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Monkey to human comparative anatomy of the frontal lobe association tracts

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ABSTRACT

The greater expansion of the frontal lobes along the phylogeny scale has been interpreted as the signature of evolutionary changes underlying higher cognitive abilities in humans functions in humans. However, it is unknown how an increase in number of gyri, sulci and cortical areas in the frontal lobe have coincided with a parallel increase in connectivity. Here, using advanced tractography based on spherical deconvolution, we produced an atlas of human frontal association connections that we compared with axonal tracing studies of the monkey brain. We report several similarities between human and monkey in the cingulum, uncinata, superior longitudinal fasciculus, frontal aslant tract and orbito-polar tract. These similarities suggest to preserved functions across anthropoids. In addition, we found major differences in the arcuate fasciculus and the inferior fronto-occipital fasciculus. These differences indicate possible evolutionary changes in the connectational anatomy of the frontal lobes underlying unique human abilities.

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1. Introduction

Comparative anatomy studies have shown that the frontal lobes have expanded more than any other brain region along the phylogeny scale, reaching its greatest relative size in great apes and humans (Semendeferi et al., 2002). The relative volume expansion along the phylogeny scale is also

accompanied by changes in other anatomical features, such as increase in the gyrification index (Zilles et al., 1988, 1989), cortical volume (Hofman, 1985, 1988) and density of synapses (Rockel et al., 1980; Chklovskii et al., 2002; DeFelipe et al., 2002; Emes et al., 2008). In addition, other changes such as the increase in relative size of area 10 (Semendeferi et al., 2001; Petrides et al., 2012, this issue) and the relative quantity of

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frontal white matter (i.e. frontal hyperscaling of white matter; Smaers et al., 2010, 2011) have been reported as primary factors underlying the evolution of primate brain architecture. This suggests that the evolution of complex human cognitive abilities is mediated by frontal connectivity (Sherwood et al., 2005). Most of the evidences related to the hyperscaling of the frontal connections are derived from volumetric measures of the entire frontal lobe. Whether such anatomical differences are general or specific to distinct pathways is unknown.

The connectivity of the monkey frontal lobe has been studied in detail using axonal tracing (Yeterian et al., 2012, [this issue](#)). The monkey pattern of connectivity is often transposed to humans, an assumption that may not hold true, especially for the frontal lobes. Axonal tracing methods are not suitable to study human connections, recent developments in diffusion imaging tractography (Le Bihan and Breton, 1985; Moseley et al., 1990; Basser et al., 1994; Jones et al., 1999; Mori et al., 1999) offer a valid alternative to visualise the in vivo organisation of human brain pathways. Preliminary tractography studies suggest that some connections (e.g., uncinate fasciculus) as described in the monkey brain, are also found in the human brain (Catani et al., 2002). Other tracts have been described in humans but not in monkeys (e.g., inferior fronto-occipital fasciculus; Catani 2007; Schmahmann and Pandya, 2007; Schmahmann et al., 2007). However, direct comparisons between the detailed anatomical connections of the human and monkey brain are not available.

Therefore in this study, we used tractography to build an atlas of human frontal connections for a direct comparison with a recent atlas of the fibres pathways of the monkey brain (Schmahmann and Pandya, 2006). To increase the quality of the in vivo human reconstructions, we have used tractography based on Spherical Deconvolution (SD) imaging (Tournier et al., 2004; Dell'Acqua et al., 2007). SD is a new method that has recently been developed to partially overcome the limitations of classical diffusion tensor tractography (Basser et al., 2000; Jones, 2008). It has the ability to identify and quantify the orientation of different populations of fibres within a single voxel (Tournier et al., 2007; Dell'Acqua et al., 2010). Preliminary results using SD tractography show anatomical features that have close correspondence to axonal tracing studies (Dell'Acqua et al., 2008; Thiebaut de Schotten et al., 2011a). In this study the main association tracts of the human frontal lobe derived from SD tractography are compared to classical axonal tracing findings of equivalent tracts in the monkey brain. Our aim is to highlight human–simian similarities and differences, in order to understand the anatomical substrates underlying development of higher cognitive functions.

2. Method

2.1. Magnetic resonance data acquisitions

A single 29-year-old, right-handed subject (the first author) gave informed consent to participate to this study.

A total of 70 near-axial slices were acquired on a Siemens 3 Tesla TRIO TIM system equipped with a 32-channel head coil. We used an acquisition sequence, fully optimised for advanced tractography of diffusion-weighted imaging (DWI), which

provided isotropic ($2 \times 2 \times 2$ mm) resolution and coverage of the whole head. The acquisition was peripherally-gated to the cardiac cycle with an echo time (TE) = 85 msec and repetition time (TR) equivalent to 24 RR intervals. At each slice location, 3 images were acquired with no diffusion gradient applied. Additionally, 64 diffusion-weighted images were acquired at each slice location, in which gradient directions were uniformly distributed in space. The diffusion weighting was equal to a b -value of 2000 sec mm^{-2} . To increase signal to noise ratio (SNR) the whole acquisition was repeated 4 times. Raw diffusion-weighted data were up-sampled to $1 \times 1 \times 1$ mm with a 3rd order b -spline interpolation. An axial three-dimensional MPRAGE dataset covering the whole head was also acquired (176 slices, voxel resolution = $1 \times 1 \times 1$ mm, TE = 4.2 msec, TR = 2.3 msec, flip angle = 9°).

2.2. Correction of motion and eddy current distortion, and estimation of the fibre orientation distribution

The 4 repeated DWI datasets were concatenated, simultaneously registered, and corrected for subject motion and geometrical distortions using ExploreDTI (<http://www.exploredti.com>; Leemans and Jones, 2009). A SD (Tournier et al., 2004, 2007) approach was chosen to estimate multiple orientations in voxels containing different populations of crossing fibres (Alexander, 2006). SD was calculated applying the damped version of the Richardson–Lucy algorithm (Dell'Acqua et al., 2010). The high SNR of the data allowed us to apply a relatively low regularisation threshold equal to $\eta = .01$ without an excessive increase of spurious fiber orientation distribution (FOD) components. We used a fibre response function equivalent to a tensor of $[1.5 \ .3 \ .3] \times 10^{-3} \text{mm}^2 \text{ sec}^{-1}$, 200 algorithm iterations and $\nu = 8$ as previously optimised in (Dell'Acqua et al., 2010). Fibre orientation estimates were obtained by selecting the orientation corresponding to the peaks (local maxima) of each FOD profile. To exclude spurious local maxima, we applied an absolute and a relative threshold. A first “absolute” threshold was used to exclude small local maxima due to noise or isotropic tissue. This threshold is three times the amplitude of a spherical FOD obtained from a grey matter isotropic voxel. A second “relative” threshold of 5% of the maximum amplitude of the FOD was applied to remove the remaining local maxima with values greater than the absolute threshold (Dell'Acqua et al., 2009).

2.3. Tractography algorithm

Whole brain tractography was performed selecting every brain voxel with at least one fibre orientation as a seed voxel. From these voxels and for each fibre orientation streamlines were propagated using an Euler integration with a step size of .5 mm and an angular threshold of 45° . When entering a region with crossing white matter bundles, the algorithm followed the orientation vector of least curvature (as described in Schmahmann et al., 2007). Streamlines were halted when a voxel without fibre orientation was reached or when the curvature between two steps exceeded a threshold of 45° . SD, fibre orientation vector estimation and tractography were performed using in house software developed with Matlab 7.8 (<http://www.matwork.com>).

2.4. MPRAGE dataset and tractography registration to the MNI

The skull was extracted from the MPRAGE dataset using Brain Extraction Tool (BET) provided in FMRIB Software Library (FSL, <http://www.fmrib.ox.ac.uk/fsl>). The skull-stripped MPRAGE dataset was then registered to the B0 volume of the diffusion-weighted dataset using affine (FMRIB's Linear Image Registration Tool, FLIRT) deformation provided in FSL. The registered MPRAGE dataset was then normalised to the stereotaxic Montreal Neurological Institute space (MNI, <http://www.bic.mni.mcgill.ca/>), using affine deformations to the MNI template as provided in FSLview (MNI152_T1_1mm_brain). A similar approach has been described in a previous study (Thiebaut de Schotten et al., 2008).

The full brain tractography was normalised to the MNI space using the transformation matrix derived from the process of normalisation of the registered MPRAGE dataset with the tool "Transform Track" provided in Diffusion Toolkit (<http://www.trackvis.org>; Wedeen et al., 2008).

Binary visitation masks were created for each of the tracts. Binary visitation maps were created from the tractography results by assigning each voxel a value of 1 or 0 depending on whether the voxel was intersected by the streamlines of the tract (Ciccarelli et al., 2003; Catani et al., 2007; Lawes et al., 2008; Thiebaut de Schotten et al., 2011b).

A 3d rendering of the brain and high contrast coronal slices were created in the MNI using the T1 pipeline in Brainvisa (<http://brainvisa.info>).

2.5. Tractography dissections of the human brain

Tractography dissections were performed by two expert neuroanatomists who combined the information provided from a monkey brain atlas (Schmahmann and Pandya, 2006) and a recent human brain atlas (Catani and Thiebaut de Schotten, *in press*). A one-region of interest (ROI) approach was used for the cingulum. A two-ROIs approach was used for the uncinate and the inferior fronto-occipital fasciculus as described in Catani and Thiebaut de Schotten (2008). A multiple ROIs approach was used to isolate the three components of the Superior Longitudinal Fasciculus as described in Thiebaut de Schotten et al. (2011a).

A two-ROIs approach was used to separate subcomponents of the arcuate fasciculus (Catani et al., 2005, 2007; Glasser and Rilling, 2008). A two-ROIs approach was also used to extract the frontal aslant tract connections from the Broca territory to the supplementary motor area (SMA) and PreSMA (Lawes et al., 2008; Oishi et al., 2008). For the orbito-polar tract the two ROIs were drawn in the frontal pole and in the post-orbital gyrus.

2.6. Meta-analyses of the rhesus monkey atlas

The monkey maps of the cingulum (Fig. 1), superior longitudinal fasciculus (Fig. 2), arcuate fasciculus (Fig. 3), inferior fronto-occipital fasciculus (Fig. 4), uncinate fasciculus (Fig. 5), frontal aslant tract (Fig. 6) and orbito-polar tract (Fig. 7), are derived from an atlas of monkey brain. The atlas uses an anterograde tract-tracer technique, using a radiolabeled

isotope (Schmahmann and Pandya, 2006). This tracer shows connections emerging from the injected site an projection to cortical areas. Projection, commissural and irrelevant association fibres have been removed for visualisation purposes.

For the cingulum, coronal slices of monkey case 22 (Vogt and Pandya, 1987; Schmahmann and Pandya, 2006) were used and only association fibres coloured in red (see Fig. 1). Case 22 was injected in the retrosplenial cortex (areas 23 and 30).

For the first branch of the superior longitudinal fasciculus (SLF I), coronal slices of cases 1 and 2 were used and only association fibres coloured in red (Seltzer and Pandya, 1980; Pandya and Seltzer, 1982; Schmahmann and Pandya, 2006) (see Fig. 2). Case 1 was injected in the medial convexity of the superior parietal lobule (areas PGm and PEc) and case 2 in the caudal superior parietal lobule (areas PEc and PE).

For the second branch of the superior longitudinal fasciculus (SLF II), coronal slices of cases 3 and 4 were used and only association fibres coloured in yellow (Seltzer and Pandya, 1980; Pandya and Seltzer, 1982; Schmahmann and Pandya, 2006) (see Fig. 2). Case 3 was injected in the caudal superior parietal lobule more laterally than case 2 (lateral portion of area PEc), and case 4 was injected in the inferior parietal lobule (areas PG and Opt).

For the third branch of the superior longitudinal fasciculus (SLF III), coronal slices of cases 5 and 6 were used and only association fibres coloured in green (Seltzer and Pandya, 1980; Pandya and Seltzer, 1982; Schmahmann and Pandya, 2006) (see Fig. 2). Case 5 was injected in the rostral inferior parietal lobule (area PF) and case 6 in the middle part of the parietal operculum (ventral portion of area PF).

For the arcuate fasciculus, coronal slices of cases 7–9 were used and only association fibres coloured in red (Seltzer and Pandya, 1978, 1989; Galaburda and Pandya, 1983; Schmahmann and Pandya, 2006) (see Fig. 3). Case 7 was injected in the caudal part of the superior temporal gyrus (area Tpt) and case 8 more ventrally, in the caudal part of the superior temporal gyrus (areas Tpt and paAlt). Case 9 was injected in the lateral part of the cortex of the upper bank of the superior temporal sulcus (area TPO), the ventral part of the superior temporal gyrus (area TAa) and the caudal part of the primary auditory area in the supratemporal plane (area KA).

For the longitudinal fibres of the external/extreme capsule, coronal slices of cases 31 and 32 were used and only association fibres coloured in red (Petrides and Pandya, 1994; Schmahmann and Pandya, 2006) (see Fig. 4). Case 31 was injected in the prefrontal cortex above the midportion of the principal sulcus (area 9/46d) and case 32 below the midcaudal portion of the principal sulcus (area 9/46v).

For the uncinate, coronal slices of cases 13 and 14 were used and only association fibres coloured in red (Seltzer and Pandya, 1978; Schmahmann and Pandya, 2006) (see Fig. 5). Case 13 was injected in the ventral temporal region (area TF) and case 14 in the cortex of the lower bank of the superior temporal sulcus (area IPa).

For the frontal aslant tract, coronal slices of case 25 were used and only association fibres coloured in red (Petrides and Pandya, 1994; Schmahmann and Pandya, 2006) (see Fig. 6). Case 25 was injected in the ventral part of the precentral gyrus (area 4) corresponding to the area of the face.

For the orbito-polar tract, coronal slices of case 33 were used and only association fibres coloured in red (Petrides and

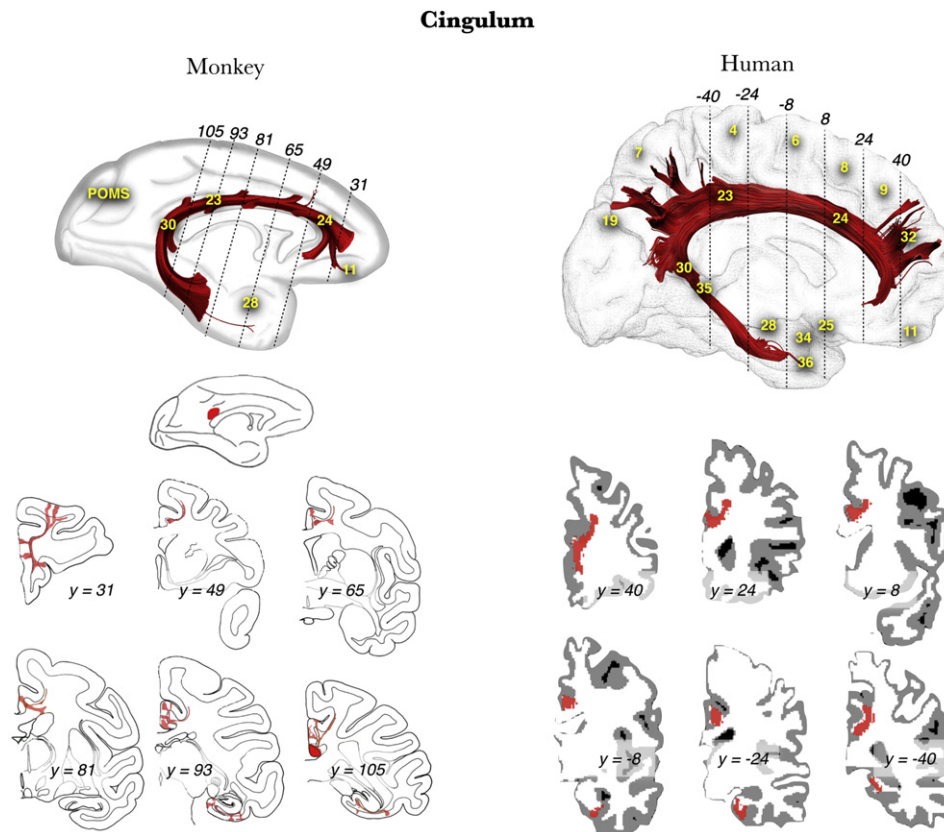


Fig. 1 – Reconstruction of the cingulum: comparison between post-mortem axonal tracing in monkey (case 22 modified from Schmahmann and Pandya, 2006) and human in vivo SD tractography shows simian-human similarities.

Pandya, 1994; Schmahmann and Pandya, 2006) (see Fig. 7). Case 33 was injected in the orbital frontal cortex, encroaching posteriorly on the insular proisocortex (area 47/12).

3. Results

In the human brain, we were able to identify all major long-range association pathways previously described in the monkey brain. We were also able to visualize short-range intralobar frontal connections. For the monkey brain, the cortical projection are indicated using a contemporary international nomenclature (Von Bonin and Bailey, 1947; Paxinos et al., 1999; Schmahmann and Pandya, 2006) while for the human brain we used Brodmann areas (Brodmann, 1909). Correspondence between the two nomenclatures applied to the frontal lobe are discussed in detail in Petrides et al. (this issue).

3.1. Long-range association pathways

Long-range association pathways are defined in this study as inter-lobar connections (i.e. between frontal and other lobes). Long-range association pathways of the frontal lobe include the cingulum (Fig. 1), the superior longitudinal fasciculus (Fig. 2), the arcuate fasciculus (Fig. 3), the inferior fronto-occipital fasciculus (Fig. 4) and the uncinate fasciculus (Fig. 5).

3.1.1. Cingulum bundle

In humans, the cingulum is a sickle-shaped tract composed of fibres of different lengths. The longest fibres run from the amygdala, uncus (BA 35) and parahippocampal gyrus (BA 36 and 30) to sub-genual areas of the orbito-frontal lobe (BA 25 and 11) (Crosby et al., 1962; Nieuwenhuys et al., 2008). Shorter fibres, that join and leave the cingulum along its length, connect to adjacent areas of the cingulated cortex (BA 23 and 24), superior medial frontal gyrus (BA 32, 6, 8 and 9), paracentral lobule (BA 4), precuneus (BA 7), cuneus (BA 19), lingual (BA 18 and 19), and fusiform gyri (BA 19 and 37) (Dejerine, 1895; Nieuwenhuys et al., 2008). The cingulum can be divided into an anterior-dorsal component (the blade of the sickle), which forms most of the white matter of the cingulate gyrus, posterior precuneus (BA 7 and 19), and a posterior-ventral component (the handle of the sickle) running within the parahippocampal gyrus (BA 34 and 28), retrosplenial cingulate gyrus (BA 26, 19 and 30) (Fig. 1).

In the monkey brain, the cingulum has a very similar shape to humans, and its dorsal projections terminate in the rostral cingulate cortex (area 24), orbital cortex (area 11) and medial parietal cortex (area PG/Opt). The ventral component of the cingulum projects posteriorly to the parietal occipital medial sulcus (POMS) and ventrally to the presubiculum, parahippocampal gyrus, entorhinal cortex (area 28) and amygdala (Mufson and Pandya, 1984; Vogt and Pandya, 1987; Schmahmann and Pandya, 2006).

Overall the anatomy of the cingulum is highly conserved between humans and monkeys.

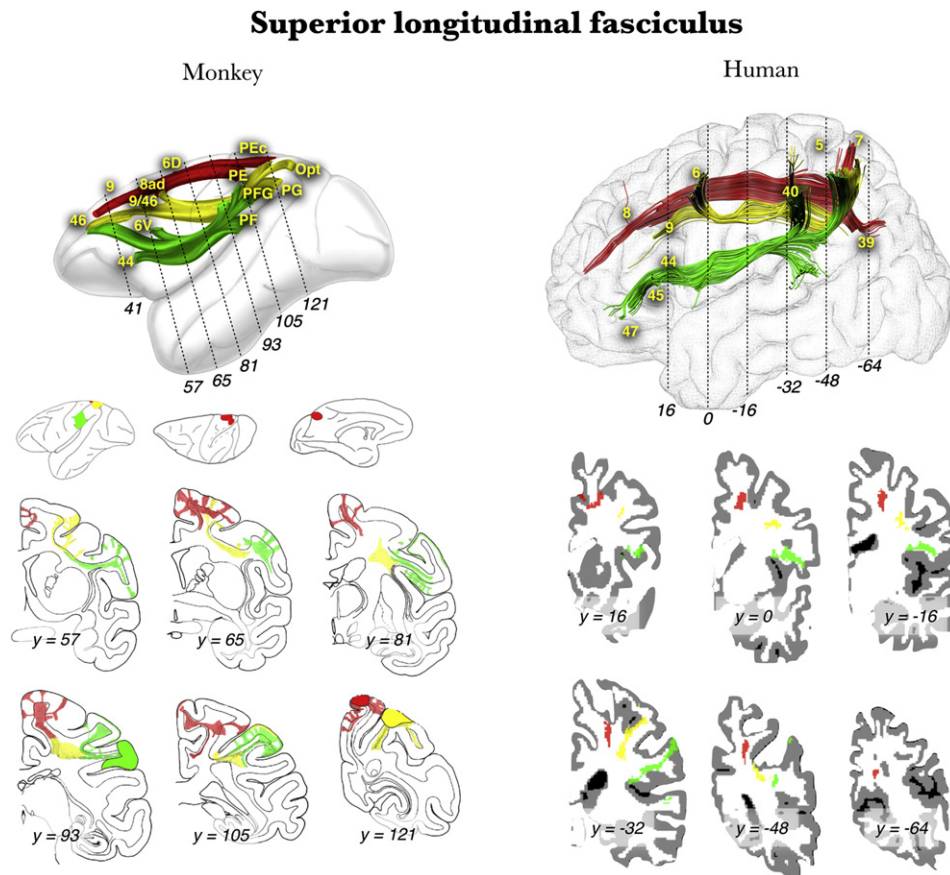


Fig. 2 – Reconstructions of the three branches of the superior longitudinal fasciculus (first branch in red, second branch in yellow and third branch in green): comparison between post-mortem axonal tracing in monkey (cases 1–6 modified from Schmahmann and Pandya, 2006) and human in vivo SD tractography suggests simian-human similarities for the three SLF branches.

3.1.2. Superior longitudinal fasciculus

The superior longitudinal fasciculus has three distinct branches (Petrides and Pandya, 1984). In humans, the first branch of the superior longitudinal fasciculus (SLF I) connects to the superior parietal lobule and precuneus (BA 5 and 7), to the superior frontal (BA 8, 9, 32) and perhaps to some anterior cingulate areas (BA 24). The second branch (SLF II) originates in the anterior intraparietal sulcus and the angular gyrus (BA 39 and 40) and terminates in the posterior regions of the superior and middle frontal gyrus (BA 6, 8, 9). The third branch (SLF III) connects the intraparietal sulcus and inferior parietal lobule to the inferior frontal gyrus (BA 44, 45, 47) (Fig. 2).

In the monkey the three branches have a similar anatomy. The SLF I connects the superior frontal gyrus (MII, area 6D and 9) to the posterior medial (area PGm) and caudal superior parietal lobule of the monkey brain (area PE and PEc). The SLF II originates from the dorsolateral prefrontal cortex (areas 6D, 8Ad, 9/46, and 46) and ends in the occipito-parietal area (area POa) and the caudal inferior parietal lobule (area PG/Opt, equivalent to human angular gyrus). The SLF III links the posterior part of the inferior frontal gyrus (area 6V and area 44) to the rostral portion of the inferior parietal lobule (areas PF, POa, PFG and PFop).

Overall, the anatomy of the SLF is highly conserved between humans and monkeys.

3.1.3. Arcuate fasciculus

In humans, the longest fibres of the arcuate fasciculus connect the posterior regions of the frontal lobe to the temporal lobe (Catani et al., 2002, 2005; Parker et al., 2005). A subset of connections links the most posterior part of the superior temporal gyrus (BA 41 and 42) to the inferior frontal gyrus (BA 44 and 45). A larger subset of connections links the middle and inferior temporal gyri (BA 21, 22 and 37) to the inferior precentral (BA 6) and posterior regions of the middle and inferior frontal gyrus (BA 8, 9, 44 and 45).

In the monkey brain, the arcuate connects the caudal part of the superior temporal gyrus (Tpt) and the dorsal part of area 8 (area 8Ad), area 46, and 6. More recent investigation also revealed arcuate connections to area 44 arising from the superior temporal sulcus next to Tpt (Petrides and Pandya, 2009).

Overall, the arcuate fasciculus shows significant differences between human and monkey brains, with the projection to middle and inferior temporal gyrus being absent in monkey (Fig. 3).

3.1.4. Inferior fronto-occipital fasciculus

In humans, the fronto-occipital fasciculus is a long-ranged bowtie-shaped tract that originates from the inferior and medial surface of the occipital lobe (BA 19 and 18), with a minor contribution probably from the medial parietal lobe

Arcuate

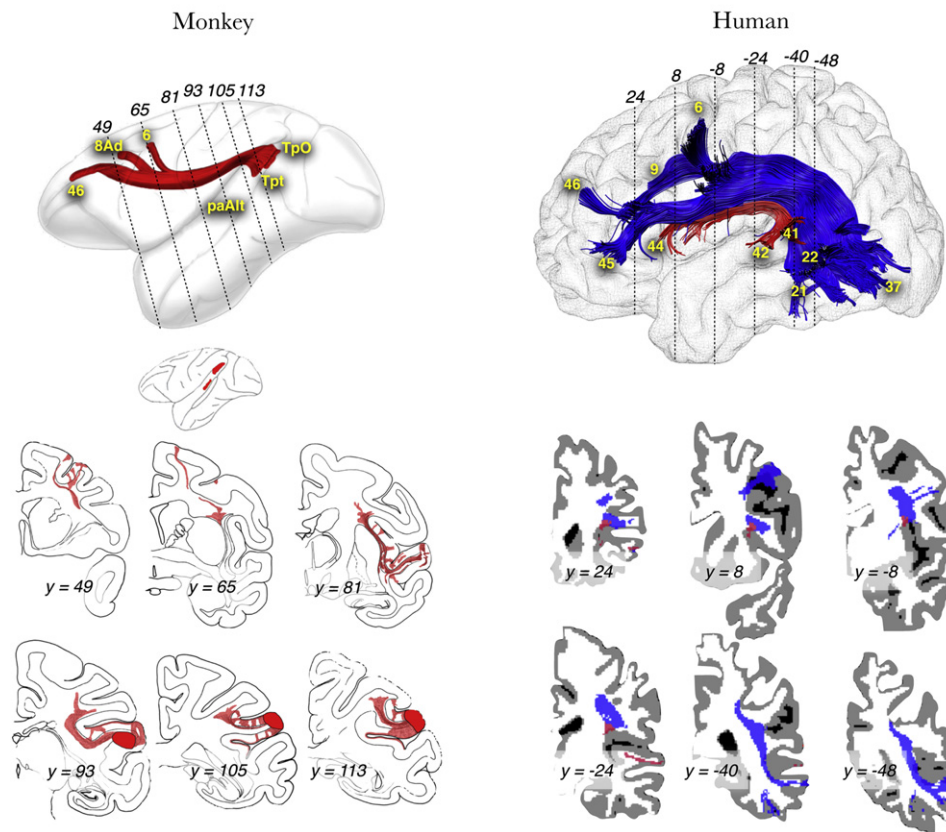


Fig. 3 – Reconstruction of the arcuate fasciculus: comparison between post-mortem axonal tracing in monkey (cases 7–9 modified from Schmahmann and Pandya, 2006) and human in vivo SD tractography. Common anatomical features between human and monkey are reconstructed in red whereas anatomical differences have been coloured in blue.

(Catani et al., 2002; Martino et al., 2010). As it leaves the occipital lobe and enters the temporal stem, the inferior fronto-occipital fasciculus narrows in section and its fibres gather at the level of the external/extreme capsule just above the uncinate fasciculus. Because the diffusion imaging lacks resolution, it cannot discriminate extreme from external capsule. As it enters the frontal lobe, its fibres spread to form a thin sheet, curving dorsolaterally that terminates mainly in the inferior frontal gyrus. The most ventral fibres continue anteriorly and terminate in the medial fronto-orbital region (BA 11) and the frontal pole (BA 10) (Catani et al., 2002). In the tractography reconstruction presented in Fig. 4, the most dorsal fibres terminate in the rostral portion of the superior frontal gyrus (rostral portion of BA 9).

In the monkey brain, because the autoradiographic technique shows axons, it can discriminate extreme from external capsule. The fibres passing through the extreme capsule (EmC) connect the middle superior temporal region (areas IPa, TAa and TPO) and the caudal inferior temporal region (area 19) with the caudal parts of the orbital cortex (area 47/12), the ventro-lateral prefrontal cortex (area 9/46 and 45) and the frontal pole (area 10) (Petrides and Pandya, 1988; Ungerleider et al., 1989; Schmahmann and Pandya, 2006).

Hence, whilst the anterior projections of the extreme capsule in the monkey overlap with those of the human

inferior fronto-occipital fasciculus, the posterior projections do not reach the occipital lobe.

3.1.5. Uncinate fasciculus

In humans, the uncinate fasciculus is a hook-shaped tract that connects the anterior part of the temporal lobe (BA 38) with the orbital (BA 11 and 47) and polar (BA 10) frontal cortex. In the tractography reconstruction presented in Fig. 5, the fibres of the uncinate originate from the temporal pole (BA 38), uncus (BA 35), parahippocampal gyrus (BA 36 and 30), and amygdala. After a U-turn, the fibres of the uncinate enter the anterior floor of the external capsule between the insula and the putamen. Here, the uncinate runs inferiorly to the fronto-occipital fasciculus before entering the orbital region of the frontal lobe, where it splits into a ventro-lateral branch, which terminates in the lateral orbito-frontal cortex (BA 11 and 47), and an antero-medial branch that continues towards the cingulate gyrus (BA 32) and the frontal pole (BA 10) (Dejerine, 1895; Klingler and Gloor, 1960; Crosby et al., 1962).

The monkey uncinate connects the ventro-lateral prefrontal (area 47/12) and the orbital cortex (areas 11 and 13) to the temporal pole, amygdala, and the parahippocampal gyrus (area 35 and 28).

Overall the anatomy of the uncinate is highly conserved between humans and monkeys.

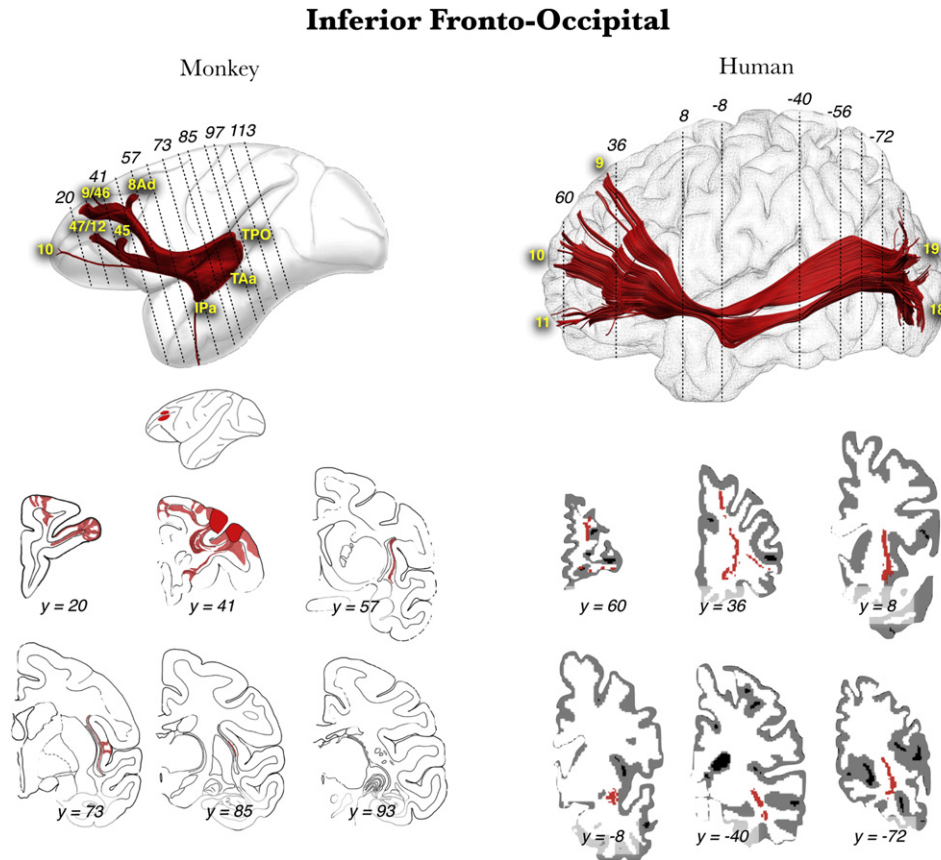


Fig. 4 – Comparison between post-mortem axonal tracing of the extreme capsule fibres in monkey (cases 31 and 32 modified from Schmahmann and Pandya, 2006) and human in vivo SD tractography of the inferior fronto-occipital fasciculus. The two tracts pass through the external capsule and project to similar frontal regions. Their posterior projections are however, different; the external capsule project to the temporal lobe while the inferior fronto-occipital to the occipital lobe.

3.2. Short-range association pathways

A number of intra-lobar connections link different areas of the frontal lobe (Catani et al., 2012, issue 2). Many of these connections are U-shaped fibres linking adjacent gyri. There are also longer intra-lobar fibres connecting distant gyri within the frontal lobe. Among these connections, the “frontal aslant tract” (Fig. 6) and the “frontal orbito-polar tract” (Fig. 7) are presented below in our study.

3.2.1. Frontal aslant tract

The frontal aslant tract resembles a baseball glove. It connects the most posterior part of Broca’s territory (i.e. precentral cortex, BA 6, pars opercularis, BA 44) in the inferior frontal gyrus with the SMA and pre-SMA in the superior frontal gyrus (BA 8 and 6) (Lawes et al., 2008; Oishi et al., 2008).

In the monkey brain, a group of fibres originates in the ventral part of the precentral gyrus (areas 6V and 44) and projects to the SMA in the superior frontal gyrus (areas 6D and 8B) (Petrides and Pandya, 1994; Schmahmann and Pandya, 2006). These fibres are very similar to the human frontal aslant tract (Fig. 6).

3.2.2. Frontal orbito-polar tract

In humans the frontal orbito-polar bundle is a ventral tract connecting posterior (BA 25 and 11) and anterior orbitofrontal gyri (BA 11) and the frontal pole (BA 10).

In monkey, the frontal orbito-polar tract connects the posterior orbital frontal cortex (area 25) to the frontal pole (area 10) (Petrides and Pandya, 1994; Schmahmann and Pandya, 2006).

Overall the anatomy of the frontal orbito-polar tract is highly similar between humans and monkeys (Fig. 7).

4. Discussion

In this study, a direct comparison of the major frontal lobe connections between monkey and human suggests the following: (i) the majority of the frontal lobe connections described in the monkey brain using axonal tracing can be visualised in the human brain using SD tractography; (ii) overall a general correspondence between human and monkey connective anatomy is observed for the short and long-range frontal connections; (iii) major differences were

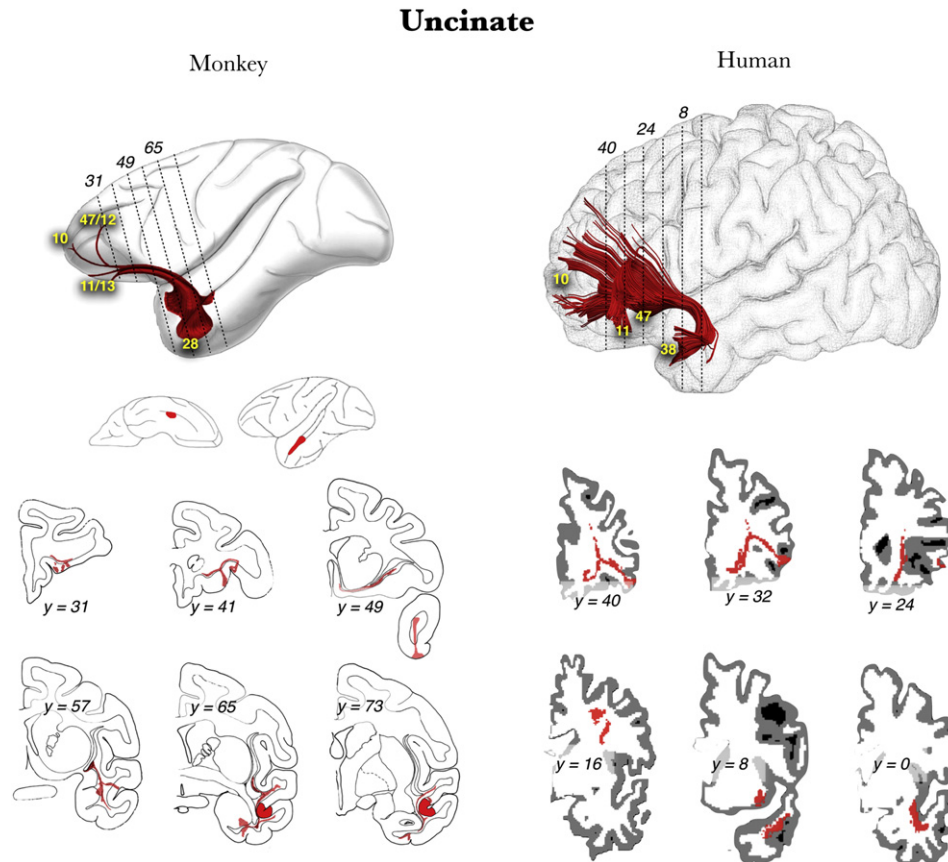


Fig. 5 – Reconstructions of the uncinate: comparison between post-mortem axonal tracing in monkey (cases 13 and 14 modified from Schmahmann and Pandya, 2006) and human in vivo SD tractography suggests simian-human similarities.

found for the arcuate fasciculus and the inferior fronto-occipital fasciculus, which may underlie unique human cognitive functions.

Human–simian similarities were found for the anatomy of the superior longitudinal fasciculus, the uncinate fasciculus and the cingulum.

The superior longitudinal fasciculus connects frontal and parietal regions that activate in tasks involving visuo-spatial processing (Corbetta and Shulman, 2002; Shulman et al., 2009, 2010), sensory-motor integration (Buccino et al., 2004; Johnson-Frey et al., 2005; Bohlhalter et al., 2009), working memory (Ungerleider et al., 1998; Marklund et al., 2007; Volle et al., 2008), and eye movement (Corbetta, 1998; Berman et al., 1999; Petit and Haxby, 1999). Lesions to the superior longitudinal connections manifest with neglect (Gaffan and Hornak, 1997; Thiebaut de Schotten et al., 2005; Doricchi et al., 2008), apraxia (Goldenberg, 2003; Heilman and Watson, 2008; Goldenberg and Spatt, 2009), working memory impairment (Levy and Goldman-Rakic, 1999; Curtis, 2006; Sepulcre et al., 2009), optic ataxia and oculomotor dysfunction (Buneo et al., 2002; Karnath and Perenin, 2005; Blangero et al., 2010). These deficits can be frequently observed in humans and produced experimentally in monkeys.

The uncinate fasciculus is involved in processing, encoding and retrieving percepts and memories with strong emotional valence (Gaffan and Wilson, 2008; Ross, 2008). Functional studies in humans revealed activation of the fronto-temporal

network mediated by the uncinate in tasks involving integration of emotional material (Hung et al., 2010; Park et al., 2010), recall of emotionally stimulating memories (Spoont et al., 2010), estimation of risks (Vorhold et al., 2007) or watching fearful faces (Grèzes et al., 2007; Pichon et al., 2009). Lesions to the uncinate connections lead to episodic memory disorders (Horel, 1978; Eacott and Gaffan, 1992; Levine et al., 1998; Fink et al., 2010) and antisocial behaviour (Dicks et al., 1969; Price et al., 2008; Craig et al., 2009; Sundram et al., 2012, this issue; Zappalà et al., 2012, this issue) both in humans and experimental conditions in monkeys.

Human–simian similarities were also found for the cingulum. The dorsal cingulum connects the anterior cingulate and medial prefrontal cortex with the posterior cingulate and precuneus cortex. These regions show decreased activation during goal-directed tasks (i.e., default network) both in humans (Raichle et al., 2001; Greicius et al., 2009) and monkeys (Vincent et al., 2007; Buckner et al., 2008). The cingulum also contains longer fibres, which run from the anterior cingulate and medial prefrontal cortex to the anterior temporal gyrus. Lesion to these fibres manifest with apathy and tameness both in monkeys (Glees et al., 1950) and humans (Moniz, 1937).

Our dissection suggests that human–simian similarities extend also to the frontal short-range fibres of the frontal orbito-polar (FOP) and frontal aslant tract (FAT). The functions of these two tracts are not known. The frontal orbito-polar connects the posterior orbital gyrus, including the olfactory

Frontal Aslant Tract

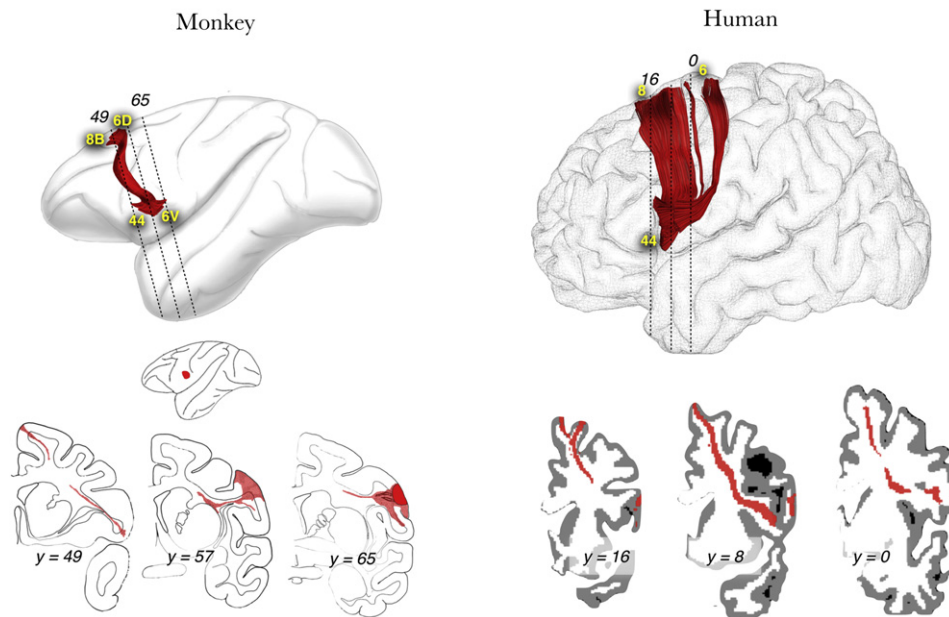


Fig. 6 – Reconstructions of the frontal aslant tract: comparison between post-mortem axonal tracing in monkey (case 25 modified from Schmahmann and Pandya, 2006) and human in vivo SD tractography shows simian-human similarities.

cortex, with the anterior orbito-frontal gyrus and inferior frontal pole. The frontal pole mainly shows an increase of activation in tasks that require maintaining information in mind while doing something else (Koechlin et al., 1999; Burgess et al., 2007). Patients with a lesion in the frontal pole manifest difficulties in multitasking (Burgess et al., 2000) and prospective memory (Volle et al., 2011). The orbito-frontal cortex is involved in reward behaviour associated with sensory (e.g., taste), multimodal and abstract reinforcers (e.g., monetary gain and loss) (Kringelbach, 2005; Palminteri et al., 2009). Lesions to the orbito-frontal cortex manifest with insensitivity to future consequences both in humans (Bechara et al., 2000; Zappalà et al., 2012, this issue) and monkeys (Iversen and Mishkin, 1970).

The frontal aslant tract connects the frontal operculum with the SMA. Cortical stimulation of the frontal operculum elicits orofacial movements in the monkey brain (Huang et al., 1989) and phonemic paraphasias in the human brain (Duffau, 2012, this issue). Cortical recording in the SMA shows different classes of neurons associated with batches of sequential movement (Donchin et al., 1971; Rizzolatti et al., 1988; Tanji and Shima, 1994). Patients with lesions extending to the FAT manifest with impaired fluency and mutism (Bates et al., 2003; du Boisgueheneuc et al., 2006). These data suggest that the frontal aslant tract is involved in motor planning (Eccles, 1982; Boecker et al., 1998), including vocalisation and speech (Alario et al., 2006).

In summary our findings suggest that humans and monkeys share a similar anatomy for tracts associated with functions that the two species have in common.

For two other long-range tracts, such as the arcuate fasciculus and the inferior fronto-occipital fasciculus, clear anatomical differences were observed. Although these differences may

be due to the limitations of the methods (discussed in detail further) and need to be confirmed in larger sample, we will discuss here their potential functional interpretation on the phylogeny scale. The arcuate fasciculus connects the posterior temporal lobe to the latero-inferior frontal lobe. A subcomponent of the arcuate fasciculus starting from the superior temporal gyrus is observed in both monkey and human. The dorsal part of this subcomponent of the arcuate fasciculus mediate spatiotemporal processing and the ventral part is involved in stimulus identification (Aboitiz and García, 2009). The majority of the fibres of the arcuate fasciculus project to the middle and inferior temporal gyri in human but not in monkey. Degeneration of the fibres of the arcuate fasciculus manifests with language disorders (Catani et al., 2003; Berthier et al., in press; Bizzi et al. 2012, in press). This finding support the theory that changes in the strength of connections between posterior temporal and inferior frontal regions have increased in the phylogeny scale, allowing a direct link between posterior regions specialised for auditory and visual word perception to frontal regions controlling orofacial movements (Aboitiz and Garcia, 1997; Aboitiz and García, 1997; Cohen et al., 2000; Epelbaum et al., 2008).

The inferior fronto-occipital fasciculus can be easily dissected in humans using post-mortem blunt dissections (Trolard, 1906; Curran, 1909; Lawes et al., 2008; Martino et al., 2010) and in vivo tractography (Catani et al., 2002; Wakana et al., 2004; Catani and Thiebaut de Schotten, 2008; Lawes et al., 2008; Urbanski et al., 2008; Pugliese et al., 2009). The absence of the inferior frontal-occipital fasciculus in the monkey brain has led to the hypothesis that this tract may be unique to the human brain (Catani, 2007). The projections of the inferior fronto-occipital fasciculus to the area 10 may also

Orbito-Polar Tract

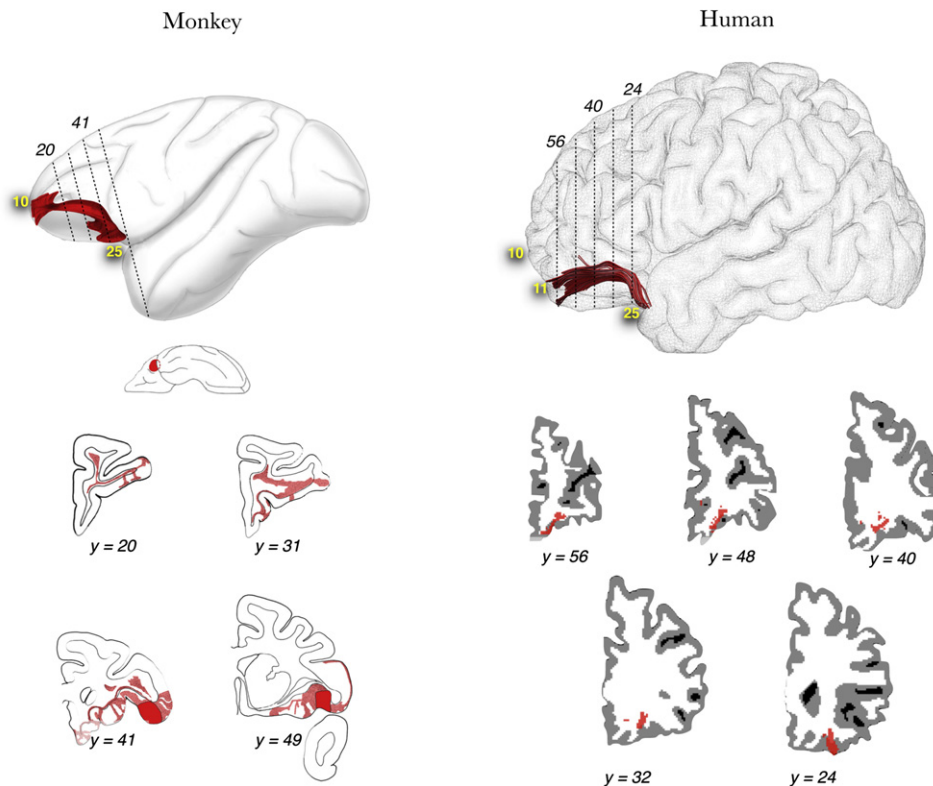


Fig. 7 – Reconstructions of the frontal orbito-polar tract: comparison between post-mortem axonal tracing in monkey (case 33 modified from Schmahmann and Pandya, 2006) and human in vivo SD tractography suggests simian-human similarities.

explain the larger relative size of area 10 in humans (Semendeferi et al., 2001) and the in relative increase of frontal white matter (Smaers et al., 2010, 2011). The functions of the inferior fronto-occipital fasciculus remain largely unknown. It has been suggested that the inferior fronto-occipital fasciculus could play a role in the rapid top-down modulation of visual processing in general (i.e., not restricted to processing emotional value of visual percepts) (Pins and Ffytche, 2003; Bar et al., 2006), including top-down amplification of visual percepts characteristic of conscious visual processing (Dehaene et al., 2006) and executive control of voluntary visual recall (Tomita et al., 1999). The inferior fronto-occipital fasciculus could also mediate interaction between the occipital and frontal areas in states of reduced consciousness. For example, Braun et al. (1998) demonstrated that rapid eye movement (REM) sleep is associated with activation of the extrastriate visual cortices, particularly within the ventral processing stream, and concomitant reduction of activity in lateral orbital and prefrontal cortex. The role of the inferior fronto-occipital fasciculus in sleep is also suggested by patients with an acquired inability to dream (anoreria) following lesions of the lateral orbito-frontal cortex (Solms, 1997). Other roles of the inferior fronto-occipital fasciculus remains to be clarified such as its participation in mental rotation (Schendan and Stern, 2008), space-directed attention (Urbanski et al., 2008, 2011), reading (Shaywitz et al., 2002; Mechelli et al., 2004), and semantic processing (Duffau et al., 2005).

The extreme capsule is considered as a separate bundle in the monkey literature. In humans the extreme capsule contains many fibres, the majority of which project to posterior temporal and occipital areas through the uncinate and the inferior fronto-occipital fasciculus. It is possible, however, that some projections of the inferior fronto-occipital fasciculus branches ends in the superior temporal lobe, thus representing the human equivalent of the extreme capsule fasciculus described in the monkey. This tract has been recently linked to language functions (Makris and Pandya, 2009) and could correspond to the ventral semantic pathway described in the human brain (Duffau, 2005; Saur et al., 2008).

In summary the differences we found in the anatomy of the arcuate fasciculus and inferior fronto-occipital fasciculus suggest that these tracts may underpin functions unique to humans.

In this study, the human–simian comparison we provide is based on two distinct methods for reconstructing fibre pathways. Some of the findings may therefore be related to the different methodological approaches, rather than reflecting true anatomical differences. For example, axonal tracing allows for the identification of single axon trajectories (Schmahmann and Pandya, 2006) and detailed description of their cortical terminations, whereas SD tractography is based on the diffusion signal acquired from relatively large voxels containing multiple axonal bundles, and is limited in reconstructing tracts approaching cortical regions. This methodological difference

may account for tracts that were identified in the monkey, but not in the human brain. Despite the above limitations, we show that the majority of frontal lobe connections described in the monkey brain through axonal tracing, can be also visualised in the human brain using SD tractography.

This study did not account for inter-individual variability and gender differences as human inter-individual variability data are drawn from one single subject. Inter-subject variability of white matter tracts in the human brain has been previously studied with diffusion tensor tractography and showed lower degree of variability in the central portion of the tracts, and a higher degree of variability in the peripheral regions (Thiebaut de Schotten et al., 2011b). The same study reported gender differences for the long segment, which is more left lateralized in males as compared to females. Future studies will need to examine interindividual variability using SD tractography.

Another limitation of this study is related to the visualisation of the trajectories of the individual tracts based on the drawings derived from histological sections of a monkey brain atlas. Single tracts on coronal slices can be difficult to identify visually and may lead to errors in labelling. In the monkey brain, the reconstruction of a single tract is based on patchy injections in individual cortical areas that do not cover the whole brain, especially in the most ventral areas. This methodological difference may account for tracts identified in the human brain, but not in monkeys, such as the inferior fronto-occipital fasciculus and some components of the arcuate fasciculus. Future ad-hoc studies using axonal tracing are needed to confirm the presence of tracts that are found in the human brain, whilst absent in the monkey brain.

We used SD tractography to overcome some of the limitations of current tractography methods based on the diffusion tensor model. In voxels with crossing, kissing or fanning fibres, the tensor model is unable to describe the complexity of white matter organisation. Consequently, the resultant tractography reconstructions are likely to contain erroneous results (Basser et al., 2000; Catani, 2007; Jones, 2008). SD models the diffusion signal as a distribution of multiple fibre orientations, and is therefore able to resolve fibre crossing in regions with two or more tracts. Tractography reconstructions based on SD help to reduce false negatives (=ineffective tracking of pathways that do exist) but are likely to generate false positives (=tracking of pathways that do not exist). In our study, the inferior fronto-occipital fasciculus and the arcuate are unlikely to represent flawed reconstructions, as the existence of these tracts in the human brain is supported by post-mortem dissections (Türe et al., 2000; Lawes et al., 2008) and cortico-cortical recording in epileptic patients (Kawasaki et al., 2001; Matsumoto et al., 2004). Finally, in this study we focused on association pathways without analysing of the projection and commissural (Berlucchi, 2012, this issue) tracts that are also important for cognition and behaviour such as fronto-striatal (Krause et al., 2012 this issue; Langen et al., in press; Cubillo et al., in press) and thalamocortical pathways (Muircheartaigh and Richardson, in press).

In conclusion, in this study we tried to bridge the gap between human and monkey neuroanatomy of frontal lobe association tracts. Our preliminary findings suggest that most of the association tracts in the frontal lobe are similar between

the two species. These tracts may therefore underlie functions that are conserved along the phylogeny scale. Conversely, some segments of the arcuate fasciculus and the inferior fronto-occipital fasciculus, which are not identified in the monkey brain, may be related to unique human abilities. Future studies with larger samples are necessary to understand the variability of those tracts and their correlation with behaviour.

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