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Individual differences in white matter anatomy predict dissociable components of reading skill in adults☆

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ABSTRACT

We used diffusion tensor imaging (DTI) to investigate relationships between white matter anatomy and different reading subskills in typical-reading adults. A series of analytic approaches revealed that phonological decoding ability is associated with anatomical markers that do not relate to other reading-related cognitive abilities. Thus, individual differences in phonological decoding might relate to connectivity between a network of cortical regions, while skills like sight word reading might rely less strongly on integration across regions. Specifically, manually-drawn ROIs and probabilistic tractography revealed an association between the volume and integrity of white matter underlying primary auditory cortex and nonword reading ability. In a related finding, more extensive cross-hemispheric connections through the isthmus of the corpus callosum predicted better phonological decoding. Atlas-based white matter ROIs demonstrated that relationships with nonword reading were strongest in the inferior fronto-occipital fasciculus and uncinate fasciculus that connect occipital and anterior temporal cortex with inferior frontal cortex. In contrast, tract volume underlying the left angular gyrus was related to nonverbal IQ. Finally, connectivity underlying functional ROIs that are differentially active during phonological and semantic processing predicted nonword reading and reading comprehension, respectively. Together, these results provide important insights into how white matter anatomy may relate to both typical reading subskills, and perhaps a roadmap for understanding neural connectivity in individuals with reading impairments.

Introduction

Reading is a complex skill that requires integration of multiple cognitive abilities and processes, including visual perception, letter-sound knowledge, word meaning, and attention. Not surprisingly, neuropsychology has identified multiple brain regions subserving reading, presumably due to the different types of knowledge represented. Most recently, evidence has come from fMRI studies that have sought to identify how different cortical regions are associated with different subcomponents of reading processes. We and others have recently identified ways in which the engagement of cortical regions subserving reading can vary in the normal population of readers, and in a way that reflects individual differences in reading subskills (Clements-Stephens et al., 2012; Welcome and Joanisse, 2012). There is increasing interest in the gray matter sources of individual differences in reading (Welcome et al., 2011) as they permit us to better assess the contribution of specific neural subregions to specific cognitive subskills. However, questions remain about how individual differences in reading are linked to white matter tracts responsible for the coordination of these many cortical regions during reading.

It has long been hypothesized that efficient language processing relies on white matter pathways to connect distant cortical regions (Wernicke, 1874). This hypothesis has been supported by lesion data demonstrating that disconnections of language-relevant cortex can produce reading deficits even if the cortical regions themselves are spared (Dejerine, 1892). In the present study, we focus on reading ability in humans, an ability that critically relies on the ability to coordinate multiple brain regions supporting different sub-processes (Sandak et al., 2012). We have taken advantage of recent advances in diffusion tensor imaging (DTI) analyses to explore the hypothesis that individual differences in white matter pathway volume and integrity can predict component reading skills in typical-reading adults. DTI-weighted MRI scans permit the characterization of water diffusivity in the brain, and are thus well suited to characterizing the integrity of white matter tracts at a scale of 1–3 mm. We explored relationships between skill in different aspects of reading and white matter tracts identified using DTI in order to tease apart the roles of various white matter pathways in reading.

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Various white matter pathways have been associated with language both because of their anatomy and as consequences of lesions. While the focus of some studies has been spoken language, and others have focused on reading, there is reason to believe that linked mechanisms are engaged by both spoken language and written language. Specifically, both require phonological and semantic processing, two processes which appear to be subserved by partially distinct cortical networks. The pathway most frequently associated with language is the arcuate fasciculus (AF), which travels between the ventrolateral frontal lobe and superior/middle temporal regions, connecting classical Broca's and Wernicke's areas. It has been hypothesized that this pathway is involved with sensory-motor mapping of spoken language (Saur et al., 2008) and subcortical stimulation along the AF has been show to result in phonological disturbances (Duffau et al., 2002). Recent DTI work suggests that the AF can be divided into a direct pathway (traversing the whole path) and an indirect pathway in which separate portions travel between frontal and inferior parietal regions and between inferior parietal and temporal regions (Catani et al., 2005). Evidence from aphasic patients suggests that damage to the direct pathway results in difficulty processing phonological aspects of language, while damage to the indirect pathway results in difficulties with semantic aspects (Catani et al., 2005).

In addition to the AF, neuroimaging data suggest that other white matter pathways may also be involved in processing language, particularly word-based semantic memory (Duffau et al., 2005; Saur et al., 2008) and written word forms (Cohen and Dehaene, 2004). In a patient with acquired pure alexia as a result of surgery, the inferior longitudinal fasciculus degenerated while the AF remained intact (Epelbaum et al., 2008). This finding suggests that pathways other than the AF between occipital and temporal cortex are necessary for efficient reading. Anatomical alteration of the uncinate fasiculus, which connects the anterior temporal lobe with ventral frontal regions, has also been associated with difficulties in picture naming (Grossman et al., 2004; Lu et al., 2002). Finally, subcortical stimulation of the inferior fronto-occipital fasciculus, which passes through the temporal lobe, induced semantic paraphasias (Mandonnet et al., 2007).

Further, there is evidence that white matter anatomy is disrupted in children and adults with dyslexia. Adults with poor reading skills showed less fractional anisotropy (FA, an indicator of white matter coherence as measured by DTI) in bilateral temporo-parietal regions than typical readers (Klingberg et al., 2000). In adults with a history of reading and spelling difficulties, FA was reduced in bilateral fronto-temporal regions as well as a left temporo-parietal region (Steinbrink et al., 2008). When FA was examined within specific white matter ROIs, the posterior superior longitudinal fasciculus showed decreased FA in children with dyslexia (Carter et al., 2009), while FA within the arcuate fasciculus was negatively correlated with phonological awareness (Yeatman et al., 2011). A tract-based spatial statistics approach revealed broader reductions in bilateral white matter tracts in frontal, temporal, parietal, and occipital regions in adults with dyslexia (Richards et al., 2008).

One question that arises from prior findings of alterations in white matter anatomy in individuals with dyslexia is whether these differences in white matter anisotropy and/or coherence reflect the tail end of a normal distribution throughout the population, or are a marker of frankly atypical neural organization in dyslexia. Such a question motivates our current interest in individual differences within the population of normal-range readers. In this view, the language disruptions that come about as a result of lesions represent an extreme version of brain/behavior relationships that exist across the spectrum of language skill. Prior work supports the view that connectivity differences associated with dyslexia are mirrored by relationships between individual differences in reading and white matter microstructure. Word reading ability was positively correlated with FA in left temporo-parietal white matter in children (Beaulieu et al., 2005) and adults (Klingberg et al., 2000). In the ROI identified in adults by Klingberg et al., children showed relationships between FA and coherence and standardized measures of word reading, nonword reading, spelling, and rapid naming (Deutsch et al., 2005). Children with dyslexia whose reading improved over time showed greater FA in the right superior longitudinal fasciculus, suggesting that greater integrity of this right hemisphere pathway supported reading improvement (Hoeft et al., 2011). Similarly, FA in the left anterior centrum semiovale increased with improvement in phonological decoding as a result of reading remediation in 8–10 year old poor readers (Keller and Just, 2009).

While there appears to be consensus that left temporo-parietal white matter organization is related to general reading skill, the precise nature of this relationship remains unclear. While the majority of fibers in the temporo-parietal region identified by Klingberg et al. (2000) had an anterior–posterior orientation, and could thus be part of the arcuate fasciculus, other studies have noted that the majority of fibers in regions that show associations with reading have an inferior–superior orientation, consistent with the corona radiata (Beaulieu et al., 2005; Deutsch et al., 2005).

Given the multiple proposed roles of temporal lobe white matter pathways in reading, we investigated whether a clearer picture might emerge if we considered associations between anatomy and different subcomponents of reading skills separately. On this view, brain–behavior relationships might vary anatomically based on component reading skills, i.e., phonological decoding versus reading comprehension. Here, we explored relationships between white matter anatomy and speeded recognition of real words (sight word efficiency), speeded reading of nonwords (phonemic decoding efficiency), and reading comprehension. These measures were selected to tease apart various aspects of reading skill, and indeed show partially distinct relationships with patterns of brain activation (Welcome and Joanisse, 2012). As such, we explored whether associations with white matter microstructure were specific to these reading subskills. Our study also included a test of nonverbal IQ, which helped identify the extent to which apparent effects went beyond more general differences in global cognitive ability.

It is also apparent that the choice of method of measuring white matter anatomy can influence the nature of the results. Most studies of white matter involvement in reading have to date employed measures of FA and/or voxel-wise coherence using deterministic algorithms. However, there is also growing interest in a somewhat newer approach of probabilistic tractography, which examines the microstructural properties and connectivity of white matter within specific anatomical regions of interest. A challenge of imaging white matter tracts has been the concern that the size of these tracts is appreciably smaller than what can be imaged by conventional MRI scanners, yielding some indeterminacy in identifying the direction of individual fibers being imaged. Earlier work in tractography used deterministic algorithms that provided a “best guess” at fiber orientation. Probabilistic tractography provides some advantage by additionally deriving information regarding the confidence with which a pathway is identified (Dudink et al., 2008). Such algorithms are more resistant to noise as errant paths tend to not be repeated as often as legitimate paths (Behrens et al., 2007). A probabilistic approach also allows tracking of fibers nearer to areas of low anisotropy such as gray matter, rather than being restricted to regions in which fiber direction is more certain (Behrens et al., 2003b; Conturo et al., 1999). These differences may result in improved ability to track temporal lobe pathways. For instance, in one recent study, deterministic tractography identified the right arcuate fasciculus in 34/55 subjects, while probabilistic tractography identified this structure in every subject (Yeatman et al., 2011).

Probabilistic tractography requires the use of anatomical seed regions to serve as either originator and/or waypoint regions. One challenge to this approach is the optimal method for choosing these seed regions. To address this challenge, we used a variety of approaches, including manually-defined cortical ROIs, atlas-based white matter ROIs, and functionally-defined ROIs as seed regions for probabilistic tractography. Using multiple approaches allowed us to investigate the