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Research report

Decoding levels of representation in reading: A representational similarity approach

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ABSTRACT

Multiple levels of representation are involved in reading single words: visual representations of letter shape, orthographic representations of letter identity and order, phonological representations of the word's pronunciation, and semantic representations of its meaning. Previous lesion and neuroimaging studies have identified a network of regions recruited during word reading, including ventral occipital-temporal regions and the angular gyrus (AG). However, there is still debate about what information is being represented and processed in these regions. This study has two aims. The first is to help adjudicate between competing hypotheses concerning the role of ventral occipital cortex in reading. The second is to adjudicate between competing hypotheses concerning the role of the AG in reading. Participants read words in the scanner while performing a proper name detection task and we use a multivariate pattern analysis technique for analyzing fMRI data – representational similarity analysis (RSA) – to decode the type of information being represented in these regions based on computationally explicit theories. Distributed patterns of activation in the left ventral occipitotemporal cortex (vOT) and the AG show evidence of some type of orthographic processing, while the right hemisphere homologues of the vOT supports visual, but not orthographic, information processing of letter strings. In addition, there is evidence of left-lateralized semantic processing in the lvOT and evidence of top-down feedback in the lvOT. Taken together, these results suggest an interactive activation theory of visual word processing in which both the lvOT and lAG are neural loci of an orthographic level of representations.

Reading is a remarkable human invention. It allows our brains to transform patterns of retinal stimulation into abstract representations of words (i.e., meanings and pronunciations). The processes by which these transformations occur are complex, heavily debated, and the focus of extensive research in the cognitive sciences (see Adelman, 2012; Carreiras, Armstrong,

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Perea, & Frost, 2014; Frost, 2012 for recent reviews). Despite important differences that are beyond the scope of this article, theories tend to agree on the different types of representations engaged during reading. Low-level *visual* representations of the stimulus code all visual inputs into basic visual features such as oriented edges. *Phonological* representations encode the sequence of sounds that correspond to the word being verbalized. *Semantic* representations denote the meaning of the word. Between the visual processing of the stimulus and the semantic and phonological processing of the word are a series of levels of representations – grouped into a broad category of *orthographic* representations – involved in processes such as recognizing letter identities and their order or recognizing which sequences of letters are familiar words (Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001). Reading can therefore be viewed as a series of translational processes, converting visual characteristics to orthographic representations, which in turn serves as a means to generate higher order representations (e.g., phonological and semantic).

One striking aspect of reading is how distinct these different levels of representation are from each other. It is well known that the relationship between a word's phonology (or its orthography) and its semantics is largely arbitrary (e.g., Monaghan, Christiansen, & Fitneva, 2011). In fact, visual and orthographic representations can also be unrelated. For example, the letters d and b are similar to each other at a visual level of representation, while d and D share fewer visual features. In contrast, at orthographic levels, d and D are examples of the same letter identity, while d and b are not and thus map onto different representations (Rothlein & Rapp, 2014). In a language like English, orthography and phonology can have an opaque relationship, with words like *through, though, thought* and *tough* highly similar in their orthographic representations but dissimilar in their phonological representations. Meanwhile words like *through* and *grew* have similar representations at a phonological level, despite having little overlap at orthographic levels.[1]

A well-articulated map of the regions of cortex associated with single word reading has emerged over the past 25 years (Fiez & Petersen, 1998; Price, 2012; Turkeltaub, Eden, Jones, & Zeffiro, 2002). These areas cover a large left hemisphere network including the angular gyrus (AG); supramarginal gyrus; ventral occipitotemporal cortex (vOT); inferior, middle and superior temporal gyri; extrastriate occipital cortex; lingual gyrus; and left inferior frontal gyrus (triangularis and opercularis). The areas identified by functional neuroimaging largely have been corroborated by lesion studies, with brain damage to each of these regions associated with selective impairments in the ability to read words (e.g., Hillis & Rapp, 2004; Philipose et al., 2007). However, a full understanding of the neural correlates of reading requires both identifying the cortical regions that respond to visual words, and also the level(s) of representation associated with these regions. There is general consensus about which cortical regions are broadly associated with reading, yet extensive debate about the type of information processing goes on in those regions. In particular, the roles of two regions – the left ventral occipitotemporal region and the left AG – have been debated extensively in the literature over the past several decades.

Left ventral occipitotemporal region (lvOT). Functional neuroimaging (see Dehaene & Cohen, 2011; Price & Devlin, 2011) and lesion studies (Cohen et al., 2003; Leff et al., 2001) have provided consistent evidence that the lvOT is involved in reading. The most familiar interpretation of the function of this region comes from Dehaene and Cohen (2011, see also McCandliss, Cohen, & Dehaene, 2003; Cohen & Dehaene, 2004), who argue that this region is the “visual word form area” (VWFA).

According to the VWFA hypothesis, activation in this region during reading tasks reflects engagement of orthographic processing. Support for this hypothesis is that this region shows neural adaptation for cross case priming (e.g., rage – RAGE), suggesting a level of representation that abstracts away from visual features (Dehaene et al., 2004, 2001). In contrast, the right homologue of the region shows sensitivity to cross-case neural adaptation only when the upper and lower case forms of the letters are visually similar (Dehaene et al., 2004), indicating that this region processes visual not orthographic information. Furthermore, activation in the lvOT is sensitive to language-specific orthographic constraints, like the frequency of specific letter combinations (Binder, Medler, Westbury, Liebenthal, & Buchanan, 2006; Vinckier et al., 2007), which are variables that have been linked to orthographic representations. Finally, individuals who have highly selective impairments in recognizing letter identities or familiar written words frequently have damage to this region (Pflugshaupt et al., 2009; Tsapkini, Vindiola, & Rapp, 2011).

However, not all evidence so clearly supports the VWFA hypothesis. The region does not respond selectively to written words, also showing greater response to objects and faces compared with scrambled objects or scrambled faces, even in highly literate participants (Moore & Price, 1999; Nestor, Plaut, & Behrmann, 2011; Song, Hu, Li, Li, & Liu, 2010; Turkeltaub, Flowers, Lyon, & Eden, 2008; Vogel, Petersen, & Schlaggar, 2012). While the region shows cross-case priming, it shows comparable levels of neural adaptation when a written word is preceded by a picture with the same name, or vice-versa (Kherif, Josse, & Price, 2011). Along similar lines, many individuals with damage to the lVOT also have difficulty when naming objects (Hillis et al., 2005; Starrfelt & Gerlach, 2007) or mild face recognition impairments (Behrmann & Plaut, 2014). Taken together, these results suggest that if activation in the region reflects one unified level of representation across all tasks, it is likely not specifically an orthographic level of representation. Even results that purportedly support the VWFA hypothesis do not selectively implicate the area in an orthographic level of representation. For example, in the cross-case neural adaptation experiments, the upper and lower case forms of the same words (e.g., rage – RAGE) are represented as identical at orthographic, semantic and phonological levels of representation. Therefore, the observed adaptation could indicate that the region is involved in any of these levels of representation.

[1] Note that this logic cannot distinguish between different levels of orthographic representation. The words *through*, *though*, *thought* and *tough* are all familiar words with similar sequences of letter identities. They are similar to each other at a level of orthographic representation that represents the letter identities in the written stimulus and their order. They are also similar to each other at the level of orthographic lexicon, or the long-term memory system that stores the spellings of familiar words.