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Structural properties of the ventral reading pathways are associated with morphological processing in adult English readers

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ABSTRACT

Morphological processing, the ability to extract information about word structure, is an essential component of reading. Functional MRI studies have identified several cortical regions involved in morphological processing, but the white matter pathways that support this skill remain unknown. Here, we examine the relationship between behavioral measures of morphological processing and microstructural properties of white matter pathways. Using diffusion MRI (dMRI), we identified the major ventral and dorsal reading pathways in a group of 45 adult English readers. The same participants completed a behavioral battery that included a morphological task and measures of phonological and orthographic processing. We found significant correlations between morphological processing skill and microstructural properties of the ventral, but not dorsal, pathways. These correlations were detected primarily in the left hemisphere, and remained significant after controlling for phonological or orthographic measures, suggesting some level of cognitive specificity. Morphological processing of written words thus appears to rely on ventral pathways, primarily in the left hemisphere. This finding supports the contribution of morphological processing to lexical access and comprehension of complex English words.

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1. Introduction

Reading is a complex human behavior which has become an essential skill in modern everyday life. It entails mapping between arbitrary visual symbols (written words) and their

corresponding sounds and meanings. For reading to be efficient, it requires the coordinated operation of several perceptual, cognitive and linguistic processes. According to some accounts, one of these processes is morphological processing, in which complex words are decomposed into basic

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components, called morphemes. Morphemes are meaningful letter strings that can be combined to create complex words (e.g., ‘play’ + ‘ful’ + ‘ly’). A common distinction is made between inflectional and derivational morphemes: Inflectional morphemes are added to the stem to modulate its syntactic features (e.g., tense, as in ‘played’, or person, as in ‘plays’), allowing it to agree with other words in the sentential context. Derivational morphemes, on the other hand, modulate the meaning of the stem to generate new meanings (e.g., replay, playful, player). Both inflectional and derivational morphemes typically modulate the stem in a consistent, predictable manner, thus providing valuable cues for mapping written word forms to their meaning (Rastle, Davis, Marslen-Wilson, & Tyler, 2000; Rastle, 2018).

Most theoretical models of reading, both modular and connectionist, fail to assign an explicit role to morphological processing (Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001; Harm & Seidenberg, 2004; Perry, Ziegler, & Zorzi, 2010; Plaut, McClelland, Seidenberg, & Patterson, 1996). However, accumulating behavioral evidence suggests that morphological processing plays an important part in skilled reading. For example, morphological awareness, the ability to recognize and manipulate morphemes within complex stimuli, has been repeatedly shown to predict reading skills in children (Carlisle, 2000; Deacon & Kirby, 2004; Kirby et al., 2012; McBride-Chang, Wagner, Muse, Chow, & Shu, 2005; Nagy, Berninger, & Abbott, 2006; Saiegh-Haddad & Geva, 2008; Siegel, 2008) as well as in adults (Law, Wouters, & Ghesquière, 2015; Tighe & Binder, 2015), even after controlling for other factors, such as phonological awareness. In addition, it has been suggested that morphological knowledge can be used by poor readers to overcome reading difficulties, so morphology may be used as a compensatory mechanism (Arnbak & Elbro, 2000; Casalis, Colé, & Sopo, 2004; Cavalli, Duncan, Elbro, El Ahmadi, & Colé, 2016; Elbro & Arnbak, 1996; Martin, Frauenfelder, & Colé, 2014). This notion is further supported by intervention studies showing that poor readers particularly benefit from morphological instruction (Bowers, Kirby, & Deacon, 2010; Goodwin & Ahn, 2010; Taha & Saiegh-Haddad, 2015). Despite this growing body of research, the neural underpinnings of morphological processing and its place within the broader pathways supporting reading in the brain remain poorly understood.

The neural pathways underlying skilled reading have been the focus of extensive research in recent years (Dehaene & Dehaene-Lambertz, 2016; Dehaene, 2009; Rueckl et al., 2015; Taylor, Rastle, & Davis, 2013; Wandell & Le, 2017; Wandell & Yeatman, 2013). Several functional neuroimaging studies contribute to the predominant view that skilled reading is supported by two complementary routes, the dorsal and ventral streams (Cohen, Dehaene, Vinckier, Jobert, & Montavont, 2008; Cummine et al., 2015; Dehaene, 2009; Jobard, Crivello, & Tzourio-Mazoyer, 2003; Taylor et al., 2013). The dorsal reading stream is thought to support phonological processing and the conversion of print to sound (e.g., Booth et al., 2002; Hickok & Poeppel, 2007; Saur et al., 2008; Taylor, Rastle, & Davis, 2014), while the ventral reading stream comprises regions involved in the visual analysis of written words (Ben-Shachar, Dougherty, Deutsch, & Wandell, 2011; Binder, Medler, Westbury, Liebenthal, & Buchanan, 2006;

Glezer, Jiang, & Riesenhuber, 2009; McCandliss, Cohen, & Dehaene, 2003; Vinckier et al., 2007) as well as access to meaning (Binney, Embleton, Jefferies, Parker, & Lambon Ralph, 2010; Carlson, Simmons, Kriegeskorte, & Slevc, 2014; Pugh et al., 2000; Visser, Jefferies, & Lambon Ralph, 2010; Visser, Jefferies, Embleton, & Lambon Ralph, 2012). This dual-stream model of reading is further supported by diffusion MRI studies, linking microstructural properties of the dorsal reading pathways to phonological processing (Saygin et al., 2013; Vanderauwera, Vandermosten, Dell’Acqua, Wouters, & Ghesquière, 2015; Yeatman et al., 2011) while the ventral white matter pathways are associated with semantic processing and lexical access (Cummine et al., 2015; Harvey & Schnur, 2015; Nugiel, Alm, & Olson, 2016). It is yet unclear how morphological processing fits into this dual-stream view of the reading pathways.

A small body of literature addressed the cortical regions involved in morphological processing of written words. Several magnetoencephalography (MEG) studies implicate the left ventral reading pathways in morphological processing of written words. These studies report early (M170) morphological effects originating in left ventral occipitotemporal cortex (Lehtonen, Monahan, & Poeppel, 2011; Lewis, Solomyak, & Marantz, 2011; Solomyak & Marantz, 2010), as well as a later morphological component (M350), associated with the left middle temporal gyrus (MTG) (Fruchter & Marantz, 2015; Pylkkänen, Feintuch, Hopkins, & Marantz, 2004) or inferior temporal gyrus (ITG) (Cavalli, Colé, Badier, Zielinski, Chanoine, & Ziegler, 2016). Further support for ventral stream involvement in morphological processing is provided by functional MRI studies employing visual masked priming. These studies reveal effects of morphological priming in ventral regions, in particular the anterior middle occipital gyrus (A-MOG), fusiform gyrus and MTG (Devlin, Jamison, Matthews, & Gonnerman, 2004; Gold & Rastle, 2007). The functional evidence thus suggests engagement of regions along the ventral reading pathways in morphological processing, in alignment with the view that morphological knowledge is primarily a ventral capacity (Rastle, 2018).

To date, direct evidence for the involvement of a specific set of white matter tracts in morphological processing is lacking. White matter fiber tracts support information transfer from one cortical region to another, hence their properties and organization are of great importance for cognitive processes that require integration of multilevel information from distant regions. For example, reading related skills are associated with white matter microstructure, both in dorsal (Saygin et al., 2013; Yeatman et al., 2011) and in ventral reading pathways (Cummine et al., 2015; Horowitz-Kraus, Wang, Plante, & Holland, 2014). The goal of the current study was to identify the white matter pathways associated with morphological processing abilities in typical adult English readers, and examine the extent of functional specificity in these pathways. To this end, we identified major dorsal and ventral fiber tracts using diffusion MRI (dMRI), and examined the associations between their structural properties and a behavioral measure of morphological sensitivity. Based on the theoretical considerations discussed above and prior functional findings, we hypothesized that morphological processing relies on ventral stream connectivity. Therefore, we

expect behavioral measures of morphological processing to correlate with properties of the ventral reading pathways.

To date, most studies of the reading pathways were conducted in developmental populations (Beaulieu et al., 2005; Broce, Bernal, Altman, Tremblay, & Dick, 2015; Niogi & McCandliss, 2006; Saygin et al., 2013; Travis, Adams, Kovachy, Ben-Shachar, & Feldman, 2016; Travis, Ben-Shachar, Myall, & Feldman, 2016; Travis, Leitner, Feldman, & Ben-Shachar, 2015; Vanderauwera et al., 2015; Yeatman et al., 2011; Yeatman, Dougherty, Ben-Shachar, & Wandell, 2012) or clinical populations (Harvey & Schnur, 2015; Harvey, Wei, Ellmore, Hamilton, & Schnur, 2013; Klingberg et al., 2000; Vandermosten et al., 2012). By nature, these populations provide a large range of cognitive abilities, thus facilitating the detection of associations with measures of white matter microstructure. To the best of our knowledge, only three studies report associations between white matter structure and reading skills in typical adults (Cummine et al., 2015; Welcome & Joanisse, 2014) or adolescents (Horowitz-Kraus et al., 2014). The paucity of findings in the healthy adult population may stem from the fact that healthy adults often perform at ceiling in standardized reading tasks. Low behavioral variability poses a major challenge in studying neuro-behavioral associations in the typical population.

To overcome this difficulty, we sought a sensitive and robust morphological paradigm that provides considerable variability even in adult skilled readers. We capitalized on the morpheme interference effect (MIE), a well-established behavioral phenomenon that yields highly variable performance in typical adults (Crepaldi, Rastle, & Davis, 2010; Dawson, Rastle, & Ricketts, 2017; Taft & Forster, 1975). In this task, participants perform lexical decisions on pseudowords that comprise a real stem, and either a real suffix (e.g., *towerly*) or a non-morphological ending (e.g., *towerla*). Participants who rely more heavily on their morphological knowledge typically make more errors and respond slower to pseudowords that incorporate a real suffix. The effect is quantified as the difference in performance between the suffixed and control conditions. Higher MIE thus reflects stronger reliance on morphological knowledge in visual word recognition. While this paradigm focuses on the responses to pseudowords, the standard interpretation is that the real morphemes (embedded within the pseudowords) elicit morpheme recognition and subsequent access to the lexicon (Dawson et al., 2017). Thus, lexical access is critically involved in this task, regardless of the non-lexical status of the stimuli.

In the current study, healthy adult English readers completed the MIE task as well as dMRI scans (in separate sessions). We identified major white matter tracts within the dorsal and ventral streams in each participant and extracted their microstructural properties. We next tested whether these properties correlate with morphological processing skills, as quantified by the MIE task. In line with the proposal that morphological knowledge supports efficient access to meaning (e.g., Rastle, this volume), we hypothesized that MIE scores correlate specifically with white matter tracts along the ventral, print-to-meaning, reading stream. Specificity of the associations is assessed via partial correlations, controlling for measures of phonological and orthographic processing.

2. Methods

2.1. Participants

49 English speaking adults participated in this study (mean age 21.27 ± 2.38 years, age range 19–35, 9 males). Participants were right handed and without any history of diagnosed learning disabilities or neurological conditions. Participants were paid for their time and travel expenses. The research was approved by the Ethics Committee of Royal Holloway, University of London, and all participants signed a written informed consent before participating.

2.2. Behavioral assessment

Participants were recruited as part of a larger research project (Taylor, Davis, & Rastle, 2017) which included extensive behavioral assessment and MRI scans, conducted in separate sessions. In addition to the MIE task (see below), we included in the current analysis two standardized tests that tap into separate components of skilled reading: decoding and fluency (for details see section 2.2.2). Additional background measures are reported in [Supplementary Table 2](#). The behavioral assessment took place in a quiet room and lasted approximately 1 h.

2.2.1. MIE task

Participants completed a lexical decision task that included 60 suffixed pseudowords (e.g., *towerly*), 60 pairwise-matched control pseudowords with a non-morphological ending (e.g., *towerla*), and 120 real words. The pseudoword stimuli constitute two conditions from Crepaldi et al. (2010), Experiment 1, excluding 4 stimulus pairs, such that participants were presented with the same number of words and pseudowords (the full list of stimuli is provided in Crepaldi et al., Appendix A). Suffixed and control pseudowords were carefully matched on measures of orthographic similarity to real words, including Coltheart's N (i.e., the number of real word neighbors that differ from the target string by a single letter substitution; Coltheart et al., 1977), and orthographic Levenshtein distance to the nearest real word neighbor (Yarkoni, Balota, & Yap, 2008).

The task began with 8 practice trials. Each trial started with a fixation cross presented at the center of the screen for 500 msec, followed by the target string on which the participant had to make a lexical decision. The target string remained on the screen until the participant issued a response or until a timeout of 2500 msec has elapsed. There was a 500 msec interstimulus interval between trials. Stimulus presentation and response collection were controlled by DMDX software (Forster & Forster, 2003). A two-button response box was used to record participants' lexical decisions. Participants were instructed to press the right button if the target string was a real word and the left button if it was a pseudoword. Stimulus presentation order was randomized by DMDX without any constraints.

Our variable of interest, morphemic cost, was defined as the difference in performance (accuracy or RT) between suffixed and control pseudowords. For each participant, accuracy

cost (henceforth MIE-Acc) was calculated by subtracting the percentage of correct responses to suffixed pseudowords from the percentage of correct responses to control pseudowords. Similarly, raw RT cost was calculated by subtracting the mean RT for control pseudowords from that of the suffixed pseudowords. When calculating mean RT for each condition, only item pairs that incurred an accurate response for both items were taken into account. Raw RT cost was then normalized by the participant's overall RT (where overall RT is the mean RT across all correct responses). Dividing by the overall RT accounted for individual differences in response speed (see [Supplementary Table S1](#)). Thus, the term MIE-RT refers henceforth to the difference between the RT to suffixed and control pseudowords, divided by the overall RT.

2.2.2. Additional reading and phonological measures

Participants completed the nonword repetition subtest from the Comprehensive Test of Phonological Processing (CTOPP2), which includes 30 items, gradually increasing in length ([Wagner, Torgesen, & Rashotte, 1999](#)). Responses were scored by two independent raters. The inter-rater agreement, measured by the correlation across participants, was .66. On average, raters disagreed on 2.37 items per participant. To resolve these disagreements, one rater listened to the responses again and made a decision as to which rating was correct. In addition, participants completed the TOWRE sight word efficiency test, which assesses the number of words participants can read aloud in 45 sec (total number of words in the list = 108) ([Torgesen, Rashotte, & Wagner, 1999](#)). For both tests, the final scores were scaled according to the norms of the appropriate age group (17–24 years).

2.3. MRI data acquisition

Magnetic Resonance Imaging (MRI) data were collected using a 3T Siemens Trio scanner (Siemens Medical Systems, Erlangen, Germany), with a 32-channel head coil. A standard dMRI protocol was applied by means of a single-shot spin-echo diffusion-weighted echo-planar imaging sequence (63 axial slices, each 2 mm thick, no gap; FOV = 192 mm, image matrix size = 128 × 128 providing a cubic resolution of ~2 × 2 × 2 mm). 64 diffusion-weighted volumes ($b = 1000 \text{ sec/mm}^2$) and one reference volume ($b = 0 \text{ sec/mm}^2$) were acquired using a standard diffusion direction matrix. Total scan time for the dMRI sequence was 8:52 min.

High resolution T1-weighted anatomical images were also acquired for each participant using a magnetization prepared rapid acquisition gradient echo (MPRAGE) protocol (TR = 2,250 msec, TE = 2.99 msec, flip angle = 9°, 1 mm thick slices, 256 × 240 × 192 matrix, voxel size: 1 × 1 × 1 mm).

2.4. Data analysis

2.4.1. MRI preprocessing

Data preprocessing was conducted using 'mrDiffusion', an open source package (<http://web.stanford.edu/group/vista/cgi-bin/wiki/index.php/MrDiffusion>) and Matlab 2012b (The Mathworks, Nattick, MA).

As a first step, T1 images were aligned to the anterior commissure–posterior commissure (AC-PC) orientation.

Diffusion weighted images were corrected for eddy-current distortions and head motion ([Rohde, Barnett, Basser, Marengo, & Pierpaoli, 2004](#)). Diffusion weighted volumes were registered to the non-diffusion weighted (b_0) volume, which was registered to the T1 image using a rigid body mutual information maximization algorithm (implemented in SPM8; [Friston & Ashburner, 2004](#)). Then, the combined transform resulting from motion correction, eddy-current correction and anatomical alignment was applied to the raw diffusion data once. Next, the table of gradient directions was appropriately adjusted to fit the resampled diffusion data ([Leemans & Jones, 2009](#)). The raw diffusion data was then fitted with the tensor model using a standard least-squares algorithm. Four maps were calculated based on the estimated eigenvalues ($\lambda_1, \lambda_2, \lambda_3$) of the tensor in each voxel: Fractional anisotropy (FA) was calculated as the normalized standard deviation of the eigenvalues ([Basser & Pierpaoli, 1996](#)); Mean diffusivity (MD) was calculated as the average of all three eigenvalues; Axial diffusivity (AD) and radial diffusivity (RD) were calculated as the diffusivity along the principal axis (λ_1), and as the average diffusivity along the two secondary axes (λ_2, λ_3), respectively.

2.4.2. Tract identification and segmentation

Our analysis approach used tractography in the native space of each participant for individual tract identification, followed by diffusivity value extraction along each tract and correlation evaluation between diffusivity values and cognitive measures of the same participants. In line with the dual stream framework, we focused on three ventral and two dorsal-stream tracts. Ventrally, we identified the inferior fronto-occipital fasciculus (IFOF), the inferior longitudinal fasciculus (ILF), and the uncinate fasciculus (UF), all previously implicated in the ventral semantic system ([Harvey & Schnur, 2015; Mehta et al., 2016; Moritz-Gasser, Herbet, & Duffau, 2013](#)). Dorsally, we identified the fronto-temporal and fronto-parietal segments of the arcuate fasciculus (AF_{ft} and AF_{fp} , respectively), previously associated with decoding and phonological processing ([Horowitz-Kraus et al., 2014; Vandermosten et al., 2012; Yeatman et al., 2011; Yeatman, Dougherty, Ben-Shachar, et al., 2012; Yeatman, Dougherty, Myall, Wandell, & Feldman, 2012](#)). For each participant, the 5 tracts were segmented bilaterally.

In order to segment these tracts and quantify their diffusion parameters, we used the Automatic Fiber Quantification ('AFQ') package ([Yeatman, Dougherty, Myall, et al., 2012](#)). AFQ consists of the following steps: (1) Whole brain fiber tractography, (2) Tract segmentation based on template defined regions of interest (ROIs) warped to individual brains, and automatic cleaning of fiber outliers, and (3) Quantification of diffusion properties along each tract. Whole brain tracking (step 1) was initialized from a whole brain white matter mask ($FA > .2$), using deterministic Streamlines Tractography (STT), with a 4th-order Runge–Kutta path integration method and 1 mm step size ([Basser, Pajevic, Pierpaoli, Duda, & Aldroubi, 2000; Mori, Crain, Chacko, & Van Zijl, 1999; Press, Teukolsky, Vetterling, & Flannery, 2002](#)). Stopping criteria for the tracking algorithm were defined as $FA < .2$ or an angle greater than 30° between the last and the next step direction.

Minimum and maximum streamline length were set to 20 mm and 250 mm, respectively.

Tract segmentation (step 2) was achieved using a two-waypoint ROI procedure as defined by [Wakana et al. \(2007\)](#). First, an estimated non-linear transformation was applied to automatically warp predefined ROIs from the Montreal Neurological Institute (MNI) T2 template into each individual's native space. Then, streamlines tracked from the entire brain (step 1) were intersected with the individual ROIs, using logical AND operations, to identify the streamlines that pass through both ROIs. The resulting tract was cleaned automatically, using a statistical outlier rejection algorithm that removed streamlines that were at least 4 standard deviations longer than the mean tract length, or that deviate by more than 5 standard deviations in distance from the core of the tract. This process was repeated 5 times (see [Yeatman, Dougherty, Myall, et al. \(2012\)](#) for details regarding the automatic segmentation method).

Individual tracts were visually inspected using Quench, an interactive 3D visualization tool ([Akers, 2006](#)); (<http://web.stanford.edu/group/vista/cgi-bin/wiki/index.php/QUENCH>). Visual inspection revealed that the automatically cleaned AF_{fp} still contained streamlines that did not fit the tract definition. These were cleaned manually following [Tsang, Dougherty, Deutsch, Wandell, and Ben-Shachar \(2009\)](#).

Lastly, diffusion properties were quantified for all resulting tracts (step 3). Diffusion properties were calculated at 100 equidistant nodes along the central portion of each tract. While tract endpoints may vary greatly across individuals, the portion of the tract enclosed by the ROIs is highly consistent. Therefore, we restricted the analysis of diffusion properties to the core of each tract (in between the two ROIs), with the exception of the UF. For the UF, restricting the analyses to the segment enclosed by the ROIs overlooks the entire frontal portion of the tract. Therefore, we extracted diffusivity measures along the entire trajectory of the UF (ROI placement for each tract is demonstrated in [Supplementary Figure S1](#)). The resulting FA and MD profiles extracted from each tract were subject to further statistical analyses as described below.

2.4.3. Brain-behavior correlation analyses

As a first step, we tested whether the average diffusion properties of each tract were correlated with morphemic cost. For each tract, diffusion parameters (FA and MD) were averaged across the nodes, to obtain mean tract-FA and mean tract-MD scores for each individual. We then calculated Spearman's correlations between these measurements and morphemic cost (both MIE-Acc and MIE-RT). Next, to improve specificity, we calculated Spearman's correlation coefficients between morphemic cost and FA (or MD) in each node along the tract profile. Spearman's correlation was used because the distribution of morphemic cost did not pass the normality criterion (as indicated by a Kolmogorov–Smirnov test). Significance was corrected for 100 comparisons using a nonparametric permutation method, yielding a family-wise error (FWE) corrected alpha value of .05 ([Nichols & Holmes, 2003](#)). Across the tracts, we controlled the false discovery rate (FDR) at a level of 5% ([Benjamini & Hochberg, 1995](#)).

Importantly, neither FA nor MD directly map onto a single biological property, and their values are affected by a

multitude of factors, like axonal diameter, axonal density, myelination and tissue architecture ([Assaf & Pasternak, 2008](#)). Some of these factors affect FA in opposing directions. For example, elevated myelin content, which contributes to reliable and timely transmission of neuronal signals, leads to increased FA values, because myelin hinders inter-cellular diffusivity. On the other hand, thicker axons, which contribute to faster transmission speed, lead to decreased FA values. Previous literature reports both positive and negative correlations between FA and reading related skills (e.g., [Frye et al., 2011](#); [Arrington, Kulesz, Juranek, Cirino, & Fletcher, 2017](#); [Welcome & Joanisse, 2014](#); [Yeatman, Dougherty, Ben-Shachar, et al., 2012](#); [Yeatman, Dougherty, Myall, et al., 2012](#)). It is thus difficult to predict in advance the expected direction (positive/negative) of correlations between morphemic cost and FA or MD. To interpret the direction of the observed associations post-hoc, we further extracted axial diffusivity (AD) and radial diffusivity (RD) values from clusters that showed significant correlations with morphemic cost. We then calculated Spearman's correlations between morphemic cost and mean AD or mean RD in each cluster. AD and RD are still modulated by several factors, but they help draw a fuller picture of the data and propose potential linking hypotheses to the underlying biological structure.

Lastly, to test the specificity of the associations found with morphemic cost, we followed up on significant correlations by calculating partial correlations. Within each significant cluster, we calculated the correlation between morphemic cost and FA (or MD), while controlling for phonological memory or for sight word efficiency (see section 2.2.2 for the definition of these measures).

3. Results

Three participants failed to reach the accuracy criterion (at least 85% correct responses) on the MIE task, and were subsequently removed from further analyses. An additional subject was an outlier in terms of age (5 standard deviations older than the sample's mean age), and showed extreme mean tract-MD values in 3 of the tracts of interest. We therefore excluded this subject from analysis as well. The results are reported for the remaining 45 participants (mean age 20.98 ± 1.37 years, age range 19–25, 8 males).

3.1. Behavioral results

Participants performed the lexical decision task at a high level of accuracy ($94 \pm 2.8\%$, range 87–99%). To assess individual variability in the sensitivity to morphological structure, we calculated morphemic cost as the difference in performance between the suffixed and control pseudoword conditions, both in terms of accuracy (MIE-Acc) and RT (raw MIE-RT). Large individual variability was observed in both measures of morphemic cost (MIE-Acc: $9.89 \pm 5.5\%$, range 0–26%; raw MIE-RT: 82 ± 58 msec, range –43–232 msec; see [Supplementary Table S2](#)). Importantly, MIE-Acc was not correlated with participants' overall speed (mean RT on all correct responses) in the lexical decision task ($r = -.01$, n.s.), ruling out alternative interpretation of the MIE as reflecting a

general speed-accuracy trade off. In contrast, raw MIE-RT was strongly correlated with overall speed ($r = .51, p < .005$), probably because slower responders show longer reaction times in all conditions, allowing for greater differences to emerge between the conditions. To account for variability in overall response speed, we normalized individual's raw MIE-RT measure by dividing it by the participant's mean RT, averaged across all correct responses (to words and pseudo-words alike). This normalized measure (henceforth MIE-RT: $.11 \pm .07$, range $-.07-.28$) was used for subsequent correlation analyses, after excluding negative MIE-RT scores ($N = 3$). Measures of morphemic cost (MIE-Acc, MIE-RT) did not show any significant correlation with other measures collected in the behavioral battery (see [Supplementary Table S3](#)). This suggests that the MIE taps into a unique component of reading.

3.2. Associations between morphemic cost and FA

[Fig. 1](#) depicts the ten tracts of interest in a sample subject. The tracts were successfully detected in nearly all participants, with few exceptions (the right IFOF could not be traced in one participant, the right AFft in five participants, and the left AFfp in 2 participants). As a first step, we assessed the associations between mean tract-FA (see section 2.4.3) and morphemic cost, but no significant correlation was detected. Previous studies have shown that diffusion properties, and FA in particular, vary considerably along the major cerebral tracts ([Yeatman et al., 2011](#)). Estimating diffusion profiles along the tracts provides enhanced sensitivity for detecting localized brain-behavior correlations, which go beyond mean tract-FA or tract-MD values. Thus, we examined the associations between local FA values along the trajectory of each tract and morphemic cost.

Indeed, significant correlations with local FA values were detected along bilateral ventral tracts. Specifically, MIE-Acc was negatively correlated with local FA values in clusters within the IFOF, bilaterally (FWE corrected for 100 comparisons along the tract; see [Fig. 2](#) and [Table 1](#)). The location of the significant clusters along the tracts is visualized in [Fig. 2](#) (panels a, c). The distribution of individual values and the

pattern of covariation between MIE-Acc scores and FA values extracted from significant clusters is visualized in panels b and d of this Figure. The correlations between mean cluster-FA and MIE-Acc remained statistically significant after controlling FDR at $q < .05$ across the tracts. The correlations also remained significant after controlling for mean tract-FA of the homologous tract. No significant correlations were found between FA and MIE-RT in any of the analyzed tracts, when controlling the familywise error (for 100 nodes within tract) at $p < .05$.

3.3. Associations between morphemic cost and MD

The analysis of associations between MD and morphemic cost revealed a similar pattern of results. First, and similarly to the analysis of mean tract-FA, no significant correlations were detected between mean tract-MD and morphemic cost. However, an analysis of Spearman's correlations along the trajectory of each tract revealed several significant clusters along the ventral (but not dorsal) tracts (see [Tables 1 and 2](#)). Specifically, MIE-Acc was positively correlated with MD in clusters within the left UF and left ILF. [Fig. 3](#) depicts the location of the significant clusters along the tracts (panels a, c), and the pattern of covariation between MIE-Acc scores and MD values extracted from the significant clusters. Correlations between mean cluster-MD and MIE-Acc remained statistically significant after controlling FDR across the tracts at $q < .05$. In addition, MD was also correlated with MIE-RT in clusters within the left ILF and UF (bilaterally). [Fig. 4](#) depicts the location of the significant clusters along the tracts (panels a, c, e), and the pattern of covariation between MIE-RT scores and MD values extracted from the significant clusters. Correlations between mean cluster-MD and MIE-RT remained statistically significant after controlling the FDR across the tracts at $q < .05$. In sum, morphemic cost was positively correlated with MD in several clusters within the ventral tracts, primarily in the left hemisphere.

3.4. Post hoc correlations with AD and RD

To further investigate the source of the correlations between morphemic cost and measures of white matter

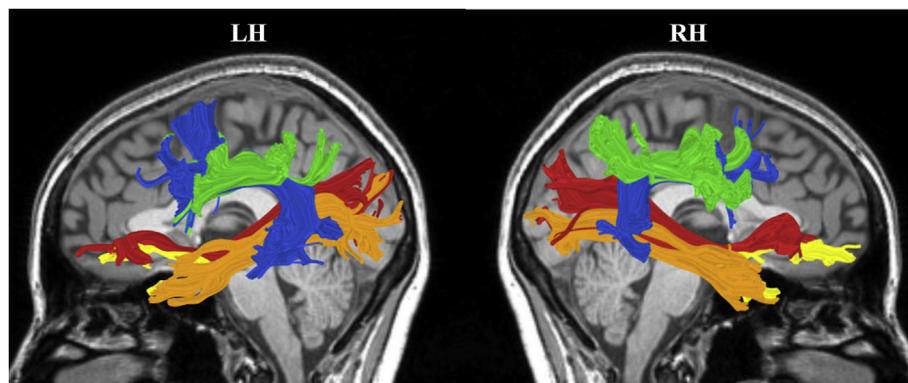


Fig. 1 – Dorsal and ventral tracts of interest. Shown are the bilateral tracts identified in a single subject (female, 20), overlaid on a midsagittal T1 image. The dorsal tracts identified are the fronto-temporal (blue) and fronto-parietal (green) segments of the arcuate fasciculus. The ventral tracts identified are the inferior longitudinal fasciculus (orange), the inferior fronto-occipital fasciculus (red) and the uncinate fasciculus (yellow). LH- left hemisphere, RH- right hemisphere.

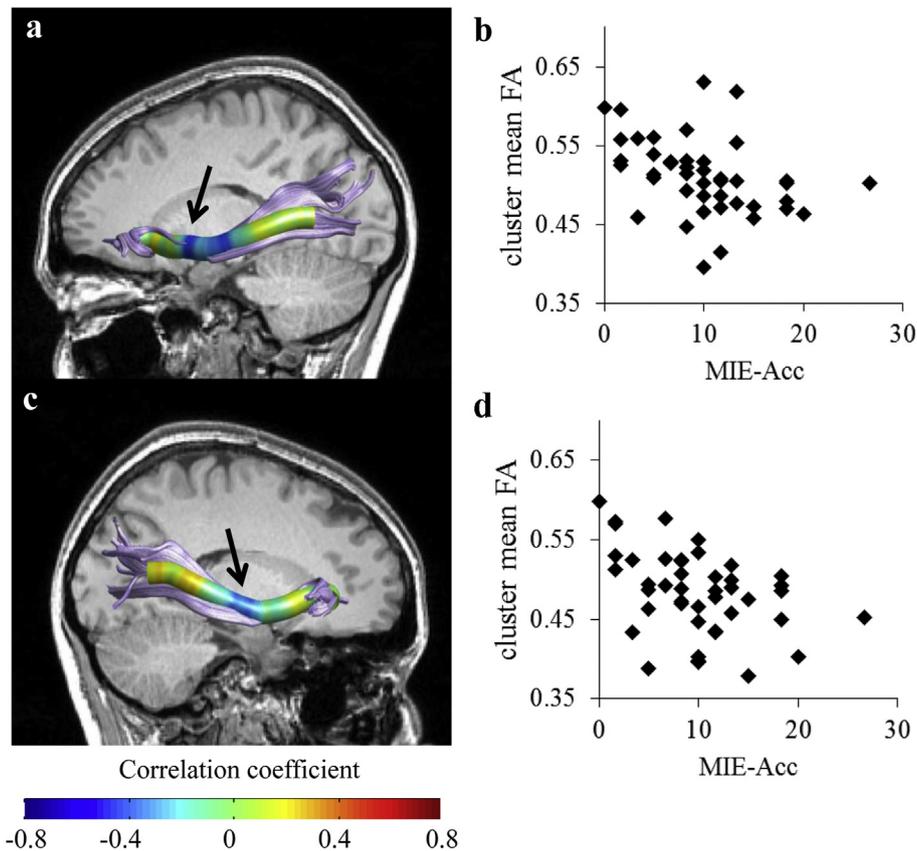


Fig. 2 – Morphemic cost (MIE-Acc) is negatively correlated with FA in IFOF clusters, bilaterally. (a, c) Spearman's correlation coefficients ($N = 45$) are visualized in 100 nodes along the left IFOF (a) and right IFOF (c). Black arrows denote the location of significant clusters after family-wise error correction across the 100 nodes (left IFOF: nodes 42–58; right IFOF: nodes 46–60). (b, d) Scatter plots showing the association between MIE-Acc (as defined in the results text) and the mean FA in the significant cluster of nodes, in left IFOF (b) and right IFOF (d). These scatter plots are shown for visualization purposes, significance is calculated along the trajectory of the tracts. IFOF- inferior fronto-occipital fasciculus.

microstructure, we examined, separately, the pattern of association between morphemic cost and each diffusivity sub-component: AD and RD. In the clusters that showed significant correlations with FA, we found significant positive correlations between MIE-Acc and mean cluster RD, not with

AD (see Fig. 5, Table 1). The clusters that showed significant correlations with MD exhibit a more complex picture, such that some of the MD correlations were explained by RD associations and other by AD (see Fig. 6, Table 1 for MIE-Acc clusters and Fig. 7, Table 2 for MIE-RT clusters).

Table 1 – Clusters in ventral tracts show significant Spearman's correlations with MIE-Acc.

White matter tract	location of significant cluster	rs	95% CI	AD rs	RD rs	partial correlations	
						NWrep rs	SWE rs
FA clusters							
Left IFOF	42–58	-.50**	[-.7, -.22]	-.26	.43**	-.51*§	-.52*§
Right IFOF	46–60	-.42**	[-.65, -.12]	-.27	.34*	-.42*§	-.41*§
MD clusters							
Left ILF	30–44	.45**	[.14, 0.66]	.21	.37*	.44*§	.46*§
Left UF	21–42	.46**	[.15, 0.68]	.14	.48**	.46*§	.47*§

NWrep- CToPP nonword repetition subtest scaled scores. SWE- TOWRE sight word efficiency scaled scores. * $p < .05$, FDR corrected for 4 clusters; ** $p < .01$, FDR corrected for 4 clusters; *§ $p < .01$, FDR corrected for 8 comparisons (4 clusters*2 behavioral variables).

Table 2 – Clusters in ventral tracts show significant Spearman's correlations with MIE-RT.

White matter tract	location of significant cluster	rs	95% CI	AD rs	RD rs	partial correlations	
						NWrep rs	SWE rs
MD clusters							
Left ILF	11–25	.45**	[.14, .67]	.26	.44**	.44*§	.43*§
Left UF	76–94	.38*	[.05, .63]	.51**	.25	.41*§	.38*§
Right UF	7–24	.41**	[.09, .65]	.35*	.38*	.41*§	.39*§

NWrep- CToPP nonword repetition subtest scaled scores. SWE- TOWRE sight word efficiency scaled scores. * $p < .05$, FDR corrected for 3 clusters; ** $p < .01$, FDR corrected for 3 clusters; *§ $p < .05$, FDR corrected for 6 comparisons (3 clusters*2 behavioral variables).

3.5. Specificity of correlations with morphemic cost

To test the level of cognitive specificity of the associations reported so far, we repeated the same correlation analyses (between morphemic cost and FA or MD) while controlling for individual performance on the CToPP nonword repetition subtest, a common index of phonological memory. In a separate analysis, we partialled out participants' scores on the sight word efficiency subtest (TOWRE), a timed measure of

reading aloud. We selected these control measures a-priori, before conducting the association analyses with any diffusivity measures, because these cognitive measures assess well known components of reading, and yield sufficient variability in the current adult sample (see [Supplementary Table S1](#)). The correlations between FA and MIE-Acc remained significant after controlling for either of these measures, both in the left and right IFOF. The same was true for the correlations between MD and MIE-Acc, both in the left ILF and in the left UF.

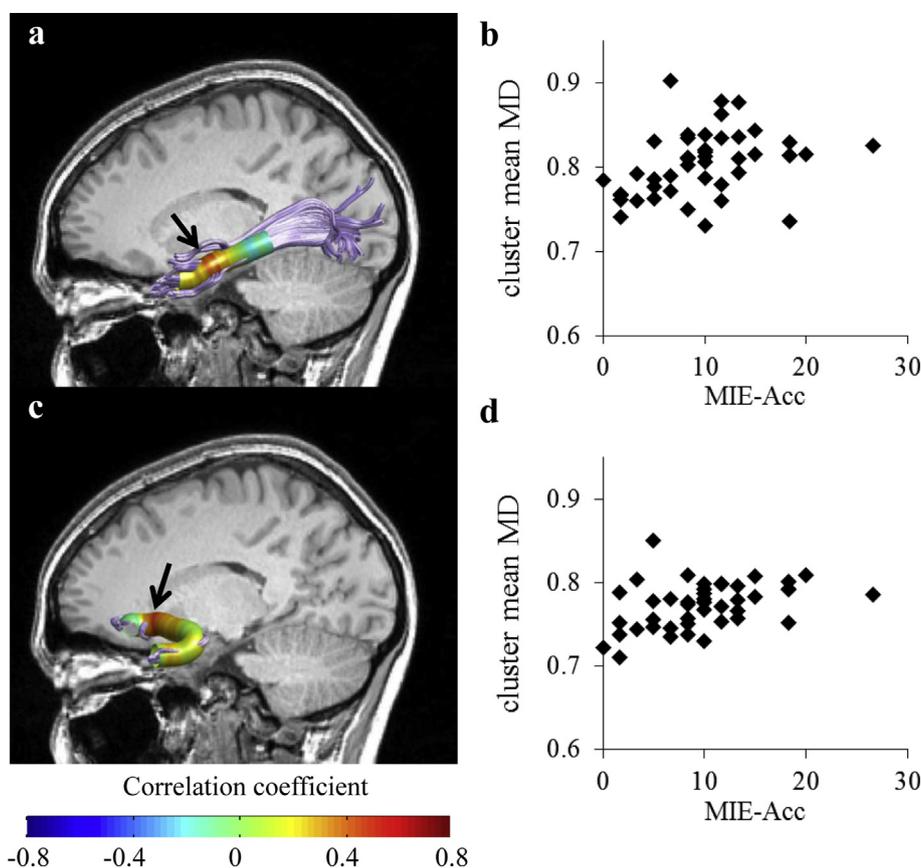


Fig. 3 – Morphemic cost (MIE-Acc) is positively correlated with MD in left ILF and UF clusters. (a, c) Spearman's correlation coefficients (N = 45) are visualized in 100 nodes along the left ILF (a) and left UF (c). Black arrows denote the location of significant clusters after family-wise error correction across the 100 nodes (left ILF: Nodes 30–44; left UF: Nodes 21–42). (b, d) Scatter plots showing the association between MIE-Acc (as defined in the results text) and the mean MD in the significant cluster of nodes, in left ILF (b) and left UF (d). These scatter plots are shown for visualization purposes, significance is calculated along the trajectory of the tracts. ILF- inferior longitudinal fasciculus. UF- Uncinate Fasciculus.

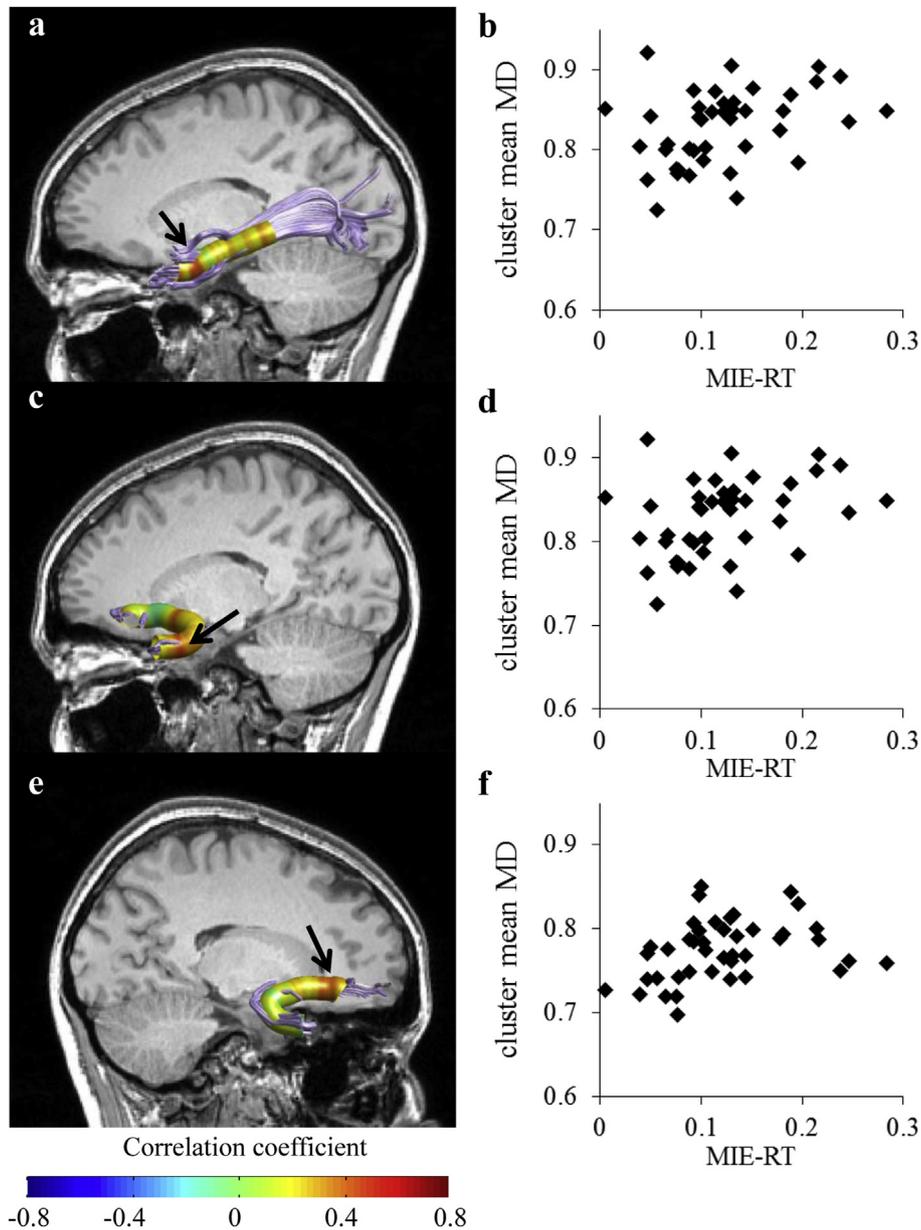


Fig. 4 – Morphemic cost (MIE-RT) is positively correlated with MD in left ILF and bilateral UF clusters. (a, c, e) Spearman's correlation coefficients ($N = 42$) are visualized in 100 nodes along the left ILF (a), left UF (c) and right UF (e). Black arrows denote the location of significant clusters after family-wise error correction across the 100 nodes (left ILF: Nodes 11–25; left UF: Nodes 76–94; right UF: Nodes 7–24). (b, d, f) Scatter plots showing the association between MIE-RT (as defined in the results text) and the mean MD in the significant cluster of nodes, in left ILF (b), left UF (d) and right UF (f). These scatter plots are shown for visualization purposes, significance is calculated along the trajectory of the tracts. ILF- inferior longitudinal fasciculus. UF- Uncinate Fasciculus.

These partial correlations are reported in Table 1, and are visualized as scatter plots in Supplementary Figures S2-S3. All partial correlations with MIE-Acc were significant at a level of $q < .01$, FDR corrected for 8 comparisons (4 clusters * 2 behavioral measures). The significant clusters between MIE-RT and MD also remained significant after controlling for these measures (see Table 2 and Supplementary Figure S4). All partial correlations with MIE-RT were significant at a level of $q < .05$, FDR corrected for 6 comparisons (3 clusters * 2 behavioral measures).

4. Discussion

The aim of the current study was to shed light on the white matter underpinnings of morphological processing in typical adult readers. Correlations were found between morphological processing, quantified by the MIE task, and diffusivity measures within major fiber tracts that belong to the ventral reading stream: the IFOF (bilaterally), UF (bilaterally), and left ILF. Within the dual-stream model of reading, as well as in

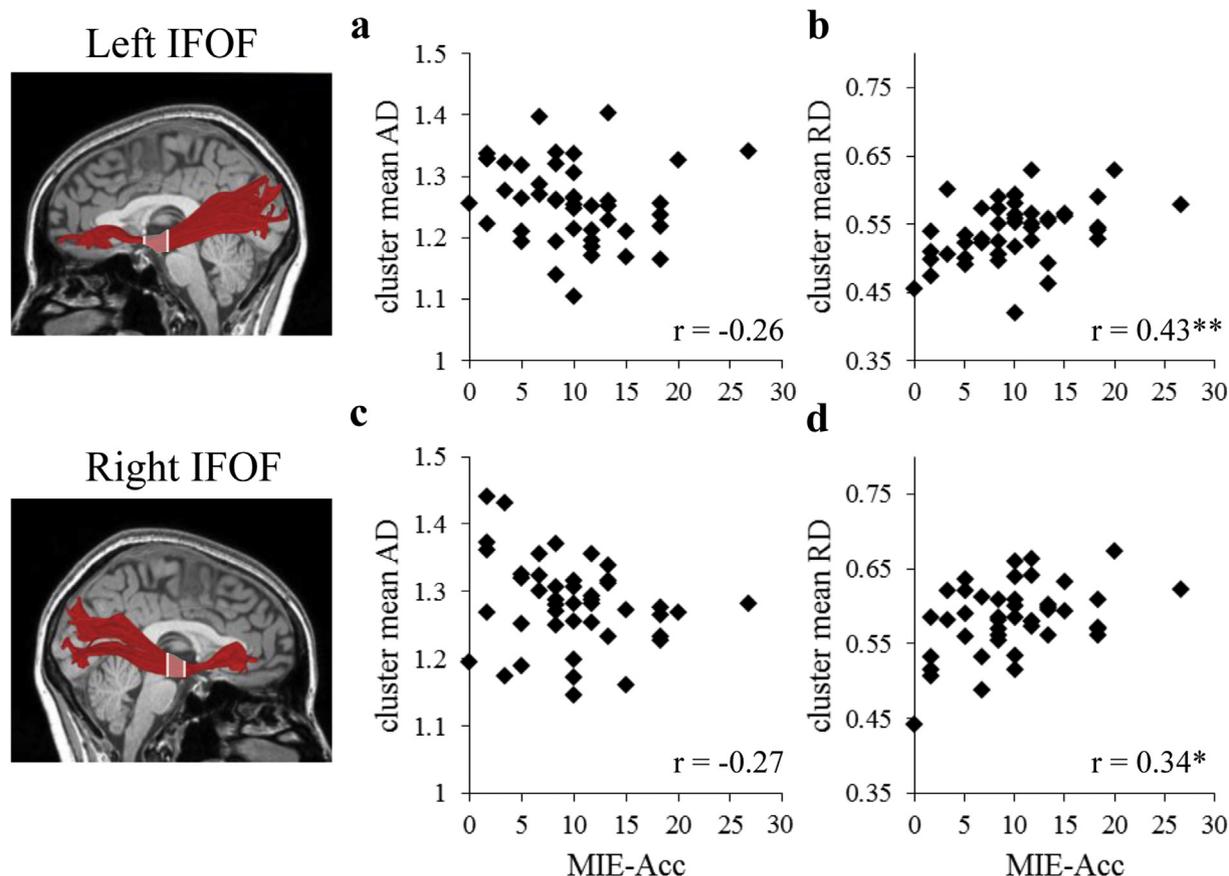


Fig. 5 – Correlations between morphemic cost (MIE-Acc) and FA are explained by positive associations with radial diffusivity, not axial diffusivity. Scatter plots show the association between morphemic cost and mean axial diffusivity (AD; panels a, c) or mean radial diffusivity (RD; panels b, d) within clusters showing a significant correlation between FA and MIE-Acc. Tractograms on the left demonstrate the relevant pathway in a single participant. Shaded regions indicate the location of the significant cluster in each tract. In all significant clusters, morphemic cost showed a significant positive correlation with RD but not with AD. * $p < .05$, ** $p < .005$, FDR corrected for 4 clusters.

models of speech processing, these ventral pathways are typically associated with access to meaning (Cohen et al., 2008; Hickok & Poeppel, 2007; Mishkin, Ungerleider, & Macko, 1983; Rauschecker & Scott, 2009; Saur et al., 2008; Taylor et al., 2013). The finding that sensitivity to word structure is associated with microstructural properties of the ventral reading tracts is in accordance with the view that morphology facilitates access from visual word forms to their meaning (Rastle, 2018).

In the current study, sensitivity to written word structure was not associated with dorsal-stream tracts. It is still unclear if these findings generalize to other tasks, stimulus- and response-modalities. Specifically, morphological processing of spoken words may recruit the dorsal stream to a greater extent. Functional MRI studies of morphological processing using the auditory modality have reported activations in cortical regions within the dorsal pathway (e.g., Arredondo, Ip, Shih Ju Hsu, Tardif, & Kovelman, 2015; Bozic, Tyler, Su, Wingfield, & Marslen-Wilson, 2013). Thus, the involvement of dorsal-stream tracts in morphological processing may be modulated by task, stimulus and response modality. This remains to be tested directly in future studies.

The tracts that were found to be associated with morphological processing in the current study were previously linked to different aspects of semantic processing, both in clinical and in healthy populations. For example, direct electrostimulation to the left and right IFOF induces semantic errors (Herbet, Moritz-Gasser, & Duffau, 2016; Moritz-Gasser et al., 2013; Sarubbo et al., 2015). Along the same lines, patients with the semantic variant of primary progressive aphasia (svPPA) typically suffer from disruptions to the IFOF, while patients diagnosed with non-fluent PPA exhibit decreased FA in dorsal white matter (Agosta et al., 2013; Galantucci et al., 2011). FA of the IFOF correlates negatively with naming abilities in stroke patients, even after controlling for lesion volume (Harvey & Schnur, 2015). In healthy adults, several studies report correlations between IFOF microstructure and aspects of semantic processing (De Zubicaray, Rose, & McMahon, 2011; Nugiel et al., 2016; Rollans, Cheema, Georgiou, & Cummine, 2017), while others report its association with orthographic processing (Rollans et al., 2017; Vandermosten et al., 2012; Welcome & Joanisse, 2014).

A wider set of functions is attributed to the ILF. This tract traverses the temporal lobe and includes long range

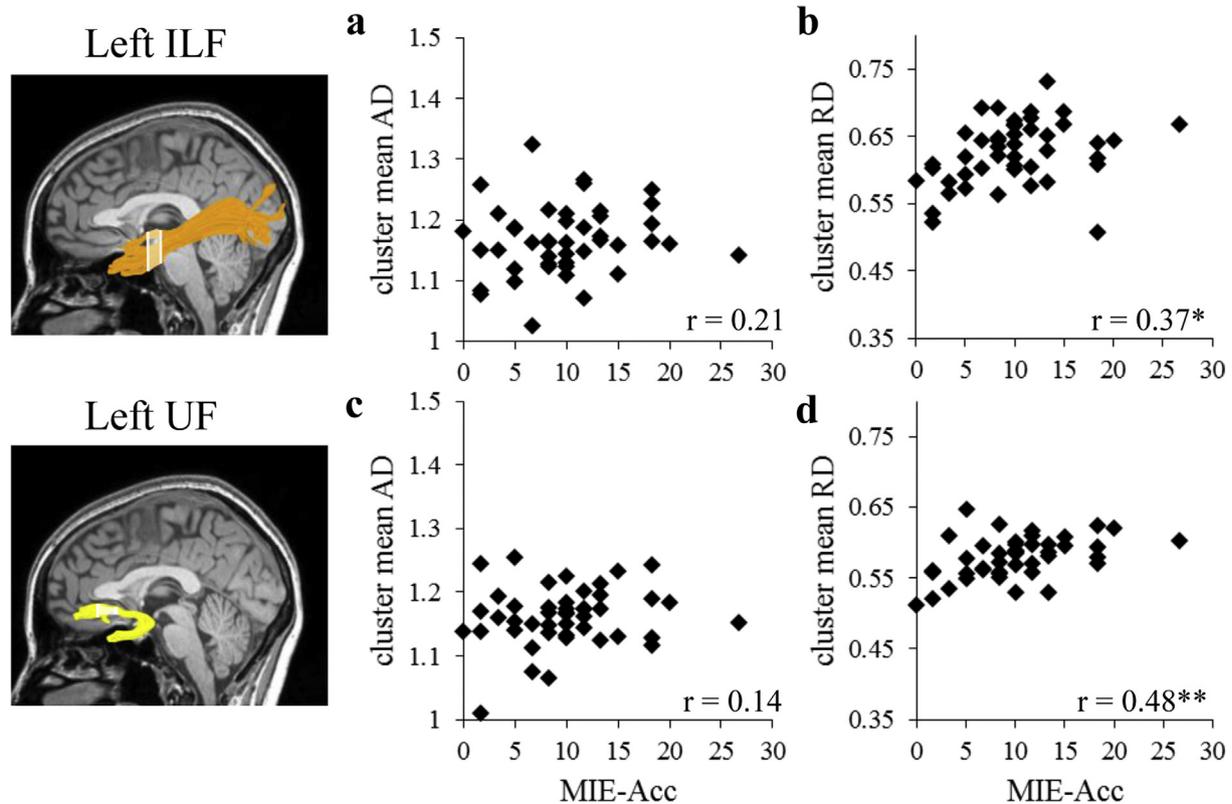


Fig. 6 – Correlations between morphemic cost (MIE-Acc) and MD are explained by positive associations with radial diffusivity, not axial diffusivity. Scatter plots show the association between morphemic cost and mean axial diffusivity (AD; panels a, c) or mean radial diffusivity (RD; panels b, d) within clusters showing a significant correlation between MD and MIE-Acc. Tractograms on the left demonstrate the relevant pathway in a single participant. Shaded regions indicate the location of the significant cluster in each tract. In all significant clusters, morphemic cost showed a significant positive correlation with RD but not with AD. * $p < .05$, ** $p < .005$, FDR corrected for 4 clusters.

connections between occipital and anterior temporal regions (Catani, Jones, Donato, & Ffytche, 2003). In healthy adults, diffusivity in the ILF correlates with visual processing of complex stimuli, in particular with perception of faces and places (Gomez et al., 2015; Tavor et al., 2014). Its proximity to the Visual Word Form Area makes the ILF a good candidate to carry information relevant for visual analysis of words (Yeatman, Rauschecker, & Wandell, 2013). Indeed, several dMRI studies have found the microstructure of the ILF to be associated with reading skills, both in children (Yeatman, Dougherty, Ben-Shachar, et al., 2012) and in adults (Horowitz-Kraus et al., 2014). Lastly, there is some evidence for the involvement of the ILF in semantic processing, yet the findings are mixed and are likely modulated by task choice (Harvey & Schnur, 2015; Herbet, Moritz-Gasser, Boisseau, Duvaux, Cochereau, & Duffau, 2016; Mehta et al., 2016; Nugiel et al., 2016). In sum, current evidence suggests that the ILF contributes to visual analysis of complex stimuli, including written words.

The third ventral tract we targeted, the UF, connects regions in the anterior temporal lobe with inferior frontal and orbital cortices (Catani & Thiebaut de Schotten, 2008). In aphasic patients, FA of the left UF correlates positively with several word-picture matching tasks, which require subjects to select a semantically related picture while rejecting

potential distractors (Harvey et al., 2013). Interestingly, several studies in healthy adults found that properties of the UF correlate with the ability to learn novel visual associations (Alm, Rolheiser, & Olson, 2016; Metoki, Alm, Wang, Ngo, & Olson, 2017; Thomas, Avram, Pierpaoli, & Baker, 2015). These findings suggest a role for the UF in visual processing and in encoding relationships between objects, in tasks that do not involve reading. On the other hand, a recent dMRI study in healthy adults found that diffusivity of the left UF is associated with word reading speed, but not with nonword reading speed, suggesting that the left UF is involved in visual word recognition and lexical access (Cummine et al., 2015). As a whole then, the literature supports a role for the left UF and left ILF in high level visual processing of complex objects, including written words, but their specific critical contribution to language processing is still under debate (Duffau, Gatignol, Moritz-Gasser, & Mandonnet, 2009; Duffau, Herbet, & Moritz-Gasser, 2013; Mandonnet, Nouet, Gatignol, Capelle, & Duffau, 2007; Papagno et al., 2011).

The associations we find between microstructural properties of the ventral tracts and morphological processing are in line with theoretical models that propose that lexical retrieval and access to meaning are morpheme-based (Fruchter & Marantz, 2015; Taft & Forster, 1975). These results also fit well with functional imaging studies that show morphological

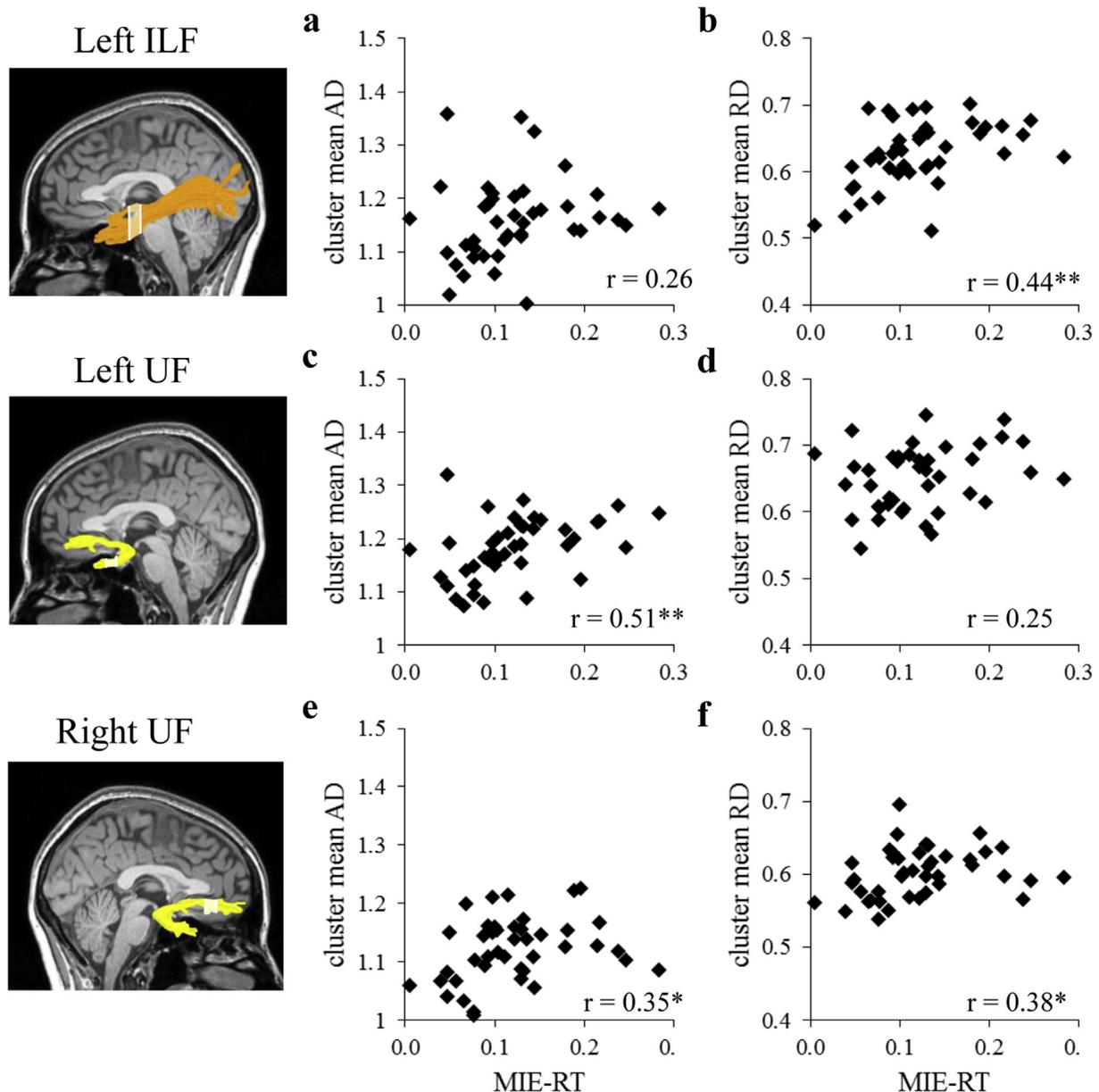


Fig. 7 – Correlations between morphemic cost (MIE-RT) and MD in different ventral tracts are explained by positive associations with either radial diffusivity or axial diffusivity. Scatter plots show the association between morphemic cost and mean axial diffusivity (AD; panels a, c, e) or mean radial diffusivity (RD; panels b, d, f) within clusters showing a significant correlation between MD and MIE-RT. Tractograms on the left demonstrate the relevant pathway in a single participant. Shaded regions indicate the location of the significant cluster in each tract. * $p < .05$, ** $p < .005$, FDR corrected for 3 clusters.

effects along the ventral occipitotemporal cortex (Cavalli, Colé, et al., 2016; Gold & Rastle, 2007; Lehtonen et al., 2011; Solomyak & Marantz, 2010). In the context of visual word recognition, morphemes form an intermediate level between the visual symbols of a writing system and whole words. The association of morphological processing with anterior segments of occipitotemporal white matter is thus compatible with the reported hierarchy of selectivity along the posterior–anterior axis of the occipitotemporal cortex, where posterior regions in the occipitotemporal sulcus demonstrate sensitivity to letter shapes and word visibility (Ben-Shachar,

Dougherty, Deutsch, & Wandell, 2007; Ben-Shachar et al., 2011) while more anterior regions in the fusiform gyrus respond to larger orthographic units and lexical-semantic information (Dehaene, Cohen, Sigman, & Vinckier, 2005; Thesen et al., 2012; Vinckier et al., 2007; van der Mark et al., 2009). Here, we were able to localize the correlations specifically to anterior portions of the ventral tracts by inspecting the diffusion profile along each tract trajectory. This demonstrates the utility of employing spatially sensitive methods when investigating white matter correlates of cognitive processes.

Morphemic cost indicates the level of sensitivity to the presence of familiar morphemes within orthographic stimuli. Higher morphemic cost therefore reflects stronger reliance on morphological cues in visual word recognition, which is considered beneficial for skilled reading in English. Although in the current study morphemic cost was not correlated with an independent measure of word reading (TOWRE sight word efficiency, see [Supplementary Table S3](#)), such standardized tests may not be appropriate to test this link as they contain only monomorphemic words. Future studies should incorporate measures of natural reading to shed light on the relationship between sensitivity to morphological structure and reading skill. Critically, in natural reading conditions, morphological processing does not operate in isolation. Many factors affect written word recognition, including orthographic, phonological and lexical-semantic processing. A related important question that we address here concerns the functional segregation between these components. We found that morphemic cost did not correlate with other behavioral measures across participants (see [Supplementary Table S3](#)), suggesting that it taps into a distinct component of reading. Moreover, the correlations found between morphemic cost and ventral tract microstructure remained significant after controlling for other factors that contribute to reading (nonword repetition, sight word efficiency). Together, these findings suggest some degree of functional specificity in the neural pathways that implement morphological processing.

The goal of the current study was to characterize the white matter pathways underlying morphological processing in typical adult readers. White matter involvement in reading related skills may be different in adults compared to children, and was previously shown to change with development ([Yeatman, Dougherty, Ben-Shachar, et al., 2012](#)). It therefore remains to be seen whether our findings in adults generalize to children in the first stages of reading acquisition. One interesting proposal postulates that successful reading acquisition entails a transition from reliance on the dorsal pathway to the ventral pathway ([Pugh et al., 2000](#)). If this is the case, then correlations with ventral tracts will emerge late in reading acquisition, while correlations with dorsal tracts reported in children will fade once learners have successfully reached reading proficiency. The idea that the dorsal tracts contribute particularly to the learning phase of language and reading is supported by studies that demonstrate that in adults, correlations with dorsal tracts emerge in tasks that require learning of novel vocabulary and phonology ([Hofstetter, Friedmann, & Assaf, 2017](#); [Lopez-Barroso et al., 2013](#); [Mamiya et al., 2016](#); [Vaquero, Rodríguez-Fornells, & Reiterer, 2017](#)). Future studies will be necessary to test the notion that the association between morphology and ventral reading pathways emerges at a later phase of skilled reading, with the development of long term morphological knowledge.

In the current study, sensitivity to morphological information was negatively correlated with FA and positively correlated with MD. The direction of these correlations might seem counter-intuitive, because FA is sometimes considered an index of “fiber integrity” (but see [Jones, Knösche, & Turner, 2013](#), for an opposing view). However, FA is modulated by multiple underlying biological factors, including axonal diameter, axonal density, myelination, and tissue

organization ([Assaf & Pasternak, 2008](#); [Barazany, Basser, & Assaf, 2009](#); [Beaulieu, 2002](#); [Budde & Annesse, 2013](#); [Pierpaoli & Basser, 1996](#); [Pierpaoli et al., 2001](#)). Some of these factors are inversely related to FA, but positively related to the speed and efficiency of information transfer. For example, thicker axons are associated with faster signal conduction, larger RD and lower FA ([Barazany et al., 2009](#); [Horowitz et al., 2014](#)). Notably, negative correlations between FA and cognitive processes are not uncommon and were previously reported in dorsal, ventral, callosal and cerebellar white matter pathways ([Alm et al., 2016](#); [Blecher, Tal, & Ben-Shachar, 2016](#); [Dougherty et al., 2007](#); [Frye et al., 2011](#); [Harvey & Schnur, 2015](#); [Tavor et al., 2014](#); [Travis et al., 2015](#); [Yeatman et al., 2011](#)). Here, our post-hoc analysis revealed that in the significant FA clusters, the correlations stemmed from a positive relationship with RD. Variations in axonal diameter may provide a possible interpretation for this finding, because thicker axons might lead to improved conduction and information transfer ([Horowitz et al., 2014](#)), resulting in better performance. This explanation cannot be tested directly here, but remains to be explored in future studies. The same analysis revealed a more complex picture for the significant MD clusters, with some of them driven by a positive relationship with RD and others with AD. Quantitative imaging methods that probe more directly into specific tissue properties will help tease apart the biological factors driving the correlations between cognitive performance and diffusion properties ([Assaf, Blumenfeld-Katzir, Yovel, & Basser, 2008](#); [De Santis, Assaf, Evans, & Jones, 2014](#); [Mezer et al., 2013](#); [Zhang, Schneider, Wheeler-Kingshott, & Alexander, 2012](#)).

A final intriguing question raised by our findings concerns the potential generalization of the current findings across orthographies and morphological systems. Languages vary in several aspects of morphological structure, for example, the manner in which morphemes combine (e.g., linearly or non-linearly) and the prevalence of morphologically complex words in common language use. These properties may influence the way morphological information is represented in the writing system ([Frost, 2012](#)). English is a language where spelling preserves morphological information at the expense of orthographic-phonological consistency ([Aronoff, Berg, & Heyer, 2016](#); [Berg, Buchmann, Dybiec, & Fuhrhop, 2014](#); [Frost, 2012](#); [Rastle, 2018](#)). Other European languages, like Finnish or Italian, have transparent spelling-sound correspondence rules, which may decrease the need to rely on morphology during reading acquisition. In Semitic languages like Arabic and Hebrew, morphological structure is non-linear, such that the root morpheme is embedded within a morphological pattern that provides a phonological template. In these languages phonological information is underspecified in writing, such that morpheme recognition provides crucial cues for the phonological decoding of written words ([Frost, 2012](#); [Frost, Katz, & Bentin, 1987](#)). Skilled readers of Hebrew or Arabic may therefore utilize morphological structure more heavily even for ortho-phonological decoding, so these readers may show morphological associations within the dorsal reading pathways as well. This hypothesis converges with more dorsal patterns of activation reported in fMRI studies of morphological processing in Hebrew readers ([Bick, Frost, & Goelman, 2010](#); [Bick, Goelman, & Frost, 2011](#)).

compared to English (Bick et al., 2011; Bozic, Marslen-Wilson, Stamatakis, Davis, & Tyler, 2007; Gold & Rastle, 2007).

In conclusion, the current study highlights the contribution of the ventral reading pathway to morphological processing. It delineates, for the first time, the white matter pathways involved in morphological processing in adult skilled readers, and supports the view that morphological knowledge plays a key part in mapping print to meaning. It remains to be seen whether these findings generalize to other populations, including developmental and clinical populations, and whether the results converge across different orthographies and morphological systems.

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Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.cortex.2018.06.011>.

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