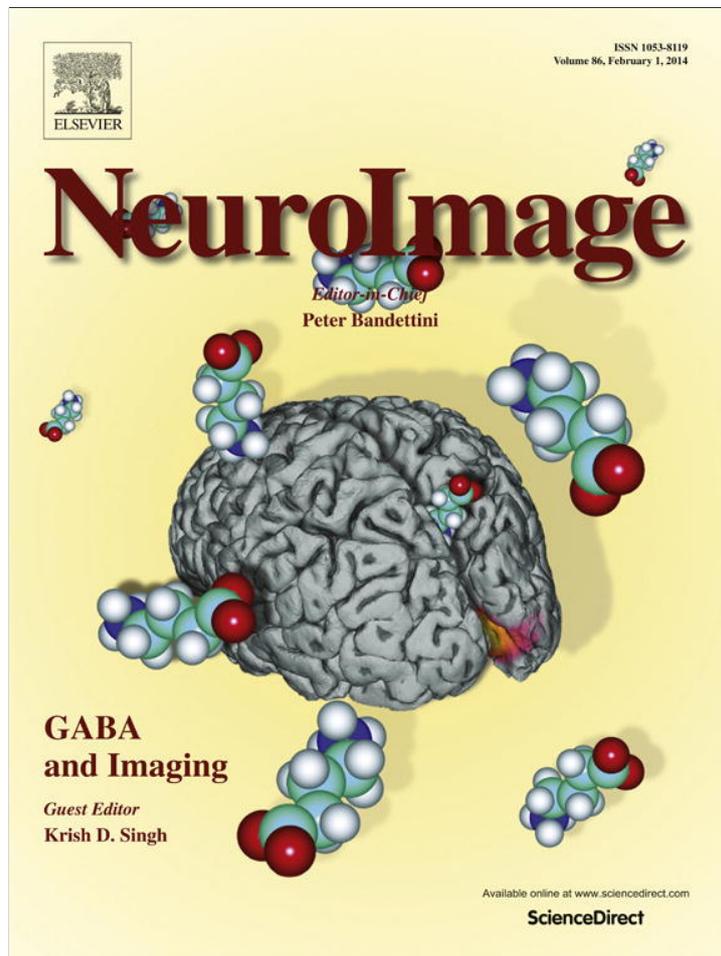


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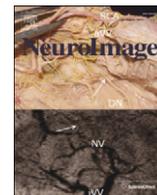
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Separate parts of occipito-temporal white matter fibers are associated with recognition of faces and places

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ABSTRACT

A central finding of functional MRI studies is the highly selective response of distinct brain areas in the occipital temporal cortex to faces and places. However, little is known about the association of white matter fibers with the processing of these object categories. In the current study we used DTI-based tractography to reconstruct two main fibers that connect the occipital lobe with the anterior temporal lobe (inferior longitudinal fasciculus-ILF) and with the frontal lobe (inferior fronto-occipital fasciculus-IFOF) in normal individuals. In addition to MRI scans subjects performed face, scene and body recognition tasks outside the scanner. Results show that recognition of faces and scenes were selectively associated with separate parts of the ILF. In particular, face recognition was highly associated with the fractional anisotropy (FA) of the anterior part of the ILF in the right hemisphere. In contrast, scene recognition was strongly correlated with the FA of the posterior and middle but not the anterior part of the ILF bilaterally. Our findings provide the first demonstration that faces and places are not only associated with distinct brain areas but also with separate parts of white matter fibers.

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Introduction

The ventral visual cortex contains several areas that show a highly selective response to certain object categories. These regions include areas selective for faces, bodies and scenes (for review see Kanwisher, 2010; Op de Beeck et al., 2008). Functional MRI (fMRI) studies have provided the primary source of information about the existence of such functional specialization and its anatomical organization. In particular, a much stronger response to faces than non-face objects has been found in the lateral occipital cortex, the fusiform gyrus and the superior temporal sulcus (for review see Kanwisher and Yovel, 2006) that is typically larger over the right than the left hemisphere (Yovel et al., 2008). More recently face-selective areas were also reported in the anterior temporal lobe (Pinsk et al., 2009; Rajimehr et al., 2009; Tsao et al., 2008) and the lateral prefrontal cortex (Avidan et al., 2005; Tsao et al., 2008). Similar selectivity to scenes was found in the parahippocampal gyrus (Epstein and Kanwisher, 1998), the retrosplenial cortex (Bar and Aminoff, 2003; Epstein, 2008) and the transverse occipital sulcus (Hasson et al., 2003; Epstein et al., 2005). Finally, body-selective areas were found next to the face-selective area in the fusiform gyrus

(Peelen and Downing, 2005; Schwarzlose et al., 2005) and the extrastriate occipital cortex (Downing et al., 2001).

Whereas this robust object-category selectivity has been extensively reported in numerous functional MRI studies an open question is whether the structural connections between those regions are also selective to the object category. Using diffusion weighted imaging and tensor analysis (Basser and Jones, 2002; Basser et al., 1994), recent studies suggest that indeed structural connectivity patterns and function categorization of the visual system are linked. For example, Saygin et al. have shown that white matter connectivity patterns may predict by itself the fusiform face-selectivity categorization (Saygin et al., 2011). Other studies have looked into the connectivity patterns either among different face-selective regions (Gschwind et al., 2011) or of face areas with non-face areas such as areas that process voice information (Blank et al., 2011).

While these studies inspected the macroscopic connectivity or probability for connectivity between regions, less attention was put on the micro-structural characteristics of these connections. Diffusion weighted imaging enables the estimation of several micro-structure parameters, the most common of them is fractional anisotropy (FA) which reflects, generally, fiber ordering (Assaf and Pasternak, 2008; Basser and Pierpaoli, 1996; Beaulieu, 2002). This micro-structural measure has been shown to be associated with various cognitive tasks (Dougherty et al., 2007; Frye et al., 2010; Lebel et al., 2010; Rudebeck et al., 2009; Sasson et al., 2010; Tuch et al., 2005).

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The inferior longitudinal fasciculus (ILF) and the inferior longitudinal fasciculus (IFOF) are the main fiber tracts that project through the occipito-temporal cortex and connect the occipital lobe to the temporal and frontal lobes, respectively (Thiebaut de Schotten et al., 2012b). The ventral visual stream, which processes visual information for the purpose of identification, follows the course of the ILF (Mishkin et al., 1983). The relevance of both the ILF and IFOF to face recognition was previously reported (Thomas et al., 2009).

In this study we explored whether the micro-structural properties of these specific occipito-temporal (ILF) and occipito-frontal (IFOF) projections are indicative of the visual system's object selectivity. Using the inter-subject variability in performance in an object recognition task (including stimuli for faces, scenes and bodies) we examined the role of white matter micro-structure (of the abovementioned fiber systems) in this cognitive phenomenon.

Materials and methods

Subjects

Twenty two healthy undergraduate students (ages 18–34; mean age = 24.7; SD = 3.2; six males, two left handed) participated in this study. Two subjects were excluded from the study, one of them due to severe image artifacts and the other because of poor performance on face recognition tasks (more than 2 standard deviations below average, in the range of prosopagnosia). Subjects received course credit for their participation in the behavioral study performed outside the scanner and \$12/h for participation in the MRI scan. Subjects had intact vision and no history of neurological diseases or psychological disorders. Subjects signed a consent form that was approved by the Tel-Aviv Medical Center Helsinki committee.

Procedure

Behavioral experiments

Subjects completed old/new recognition tasks for faces, scenes and bodies, in addition to other visual perception tasks designed to test different hypotheses.

Old/new object recognition tests. The old/new recognition test is composed of 2 phases: a study phase and a test phase. The study phase includes 20 stimuli. Each stimulus is presented for 500 ms followed by an inter-stimulus interval of 1500 ms before the presentation of the next stimulus. Participants were asked to look at the images and try to memorize them. Immediately after the study phase ends the test phase begins. The test phase includes 30 stimuli, each is presented for 500 ms followed by an inter-stimulus interval of 1500 ms. Of the 30 stimuli, 15 were presented in the study phase ('old') and 15 were new stimuli. Participants were asked to press one key if they thought they saw an old stimulus and another key for a new stimulus. We presented three such old/new recognition tests each presenting one of 3 different stimulus categories: faces, scenes or headless bodies. The order of the 3 memory tests was counterbalanced across subjects.

MRI acquisition

The MRI scan was performed in a separate session from the behavioral testing. The datasets were collected on a 3 T scanner (GE, Milwaukee WI) using a diffusion-weighted spin-echo echo-planar-imaging (DWI-EPI) pulse sequence. The dataset had the following parameters: TE = 80 ms; TR = 17,000 ms; $\Delta/\delta = 33/26$ ms; $b = 1000$ s/mm², with 19 noncolinear diffusion gradient orientations in addition to a nonweighted image (b_0). The images had a field of view (FOV) = 200×200 mm², over an 80×80 matrix, with 48 slices. Slice thickness was 2.5 mm, with no gap and a total scan time of about 10 min.

Data analysis

Recognition tasks

Old/new tasks. Percentage of correct responses averaged across old stimuli (i.e. an old response for a stimulus that was presented in the study phase) and new stimuli (i.e. a new response for a stimulus that was not presented in the study phase) was calculated for each subject for each of the old/new recognition tasks.

DTI analysis

All of the DWIs were coregistered using SPM2 (UCL, London, UK) to correct for head motion. Gradient orientations were compensated prior to the b-matrices calculation to account for the rotation component of the registration. The datasets were further normalized to the MNI coordinates, using 12-parameter affine transformation followed by non-linear transformations.

Post processing and visualization. Diffusion tensor analysis was done using an in-house software following the routine given in Basser and Pierpaoli (1998) to compute the diffusivities and the fractional anisotropy (FA) (Basser and Pierpaoli, 1996). A λ_1 map was referred to as the axial diffusivity, and the average of λ_2 and λ_3 was termed the radial diffusivity. Tractography was applied using the brute force FACT algorithm (Mori et al., 1999), terminating at voxels with FA lower than 0.2 or following tract orientation change higher than 60°. In this study we did not use a probabilistic approach as we aimed to reconstruct major fiber systems that are well defined (see below) using deterministic tractography (Catani et al., 2002; Mori and van Zijl, 2002). Tractography was used to reconstruct bilateral ILF and IFOF of each subject. Two Seed ROI were chosen on the coronal plane (one anterior and one posterior, see Figs. 1B and C), according to Mori et al.'s human white matter atlas (Mori et al., 2005). An example for a reconstructed ILF and IFOF is shown in Fig. 1A.

Statistical analysis

To avoid the large number of multiple comparisons of voxel-wise analysis, we chose an ROI-based approach by manually segmenting the fiber system into three regions: anterior, middle and posterior. For each subject we divided the fibers geometrically into three equal sections along the posterior–anterior axis. We averaged the FA for each section after excluding the 5% of the voxels that were outliers (i.e. the highest and lowest 2.5% values). All variables (i.e. the average FA of each part of the ILF and IFOF and scores in object recognition tasks) were checked for normality using the Lilliefors test, under the null hypothesis that each sample comes from a normally distributed population. At significance level of 0.05, we didn't reject the null hypothesis in any of the variables. Pearson correlation coefficients were computed between the FA of the posterior, middle and anterior parts of each fiber tract and performance on each of the object recognition tasks. False discovery rate (FDR) correction for multiple comparisons (Benjamini and Hochberg, 1995), resulted from the division of the two fibers to 3 sections each, was applied. Power analysis revealed that with a sample size of 20 and significance level of $\alpha = 0.05$, the power for rejecting the null hypothesis $H_0: \rho = 0$ whenever $|\rho| \geq 0.5$ is $1 - \beta = 0.70$.

Results

Behavioral results of the different recognition tasks are presented in Table 1. Data show overall similar performances across the three categories. Therefore, task difficulty cannot account for different correlations between DTI measures and different object categories.

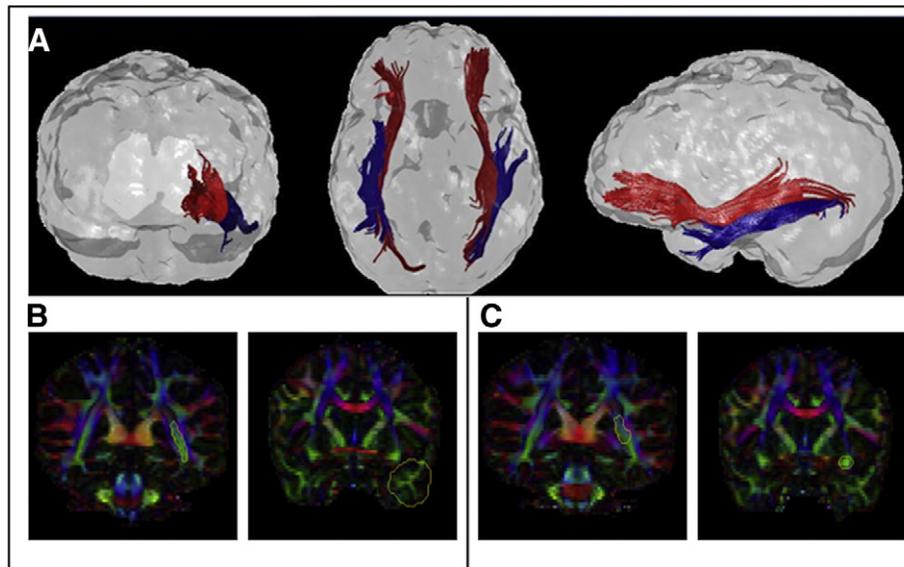


Fig. 1. (A) Tractography of the inferior longitudinal fasciculus (ILF, blue) and the inferior fronto-occipital fasciculus (IFOF, red) in frontal, axial and lateral views of the brain. Seed regions of interest (ROI) for the ILF and IFOF are shown in (B) and (C) respectively.

Correlations between behavioral and DTI measures

All correlation coefficients between recognition tasks and DTI measures are presented in Table 2 and summarized below.

Inferior longitudinal fasciculus

Fractional anisotropy

We divided the ILF into three sections and examined the correlation of each section with each of the memory tasks. Performance on the old/new face task was significantly correlated with the anterior part of the right ILF ($r = -0.60, p = 0.005$, see Fig. 2) but not with the anterior part of the left ILF or with the posterior and middle parts bilaterally. In contrast, performance on the old/new scene task was correlated with the FA of the posterior part of the fiber tracts bilaterally (right hemisphere: $r = -0.51, p = 0.02$; left hemisphere: $r = -0.66, p = 0.0015$), as well as with the middle section of the left ILF ($r = -0.52, p = 0.018$). The old/new scene task was not correlated with the anterior section of the ILF of neither hemisphere (Fig. 3). These findings suggest that recognition abilities for faces and places are associated with different sections of the ILF.

Axial and radial diffusivities

FA is a measure of the variance between the principal diffusivities (λ_1, λ_2 or λ_3). Thus, high FA values may reflect either high axial diffusivity, low radial diffusivity or both (Pierpaoli and Basser, 1996). Accordingly, the abovementioned correlations of behavior and FA may therefore reflect correlations with axial or radial diffusivities alone or with both of these measures together. To better understand the origin of the FA results, we also examined the correlations with the axial and radial diffusivities in fiber sections that showed significant behavior-

Table 1

Behavioral results.

	Face recognition	Scene recognition	Body recognition
Mean	0.79	0.74	0.78
Standard deviation	0.11	0.10	0.09

Average performance level and standard errors in old/new recognition tests for faces, scenes and bodies. The score was calculated as the proportion of correct answers in each test.

FA correlations. In the anterior right ILF we found significant positive correlation between the old/new face recognition score and radial diffusivity ($r = 0.452, P = 0.045$). Additionally, old/new scene recognition was correlated with radial diffusivity of the middle left ILF ($r = 0.47, P = 0.036$). No correlations were found between any of the recognition tasks and axial diffusivities.

Inferior fronto-occipital fasciculus

None of the recognition tasks was correlated with the FA of the IFOF (see Table 2).

As the IFOF is longer than the ILF, we also divided it into 4 sections instead of 3 in order to make each segment more comparable to the ILF segments. Nevertheless, we found no significant correlations between these 4 segments with performance on any of the object category memory tasks.

Discussion

Our findings reveal an association between object recognition abilities and microstructural characteristics of white matter fiber tracts in

Table 2

Correlations between FA of fiber tracts sections and recognition tasks.

			Face recognition	Scene recognition	Body recognition
Right ILF	FA	Anterior	-0.60*	-0.06	0.09
		Middle	-0.21	-0.22	0.14
		Posterior	0.30	-0.51*	-0.03
Left ILF	FA	Anterior	-0.29	0.01	0.45
		Middle	-0.02	-0.52*	0.20
		Posterior	-0.12	-0.66*	-0.24
Right IFOF	FA	Anterior	-0.14	-0.08	0.18
		Middle	-0.34	-0.15	0.05
		Posterior	0.33	-0.35	0.17
Left IFOF	FA	Anterior	-0.16	0.09	-0.10
		Middle	-0.12	-0.29	0.10
		Posterior	-0.37	-0.30	0.19

Pearson correlation coefficients were computed for the average FA of the anterior, middle and posterior sections of the reconstructed inferior longitudinal fasciculus (ILF) and inferior fronto-occipital fasciculus (IFOF), with recognition tasks scores.

* $p < 0.05$ (corrected for multiple comparisons using FDR).

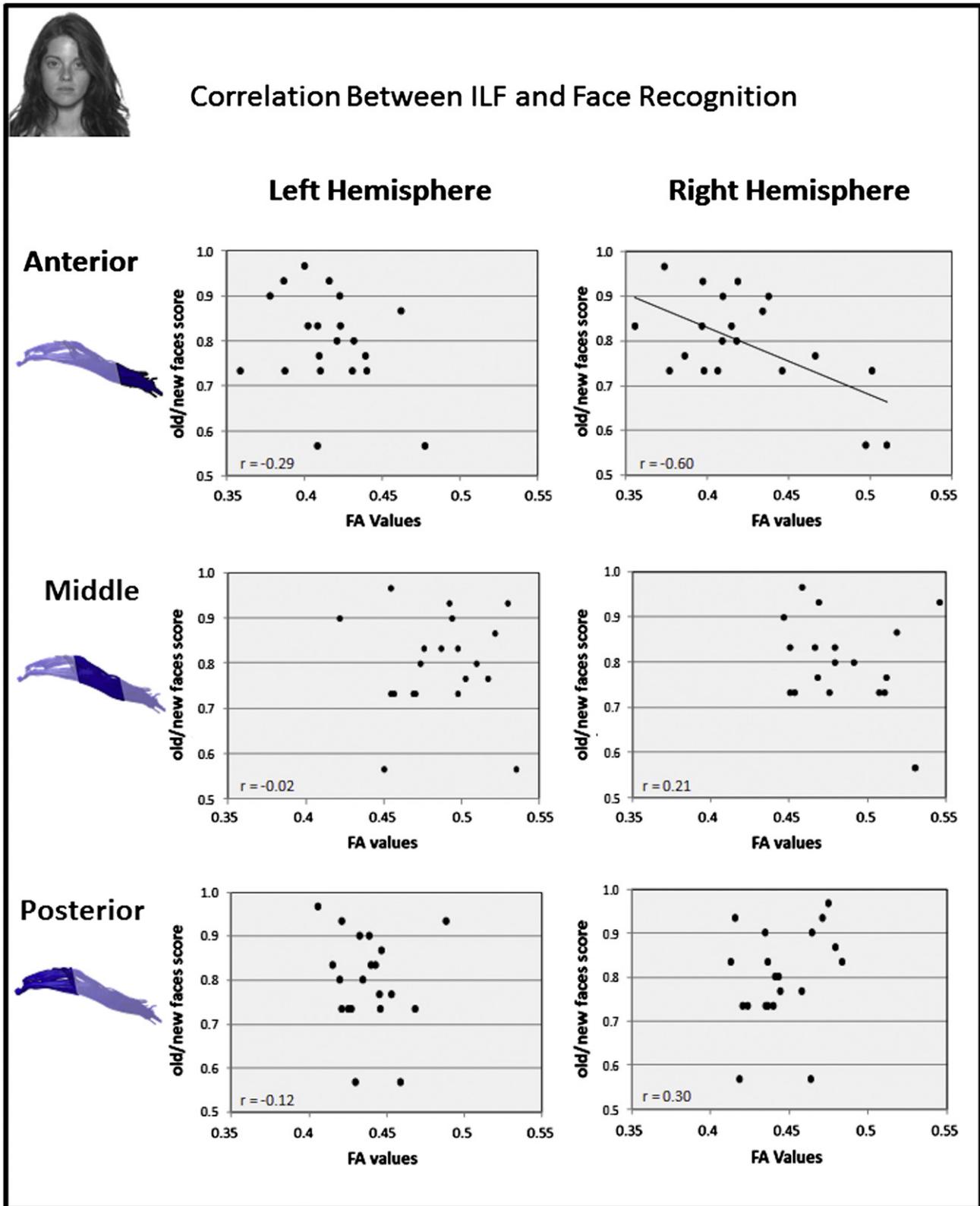


Fig. 2. Correlation between the fractional anisotropy (FA) of the inferior longitudinal fasciculus (ILF) and performance on the old/new face recognition task: Face recognition was correlated with the FA of the anterior and not middle or posterior ILF within the right hemisphere. Face recognition was not correlated with the FA of the left ILF.

the ventral occipito-temporal cortex. These results provide the first demonstration that faces and places are not only associated with selective neural response of distinct brain areas in the occipito-temporal cortex as seen with functional MRI, but also with micro-structural

characteristics of white matter fibers that connect the occipital and anterior temporal cortex. This observation implies that the functional selectivity affects not only the connectivity pattern (Saygin et al., 2011) but also the composition of the fiber system (which is reflected by the

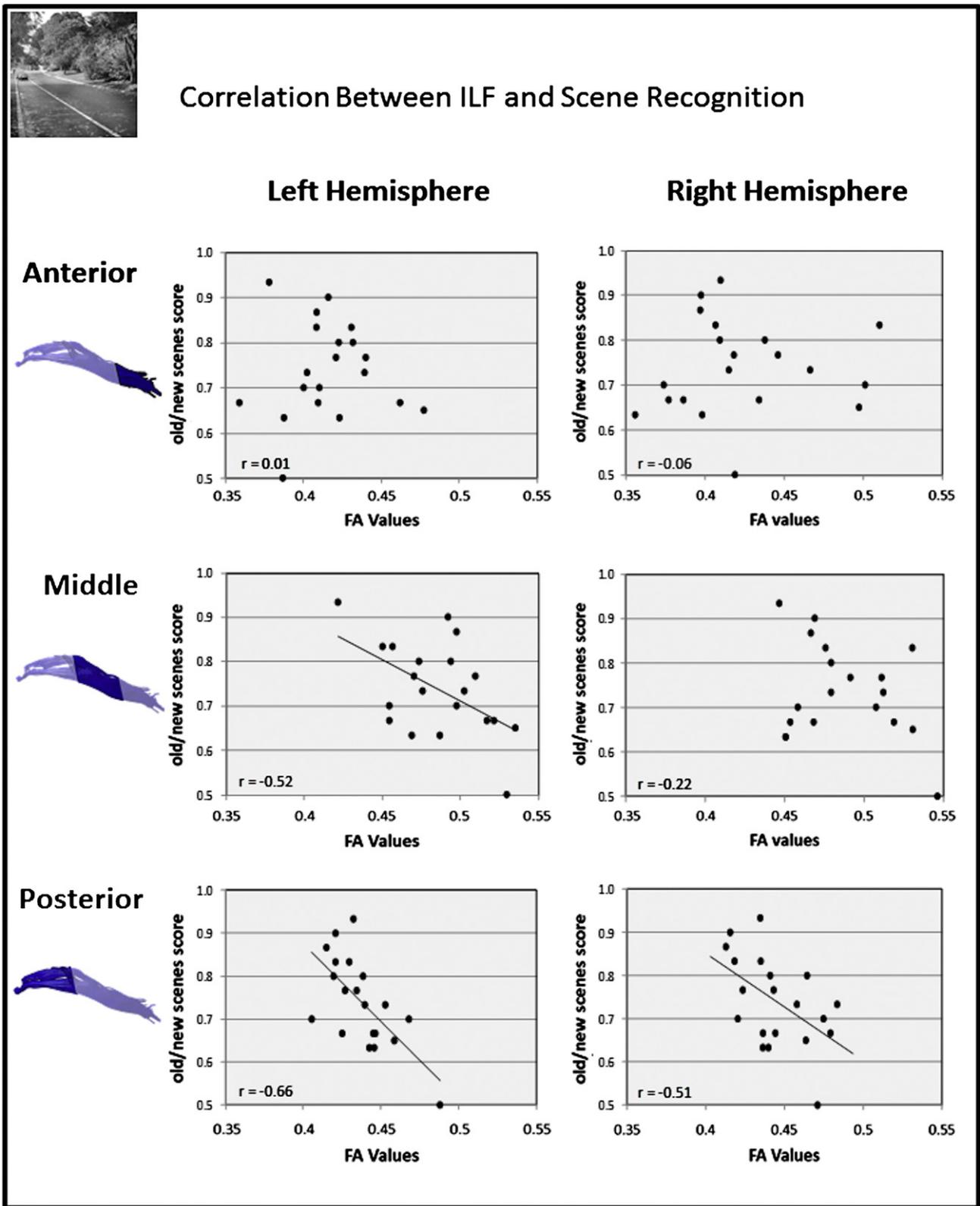


Fig. 3. Correlation between the fractional anisotropy (FA) of the inferior longitudinal fasciculus (ILF) and performance on the old/new scene recognition task: Scene recognition was correlated with the FA of the middle and posterior, but not anterior, ILF, bilaterally.

diffusion quantitative measures). Importantly, our observations suggest that different sections of the ILF are associated with different object categories indicating that this fiber system is composed of several bundles, each having different functional specialization.

Different parts of the ILF are associated with different object categories

We found different patterns of association of white matter fibers with different object categories: while scene recognition was correlated

with diffusion properties of the ILF in both hemispheres, face recognition was correlated only with the right ILF. The correlation of face recognition with the right but not the left ILF is consistent with the dominance of the right hemisphere in face recognition (Luh et al., 1991; Rhodes, 1985; Sergent and Bindra, 1981). This right hemisphere superiority has been demonstrated both with fMRI that typically show larger face activations over the right than left hemisphere (Kanwisher et al., 1997; Yovel et al., 2008) as well as in behavioral studies showing better performance for faces presented in the left than the right visual fields (Levine et al., 1988; Levy et al., 1972, 1983; Rhodes, 1985; Sergent and Bindra, 1981).

Dissociation between faces and scenes was also found in the posterior–anterior axis. Face recognition was highly correlated with the anterior part of the right ILF, whereas scene recognition was highly correlated with the middle and posterior parts bilaterally. Correlation between the anterior section of the ILF and face recognition is consistent with recent studies which revealed a face-selective area in the anterior temporal lobe (Tsao et al., 2008; Axelrod and Yovel, 2013). This region is considered to be homologs to the anterior temporal face patch found in macaque (see also Pinsk et al., 2009; Rajimehr et al., 2009) and has been shown to be tuned to the processing of face identity (Freiwald and Tsao, 2010). In a voxel-based morphometry (VBM) study, Garrido et al. (2009) also suggest the involvement of an anterior temporal region in face recognition ability. Consistent with these findings, Krigerskorte and colleagues have recently revealed that voxels in the anterior temporal lobe but not in the core face-selective network, showed beyond chance classification of face identity information (Kriegeskorte et al., 2007) and suggest that anterior rather than posterior face areas are engaged in face recognition. Recently, however, Nestor and colleagues showed that in addition to the anterior temporal cortex, the fusiform face area also showed beyond chance classification of face-identity information (Nestor et al., 2011). This further implies the importance of connectivity between occipito-temporal face-selective regions and anterior areas. Taken together, these findings suggest a role for the anterior temporal lobe in face recognition abilities in particular over the right hemisphere and are consistent with our findings that diffusion properties of the right anterior temporal white matter are correlated with behavioral measures of face recognition.

In addition to the correlations that we found with face recognition abilities, diffusion properties were also correlated with recognition abilities of scenes. In strong contrast to the correlation that we found with face recognition abilities in the right anterior ILF, scene recognition was associated with diffusion properties in posterior and middle sections of the ILF in both hemispheres. These findings may be consistent with the location of scene selective areas that are found in the occipital lobe (TOS), the retrosplenial region (RSC) and the mid temporal cortex (PPA). To the best of our knowledge no scene regions were reported in the anterior part of the temporal lobe. The correlation found between the scene recognition task and the FA of the posterior ILF further implies the involvement of dorsal occipital white matter fibers, which may be connected with the TOS, in the visual processing of scenes. Finally, our data show no correlations between any section of the ILF and body recognition tasks. These findings further suggest that the diffusion properties of the FA do not reflect general object recognition abilities, but are selectively associated with different object categories that may correspond to the location of the category-selective areas in the occipito-temporal cortex.

Significance of correlations of FA with recognition abilities

The correlations that we found between FA and recognition abilities were negative. Thus, high FA values were associated with lower recognition scores. These findings contrast with Thomas et al. (2008) that found lower FA values in individuals with prosopagnosia than in controls. However, a close inspection of the scatterplot of the healthy control group alone shows that despite the fact that as a group they

showed a higher FA value, within the control group such a relation does not exist. These findings suggest that differences between normal and pathological groups are not necessarily comparable to differences within the normal population.

Furthermore, although FA is considered a micro-structure probe of white matter, the cellular correlates of FA are not clear and therefore the biological interpretations of these results are not certain. Many factors may affect water anisotropy and consequently the FA value of a given fiber (myelin, cell membrane, axonal diameter and density, etc.) (Assaf and Pasternak, 2008; Barazany et al., 2009; Beaulieu, 2002; Song et al., 2005), and each of these factors can influence axonal conduction velocity (Hursh, 1939; Waxman and Bennett, 1972) and thereby relate to cognitive performance (Thiebaut de Schotten et al., 2011). For example, the thickness of the myelin layer and the diameter of the axon are positively correlated with conduction velocity, but have opposite correlations with FA. Specifically, while the myelin layer hinders water diffusion perpendicular to the axons and therefore positively correlated with FA, the axon diameter is negatively correlated with FA. Thus, the fact that both positive (Klingberg et al., 2000; Madden et al., 2004; Thiebaut de Schotten et al., 2012a) and negative correlations (Frye et al., 2010; Lebel et al., 2010; Tuch et al., 2005) were previously found between FA and different cognitive scores may reflect different underlying biological factors. Accordingly, the low FA in prosopagnosic individuals may reflect effects of demyelination, whereas the negative correlations with FA that we found in the normal population may be related to axon diameter. Negative correlations with FA can also be associated with an increase of local connectivity which may decrease FA by increasing the crossing-fibers effect within the measured voxel. In that case, low FA will be an indication of the complexity of the tissue and not of axon diameter (Johansen-Berg, 2010; Thiebaut de Schotten et al., 2012a).

One way to uncover which of the abovementioned factors underlies the correlation between behavioral measures and FA (e.g., axon diameter, myelin content, axonal density) in our study is to separately examine the correlations of the behavioral measures with axial and radial diffusivities. Concomitantly to negative FA correlation with face recognition, we found a positive correlation between radial diffusivity with performance on face and scene recognition. Radial diffusivity has been shown to be positively associated with demyelination (Song et al., 2005) as well as with axon diameter (Barazany et al., 2009). Whereas, less myelin is not likely to positively influence behavior, our finding suggests that axon diameter might be the factor underlying the correlation between face recognition abilities and FA. Thus, the negative correlations between FA and behavioral performance suggest that better performance was associated with larger axon diameter. It is noted that other factors such as fiber complexity and geometry may also influence FA values (Johansen-Berg, 2010). Further research using advanced techniques such as CHARMED (Assaf and Basser, 2005), AxCaliber (Barazany et al., 2009) or ActiveAx (Alexander et al., 2010), measuring axon diameter and density, is required in order to fully understand the relation between tissue microstructure, diffusion MRI and behavior.

Limitations

This study uses basic DTI acquisition and analysis routines. A protocol of 19 gradient orientations, the usage of SPM2 for motion correction and the FACT algorithm for tractography are basic procedures compared with recently introduced advanced tools (high-angular-resolution diffusion imaging (HARDI) or probabilistic tractography algorithms). Although there are newer methods for motion correction, we find the used routine sufficient for our purposes. Importantly, the association between face or scene recognition with different segments of the ILF cannot be explained by motion or registration artifacts. As for the tractography routine, the main drawback of the FACT algorithm is the usage of a single tensor model with a deterministic tracing approach, hence the inability to deal with crossing fibers. However, this is not an

issue in the inferior longitudinal fasciculus (or the inferior fronto-occipital fasciculus) that can be reconstructed accurately using the FACT algorithm, as demonstrated by Catani et al. (2002) and Mori et al. (2005).

Conclusion

Our study reveals an association between micro-structural characteristics of occipito-temporal white matter to visual recognition abilities. Importantly, we found that recognition for faces and scenes was correlated with different sections of the ILF. Face recognition correlated with right anterior parts of the reconstructed tract, whereas scene recognition was correlated with its posterior and middle parts bilaterally. The ability to recognize and perceive faces requires complex mechanisms, involving several brain regions and the connectivity between them. White matter fiber tractography can be used to investigate these connections within the normal population and shed light on the way objects are being processed. The results of this study also suggest that different sections within the ILF are responsible for different visual processes which may have developed differently (within the same major pathway) to account for the different responses in object recognition of various stimuli. We conclude that although the ILF connects specific brain regions, using correlation with inter subject variability in object recognition task, the functional role of its different parts can be explored.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2013.07.085>.

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