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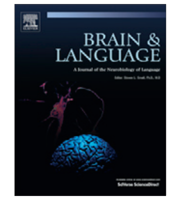

Individual differences in skilled adult readers reveal dissociable patterns of neural activity associated with component processes of reading

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ABSTRACT

We used fMRI to examine patterns of brain activity associated with component processes of visual word recognition and their relationships to individual differences in reading skill. We manipulated both the judgments adults made on written stimuli and the characteristics of the stimuli. Phonological processing led to activation in left inferior frontal and temporal regions whereas semantic processing was associated with bilateral middle frontal activation. Individual differences in reading subskills were reflected in differences in the degree to which cortical regions were engaged during reading. Variation in sight word reading efficiency was associated with degree of activation in visual cortex. Increased phonological decoding skill was associated with greater activation in left temporo-parietal cortex. Greater reading comprehension ability was associated with decreased activation in anterior cingulate and temporal regions. Notably, associations between reading ability and neural activation indicate that brain/behavior relationships among skilled readers differ from patterns associated with dyslexia and reading development.

1. Introduction

Successful reading in adults involves translating a visual code into both sound-based (phonological) and meaning-based (semantic) codes; as a result, it requires coordinating a range of mental processes. Consistent with this, advances in neuroimaging have uncovered a reading network spanning wide-ranging cortical regions. A prevailing view holds that different subcomponents of this network correspond to processes involved in accessing orthography (i.e., visual symbols and the ways in which they can be combined), phonology (i.e., sounds of language), and semantics (i.e., word meanings; (Devlin, Matthews, & Rushworth, 2003; Fiez, 1997; Price, Moore, Humphreys, & Wise, 1997; Pugh et al., 1996; Rumsey et al., 1997). In parallel with this, a separate line of research has sought to link patterns of brain activity to individual differences in reading subskills. However, the focus of these studies has been the trajectory of neural changes reflecting normal development of reading (Church, Coalson, Lugar, Petersen, & Schlaggar, 2008; Turkeltaub, Gareau, Flowers, Zeffiro, & Eden, 2003) or wide-scale neural differences in individuals with dyslexia (Brunswick, McCrory, Price, Frith, & Frith, 1999; Temple et al., 2001). In the current study we aimed to bridge these lines of research by examining how individual differences in specific reading skills among a wide range of adults relates to activation in specific brain regions engaged by reading.

1.1. Component processes of reading

Studies of reading and the brain have emphasized a group of cortical regions that are engaged during reading. Moreover, stimulus properties and task demands appear to differentially modulate activity in these regions, such that different hypotheses have been put forward concerning their function. Here we summarize some of the key findings in this regard.

The first of these is the proposal that the left ventral temporal region, including ventral extrastriate cortex and the fusiform gyrus, supports pre-lexical orthographic analysis during reading (Cohen et al., 2000). This type of analysis includes not only the recognition of individual orthographic units, but also the knowledge of how these units can be legally combined to form valid words in a language. This allows for relatively efficient recognition of familiar words, despite variations in physical characteristics such as font and case (McCandliss, Cohen, & Dehaene, 2003). Evidence that the midfusiform gyrus is involved in this type of processing comes from observations that this region shows greater activation to orthographically legal letter strings than to either nonalphabetic stimuli (Price, Wise, & Frackowiak, 1996; Puce, Allison, Asgari, Gore, & McCarthy, 1996) or to strings of letters that are orthographically illegal (Buchel, Price, & Friston, 1998; Cohen et al.,

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2002). Additionally, activity in this region is modulated during tasks that place specific demands on orthographic processing such as case judgment (Pugh et al., 1996), cross-case repetition priming (Dehaene et al., 2004), lexical decision with anagrams (Pammer et al., 2004) and reading Chinese logographic characters versus Chinese words presented in an alphabetic script ('pinyin'; (Chen, Fu, Iversen, Smith, & Matthews, 2002). Left fusiform activation in response to written language is greater in literate than illiterate adults (Dehaene et al., 2010), even when literacy was acquired in adulthood, suggesting that this region is sensitive to experience. The fusiform gyrus is also active during written and auditory spelling, which require access to word form information, than during auditory and written rhyme tasks, which do not (Booth et al., 2002). Involvement of this area in visual word form analysis is consistent with the broader role of the inferior temporal cortex in object recognition and visual expertise (Dehaene & Cohen, 2011; McCandliss et al., 2003), although it remains hotly debated whether there exists a cortical specialization for visual words to the exclusion of other orthographic stimuli and other non-visual language processing (Price & Devlin, 2003; Price & Devlin, 2011). For example, priming with picture/word pairs that do not have similar visual forms reduces activation in the fusiform gyrus (Kherif, Josse, & Price, 2011), which has been taken as evidence that this region is sensitive to top-down influences.

A second set of findings highlights the roles of left inferior frontal cortex and left temporo-parietal regions in phonological processing. Pugh and colleagues have found greater activity for rhyme judgments versus letter case judgments in the left inferior frontal gyrus (IFG) and left superior temporal gyrus (STG) (Pugh et al., 1996). Left IFG has been found to be differentially active during phonological analysis when compared with a picture-matching task using the same stimuli (Katzir, Misra, & Poldrack, 2005). Additionally, activation in the left frontal operculum is modulated by word frequency and spelling-to-sound consistency (reviewed in Fiez and Petersen (1998)). Attending to sound similarity while reading lists of phonologically related words led to greater activation in posterior portions of the left IFG than attending to meaning relationships while reading lists of semantically related words (McDermott, Petersen, Watson, & Ojemann, 2003). Similarly, left temporo-parietal activation has been associated with syllable counting (Price et al., 1996) and data from Chinese reading indicate that reading pinyin yields greater activation in bilateral inferior parietal and superior temporal cortex than reading Chinese logographic characters, due to the greater involvement of phonological decoding in reading pinyin (Chen et al., 2002). The exact roles that left IFG and temporo-parietal regions play in phonological processing remains somewhat unclear. It has been suggested that IFG activity reflects demands placed on working memory by phonological segmentation or articulatory recoding processes (Burton, Locasto, Krebs-Noble, & Gullapalli, 2005), with activation of temporo-parietal cortex reflecting grapheme-to-phoneme conversion (Blomert & Froyen, 2010; Jobard, Crivello, & Tzourio-Mazoyer, 2003). Finally, inferior frontal activation may reflect implicit access of articulatory representations (Hickok & Poeppel, 2004; Zatorre, Meyer, Gjedde, & Evans, 1996). While this model is typically applied to studies of auditory speech processing, one might also assume that this group of cortical regions represents phonological processing that abstracts away from either the visual or auditory modality.

A more complex set of regions appears to be engaged in processing words' meanings. Studies of patients with semantic dementia suggest a role for anterior temporal regions in semantic processing (Mummery et al., 2000), though the exact role this region plays in this regard is still under debate (Simmons & Martin, 2009). The semantic network likely also includes portions of the left middle temporal cortex, as this region appears sensitive to semantic judgment compared to phonological or orthographic judgments (Price et al., 1997; Pugh et al., 1996; Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996). Words with greater familiarity, meaningfulness, and number of semantic features more strongly engage the angular gyrus and posterior cingulate bilaterally, perhaps reflecting increased semantic processing of these items (Graves, Desai, Humphries, Seidenberg, & Binder, 2010). Notably, studies have also identified increased activity in portions of left inferior frontal cortex while processing semantic characteristics of words (Bookheimer, 2002; Poldrack et al., 1999). This includes living/nonliving judgments (Kapur et al., 1994), abstract/concrete decisions (Demb et al., 1995; Gabrieli et al., 1996), and verb generation (Petersen, Fox, Posner, Mintun, & Raichle, 1988). Importantly, the portion of IFG involved in semantic processing appears to lie in a distinct subregion that is anterior to the one engaged during phonological processing (Gough, Nobre, & Devlin, 2005; McDermott et al., 2003).

In spite of a considerable literature concerning the neural mechanisms related to different components of word knowledge, prior studies do present some limitations. Specifically, some studies have focused exclusively on individual component processes of visual word recognition (e.g., Cohen et al., 2000) or on how specific cortical regions respond to different word types or tasks (e.g., Graves et al., 2010). While these lines of research have been highly instructive, it can be difficult to extrapolate across this type of study to obtain a full picture of the patterns of neural activity during reading. Other studies have taken on the goal of differentiating different component processes of reading via task decomposition (Chen et al., 2002; McDermott et al., 2003; Pugh et al., 1996; Rumsey et al., 1997), taking the approach of isolating subprocesses of visual word recognition by varying both stimuli and tasks. However, this could have the effect of confounding differences in processing with differences in stimulus characteristics.

In order to investigate component processes of visual word recognition without confounding task differences and stimulus differences, the present study takes a different approach of asking subjects to perform different tasks while maintaining stimulus properties across conditions. This approach is similar to prior studies focusing on phonological versus semantic processing of familiar English words (Devlin et al., 2003; Price & Devlin, 2003; Price et al., 1997), but with additional conditions that allowed us to isolate brain regions related to orthographic processing as well.

1.2. Individual differences in reading

A separate line of research has investigated relationships between individual differences in brain activation and individual differences in reading skill. This work has typically included comparisons of individuals with reading impairment to typical readers, or tracked changes in activation associated with reading development, with a smaller number of studies focusing instead on individual differences within typical adult readers. Below we discuss the evidence for associations between such individual differences and activation associated with specific reading skills.

We first consider individual differences in the ventral portion of left inferior temporal gyrus, a region associated with orthographic processing. There is conflicting evidence regarding relationships between reading skill and activation in this region. In a magnetic source imaging study, children with dyslexia showed similar activation profiles to age-matched non-impaired readers in the left basal temporal areas (approximately BA 37) during printed word and pseudoword reading (Simos, Breier, Fletcher, Bergman, & Papanicolaou, 2000a). However, adolescents with dyslexia showed reduced activation in the fusiform gyrus bilaterally during visual rhyme judgments when compared to both reading and age matched groups (Hoeft et al., 2007). Among children aged 13–15, increased