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Shared orthographic neuronal representations for spelling and reading

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ABSTRACT

A central question in the study of the neural basis of written language is whether reading and spelling utilize shared orthographic representations. While recent studies employing fMRI to test this question report that the left inferior frontal gyrus (IFG) and ventral occipitotemporal cortex (vOTC) are active during both spelling and reading in the same subjects (Purcell et al., 2011a; Rapp and Lipka, 2011), the spatial resolution of fMRI limits the interpretation of these findings. Specifically, it is unknown if the neurons which encode orthography for reading are also involved in spelling of the same words. Here we address this question by employing an event-related functional magnetic resonance imaging-adaptation (fMRI-A) paradigm designed to examine shared orthographic representations across spelling and reading. First, we identified areas that independently showed adaptation to reading, and adaptation to spelling. Then we identified spatial convergence for these two separate maps via a conjunction analysis. Consistent with previous studies (Purcell et al., 2011a; Rapp and Lipka, 2011), this analysis revealed the left dorsal IFG, vOTC and supplementary motor area. To further validate these observations, we then interrogated these regions using an *across-task* adaptation technique, and found adaptation across reading and spelling in the left dorsal IFG (BA 44/9). Our final analysis focused specifically on the Visual Word Form Area (VWFA) in the vOTC, whose variability in location among subjects requires the use of subject-specific identification mechanisms (Glezer and Riesenhuber, 2013). Using a functional localizer for reading, we defined the VWFA in each subject, and found adaptation effects for both *within* the spelling and reading conditions, respectively, as well as *across* spelling and reading. Because none of these effects were observed during a phonological/semantic control condition, we conclude that the left dorsal IFG and VWFA are involved in accessing the same orthography-specific representations for spelling *and* reading.

Introduction

Written language is a promethean cultural invention that has allowed humans to express thoughts and communicate throughout the millennia. In modern society, reading text and writing out ideas are critically useful skills that require years of education. Naturally there are inherent differences between those cognitive and sensorimotor skills required to read words and those used to write them. Whereas reading involves the visual perception of letter strings which are mapped onto orthographic, phonological and semantic components for oral production, writing involves the translation of these concepts from orthographic representation to sequential motor commands used to generate word-specific letter sequences (Caramazza and Miceli, 1990; Ellis and Young, 1988; Rapcsak and Beeson, 2002; Rapp and Hillis, 2002; Roeltgen and Heilman, 1985). There is general agreement that semantics and phonology are not unique to either reading or spelling as they form the core cognitive functions in the spoken language system. Although it is also clear that fluent reading and spelling depend on accessing orthographic representations (i.e. the memories of the sequences of letters that comprise a word), it is not known whether these are the *same* exact orthographic representations or whether reading and spelling call upon *different* orthographic representations.

The question of independent versus shared orthographic systems for spelling and reading originated from the neuropsychology literature. Support for the independent orthography model stems from work which demonstrated that there can be damage that impairs spelling but not reading (Beauvois and Dérouesné, 1981; Roeltgen and Heilman, 1984), as well as damage that impairs reading but not spelling (e.g. Cumming et al., 1970; Friedman, 1982). Such work led to the theory that there are distinct orthographic long-term memory components for spelling and reading (Patterson and Shewell, 1987). While this suggests that there is some segregation of cognitive functions, there is also a significant body of evidence instead suggesting that there are shared

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components for orthographic processing. Specifically, there are numerous reports of brain damaged individuals with a deficit in both spelling and reading (Behrmann and Bub, 1992; Philipose et al., 2007; Rapcsak et al., 2007; Tsapkini and Rapp, 2010). In particular, the work of Behrmann and Bub (1992) described an individual with impairments in spelling and reading for the same irregular words (i.e. words with a low phoneme to grapheme probability, e.g. *yacht*), which suggests a shared orthographic long-term memory store. Furthermore, there has been a report of a treatment generalization effect in an individual with acquired dyslexia, such that there was improved performance in spelling for those words that were trained with reading (Hillis, 1993). This speaks in support of the idea that spelling and reading can access shared orthographic long-term memory representations.

Behavioral studies of spelling and reading in healthy participants also support the theory that there are shared orthographic representations used for both spelling and reading. For instance, it has been reported that, compared to words that are correctly spelled, words that are incorrectly spelled (i.e. that have low-integrity orthographic long-term memory representations) are less accurately identified during a reading lexical decision task (Burt and Tate, 2002). Furthermore, it was found that literate adults were poor at visually distinguishing misspelled words from actual words only for the words that they themselves were poor at spelling and not for words that they were good at spelling (Holmes and Carruthers, 1998). Finally, in a repetition priming study, it was found that spelling a given word primed performance on a reading task for that same word, but not for different words (Monsell and Coltheart, 1987). A parsimonious interpretation of the behavioral findings is that orthographic long-term memory representations for spelling and reading are shared.

Although the aforementioned findings predominantly support shared orthographic components for spelling and reading – in particular, orthographic long-term memories – evidence from cognitive behavioral experiments alone cannot adjudicate whether there are shared orthographic representations at the *neural* level in normal literate adults. Such a proposal requires direct investigation of the neural underpinnings of spelling and reading.

Brain imaging studies have begun to shed light on this matter, with most focused on reading and few on spelling. Considering neuroimaging studies of reading first, several meta-analyses have been conducted, providing a useful way of assimilating the most salient results. For example, the most recent of these meta-analyses was conducted in children and adults; this work reports that neuroimaging studies in adults using a variety of reading tasks show converging brain activation in the following regions: left ventral occipitotemporal cortex (vOTC), left inferior frontal cortices, left parietal cortices, bilateral supplementary motor areas (SMAs), and right cerebellum (Martin et al., 2015). The left vOTC, parietal and inferior frontal cortices are considered the canonical brain areas involved in reading, and will be considered in more detail here.

The left parietal cortex has been associated with reading and phonological processing and has been deemed critical for early reading development (Pugh et al., 2001). Specifically, the supramarginal and posterior superior temporal gyri have been identified in fMRI studies of pseudoword reading and phonological manipulation and are therefore thought to support the grapheme-phoneme conversion processes necessary for reading (e.g., Jobard et al., 2003; Simos et al., 2002). The posterior parietal cortices on the other hand have been associated with attentional processes. Generally, the left posterior parietal is thought to form a fronto-parietal network with the SMA thus forming an attentional control network involved in goal-directed cognitive functions (Corbetta et al., 2008; Spreng et al., 2010); it has recently been proposed that these regions form a fronto-parietal attentional network for reading (Martin et al., 2015).

The left IFG, on the other hand, is often associated with a more diverse set of functions during reading, including phonological, semantic, and orthographic processing. With regards to phonology, it is associated with articulatory planning required for overt reading, consistent with the classical notion of Broca's area in spoken production (Guenther, 2006; Price, 2012; Taylor et al., 2013). Furthermore, it is associated with aspects of both lexical and sublexical processing; specifically, it is involved in the selection of the correct phonological lexical representations among competing alternatives (e.g., Heim et al., 2013; Righi et al., 2010), and the sublexical mapping of individual graphemes to their corresponding phonemes (Fiez et al., 1999; Jobard et al., 2003; Poldrack et al., 1999). In the semantic domain it is associated with accessing semantic representations during reading (Binder et al., 2009; Binder and Desai, 2011; Poldrack et al., 1999), and specifically the selection of the correct semantic representations among competitors (Thompson-Schill et al., 1997). The left IFG is also involved in orthographic processing. For instance, in studies of reading, the left IFG has been shown to be sensitive to the written frequency of letter combinations (e.g. infrequent letters and common bigrams) (Vinckier et al., 2007), as well as the frequency of whole written words (Fiez et al., 1999; Kronbichler et al., 2004).

The visual word form area (VWFA) in left vOTC has gained prominence in the neuroimaging literature as being consistently and selectively activated during whole word reading (Baker et al., 2007; Cohen and Dehaene, 2004; Gaillard et al., 2006; McCandliss et al., 2003). Although the specific function of this area has been debated in recent years, the VWFA is generally thought to participate in processing learned orthographic long-term memory representations, either as one component of an extended network or as a regionally focal area that hosts neurons which process orthographic long-term-memory representations (e.g., Dehaene and Cohen, 2011; Price and Devlin, 2011). Specifically, it has been found that the VWFA is active in literate, but not illiterate adults (Dehaene et al., 2010), providing evidence that it becomes entrained to orthographic features through the process of learning to read. Further, it is functionally selective to reading words while being invariant to other features such as case, font or size (Dehaene et al., 2001; however see Wimmer et al., 2016). It has also been found that the VWFA contains neuronal populations that are selectively tuned to whole visual word representations (Glezer et al., 2009; Schurz et al., 2010), thus providing support for the idea that this site is associated with orthographic lexical input processes for reading. Together, this work fits well with the lesion studies that have identified the left vOTC as being selectively required for normal reading (Cumming et al., 1970; Gaillard et al., 2006; Sheldon et al., 2008).

Turning to spelling, a relatively smaller corpus of neuroimaging studies reveals a consistent left lateralized set of regions associated with spelling (Planton et al., 2013; Purcell et al., 2011b). One recent meta-analysis of brain areas involved in spelling (Purcell et al., 2011b) found high likelihood of activation for the central components of spelling in the left vOTC, superior temporal gyrus, intraparietal sulcus, and IFG. Of particular interest is the left IFG and vOTC, both of which have been shown to contribute to intact orthographic long-term memory processing in spelling. For instance, fMRI activation while spelling has been found to be modulated by word frequency (i.e. differences in spelling high frequency words relative to infrequently occurring words) (Rapp and Dufor, 2011; Rapp and Lipka, 2011), and by lexicality (i.e. differences in spelling real words relative to pseudowords, e.g. fodap) (DeMarco et al., 2017; Ludersdorfer et al., 2015). The modulation of neural activity due to frequency and lexicality are indicative of orthographic long-term memory because orthographic representations underlying higher frequency words are considered to be better inculcated into the orthographic long-term memory stores as compared to either low frequency words or pseudowords. This neuroimaging work is consistent with lesion literature which finds that individuals with damage to either the left IFG or the left vOTC have impaired access to orthographic long-term memories for spelling (Rapp et al., 2015).

While earlier brain-based studies of reading and spelling occurred independently of each other, more recent work has attempted to