kronbichler et al., 2004). This practice may help explain the paucity of activation findings for reading high- compared to low-frequency words.

Evidence from acquired dyslexia

Independent evidence for distinct roles for semantic processing in the AG/PC on the one hand, and the middle MTG/ITG on the other, comes from studies of acquired dyslexia. Semantic dementia (SD) is a clinical variant of frontotemporal

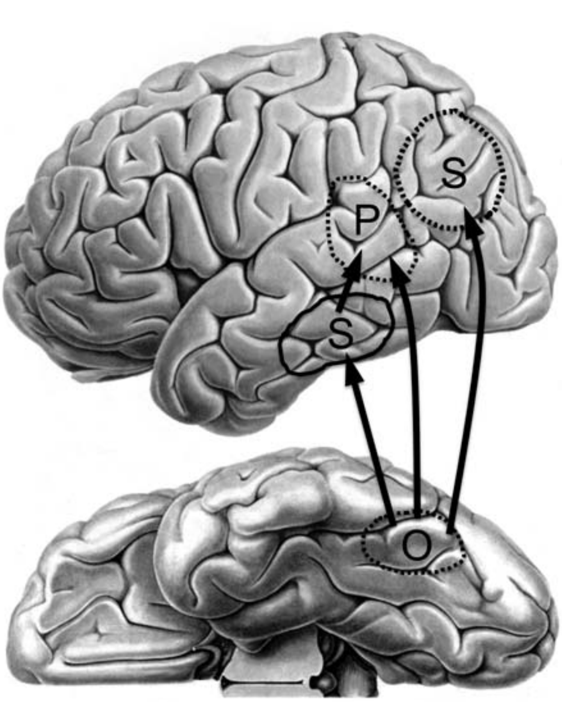

Figure 9.1 A neuroanatomical model of posterior left hemisphere pathways involved in reading aloud. Orthographic information (letter and letter string identity) is processed in the posterolateral fusiform gyrus and adjacent occipitotemporal sulcus ("O"). This information is mapped directly onto phonological representations in the posterior superior temporal region, including superior temporal sulcus and supramarginal gyrus ("P"). Low spelling–sound consistency produces enhanced activation of semantic representations in the middle and inferior temporal gyri (area "S" marked by solid line), which in turn provide input to P that assists in correct phonological retrieval. All words activate semantic representations in the angular gyrus (area "S" marked by dotted line). This latter area is modulated by word frequency and imageability but not by spelling–sound consistency, suggesting that semantic processing here supports word comprehension rather than pronunciation.

lobar degeneration, associated with both loss of semantic knowledge and atrophy of the anterior middle and inferior temporal lobes (Neary et al., 1998). SD patients tend to exhibit surface dyslexia, producing regularized pronunciations of low-consistency words (e.g., pronouncing "deaf" to rhyme with "leaf"; Patterson & Hodges, 1992). The association of surface dyslexia with the pattern of brain damage in SD is highly reliable, with the severity of surface dyslexia increasing with overall degree of semantic impairment (Woollams, Lambon Ralph, Plaut, & Patterson, 2007). Although SD patients have primarily anterior temporal lobe damage (Brambati, Ogar, Neuhaus, Miller, & Gorno-Tempini, 2009; Nestor, Fryer, & Hodges, 2006; S. M. Wilson, Brambati, et al., 2009), the posterior extent of this damage in

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the left hemisphere includes the middle MTG/ITG (Rohrer et al., 2009), an area found by Graves et al. (2010) to show increasing activity for reading aloud words of decreasing spelling–sound consistency.

Patients with Alzheimer's disease (AD), by comparison, show widespread pathology in temporal and parietal lobe areas that prominently include the medial temporal lobe, posterior cingulate/precuneus, and lateral posterior temporoparietal regions such as angular gyrus (Arnold, Hyman, Flory, Damasio, & van Hoesen, 1991), with comparative sparing of ventral and lateral anterior temporal regions (Buckner et al., 2005). In addition to this partially distinct pattern of pathology distribution, these patient groups also differ symptomatically. As discussed above, SD patients exhibit surface dyslexia. Although surface dyslexia may occur in later stages of AD (Strain, Patterson, Graham, & Hodges, 1998), AD patients more typically show preserved reading of low-consistency words (Noble, Glosser, & Grossman, 2000). Like SD patients, however, AD patients have been shown to exhibit impairment on tasks related to semantic knowledge. Specifically, AD patients produce more shared compared to distinct features for concrete concepts (Alathari, Ngo, & Dopkins, 2004), and loss of knowledge about distinguishing features may lead to a characteristic "hyperpriming" phenomenon (Chertkow, Bub, & Seidenberg, 1989; Giffard et al., 2001; Martin, 1992). Additional evidence for the erosion of distinctive relative to shared features in AD comes from the finding that AD patients show greater naming impairment for categories such as animals with many shared features, compared to objects with relatively few shared features (Whatmough et al., 2003). AD patients also show greater impairment on semantic compared to phonemic fluency tasks, despite the comparable executive control processes required by these tasks (Henry, Crawford, & Phillips, 2004; Salmon, Butters, & Chan, 1999; see also Pekkala, Volume 2, Chapter 30). Thus, although deficits in semantic processing are evident in both SD and AD, damage in SD includes the middle MTG/ITG region found by Graves et al. (2010) to be associated with consistency effects in reading aloud, and damage to this region results in surface dyslexia symptoms not typically seen in AD.

To our knowledge, only two studies have examined surface dyslexia in cases of focal brain damage. A longitudinal study of recovery from acquired dyslexia by B. A. Wilson (1994) included two cases of herpes simplex encephalitis who exhibited surface dyslexia. Although no information was given about their lesion locations, damage associated with herpes simplex encephalitis tends to concentrate in the anteromedial and ventral temporal lobes. These patients were the only two of the entire group of seven who were specifically diagnosed with surface dyslexia. A recent study by Jefferies, Rogers, Hopper, and Lambon Ralph (2010) included 13 patients with strokes that impaired semantic processing. This study examined effects of consistency and word frequency on reading aloud in both stroke and SD cohorts, finding a greater proportion of errors for less consistent and lower-frequency words in both groups. An interaction between consistency and word frequency, with a larger difference in error rate between low- and high–consistency words for those of lower frequency, was, however, found only in the SD group. Brief verbal

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descriptions of approximate lesion location were provided for 9 of the 13 stroke patients, indicating widespread damage in frontal, occipital, temporal, parietal, and subcortical areas. However, no lesion-deficit analyses were performed, leaving open the question of whether the differing response profiles were due, for example, to the stable versus progressive nature of the damage, or to the disruption of different neural structures in the patients with stroke compared to SD.

Conclusion

Although the role of semantic processing in reading aloud is controversial and is likely to remain so for some time, recent evidence from functional neuroimaging, considered alongside existing behavioral and computational studies, suggests an integral role for semantic processing in reading aloud. A set of neural areas including bilateral angular gyrus, posterior cingulate/precuneus, and left middle MTG/ITG appears to support semantic processing in several tasks, including reading aloud. Based on recent parametric and chronometric studies of reading aloud, we suggest that immediately following the initial decoding of a word's orthographic information, and likely before such decoding is completed, processing in the angular gyrus and posterior cingulate/precuneus serves to support automatic comprehension of the word, perhaps through integration and/or retrieval of its semantic features. Processing in the middle MTG/ITG, on the other hand, serves to map the retrieved semantic information onto a corresponding phonological representation for production.

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