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Anatomy is strategy: Skilled reading differences associated with structural connectivity differences in the reading network

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ABSTRACT

Are there multiple ways to be a skilled reader? To address this longstanding, unresolved question, we hypothesized that individual variability in using semantic information in reading aloud would be associated with neuroanatomical variation in pathways linking semantics and phonology. Left-hemisphere regions of interest for diffusion tensor imaging analysis were defined based on fMRI results, including two regions linked with semantic processing – angular gyrus (AG) and inferior temporal sulcus (ITS) – and two linked with phonological processing – posterior superior temporal gyrus (pSTG) and posterior middle temporal gyrus (pMTG). Effects of imageability (a semantic measure) on response times varied widely among individuals and covaried with the volume of pathways through the ITS and pMTG, and through AG and pSTG, partially overlapping the inferior longitudinal fasciculus and the posterior branch of the arcuate fasciculus. These results suggest strategy differences among skilled readers associated with structural variation in the neural reading network.

1. Introduction

Readers acquire extensive knowledge of the spellings, sounds, and meanings of words and the mappings between these codes (Harm & Seidenberg, 2004; Rayner, Foorman, Perfetti, Pesetsky, & Seidenberg, 2001). This knowledge is used in performing tasks such as determining the meaning or pronunciation of a word from print. Reading aloud has been widely studied because of its importance in early reading (Wagner & Torgesen, 1987) and because performance is often impaired in developmental dyslexia and in many types of neuropathology (Coslett, 2000; Gabrieli, 2009; Price & Mechelli, 2005). The types of computations that underlie reading aloud and their neural instantiations have been the focus of extensive research (Schlaggar & McCandliss, 2007).

Writing systems afford two ways to pronounce words from print (Fig. 1A). Pronunciations (phonology) can be computed directly (green arrow in Fig. 1A) from the written code (orthography); however, readers can also compute the meaning of a word from its spelling, and then use meaning to generate a pronunciation (red arrows in Fig. 1A), as occurs in the related domain of spoken language production (Levelt, Roelofs, & Meyer, 1999). Evidence for these mechanisms derives from several types of research, including developmental studies of learning to read (the orthography–phonology pathway develops more rapidly than the semantic pathway; Harm & Seidenberg, 1999), studies of brain-injured patients for whom one or the other pathway is more impaired (Coslett, 2000), studies in which reliance on a given pathway is changed via manipulations of instructions or stimulus materials (Hino & Lupker, 2000; Kinoshita, Lupker, & Rastle, 2004), and neuroimaging studies (Fiez, Balota, Raichle, & Petersen, 1999; Jobard, Crivello, & Tzourio-Mazoyer, 2003). Whether *skilled* readers differ in the use of these two pathways is uncertain, however. The possibility has been discussed since a classic study by Baron and Strawson (1976) examining "Chinese" (visual) vs. "Phoenician" (phonological) subtypes of readers. However, it has been difficult to obtain clear evidence for the existence of these subtypes among skilled readers of English (Brown, Lupker, & Colombo, 1994; Yap, Balota, Sibley, & Ratcliff, 2012). Many individual differences in reading aloud (e.g., in the magnitude of frequency and spelling-sound consistency effects) may arise from differences in reading proficiency, experience, and speed rather than distinct reading

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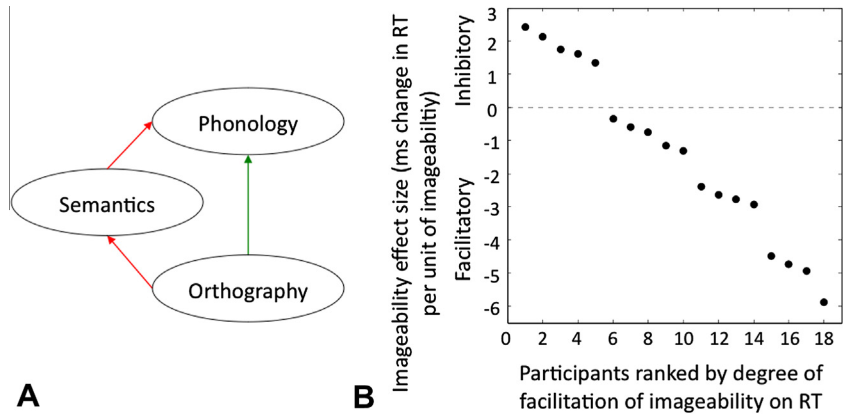

Fig. 1. Triangle model and individual effects of imageability. (A) Schematic representation of the triangle model of reading. Red and green arrows indicate different reading pathways. For reading aloud, phonology units are assumed to be phonetic features sufficient to determine speech output. (B) Individual variability in effect of imageability on RT. Increased levels of imageability facilitated reading aloud for most participants, though some showed a weak effect in the opposite direction.

styles or strategies (Seidenberg, 1985). Here we consider potential strategy differences not in terms of overt, deliberative strategy, but rather as implicit differences in reading style that develop over a lifetime of reading.

The present study examined differences among skilled readers by addressing two questions: (1) do skilled readers differ in the extent to which semantic information is used in reading aloud, and (2) are such differences associated with neuroanatomical variability within the reading network? Regarding the first question, reading aloud does not demand access to word meaning, and in dual-route models of the task (Coltheart, Curtis, Atkins, & Haller, 1993; Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001; Perry, Ziegler, & Zorzi, 2007) it plays no role. However, a computation from orthography to semantics and then from semantics to phonology might facilitate processing for some individuals or some words (Plaut, 1997; Plaut, McClelland, Seidenberg, & Patterson, 1996). Findings concerning the use of semantic information in reading aloud are mixed. Many behavioral studies have shown that variables related to semantics, such as number of meanings and rated imageability, modulate reading aloud performance at the group level (Balota, Cortese, Sergent-Marshall, Spieler, & Yap, 2004; Hino & Lupker, 1996; Hino, Lupker, & Pexman, 2002; Rodd, 2004; Shibahara, Zorzi, Hill, Wydell, & Butterworth, 2003; Strain & Herdman, 1999; Strain, Patterson, & Seidenberg, 1995; Woollams, 2005; Yap, Pexman, Wellsby, Hargreaves, & Huff, 2012). However, some of these findings have been challenged (Monaghan & Ellis, 2002), and semantic effects were not observed in other studies (Baayen, Feldman, & Schreuder, 2006; Brown & Watson, 1987; de Groot, 1989).

The triangle model of reading seems most relevant here because it has been used to address the role of semantics in reading aloud (Plaut, 1997; Plaut et al., 1996; Woollams, Lambon Ralph, Plaut, & Patterson, 2007), within a broader theory of lexical processes in reading (Seidenberg, 2012). Learning to read involves learning to compute meanings and pronunciations from print. Skilled readers develop a division of labor between components of the system that allows these codes to be computed quickly and accurately (Harm & Seidenberg, 2004). The contributions from different parts of the system vary depending on factors such as properties of the stimulus (e.g., whether it is a familiar or unfamiliar word, a homophone or homograph, a nonword); properties of the mappings between codes (orthography and phonology are more highly correlated than orthography and semantics); properties of the writing system (its orthographic "depth"), the skill of the reader, and task. Importantly, the Fig. 1 model includes two hypothesized sources of input to phonology: directly from orthography and via the orthography → semantics → phonology pathway. The orthography → phonology pathway performs functions attributed to the two pathways in the dual-route model. The orth → sem → phon pathway provides additional input during normal reading, unlike the dual-route approach (see Seidenberg & Plaut, 2006 for detailed comparisons between the models). Hence, the triangle framework seems most relevant to the goals of the current study. Before describing specific predictions, we briefly summarize some relevant studies on the neural basis of individual differences in reading.

Although neuroimaging experiments have yielded considerable evidence about components of the reading system (Binder, Medler, Desai, Conant, & Liebenthal, 2005; Fiez et al., 1999; Graves, Desai, Humphries, Seidenberg, & Binder, 2010; Hauk, Davis, & Pulvermüller, 2008; Herbster, Mintun, Nebes, & Becker, 1997; Joubert et al., 2004), and the impact of factors such as reading skill (Hoeft et al., 2007; Jobard, Vigneau, Simon, & Tzourio-Mazoyer, 2011; Kherif, Josse, Seghier, & Price, 2008), socioeconomic status (Seghier, Lee, Schofield, Ellis, & Price, 2008), and type of writing system (e.g., English vs. Chinese; Bolger, Perfetti, & Schneider, 2005), little research has examined variability among skilled readers. The Seghier et al. (2008) and Kherif et al. (2008) research yielded extensive evidence concerning brain activity during reading aloud but did not provide strong tests of the role of semantics. Both studies compared reading aloud to an unfilled rest condition. One concern with this approach is that engagement of semantic processing during rest (Binder, Desai, Graves, & Conant, 2009; Binder et al., 1999) would tend to mask activation of semantics in comparisons to reading aloud.

A study by Jobard et al. (2011) yielded some evidence for individual differences in patterns of brain activity during silent reading rather than overt naming among relatively proficient readers. Participants' performance varied on a test of verbal working memory, a task that correlates with reading and language skills (MacDonald & Christiansen, 2002). This measure negatively correlated with activation in frontal, parietal, temporal, and occipito-temporal regions identified in two meta-analyses of studies comparing reading to rest (Fiez & Petersen, 1998; Turkeltaub, Eden, Jones, & Zeffiro, 2002).

Finally, Welcome and Joanisse (2012) attempted to isolate orthographic, phonological, and semantic components of the reading system by using a series of tasks that vary in the extent to which they engage these types of information, and also examined individual differences among their participants, who showed a range of reading proficiencies. Individual differences in functional magnetic resonance imaging (fMRI) activation related to reading