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Variation in White Matter Connectivity Predicts the Ability to Remember Faces and Discriminate Their Emotions

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Abstract

Objective—The extended face network contains clusters of neurons that perform distinct functions on facial stimuli. Regions in the posterior ventral visual stream appear to perform basic perceptual functions on faces, while more anterior regions, such as the ventral anterior temporal lobe and amygdala, function to link mnemonic and affective information to faces. Anterior and posterior regions are interconnected by a long-range white matter tracts however it is not known if variation in connectivity of these pathways explains cognitive performance.

Methods—Here, we used diffusion imaging and deterministic tractography in a cohort of 28 neurologically normal adults ages 18–28 to examine microstructural properties of visual fiber pathways and their relationship to certain mnemonic and affective functions involved in face processing. We investigated how inter-individual variability in two tracts, the *inferior longitudinal fasciculus* (ILF) and the *inferior fronto-occipital fasciculus* (IFOF), related to performance on tests of facial emotion recognition and face memory.

Results—Results revealed that microstructure of both tracts predicted variability in behavioral performance indexed by both tasks, suggesting that the ILF and IFOF play a role in facilitating our ability to discriminate emotional expressions in faces, as well as to remember unique faces. Variation in a control tract, the *uncinate fasciculus*, did not predict performance on these tasks.

Conclusions—These results corroborate and extend the findings of previous neuropsychology studies investigating the effects of damage to the ILF and IFOF, and demonstrate that differences in face processing abilities are related to white matter microstructure, even in healthy individuals.

Keywords

diffusion imaging; faces; emotion; prosopagnosia; face memory; hypoemotionality

INTRODUCTION

Over the past 100 years, several neuropsychological syndromes have been attributed to disruption or disconnection of visual fiber pathways. For instance, associative visual

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agnosia, visual amnesia (a deficit in storing visual experiences in memory, but not experiences from other sensory modalities), and visual hypo-emotionality (difficulties feeling emotions for visual stimuli but not stimuli registered in non-visual modalities) have at one time or another been attributed to disconnection (reviewed by Catani et al., 2003). The logic underlying this is that brain regions involved in processing perceptual aspects of visual stimuli must interact with limbic regions that process emotion and memory for normal functioning and that disruption of the fiber pathways linking these systems can give rise to disordered processing.

One tract that is geographically positioned to connect visual perceptual processes with limbic emotion and memory processes is the inferior longitudinal fasciculus (ILF). The ILF is a monosynaptic pathway connecting ventral extrastriate regions, and in some cases portions of the inferior parietal lobe, to the anterior temporal lobe (superior, middle, and inferior gyri, as well as the uncus/parahippocampal gyrus), the hippocampus, and the amygdala.

Damage to this tract can result in visual-emotion disconnection syndromes. In one of the earliest studies, Horel and Misantone (1974) transected white matter running along the basolateral portion of the temporal lobes in three monkeys. These monkeys became hypoemotional and lost the ability to retain newly learned visual information. However, this finding must be interpreted cautiously because complete deafferentation modifies the functions of the deafferented areas, and at times causes marked neuronal atrophy (Sprague, 1966), underscoring the fact that regionally dispersed gray matter and white matter work in concert.

A small number of related studies exist in humans. First, Bauer (1982) reported on a patient with traumatic lesion affecting inferior temporal –occipital regions bilaterally. The patient had severe prosopagnosia and visual memory deficits. The patient spontaneously complained that he no longer became emotionally aroused by visual stimuli including beautiful vistas, pretty girls, and erotic images. Upon further research, it was found that he lacked skin conductance responses to emotional images presented in the visual modality, but had persevered functioning in the auditory realm. Bauer (1982) concluded that this patient's hypoemotionality was most likely due to visual-limbic disconnection (for a similar case study see Habib, 1986). Second, a study of individuals with focal lesions involving both gray and white matter found that damage to the ILF (as well as surrounding gray matter) correlated with impairments in facial emotion recognition (Philippi, Mehta, Grabowski, Adolphs, & Rudrauf, 2009; see also Baggio et al., 2012). This finding was recently replicated in a sample population consisting of individuals with traumatic brain injury (TBI; Genova et al., 2015).

These findings suggest that the ILF may serve as a conduit for visual-limbic interactions. The goal of this study was to test this hypothesis in a neurologically normal population using diffusion tensor imaging (DTI) along with deterministic tractography. DTI utilizes diffusion-weighted MR imaging (DW-MRI) to index the degree of diffusion among water molecules within human brain tissue. White matter tracts can be imaged by exploiting the diffusion properties of the myelinated axons that make up the fiber pathways. In myelinated axons, the

direction of diffusion is restricted due to the presence of myelin sheaths. DW-MRI captures the degree of restriction, called anisotropy, and provides measures of the microstructural properties of white matter such as the orientation and magnitude of diffusion within each voxel of the brain (Alexander et al., 2011; Alexander, Lee, Lazar, & Field, 2007a; Jones, 2008; Tournier, Mori, & Leemans, 2011a). Tractography allows for the visualization of white matter tracts and can be used in combination with DTI to calculate microstructural indices specific to particular white matter tracts.

We hypothesized that individual differences in facial emotional processing and face memory should correlate with ILF microstructure given that the ILF contains a streamline between ventral extrastriate cortex and temporal limbic regions. We predicted that this relationship would not be found in a control tract, the uncinate fasciculus (UF). Like the ILF, the UF connects temporal limbic regions; however, it does not originate in the extrastriate cortex. Instead, it forms a monosynaptic pathway between the anterior and medial temporal lobes and the orbitofrontal cortex (Catani & Thiebaut de Schotten, 2008). Given its geographic location, the UF has been implicated in processes related to episodic memory (Metzler-Baddeley et al., 2011; Diehl et al., 2008; McDonald et al., 2008; Niogi et al., 2008; also see Table 1 in Olson et al., 2015), and our own working hypothesis suggests that the UF is critical for integrating memory representations stored in the temporal lobes with feedback history computed in the OFC in order to facilitate memory-based decisions (Von Der Heide et al., 2013; Alm et al., 2015).

As a control task, we used a face perception task and predicted that this task would not correlate with microstructure of the ILF.

In addition to the ILF, we examined the inferior fronto-occipital fasciculus (IFOF). Like the ILF, the IFOF begins in ventral occipital lobe. However it terminates in ventral and lateral aspects of frontal cortex (Catani & Thiebault de Schotten, 2008). The IFOF is a mysterious tract; it has not been identified in non-human primates (Schmahmann & Pandya, 2007) but has been identified in humans using diffusion imaging techniques. This has led some researchers to suggest that it may be specific to humans (Catani, 2007). Electrical stimulation of this tract during neurosurgery consistently results in semantic errors (Duffau, Peggy Gatignol, Mandonnet, Capelle, & Taillandier, 2008) providing strong evidence that this tract plays a significant role in semantic memory. However, there is a hint that it may also play some role in face processing as one study reported reduced structural integrity of the right IFOF in congenital prosopagnosia (Thomas et al., 2008). In addition, two studies found a relationship between damage to the right IFOF and emotion recognition impairments (Philippi et al., 2009; Genova et al., 2015). Given these findings, combined with the general absence of a mature literature on this tract, we decided to conduct an exploratory analysis of the IFOF.

METHODS

Study participation occurred in two separate testing sessions. During the behavioral session, participants completed computerized tasks in the laboratory. Participants were tested individually. Computerized tasks were programmed in E-Prime (Version 2.0 Professional)

and presented on Dell computers. During a separate session, diffusion-weighted MRI data, as well as high-resolution anatomical scans were acquired at Temple University Hospital.

Participants

Twenty-eight healthy individuals (19 females, 9 males) between the ages of 18 and 28 (M = 21.52, SD = 2.55) volunteered for this experiment. Participants were right-handed with normal or corrected-to-normal vision and no personal history of neurological or psychological disorders as well as no such history in their first-degree relatives (ascertained via self-report). This sample was recruited from the Temple University student body.

Three substantial outliers were found across white matter indices and thus, three participants were excluded from further analyses leaving a study sample of 25 participants. Informed consent was obtained according to the guidelines of the Institutional Review Board of Temple University and participants received monetary compensation for participation in the experiment.

Tasks

1. Face Emotion Recognition—Emotion recognition abilities tend to be at ceiling in the normal population; therefore, we designed a task using morphed emotional faces to achieve a higher level of difficulty. Morphed faces were made using Fantamorph software. A neutral face and a face very clearly showing an emotion were morphed together in different proportions to create emotional faces that were progressively more difficult to perceive. For example, a face that is 60% neutral and 40% happy is more difficult to judge as happy than a 30% neutral and 70% happy face. On each trial, participants were presented with three faces of the same identity. Participants were asked to pair the target face at the top of the screen with the face showing the same amount of expression at the bottom of the screen. For each identity, there was an easy control trial which all participants completed correctly. The task consisted of 200 total trials.

2. Cambridge Face Memory Test (CFMT)—This task is used to assess the ability to store and retrieve long-term memories of faces (Duchaine & Nakayama, 2006). Participants were first familiarized with six different facial identities, each presented at 3 viewpoints during an initial encoding phase. After this, participants completed 72 3-alternative forced choice trials in which they had to identify a target face amongst two foils. The test became progressively more difficult; in the first portion, target faces are presented in the same view as seen during training; in the second portion however, target faces are presented from novel views or lighting conditions. Finally, in the third portion of the task, target faces are presented from novel views with added visual noise. Participants completed 72 total trials.

3. Face Identity Perception—Stimuli and task were taken from the Philadelphia Face Perception Battery (Thomas et. al 2008). This task consisted of morphed faces created using GenHead software (www.genemation.com/). This software creates highly realistic artificial faces across 114 parameters, each an eigenvector derived from a principal component analysis of a large database of face photographs. Additional parameters allow for control of gender, age, and ethnicity. On each trial, one sample stimulus was presented above two side-

by-side probe faces. Stimuli were morphed faces that varied along the dimension of facial identity. The task was to choose the probe stimulus that was most similar to the sample stimulus. Accuracy was emphasized, and there was an 8-second time limit per trial. On easy trials, the two stimuli were quite different from one another, while on difficult trials, the two probe stimuli were very similar. The dimension of interest was varied continuously but was later compressed into a single number that indexed one's ability to perceive small differences in face identity. The side of the "match" stimulus was counterbalanced across trials. There were 100 total trials.

Imaging

Image Acquisition—MRI scanning was conducted at Temple University Hospital on a 3.0 T Siemens Verio scanner (Erlangen, Germany) using a Siemens twelve-channel phased-array head coil. DTI data was collected using a diffusion-weighted echo-planar imaging (EPI) sequence covering the whole brain with the following imaging parameters: 55 axial slices (with no gap between slices), 2.5 mm slice thickness, voxel size = 1.967 mm × 1.967 mm × 2.5 mm, TR = 9,900 ms, TE = 95 ms, FOV = 240 mm^2, b values of 0 and 1000 s/mm^2 (one b=0 volume), 64 non-collinear directions. These parameters yielded a DTI scan lasting approximately 11 minutes.

In addition to diffusion-weighted images, high-resolution anatomical images (T1-weighted 3D MPRAGE) were also collected for each participant with the following parameters: 160 axial slices, 1 mm slice thickness, TR = 1,900 ms, TE = 2.93 ms, inversion time = 900 ms, flip angle = 9°, FOV = 256 mm. These anatomical images were co-registered to the diffusion images and used to draw regions of interest (ROIs).

DTI preprocessing—Diffusion-weighted images were pre-processed to correct for eddy currents and subject motion using an affine registration model. The b-vector matrix was adjusted based on rigid body registration, ensuring a valid computation of the tensor variables. Non-brain tissue was removed using an automated brain extraction tool (BET), and a standard least squares diffusion tensor fitting model was then applied to the data using FSL. The diffusion tensor fitting provided estimates of fractional anisotropy (FA) and mean diffusivity (MD) as well as three eigenvectors and eigenvalues. FA was computed using the following equation: $\sqrt{\frac{1}{2}}\frac{\sqrt{(\lambda_1-\lambda_2)^2+(\lambda_2-\lambda_3)^2+(\lambda_3-\lambda_1)^2}}{\sqrt{\lambda_1{}^2+\lambda_2{}^2+\lambda_3{}^2}}$, where λ_1, λ_2, and λ_3 represent the three eigenvalues respectively. MD was calculated by averaging the three eigenvalues. Axial diffusivity (AD) was represented by the principal eigenvalue (λ_1). Finally, radial diffusivity (RD) was calculated by averaging the second and third eigenvalues. Microstructural estimates were computed on individual voxels using a three-dimensional Gaussian distribution model that yielded a single mean ellipsoid for each voxel. All preprocessing was performed using FSL (Smith et al., 2004).

Whole brain deterministic tractography was performed in subject native space using the Diffusion Toolkit and TrackVis software packages (Wang, Benner, Sorensen, & Wedeen, 2007). This software uses a fiber assignment continuous tracking (FACT) algorithm (Mori, Crain, Chacko, & Van Zijl, 1999) to determine the branching and curving of the fiber tracts. The orientation of the principal eigenvector was estimated for each voxel, and nearest-

neighbor interpolation was used to step along that direction. Step length was fixed at 0.1 mm, and an angle threshold of 35 degrees was used to determine the termination point of the fiber tracts. A spline filter was used to smooth the tractography data. A multiple region of interest (ROI) based axonal tracking approach (Mori et al., 2002; C. Thomas, Humphreys, Jung, Minshew, & Behrmann, 2010; Wakana et al., 2007) was then used to delineate three fiber pathways bilaterally: the ILF, IFOF, and UF. ROIs were drawn in subject native space using the high-resolution anatomical T-1 images and the methods outlined by Thomas and colleagues (2010) and used by our lab in a prior study (Alm, 2015). Briefly, each white matter tract, two ROIs were drawn and a Boolean AND term was used to select only the fibers that passed through both of these two regions. For the ILF, one ROI was drawn in the ventral occipito-temporal cortex inferior to the lateral ventricles, while the other ROI consisted of the portion of the temporal cortex that is anterior to the point at which the fornix descends to the mammillary bodies. For the IFOF, the same ventral occipito-temporal cortex ROI was used along with an ROI in the frontal lobe, consisting of the portion located anterior to the rostrum of the callosum. Finally, for the UF, the anterior temporal lobe ROI was used along with the frontal lobe ROI (used for defining the IFOF). Mean MD, FA, AD, and RD indices were subsequently extracted from the tracts of interest.

The ILF and IFOF originate in the same region and follow similar path trajectories until the ILF curves ventrally, ending in the ATL and the IFOF curves dorsally, into the frontal lobe. There has been some debate as to whether the two are, in fact, separate fiber pathways, or rather, make up the same white matter tract (Johansen-Berg & Behrens, 2009). For these reasons, we excluded any voxels that overlapped in our tract data for the ILF and IFOF, ensuring dissociation between these fiber pathways.

Statistical Analyses—Statistical analyses were performed using SPSS (Version 21.0). Regression analyses were used to examine the relationship between microstructure of the tracts of interest and performance on the tasks described above. Accuracy was the dependent measure of interest for each of the behavioral tasks. To control for multiple comparisons, family-wise error rate was adjusted using a Bonferroni correction to adjust for simultaneous predictors in each regression model (critical $p = .05/2$; Mundfrom, Piccone, Perrett, Schaffer, & Roozeboom, 2006). All regression p-values reported were Bonferroni-corrected.

RESULTS

Behavioral data

Individual differences in accuracy across the three tasks are presented in Figure 1. Average accuracy on the face emotion task, face memory task and face identity tasks were 72.6%, 63.2%, and 76.5%, respectively. There was sufficient variability to examine individual differences, as shown in Figure 1.

DTI data

Regression models were constructed to predict participant accuracy on the three face tasks. Previous studies have shown diffuse changes in white matter microstructure throughout the whole brain as a function of age as well as general gender differences in white matter

connectivity throughout the brain (Thomas et. al, 2008; Gong et. al, 2011; Lebel et al., 2012; Ingalhalikar et al., 2014). Therefore we examined the relationship between the white matter measures in our sample with age and gender. To investigate the possibility that age could systematically vary in this dataset, each of the white matter indices measured (bilateral MD, AD, RD and FA) in the ILF and IFOF were correlated with age of the participants. To investigate possible gender differences, t-tests were performed. No significant differences were observed in any of the white matter indices (all p's > .05), thus we did not control for age or gender in subsequent analyses.

Regression models were constructed to examine whether white matter microstructure of the ILF and/or IFOF significantly predicted behavioral performance across our tasks. Each regression model consisted of bilateral white matter microstructure measurements as predictors and task performance as the dependent measure. The results of the regression analyses are presented in Table 1.

Emotion Recognition—Regression analyses revealed a significant relationship between microstructure of the ILF and emotion recognition. Specifically, AD in the right ILF significantly predicted emotional recognition performance ($\beta = -.7$, $t(22) = 2.7$, $p = .03$) such that higher AD values were associated with lower accuracy (see Figure 2). AD in the *left* ILF significantly predicted emotional recognition accuracy before controlling for multiple comparisons, but did not survive after stringently controlling for multiple comparisons ($\beta = .46$, $t(22) = 1.82$, $p = .14$). Given our sample size, it is possible that a true effect exists in the left ILF but requires greater power to be revealed. No other microstructural indices (MD, RD or FA) in the ILF predicted differences in task performance.

Individual differences in emotion recognition were also related to variability in IFOF microstructure. FA in both the left and right IFOF significantly predicted performance ($\beta = .93$, $t(22) = 2.87$, $p = .02$ and $\beta = -.91$, $t(22) = 2.8$, $p = .02$ respectively). This relationship is depicted in Figure 3 (top). AD, RD and MD in the IFOF predicted task performance.

Individual differences in emotional recognition ability were not related to microstructural differences in a control tract, the UF (p's > .05).

Face Memory—Face memory accuracy was significantly predicted by microstructural properties of the right ILF. Regression analyses revealed a negative relationship between FA in the right ILF and face memory accuracy ($\beta = -.54$ $t(22) = 2.17$, $p = .03$; See Figure 2, bottom), such that lower FA was associated with higher face memory performance. There was no significant relationship with the *left* ILF and individual differences in face memory performance (p's > .05). MD, RD and AD in the right and left ILF did not predict face memory performance.

Similarly, FA of both left and right IFOF significantly predicted face memory performance. A positive relationship emerged between the left IFOF and face memory accuracy ($\beta = 1.87$, $t(22) = 3.49$, $p = .004$), while a negative relationship emerged for the right IFOF and face memory accuracy ($\beta = -1.61$, $t(22) = 3.49$, $p = .01$). Figure 3 (bottom) depicts this

relationship. No other white matter indices measured in the IFOF predicted face memory performance.

No significant effects were observed between microstructure of the UF and face memory performance (all *p's* > .05).

Facial Identity Perception—One's ability to perceive small differences in facial identity was not predicted by microstructural differences in any of the tracts examined (all *p's* > .05).

DISCUSSION

Theoretical discussions about the involvement of visual fiber pathways in higher-order cognition have existed for years but only recently with the advent of as diffusion-weighted MRI have we been able to test these ideas. Two rare clinical disorders, visual amnesia and visual hypo-emotionality, have been attributed to white matter disconnection (reviewed by Catani et al., 2003). Using this framework, we tested the hypothesis that individual differences in inferior longitudinal fasciculus (ILF) microstructure predicted inter-individual variability in face emotion recognition and face memory. In addition we examined two other long-range white matter tracts: the inferior fronto-occipital fasciculus (IFOF) since there is a small literature linking this tract to face processing (Thomas et al., 2008), and the uncinate fasciculus (UF) as a control fiber pathway, given that our recent literature reviews found no evidence linking this tract to any of the behaviors investigated in this study (Von Der Heide et al., 2013). Our results revealed that microstructure of the right ILF and bilateral IFOF significantly predicted variability in facial emotion recognition performance, as well as face memory performance in healthy young adults. Importantly, there is some specificity to our findings since the microstructural properties of these tracts were not related to performance on a control task of facial identity perception, nor was a control fiber pathway, the UF, related to performance on any of our tasks of interest.

Like the ILF, the UF connects temporal limbic regions; however, it does not originate in the extrastriate cortex. Instead, it forms a monosynaptic pathway between the anterior and medial temporal lobes and the orbitofrontal cortex (Catani & Thiebaut de Schotten, 2008). Based on our reviews of the literature as well as empirical findings (Von Der Heide et al., 2013; Alm et al., 2015), we believe that UF function is specifically related to tasks that involve an interaction between value encoding/updating and long-term memory. Therefore, we did not expect the UF to be recruited in simple, perceptually-driven memory tasks, such as the Cambridge Face Memory Test or in face perception tests without a memory component, such as emotion recognition. Our findings are consistent with these predictions and suggest that performance on such tasks rely on fiber pathways connecting visual regions, in particular the ILF and IFOF.

Cognitive Functions Attributed to the ILF

It is important to bear in mind that white matter does not produce behavior; the electrical activity of neurons produce behavior. White matter provides the communication system that links groups of neurons to other groups of neurons. Bearing this caveat in mind, the small literature on the function of the ILF invariably links this tract to high-level vision. Consistent

with the results reported here, two prior studies reported that in humans, damage to the ILF correlates with impairments in facial emotion recognition (Genova et al., 2015; Philippi et al., 2009). In addition, our study is the first to link the ILF to face memory abilities.

However other studies have implicated the ILF in perceptual aspects of face processing, which we did not find. ILF scarring or degeneration in multiple sclerosis and/or fronto-temporal dementia correlates with face identification deficits (Grossi et al., 2012; Yamasaki et al., 2004). Also, individuals with developmental or congenital prosopagnosia have reduced structural integrity of the right ILF (Thomas et al., 2008; Grossi et al., 2012) which predicts face-recognition impairments (Thomas et al., 2008). This raises the question of why we did not observe any effects in our face identity task. One possibility is that there simply isn't enough microstructural variance in a normative sample to observe a relationship.

The communicative functions of the ILF extend beyond face processing to include functions linked to object recognition (Braem, Honoré, Rousseaux, Saj, & Coello, 2014; Shinoura et al., 2013). Two studies using intraoperative electrical stimulation have reported changes in object naming or object recognition after stimulating the ILF (Coello, 2008; Mandonnet, 2009). Naming and recognizing common objects involves integrating perceptual representations with higher-order conceptual knowledge, potentially stored in lateral regions of the anterior temporal lobe.

Finally, the ILF has been linked to visual aspects of reading. The cell bodies in extrastriate cortex from which the ILF is derived may include the visual word form area thus there is great interest in this tract among reading researchers (see Epelbaum et al., 2008; Gill-Robles et al., 2013; Yeatman et al., 2012). Zemmoura and colleagues (2015) reported that resection of the posterior portion of the ILF, connecting ventral visual cortex to the visual word form area, induced severe reading impairments. However resection of the anterior portion of the ILF, connecting the anterior and medial temporal lobes to the visual word form area, had no effect on reading. These findings should be interpreted in the context of the anatomy of the ILF, which has U-shaped fibers entering and exiting at different waypoints. As such, it is possible that different portions of the ILF have distinct functional roles.

An unexplored topic in this literature is the lateralization of function in the ILF. Coello and colleagues (2013) drew on a single case study to speculate that the left ILF is somewhat more specialized for visual tasks requiring access to language, such as object naming while the right ILF may have functions more aligned with strictly visuospatial functions. Consistent with this, our findings showed that individual differences in right, but not left, ILF microstructure predicted the ability to discern face emotions and remember faces.

Cognitive Functions Attributed to the IFOF

The literature surrounding the functionality of the IFOF is quite small, due in large part to the fact that this tract has not been identified in non-human primates (Schmahmann & Pandya, 2006). Given that this tract may be uniquely human (Catani, 2007) some researchers have posited that its function is related to a uniquely human skill: language. Almairac and colleagues (2014) reported that patients with lesions in areas consistent with the IFOF exhibited impairments on a verbal fluency task. Participants were patients who had

undergone surgery for left lateralized low-grade gliomas. Voxel-based lesion-symptom mapping (VLSM) was used to map out the spatial location of lesions across patients. When a mask of the left IFOF was overlaid onto the VLSM maps, the degree of IFOF damage correlated significantly with impairment on a verbal fluency task. This finding was specific to semantic verbal fluency, i.e. generating words belonging to a category of animals. This finding provides corroborating evidence for earlier studies during which electrical stimulation of the left IFOF during neurosurgery produced semantic paraphasias during object naming (Duffau et al., 2005; Duffau et al., 2008; Mandonnet et al., 2007).

These findings have led some researchers to conclude that the IFOF plays an important role in semantic memory. In the diffusion imaging literature, de Zubicaray and colleagues (2011) examined the relationship between IFOF microstructure and semantic memory across a cohort of healthy older adults. A whole brain white matter analysis revealed a significant positive correlation between a composite semantic memory score and FA in the left IFOF, suggesting that the IFOF is involved in semantic access.

Yet some other findings link aspects of face processing to the IFOF. Compared to healthy controls, individuals with congenital prosopagnosia exhibit significantly decreased FA in both right and left IFOF. Furthermore, the degree of face recognition impairment in these individuals correlates with reduction in the percentage of fibers in the right IFOF (Thomas et al., 2009). Damage to the IFOF, along with the ILF, has also been reported in case studies of severe prosopagnosia (e.g. Valdés-Sosa et al., 2011). In a sample of neurologically normal participants ranging in age from 18–86 years, a reduction in the number of fibers and FA of the right IFOF was related to individuals' abilities to discriminate between faces (Thomas et al., 2008).

Finally, the IFOF has also recently been implicated in emotion recognition. Philippi and colleagues (2009) investigated emotional recognition deficits using Ekman faces (Ekman, 1976) across a large sample of patients with focal brain lesions. Disconnection of the right IFOF predicted impairment on the emotion recognition task. The authors replicated this finding in a case study of a patient with damage restricted to the IFOF. Our findings are consistent with this data. Similarly, Baggio et al. (2012) reported a significant positive relationship between emotion recognition scores and FA values in the right and left IFOF. Of note, these findings were specific to sadness recognition and participants consisted of Parkinson's patients and healthy controls.

Like the ILF, it is possible that different portions of the IFOF have distinct functional roles. A recent study demonstrated that the IFOF consists of fiber bundles that terminate in various frontal and temporal regions (Sarubbo et al, 2013). The authors posit that differential termination points may yield distinct functional subcomponents of the IFOF, which potentially support discrete functions.

Limitations

The ILF and IFOF are large white matter tracts linking functionally discrete brain regions. As noted earlier, it is possible that both tracts consist of sub-tracts that serve to link domain-specific visual processing areas performing different computational metrics along the ventral

stream, and that the face-network constitutes one of these sub-tracts. Consistent with this possibility, one study has shown that different portions of the ILF are associated with recognition ability for different stimulus classes (Tavor et al., 2013). The same logic applies to the IFOF. Our study was not designed to test the finer-grained question of whether white matter from particular cortical subregions, such as the fusiform face area to the amygdala, underlies the observed associations. Future studies should consider functionally localizing cortical subregions like the visual word form area and the fusiform face area in order to discern whether subregions of the ILF participate in distinct cognitive functions.

Second, significant findings were not apparent in all DTI measures. The only relationship between white matter measures and the face memory task were found in FA. This is true for both the IFOF and ILF. In the IFOF, the only relationship between emotion recognition and white matter was also with FA. However, in the ILF, AD was the measure that predicted performance on the emotion recognition task. These results are not terribly surprising, however, as many studies report significant findings in only some white matter indices (e.g. Thomas et al., 2008).

Also, although we observed variability in participants' behavioral performance, our cohort was more homogenous than the U.S. population at large, since our participant pool consisted largely of university undergraduate and graduate students. The study of individual differences is reliant on sufficient variability in both brain and behavior, which is limited in a healthy, young population. Nevertheless, we found robust brain-behavior correlations that were consistent with the existence literature. We find this encouraging since much of the theory building in cognitive neuroscience is pursued in neurologically normal sample populations similar to the one we tested.

Finally, due to the analysis method we use in this paper (diffusion tensor imaging), we cannot conclude that some participants had better white matter connectivity than others, nor can we conclude that better or worse white matter connectivity was the cause of better performance on our tasks (Jones, 2008). Indeed, many studies report that increased microstructural measures are related to increased task performance (e.g. Alm et. Al, 2015); however, others report that decreased microstructural measures are related to increased task performance (e.g. Hoeft et. Al, 2006,). Thus, in this report we can only conclude that microstructural differences in white matter are related to task performance differences.

Conclusions

The vast majority of DTI studies investigate the functionality of white matter in clinical populations who suffer from a range of deficits and often have widespread brain pathology. Here, we examined microstructural differences in a sample of healthy young adults in order to provide a baseline for future investigators interested in understanding the behavioral significance of variability in structural connectivity. Our results show that the ILF and IFOF both play an important role in facilitating one's ability to discern facial emotions as well as one's ability to remember new faces.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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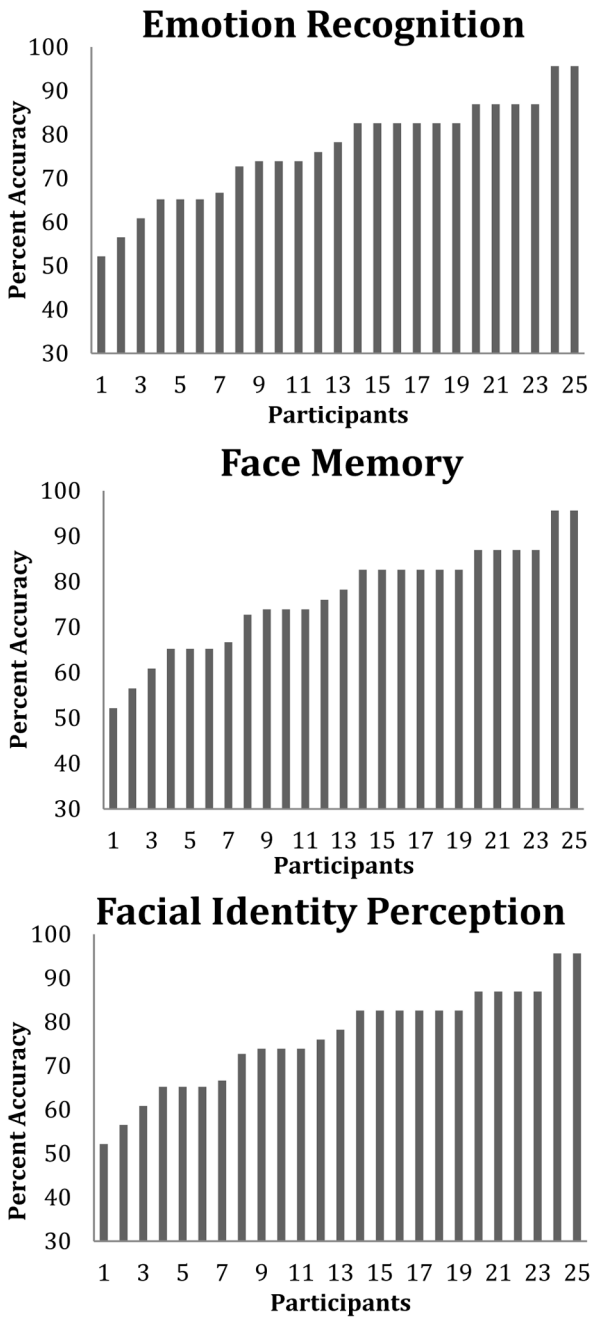

Figure 1.

Variability in scores for each task. On the x-axis is an arbitrary subject number. On the y-axis is performance accuracy. From left to right is the lowest performing participant to the highest performing participant.

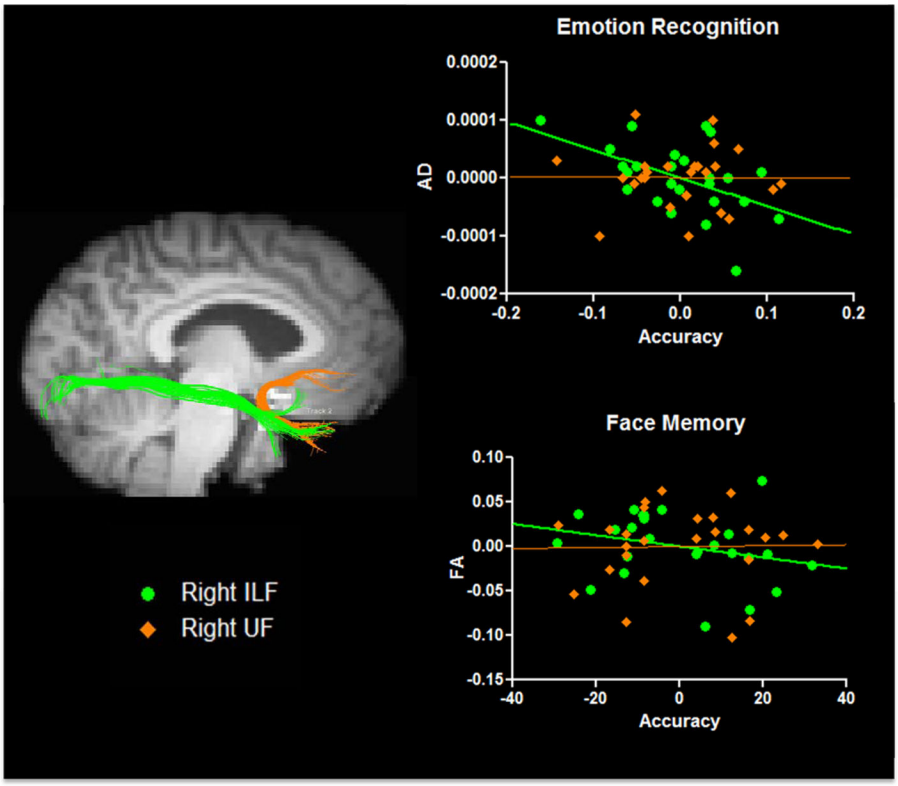

Figure 2.

Unstandardized residuals are graphed. Individual differences in ILF microstructure (green tracts and circles) predicted emotional discrimination accuracy and face memory accuracy. Variation in a control tract, the UF (orange tracts and diamonds), did not significantly predict behavioral performance in either measure.

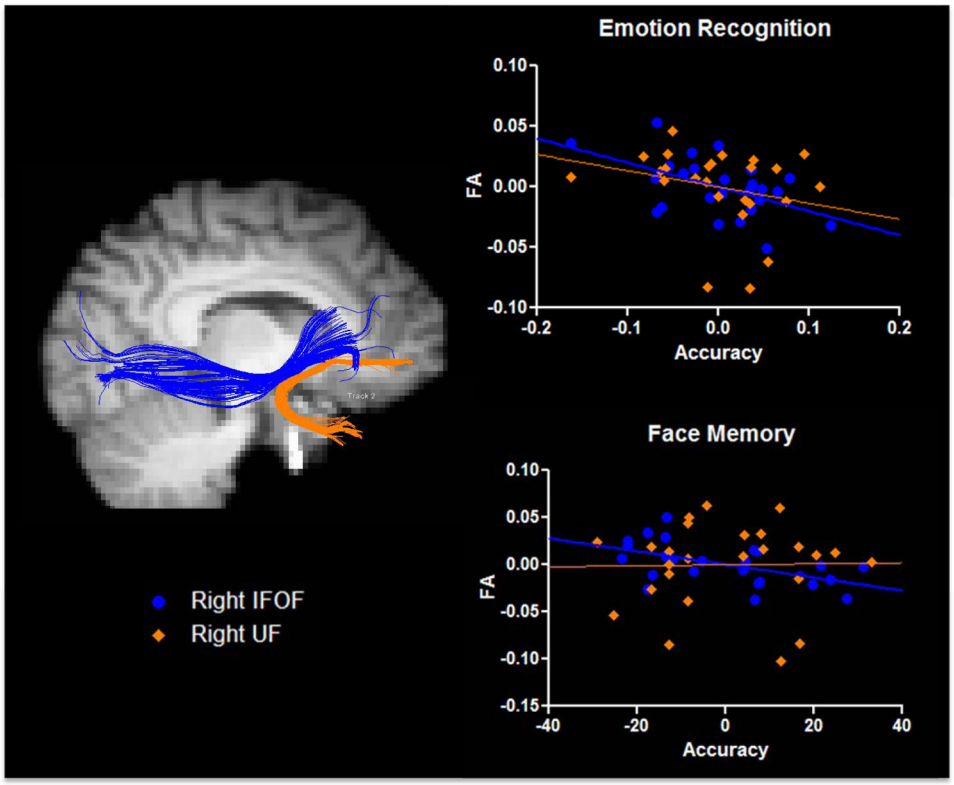

Figure 3.

Unstandardized residuals are graphed for face memory and emotion recognition tasks. Individual differences in IFOF microstructure (blue tracts and circles) predicted emotion recognition accuracy and face memory accuracy. Variation in a control tract, the UF (orange tracts and diamonds), did not significantly predict behavioral performance in either measure.

Table 1

Summary of multiple linear regression models predicting individual differences in performance on the emotional recognition, face memory, and facial identity perception tasks. Bold font and asterisks denote $p < .05$ (after controlling for multiple comparisons). FA: fractional anisotropy AD: axial diffusivity, β: standardized regression coefficient

		Inferior Longitudinal Fasiculus				Inferior Fronto-Occipital Fasiculus				Uncinate Fasiculus			
Dependent Variable	**Predictor Variables**	***β***	***t***	***F***	***R²***	***β***	***t***	***F***	***R²***	***β***	***t***	***F***	***R²***
Emotion Recognition				1.34	.11			**4.2***	**.29***			1.02	.09
	Right FA	−.38	1.56			**−.83***	**2.89***			−.27	1.33		
	Left FA	.1	.4			.87	2.81			.08	.37		
Emotion Recognition				**3.54***	**.25***			.27	.03			.4	.044
	Right AD	**−.68***	**2.66***			−.14	.43			−.22	.95		
	Left AD	.46	1.82			−.23	.07			.16	.71		
Face Memory				**6.88***	**.39***			**8.64***	**.44***			1.85	.14
	Right FA	**−.61***	**2.67***			**1.88***	**4.13***			.04	.19		
	Left FA	−.01	.044			**−1.69***	**3.72***			.38	1.92		
Face Memory				.8	.07			.22	.02			4.29	.28
	Right AD	−.31	1.12			−.04	.11			−.35	1.95		
	Left AD	.08	.3			.17	.43			.41	2.27		
Facial Identity Perception				.02	.21			.28	.03			.21	.02
	Right FA	.05	.19			−.15	.42			−.001	.004		
	Left FA	−.16	.63			.25	.71			.14	.65		
Facial Identity Perception				.14	1.7			.1	.01			.024	.26
	Right AD	−.24	.88			.14	.44			−.07	.3		
	Left AD	.49	1.79			−.1	.31			.17	.72		