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Research Report

Surface-based tractography uncovers 'what' and 'where' pathways in prefrontal cortex

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ABSTRACT

The frontal eye field (FEF) and the inferior frontal junction (IFJ) are prefrontal regions that mediate top-down functions, with mounting neuroimaging evidence suggesting that they specialize in controlling spatial versus non-spatial processing, respectively. We hypothesized that their unique patterns of structural connectivity underlie these specialized roles. To infer the localization of FEF and IFJ in standard space, we performed an activation likelihood estimation meta-analysis of functional MRI paradigms that targeted these regions. Using surface-based probabilistic tractography methods at the individual subject level, we tracked streamlines ipsilaterally from the inferred FEF and IFJ activation peaks to the dorsal and ventral visual streams mapped on the native white matter surface of 56 subjects parcellated using the multimodal atlas by Glasser et al. (2016). By contrasting FEF and IFJ connectivity likelihoods, we found predominant structural connectivity from the FEF to regions of the dorsal visual stream compared to the IFJ (particularly in the left hemisphere), and conversely, predominant structural connectivity from the IFJ to regions of the ventral visual stream compared to the FEF bilaterally. Additionally, we analyzed the cortical terminations of the superior longitudinal fasciculus to the FEF and IFJ, implicating its first and third branches as segregated pathways mediating their communication to the posterior parietal cortex. The structural connectivity fingerprints of the FEF and IFJ support the view that the two visual stream architectures extend to the posterior lateral prefrontal cortex and provide converging anatomical evidence of their specialization in spatial versus non-spatial control.

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1. Introduction

A longstanding tradition argues that in primates, the regions that mediate cognitive control and flexibility are primarily hosted in the prefrontal cortex (PFC; Chafee & Heilbronner, 2022; Luria, 1966; Miller & Cohen, 2001). The PFC cannot be fully understood in isolation, without considering its rich connectivity patterns (Fuster, 2001; Passingham & Lau, 2022). Indeed, several PFC regions form crucial hubs of brain networks with adaptive functions (Cole et al., 2013; Duncan, 2001; Yeo et al., 2011). In the human posterior lateral PFC, the frontal eye field (FEF) and the inferior frontal junction (IFJ) exhibit the characteristics of control regions that are involved in a wide array of functions ranging from attention, working memory, and other forms of cognitive control (reviewed in Bedini & Baldauf, 2021), and are responsible for biasing activity in posterior brain regions (Baldauf & Desimone, 2014; Gazzaley & Nobre, 2012; Veniero et al., 2021; Zanto et al., 2011; Zhang et al., 2018). Crucially, however, recent evidence suggests that these regions differ in their selectivity to spatial versus non-spatial information: on the one hand, the FEF predominantly encodes spatial information (Fiebelkorn & Kastner, 2020; Mackey et al., 2017; Sprague & Serences, 2013; Wang et al., 2015), whereas, on the other hand, the IFJ predominantly encodes non-spatial (i.e., feature- and object-based) information (Baldauf & Desimone, 2014; Bedini & Baldauf, 2021; O'Reilly, 2010). The functional MRI (fMRI) studies that employed multivariate pattern analysis (Peelen & Downing, 2023) to decode the attended and memorized information from the FEF and IFJ provide evidence supporting this hypothesis (discussed in Bedini & Baldauf, 2021). The dissociation in the selectivity of neural populations of these lateral prefrontal regions is in line with the model that was originally proposed by Goldman-Rakic and colleagues to understand the organization of the PFC in non-human primates based on neurophysiological and tract-tracing evidence (Constantinidis & Qi, 2018; Goldman-Rakic, 1996). In particular, the latter suggests that the dorsolateral and ventrolateral PFC are characterized by divergent patterns of anatomical connectivity to the 'what' and 'where' visual pathways (Goodale & Milner, 1992; Mishkin et al., 1983), respectively (Felleman & Van Essen, 1991; Romanski, 2004; Wilson et al., 1993; Yeterian et al., 2012). In humans, anatomical connections are primarily inferred using diffusion MRI (dMRI) tractography (Jbabdi et al., 2015; Jeurissen et al., 2019; Van Essen et al., 2014), but to date, the distinct structural connectivity patterns of the regions in the posterior lateral PFC remain elusive.

Previous dMRI studies were able to reveal that many aspects of the organization of prefrontal connectivity are preserved across the macaque and the human brain (Jbabdi, Lehman, et al., 2013; Neubert et al., 2014; Sallet et al., 2013; Thiebaut de Schotten et al., 2012), which allows researchers to formulate hypotheses motivated by comparative evidence (Mars et al., 2021). Other influential studies on the PFC focused on performing a connectivity-based parcellation to infer areal borders based on tractography (Thiebaut de Schotten et al., 2017; Tomassini et al., 2007). This technique hinges on the idea that a characteristic pattern of connectivity (i.e., the connectivity fingerprint; Passingham et al., 2002) defines each brain region (Eickhoff et al., 2018), which in turn fundamentally underlies its specialized role in cognition (Mars et al., 2018). Each PFC region's unique set of afferent and efferent connections constrain the inputs it receives (and consequently its selectivity for specific sensory information), as well as its ability to ultimately control and bias activity elsewhere in the brain to solve specific tasks (Passingham & Lau, 2022; Petrides et al., 2012).

MRI studies combining the functional localization of regions of interest at the individual subject level using fMRI, with the analysis of their structural connectivity with tractography, offered initial evidence on the involvement of long-range association pathways in mediating the functions associated with the FEF and IFJ (reviewed in Bedini & Baldauf, 2021). Of importance to the present study, the studies by Anderson et al. (2012), Szczepanski et al., 2013, and Umarova et al. (2010) provided tractography evidence of FEF wiring patterns to the posterior parietal cortex. Baldauf and Desimone (2014) showed that the connectivity likelihood with the fusiform face area and the parahippocampal place area increased in the ventrolateral PFC and near the IFJ. Collectively, these studies were important milestones suggesting that these regions communicate with the parietal and temporal cortices through distinct, reciprocal, and potentially segregated white matter pathways.

These putative pathways are known to be supported by specific white matter association bundles (Barrett et al., 2020; Thiebaut de Schotten et al., 2012) that can be delineated using virtual dissection techniques via dMRI tractography (Catani & Thiebaut de Schotten, 2008; Warrington et al., 2020). For example, a seminal dMRI study indicated that a major white matter bundle mediates the communication within the dorsal and ventral attention networks (Corbetta & Shulman, 2002; Yeo et al., 2011) is the superior longitudinal fasciculus (SLF), which is subdivided into three branches that run from the dorsomedial to the ventrolateral direction (Thiebaut de Schotten et al., 2011). Damage to the SLF often leads to visual neglect, especially in the case of right hemisphere damage (Bartolomeo & Seidel Malkinson, 2019; Doricchi et al., 2008). In addition to lesion evidence, the functions of the SLF have also been inferred by combining tractography with meta-analytic techniques. According to a large-scale study combining the virtual dissection of the SLF in 129 participants with 14 fMRI meta-analyses, the SLF1 primarily mediates 'spatial-motor', and the SLF3 'non-spatial-motor' functional components (Parlatini et al., 2017). In a comprehensive study, Sani et al. (2021) analyzed dMRI data from 263 participants released by the Human Connectome Project (HCP; Van Essen, Smith, et al., 2013) to understand the organization of the networks involved in attentional control. The authors found reliable tractography evidence that the human posterior inferotemporal area forms part of an interconnected network encompassing the FEF and the dorsal lateral intraparietal area, two well-known areas forming the core of the dorsal attention network. The authors then attempted to uncover the white matter bundles underlying these results. Interestingly, they found that the connectivity between the FEF and the dorsal lateral intraparietal area is mediated by the SLF2 and in part by the SLF3, and the connectivity between the FEF

and the posterior inferotemporal area is mediated by the posterior arcuate fasciculus and the inferior fronto-occipital fasciculus, although there was only moderate overlap with the former bundle.

Overall, the studies discussed above offer some evidence of the structural connectivity patterns of posterior lateral PFC regions (mainly the FEF, and in a more limited way, the IFJ) and the underlying white matter bundles (i.e., the SLF), and help clarify the function of these connections within the attention networks. However, these studies also faced a tradeoff between having a relatively focused sample size but with the great advantage of having regions of interest (ROIs) functionally localized at the individual level, as opposed to the ability to analyze large datasets but with regions defined at the group level or by using an atlas, which may not always represent the individual brain organization faithfully (Eickhoff et al., 2018). Even though the functional localization of ROIs at the individual level seems to be the most accurate way to overcome the issues associated with group-level analyses performed on brain templates (Coalson et al., 2018; Fedorenko, 2021), the localization of the ROIs may be impractical to scale to larger samples. As a consequence of the former limitation, another major barrier in adequately mapping the connectivity fingerprints of a brain region and relating them to its functions is the fact that most of the available brain atlases aren't tailored to incorporate information from large collections of task-based fMRI data (Eickhoff et al., 2018). To minimize these issues we first performed an activation likelihood estimation (ALE; Eickhoff et al., 2012) fMRI meta-analysis to infer the localization of FEF and IFJ in standard space. We used two sets of studies using functional localizers and other well-replicated fMRI paradigms that target these regions (as in Bedini et al., 2023), which enabled us to investigate their structural connectivity in a large dataset, such as the HCP (Van Essen, Smith, et al., 2013). Although the studies briefly reviewed here suggest that the FEF and the IFJ may communicate with posterior parietal and temporal regions through distinct and segregated pathways (Anderson et al., 2012; Baldauf & Desimone, 2014; Sani et al., 2021; Szczepanski et al., 2013; Thiebaut de Schotten et al., 2011; Umarova et al., 2010), no study has yet directly contrasted their structural connectivity to the posterior visual regions. A divergence in these connectivity patterns would be consistent with the principles of anatomical connectivity discovered in the macaque PFC (Romanski, 2004; Yeterian et al., 2012), in which case we predict that the FEF should be more likely connected to the dorsal stream, and the IFJ to the ventral stream. Such results would highlight how long-range white matter pathways underlie the functional specialization of these regions in spatial versus non-spatial control processes.

Therefore in the present study, we sought to investigate the structural connectivity fingerprints of the FEF and IFJ with posterior visual regions. We combined an ALE meta-analysis—which allowed us to infer the localization of these regions in standard space – with a surface-based probabilistic tractography analysis at the individual subject level – to contrast their connectivity likelihoods to the global dorsal and ventral visual streams. Finally, we also performed the virtual dissection of the major association bundles connecting the PFC and posterior regions (Barrett et al., 2020; Catani & Thiebaut de Schotten, 2008) to uncover the white matter pathways underlying the hypothesized connectivity patterns. We specifically focused on the cortical terminations of the SLF, as we predicted that its three branches would have distinct patterns of projections to the FEF and IFJ.

2. Materials and methods

2.1. Subjects and data sources

We used the MRI data from the HCP-MEG subjects release (Van Essen et al., 2013a; available at: https://db.humanconnectome.org). Our sample included 56 unrelated subjects (age: 22–35 years, mean = 28.66 ± 3.81; see Fig. S1 in the Supplementary Information for the selection criteria).

2.2. Localization of the FEF and IFJ seed regions

We performed an ALE fMRI meta-analysis to infer the localization of the FEF and IFJ in the MNI152 space using GingerALE (v. 3.0.2; Eickhoff et al., 2012). This analysis was carried out on part of the experiments that were included in our previous meta-analysis (Bedini et al., 2023; see Supplementary Information, Tables S1 and S2 for details), which we later refined and expanded in that study. The ALE parameters were set to $p = .01$, with a cluster-level family-wise error equal to .01 and 1000 permutations.

2.3. Streamline seeding approach

The FEF and IFJ ALE peak coordinates in the MNI152 space were non-linearly mapped using FSL FNIRT to the native dMRI space (Fig. 1A). These peaks were then projected onto each subject's white matter/grey matter (WM/GM) boundary (i.e., the native white matter surface) available in the HCP extended structural preprocessing folder as follows. We first created a sphere of a 2.5 mm radius centered around the ALE peak. Each FEF and IFJ seed therefore consisted of a 6.25 mm diameter sphere at this stage. We note that by this method, our spheres included the coordinates corresponding to the ALE peaks reported in Bedini et al. (2023). Next, we used the command-line tool surf_proj from FSL to map these spheres to the WM/GM boundary from the FreeSurfer segmentation (i.e., *h_white.gii). The latter file was mapped from the FreeSurfer space to the diffusion space using the FSL surf2surf command. We used the 'mean' method in surf_proj, and we further increased the step size by the voxel size (i.e., 1.25 mm) until each subject had identifiable vertices corresponding to the volumetric spheres (see Fig. 1A for examples). The final step size was set to 2.5 mm for every subject. Initializing the streamlines from seeds projected onto the WM/GM boundary has the advantage of mitigating some tractography biases (Sotiropoulos and Zalesky et al., 2017), including most importantly the gyral bias (Girard et al., 2014; Schilling et al., 2018; Van Essen et al., 2014).

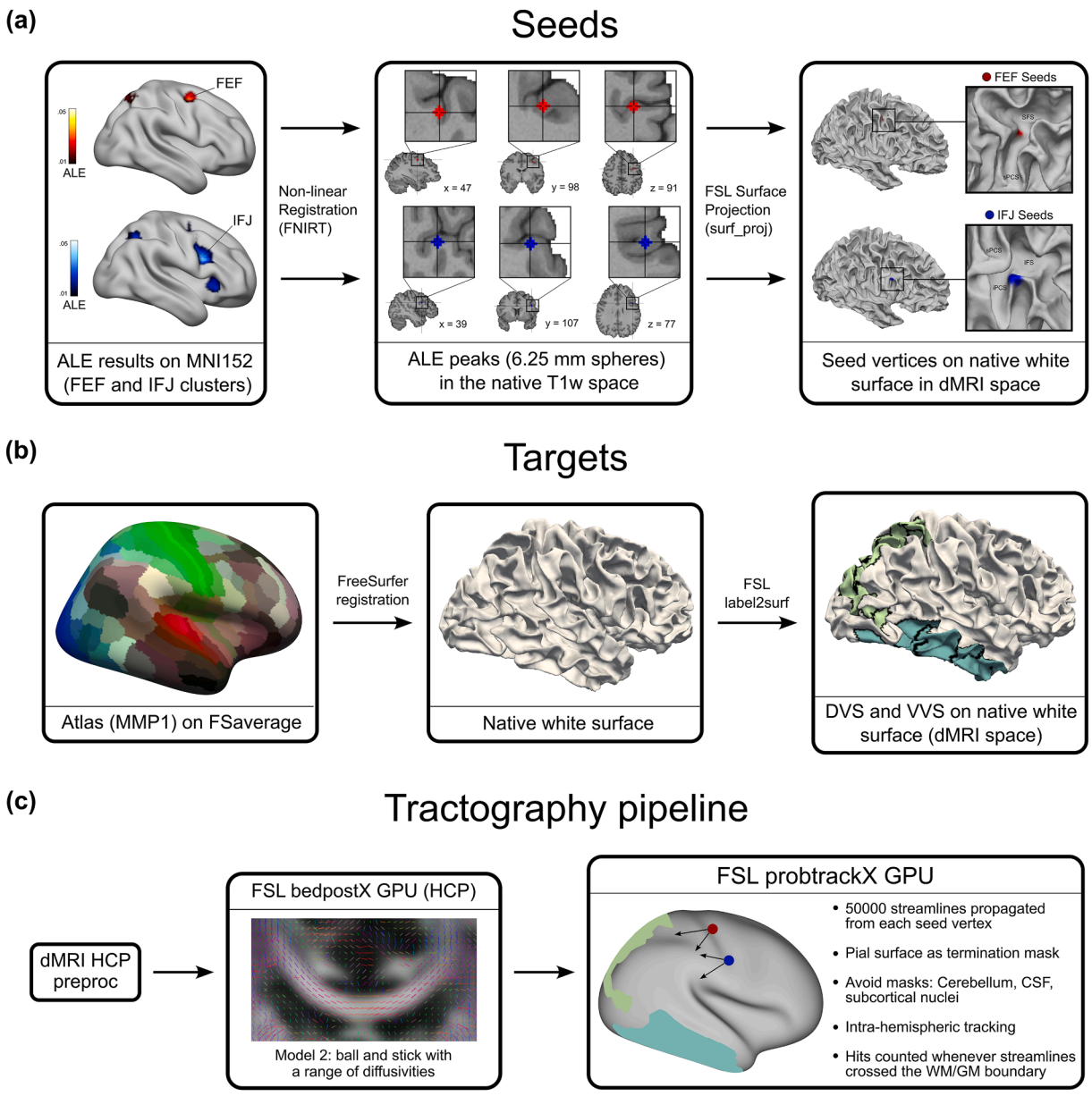

Fig. 1 – A ALE results and projection of the FEF and IFJ peaks to the WM/GM boundary of an example subject. B Mapping of the dorsal and ventral visual stream regions from the MMP1 atlas to the native white surface of the same example subject. C Overview of the surface-based tractography pipeline. From the preprocessed data, the fiber orientations were modeled by HCP's bedpostx, and we propagated streamlines ipsilaterally from each seed vertices (FEF, IFJ) in the individual subject space and counted hits on the target visual streams using FSL probtrackx GPU (Hernandez-Fernandez et al., 2019).

2.4. *Atlas selection and definition of the target regions of the two visual streams*

Recent approaches to parcellate the human cortex increasingly rely on multiple sources of information from different modalities (Eickhoff et al., 2018). The multimodal parcellation (MMP1) published by Glasser et al. (2016) provides a comprehensive understanding of the organization of the human cortex combining information about architecture, function, retinotopy, and connectivity, allowing us to systematically investigate the connectivity of the FEF and IFJ to the dorsal and ventral visual streams defined using these multimodal criteria. The MMP1 is designed to allow researchers to perform surface-based analyses (Glasser et al., 2016), an aspect that characterizes all the steps of our pipeline as we detail below. Our choice is also motivated by the fact that a fundamental property of the dorsal stream is its topographic organization, which is adequately captured in terms of the granularity (i.e., number of regions) by this atlas, allowing us to make predictions about how this feature will influence the

hypothesized connectivity patterns (see Revell et al., 2022, for considerations about descriptive and predictive validity of an atlas).

The MMP1 was projected on fsaverage (Fischl et al., 1999) by Mills, 2016 following the indications from Coalson et al. (2018) and is available at: https://figshare.com/articles/dataset/HCP-MMP1_0_projected_on_fsaverage/3498446. The resulting FreeSurfer annotation files from the MMP1 atlas were mapped to the native structural space using the scripts developed by the Neurolab, 2018 (https://figshare.com/articles/dataset/HCP-MMP1_0_volumetric_NIfTI_masks_in_native_structural_space/4249400; see Fig. 1B). We highlight that surface-based registration methods achieve much better consistency in labeling cortical areas and in capturing inter-subject variability compared to traditional volumetric methods (Coalson et al., 2018). Therefore, by using the procedure described above to map the MMP1 parcellation to the native dMRI space, we could retain high fidelity in mapping this atlas to the individual cortical anatomy. After these steps, we registered all the labels from the atlas onto each subject's white matter surface as provided by the FreeSurfer segmentation (FreeSurfer v. 6.0; Fischl, 2012) using the FSL command label2surf. To select the parcels of the MMP1 atlas that belonged to the dorsal and ventral visual streams, we consulted comparative (Kravitz et al., 2011, 2013; Mishkin et al., 1983) and human (Goodale & Milner, 1992) evidence for their definition, guided by the accompanying materials from the MMP1 publication (see Glasser et al., 2016, supplementary information #3). In addition, we took into account another defining characteristic of the dorsal visual stream, namely the presence of topographic visual organization (Wang et al., 2015), to better refine the inclusion criteria for the parcels belonging to this stream (see Table 1, and Fig. S4 in the Supplementary Information for details). We also compared our definitions to a previous study that investigated the connectivity of the extrastriate body area with these streams as defined by the MMP1 (Zimmermann et al., 2018). In contrast to that study, since we were not concerned about confounds due to the excessive proximity of the targets to the seed regions, we included additional parcels from the MMP1 that were discarded by the authors for that reason (Zimmermann et al., 2018).

2.5. *Probabilistic tractography method*

We performed all the analyses of dMRI data using FSL (v. 6.0.5; Jenkinson et al., 2012). Susceptibility-induced distortions, eddy currents, and subject motion were corrected using the HCP preprocessing pipelines (Andersson & Sotiropoulos, 2016; Van Essen, Ugurbil, & Behrens, 2013). All the dMRI data was analyzed in the subjects' native space and the original voxel resolution (i.e., 1.25 mm). First, we ran FSL DTIFIT on the preprocessed data to obtain the fractional anisotropy map, which we used for performing image registrations to the native dMRI space. To infer the connectivity likelihoods between the FEF and IFJ seeds and the target regions, we implemented the tractography pipeline in FSL, which involves two steps, namely bedpostx (Jbabdi et al., 2012) and probtrackx (Behrens et al., 2007). Since the first step is computationally intensive and given the advantages offered by the GPU implementation of bedpostx (Sotiropoulos et al., 2013), we downloaded the outputs of bedpostx released by the HCP (HCPpipelines/bedpostx) and used them as starting points for our pipeline. The following sections describe in detail our methodology to run probtrackx.

2.6. *Surface-based probabilistic tractography with GPU acceleration*

Probtrackx samples the fiber orientation estimated with bedpostx to generate a connectivity distribution between user-defined seed and target regions (Behrens et al., 2007). Importantly, probtrackx estimates how robust the connection is against noise and uncertainty, or in other words, how reproducible it is (Jbabdi & Johansen-Berg, 2011). This method allowed us to infer how likely a region is on the dominant pathway of anatomical connectivity from a seed region (Jeurissen et al., 2019). We leveraged the GPU implementation of probtrackx on a CUDA 9.2 parallel architecture, which achieves an over 200-fold acceleration compared to the CPU

Table 1 – List of the MMP1 parcels belonging to the dorsal and ventral visual streams.

Parcel	Stream	Full name	Parcel	Stream	Full name
V3A	Dorsal	Area V3A	V8	Ventral	Eight visual area
V3B	Dorsal	Area V3B	VVC	Ventral	Ventral visual complex
V6	Dorsal	Sixth visual area	PIT	Ventral	Posterior InferoTemporal
V6A	Dorsal	Area V6A	FFC	Ventral	Fusiform face complex
V7	Dorsal	Seventh visual area	VMV1	Ventral	VentroMedial visual area 1
IPS1	Dorsal	IntraParietal	VMV2	Ventral	VentroMedial visual area 2
7AL	Dorsal	Lateral area 7A	VMV3	Ventral	VentroMedial visual area 3
7PL	Dorsal	Lateral area 7P	TE1a	Ventral	Area TE1 anterior
7PC	Dorsal	Area 7PC	TE1m	Ventral	Area TE1 middle
LIPd	Dorsal	Area lateral IntraParietal dorsal	TE1p	Ventral	Area TE1 posterior
LIPv	Dorsal	Area lateral IntraParietal ventral	TE2a	Ventral	Area TE2 anterior
VIP	Dorsal	Ventral IntraParietal complex	TE2p	Ventral	Area TE2 posterior
MIP	Dorsal	Medial IntraParietal area	TF	Ventral	Area TF
IP1	Dorsal	Area IntraParietal 1	PHT	Ventral	Area PHT
V3CD	Dorsal	Area V3CD	PH	Ventral	Area PH
LO3	Dorsal	Area lateral occipital 3	TGv	Ventral	Area TG ventral
MT	Dorsal	Middle temporal area			

version (Hernandez-Fernandez et al., 2019). Overall, our general approach closely follows the study by Donahue et al. (2016) and more specifically, their method for generating the dense connectome matrix (termed dDT1 in that study). We chose to follow this tracking approach as the authors showed that it improved the agreement between measures of connectivity derived from probtrackx and retrograde tracing in the macaque, with a much higher correlation factor than previous validation studies (Donahue et al., 2016). We set probtrackx parameters as follows: 50,000 streamlines were propagated from each seed vertex (to achieve results convergence) for a maximum of 3200 steps using modified Euler integration. The curvature threshold was set to .2 (corresponding to an 80° turn) with a step length of .3125 mm (1/4 of the voxel size), and loopcheck was enabled to discard artifactual loops of the streamlines. Again similarly to Donahue et al. (2016), we also tracked the streamlines ipsilaterally, enabling us to add several anatomical constraints to tractography. We used the corpus callosum, subcortical nuclei, cerebellum, and cerebrospinal fluid masks resulting from the FreeSurfer segmentation as 'avoid' masks. The native pial surface was instead used as a 'termination' mask since this approach is effective in preventing invalid jumps of the streamlines between adjacent gyri (Hernandez-Fernandez et al., 2019). Whenever a streamline crossed the WM/GM boundary, the streamline count was increased for the cortical target corresponding to that triangular mesh. Our approach builds on the growing dMRI literature that focuses on the problem of assigning streamline terminations to cortical areas (Schilling et al., 2018; St-Onge et al., 2018; Yeh et al., 2019), and the evidence suggesting that surface-based tractography provides clear advantages when handling more complex geometrical configurations that can't be resolved using conventional volumetric techniques (Cottaar et al., 2021; Shastin et al., 2022; St-Onge et al., 2021; Yeh et al., 2019). For the control analysis focusing on the distance confounding factor, we processed our data as previously described and enabled the 'pd' flag in the probtrackx command. This flag multiplied the streamline count for each parcel by the average distance traveled by the respective streamlines from the seed, thus representing a heuristic but strict way to counteract this potential bias.

2.7. Post-processing, statistical analysis, and data visualization

Because our seeding strategy involved the propagation of the streamlines from a variable number of vertices across subjects, the total number of streamlines initialized is given by 50,000 times by the number of vertices in each seed. The raw streamline counts were summed across vertices within each target region, and we computed the ratio between the surviving streamline count and the total number of streamlines propagated from each seed region that were not discarded based on the avoid masks (termed 'waytotal' in probtrackx) to obtain a normalized streamline count (NSC) for each subject. Following that, we averaged the NSC across subjects for each seed to target region pairs. We then contrasted each seed (FEF, IFJ) to target (dorsal, ventral stream) NSC performing paired t-tests with $p = .01$ and correcting for multiple comparisons using the false discovery rate (FDR; Benjamini & Hochberg, 1995) with $q < .05$. We also performed a control analysis to account for a potential distance confound by repeating the same statistical contrasts on the distance-corrected probtrackx outputs. We performed the statistical analyses using JASP (https://jasp-stats.org), and we computed the FDR-adjusted p-values using the web utility provided by the software Seed-based d Mapping (https://www.sdmproject.com/utilities). The visualizations of the cortical connectivity values were created using Connectome Workbench (v. 1.5.0; Marcus et al., 2013). The RGB values corresponding to the difference in normalized connectivity likelihoods were generated using custom code written in MATLAB 2019b (https://www.mathworks.com) based on the diverging colormaps developed by Brewer (https://colorbrewer2.org). Finally, the raincloud plots (Allen et al., 2019) were created starting from the Python example code available at: https://github.com/pog87/PtitPrince. All the NSCs were $\log_2$-scaled for visualization convenience since we tracked streamlines from a variable number of vertices across subjects, which led to non-linear increases in the surviving streamline count.

2.8. Virtual dissection of the association white matter bundles, analysis of their asymmetries, and the cortical terminations of the SLF

Warrington et al. (2020) developed protocols for the automatic virtual dissection of the major white matter bundles in the HCP dataset. In summary, their method employs predefined waypoints, exclusion, and termination masks, and initializing probtrackx from specific seed masks enables their virtual dissection. We used this method to segment the white matter association bundles of the PFC that could potentially overlap with FEF and IFJ ALE clusters using the definitions by Barrett et al. (2020). Our bundles of interest included the three branches of the superior longitudinal fasciculus (SLF1, SLF2, and SLF3), the arcuate fasciculus (AF), and the uncinate fasciculus (UF). For this analysis, we used a subsample of 24 subjects randomly selected from the previous dataset, and it was also performed using the GPU version of probtrackx (Hernandez-Fernandez et al., 2019). We reconostructed all the white matter bundles of interest in the subject's native space. The method for the analysis of the bundles' lateralization and the associated results are reported in the Supplementary Information (p. 16). Our method to estimate the cortical projections of the three branches of the SLF involved the following steps: first, we non-linearly mapped the FEF and IFJ ALE clusters in MNI152 space to each subject's T1w image. Next, we removed all the voxels of the clusters that were found within the white matter. We then dilated these masks using a 3 mm kernel. This step was crucial to ensure that the clusters reached the white matter and closely followed previous approaches to estimating white matter bundles' terminations (e.g., Pestilli et al., 2014). To quantify the likelihood of cortical terminations to each ALE cluster, we normalized the streamline count by the number of overlapping voxels between each SLF branch and the FEF and IFJ ALE clusters separately. We contrasted the streamline count projecting to the FEF and IFJ clusters for the SLF1, SLF2, and SLF3 by performing paired t-tests with $p = .01$.

3. Results

3.1. Surface-based probabilistic tractography results

We contrasted the NSC for each seed to the ipsilateral targets separately in the left and right hemispheres using Wilcoxon's signed-rank test (w) since the data violated the normality assumption ($p < .001$; Shapiro–Wilk test). The p-values reported were corrected for multiple comparisons using the FDR ($q < .05$). Our results are summarized in Table 2, where we also report the rank–biserial correlation (rB) as a measure of our effect sizes, which is commonly adopted in case of non-parametric tests.

In the left hemisphere, the contrast between the FEF and the IFJ revealed that in the dorsal visual stream, several regions had a higher connectivity likelihood with the FEF compared to the IFJ (see Fig. 2A for example distributions in most anterior regions). Conversely, in the ventral visual stream, several regions had a higher connectivity likelihood with the IFJ compared to the FEF (see Fig. 2C). In the right hemisphere dorsal visual stream, surprisingly only one region had a higher connectivity likelihood with the FEF compared to the IFJ (see Fig. 2B), namely 7AL. On the other hand, in the ventral visual stream, again several regions had a higher connectivity likelihood with the IFJ compared to the FEF (see Fig. 2D).

To validate our results, we investigated whether they could be due to the distance between seed and target regions. Therefore, we reanalyzed our data using the probtrackx outputs where the surviving streamline count was multiplied by the average length traveled by the streamlines to reach their targets. The p values were also corrected for multiple comparisons using the FDR ($q < .05$) and are reported in the Supplementary Information (see Table S3). As a whole, they

Table 2 – FEF vs IFJ normalized connectivity likelihood contrasts for all target regions. W = Wilcoxon signed-rank test statistic (sum of ranks); rB = rank–biserial correlation (effect size). p-values are corrected for multiple comparisons using the false discovery rate method (FDR, $q < .05$). ** indicates $p < .01$; * indicates $p < .001$.**

Dorsal Visual Stream Targets							
Left hemisphere	W	*p (FDR corrected)*	*rB*	Right hemisphere	W	*p (FDR corrected)*	*rB*
7PC	1374	.00001**	.722	7PC	740	.7030	−.073
7AL	1463	.0000001***	.900	7AL	1157	.0013**	.558
LIPd	745	.0006**	.650	LIPd	462	.0807	−.329
LIPv	1221	.00003**	.706	LIPv	477	.0531	−.358
VIP	1543	.00000004***	.934	VIP	1030	.0973	.291
IP1	1319	.0000008***	.843	IP1	608	.1680	−.238
MIP	969	.000002***	.872	MIP	665	.8192	.043
7PL	1392	.0000003***	.875	7PL	854	.4305	.150
IPS1	606	.000009***	.924	IPS1	387	.5177	−.143
MT	622	.4005	.151	MT	489	.1088	−.290
LO3	834	.0185	.418	LO3	491	.5221	−.129
V7	519	.0018**	.648	V7	237	.0973	−.360
V6A	664	.0003**	.703	V6A	487	.2821	−.205
V6	297	.3761	.198	V6	173	.0748	−.418
V3CD	583	.00004**	.851	V3CD	240	.7030	−.091
V3B	316	.0001**	.945	V3B	143	.6932	−.120
V3A	452	.0827	.357	V3A	340	.0458	−.397
Ventral visual stream targets							
Left hemisphere	W	*p (FDR corrected)*	*rB*	Right hemisphere	W	*p (FDR corrected)*	*rB*
TGv	352	.0006**	−.559	TGv	95	.0000002***	−.877
TE2a	255	.00008**	−.657	TE2a	100	.0000002***	−.870
TE1a	556	.3620	−.161	TE1a	186	.00004**	−.719
TF	588	.1069	−.263	TF	276	.0003**	−.628
TE1m	348	.0037**	−.495	TE1m	128	.000002***	−.821
TE2p	520	.0769	−.300	TE2p	252	.0005**	−.620
TE1p	208	.000008***	−.739	TE1p	48	.00000003***	−.940
VVC	545	.0062**	.550	VVC	341	.8801	−.030
FFC	778	.0061**	.503	FFC	283	.0373	−.428
PH	476	.0209	−.382	PH	182	.000003***	−.772
PHT	784	.7241	.056	PHT	473	.1135	−.287
VMV3	72	.0878	.582	VMV3	44	.0818	−.537
VMV2	29	.1667	.611	VMV2	6	.0973	−.733
VMV1	22	.6294	−.200	VMV1	10	.0097**	−.853
V8	159	.0657	.514	V8	31	.0318	−.674
PIT	477	.0135	.514	PIT	221	.1145	−.336

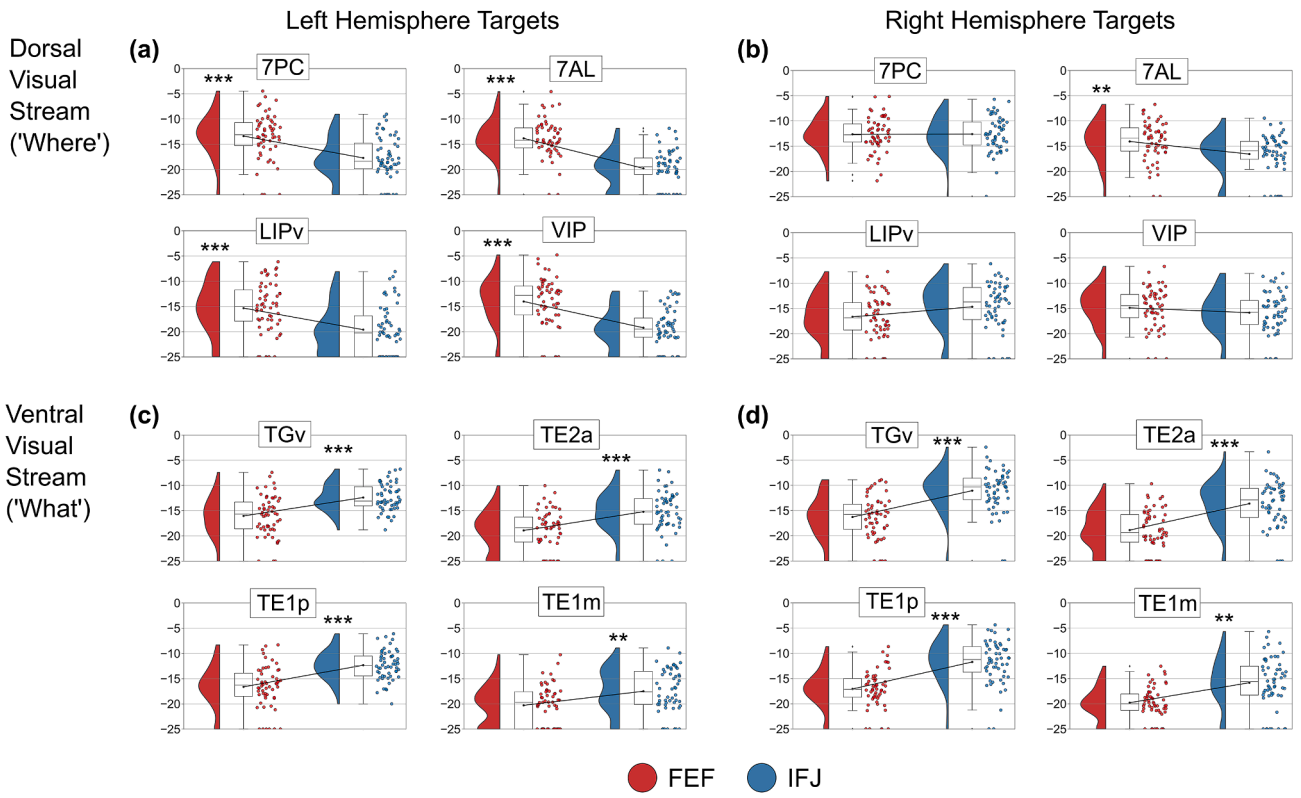

Fig. 2 – Plots of the log_2-scaled normalized streamline counts (NSC) from the frontal eye field (FEF, in red) and inferior frontal junction (IFJ, in blue) seeds to cortical targets in the most anterior portions of the dorsal and ventral visual streams in the left (panels A and C) and right hemisphere (panels B and D). Each dot represents the NSC of a subject, and the asterisks indicate significant contrasts as follows: ** = $p < .01$, *** = $p < .001$. We set −25 as an arbitrary connectivity likelihood equal to 0 for visualization purposes

overwhelmingly replicate our previous results, with 29 of the 33 significant targets parcels showing concordant results.

We summarize these results by plotting the difference between LH FEF and LH IFJ, and RH FEF and RH IFJ NSCs on the fsLR 32k surface (Van Essen et al., 2012) parcellated using the MMP1 (Fig. 3A). We indicated all the targets with significantly higher connectivity likelihood with the FEF or IFJ in the main results and the distance control analysis by asterisks in Fig. 3, panel B.

3.2. *Relationship between the FEF and IFJ ALE clusters and the cortical terminations of the three branches of the SLF*

By using the method we developed to quantify the cortical projections of the three branches of the SLF, we could contrast their estimated white matter terminations to the FEF and IFJ ALE clusters (expressed as a normalized streamline density count). Our results violated the normality assumption ($p < .001$; Shapiro–Wilk test), therefore the contrasts reported below all use the Wilcoxon's signed-rank test (w). In the left hemisphere (Fig. 4A), the SLF1 had a significantly higher number of streamlines projecting to the LH FEF than to the LH IFJ ($w = 297$, $p = 5.960 \times 10{-}7$, $r_B = .98$). In contrast, the SLF3 had a significantly higher number of streamlines projecting to the LH IFJ than to the LH FEF ($w = 8$, $p = 2.980 \times 10{-}6$, $r_B = -.947$). Similarly, in the right hemisphere (Fig. 4B), the SLF1 had a significantly higher number of streamlines projecting to the RH FEF than to the RH IFJ ($w = 279$, $p = 5.329 \times 10{-}5$, $r_B = .86$). In contrast, the SLF3 had a significantly higher number of streamlines projecting to the LH IFJ than to the LH FEF ($w = 10$, $p = 5.126 \times 10{-}6$, $r_B = -.933$). We didn't find significant differences in the SLF2 streamline projections in either hemisphere.

4. Discussion

The FEF and the IFJ are regions that continue receiving interest in the field due to their involvement in several orchestrating functions (Bedini & Baldauf, 2021). Their overarching role is to provide top-down feedback to bias activity in posterior regions in visual attention and working memory tasks (Baldauf & Desimone, 2014; Gazzaley & Nobre, 2012; Veniero et al., 2021; Zanto et al., 2011; Zhang et al., 2018). Their structural connectivity patterns remained largely elusive to date, partly due to a lack of consensus on the precise localization of these regions in standard space (Bedini & Baldauf, 2021) as well as the intrinsic limitations of dMRI tractography (Jbabdi et al., 2015; Jeurissen et al., 2019; Maier-Hein et al., 2017; Sotiropoulos &

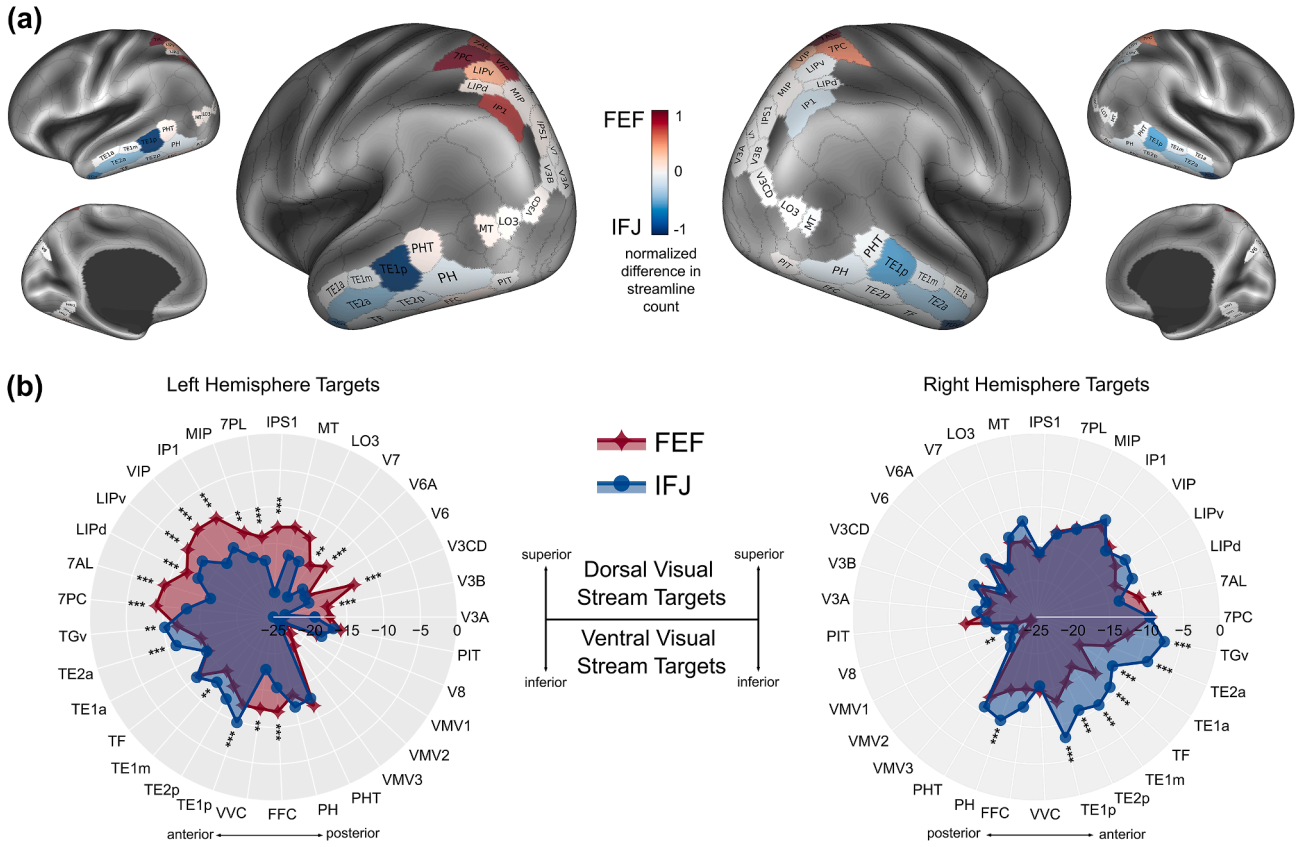

Fig. 3 – A Difference in the normalized connectivity likelihood of the FEF and IFJ with the dorsal and ventral visual streams projected on the fsLR 32k surface parcellated using the MMP1 (Glasser et al., 2016). B Polar plots of the log_2-scaled NSC of FEF and IFJ to each cortical target (we set −25 as an arbitrary 0 connectivity likelihood for visualization purposes). Asterisks indicate significant results that were replicated in the distance control analysis (= $p < .01$, *** = $p < .001$).**

Zalesky, 2017). In this study, we combined an ALE meta-analysis, which allowed us to infer the localization of the FEF and IFJ in MNI152 space, with surface-based probabilistic tractography—to uncover their structural connectivity with the dorsal and ventral visual streams (Goodale & Milner, 1992). Our meta-analysis results revealed the strongest convergence of activations at the junction of the superior frontal sulcus and superior precentral sulcus for the FEF, and at the junction of the inferior frontal sulcus and inferior precentral sulcus for the IFJ (see Bedini et al., 2023, for an extension of these results). We parcellated each participant's cortex using the MMP1 (Glasser et al., 2016) to define our target regions and we used spherical seeds centered on the FEF and IFJ ALE peaks to perform the surface-based tractography analysis. We propagated streamlines from the WM/GM boundary and we applied multiple anatomically-motivated constraints. By contrasting the connectivity likelihood of FEF and IFJ in each hemisphere to all the ipsilateral target regions, we found that in the left hemisphere, the FEF had predominant connectivity with several regions across the dorsal visual stream, whereas the IFJ had predominant connectivity with most regions of the ventral visual stream. In the right hemisphere, we found predominant connectivity of the FEF to one region of the dorsal stream, and again, a predominant connectivity of the IFJ with multiple regions of the ventral stream. We generally found the strongest divergence in these connectivity patterns in regions in the high and mid regions in the processing hierarchy of each stream, while it was almost entirely absent in early visual regions. These patterns seem to underline a gradual rather than absolute transition in the zone of the predominance of FEF and IFJ connectivity, as these regions were likely also connected to the targets in the non-dominant stream. Another striking aspect of our results is that they suggest a remarkable hemispheric asymmetry: while in the left hemisphere, they largely supported our hypothesis in both streams, in the right hemisphere, we found results in line with our prediction primarily in the ventral stream, but not in the dorsal stream. Quantitatively, these results seem to be driven by an increased connectivity likelihood of the right IFJ with the dorsal stream, as opposed to a decrease in the connectivity likelihood of the right FEF per se (see Fig. 3B and in the Supplementary Information, Fig. S6). These asymmetries potentially suggest a more robust involvement of the right IFJ in the dorsal visual stream, and fit well with a recent study that examined the structural connectivity of the dorsal and ventral attention networks, showing that these networks are right-lateralized (Alves et al., 2022). We found highly consistent results in our control analysis, where we corrected the

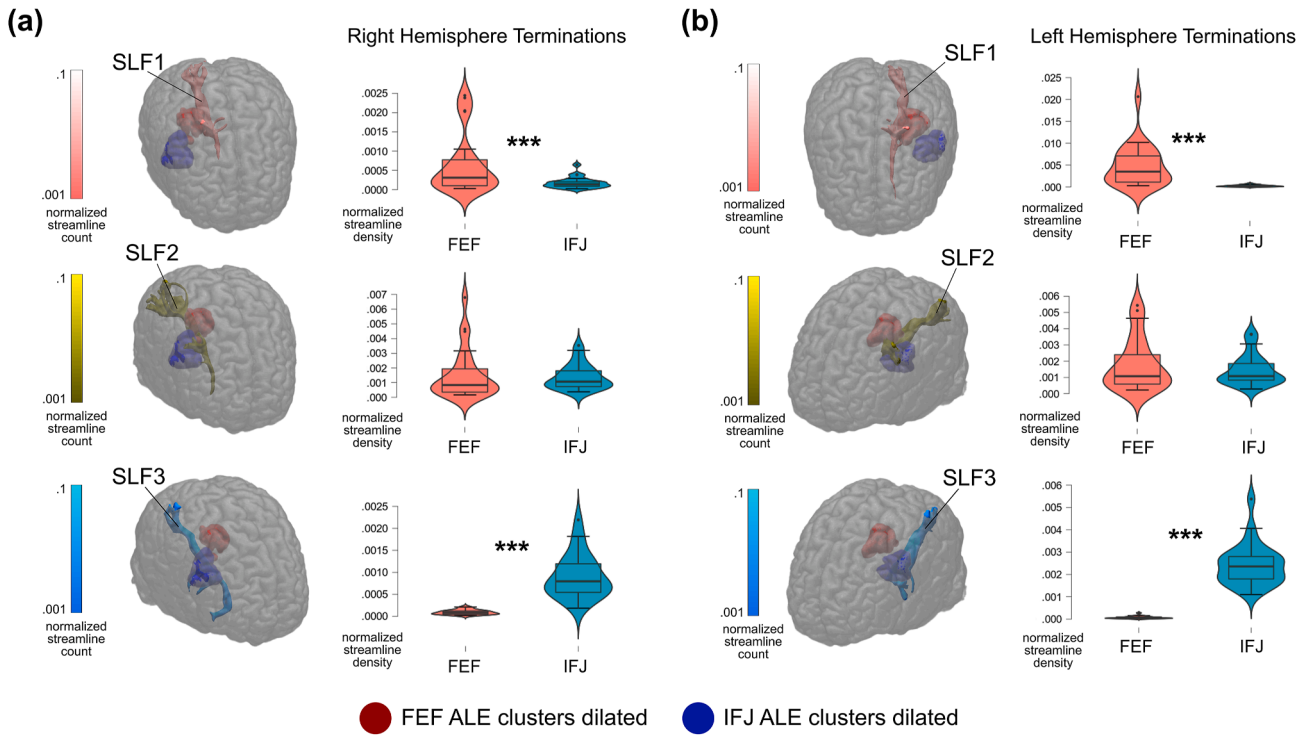

Fig. 4 – Overlay of the SLF1, SLF2, and SLF3 for an example subject with the dilated FEF (in red) and IFJ (in blue) ALE clusters, and plots of the differences in their estimated cortical terminations in the right (panel A) and left (panel B) hemisphere, respectively. Violin plots indicate the streamlines overlapping with the FEF and IFJ grey matter voxels normalized by the bundle and dilated ALE cluster voxel overlap (i.e., a streamline density count) across 24 subjects. In both hemispheres, SLF1 streamlines had a higher probability of projecting to the FEF ALE cluster, whereas SLF3 streamlines had a higher probability of projecting to the IFJ ALE cluster (* indicates $p < .001$)**

connectivity likelihoods based on the average distance traveled by the streamlines to reach their targets from the seeds, thus ruling out this potential confound.

Taken together, our findings reveal a reliable anatomical motif of segregated long–range pathways connecting the FEF and IFJ to the dorsal and ventral visual streams. These results are in agreement with the tracer evidence from the macaque model (Gerbella et al., 2010; Schall et al., 1995; Stanton et al., 1993; Webster et al., 1994; Yeterian et al., 2012). As proposed by Goldman-Rakic and colleagues based on the comparative evidence at the time (Romanski, 2004; Wilson et al., 1993), they suggest that the two visual stream architecture may also extend into the human PFC. Using a virtual dissection approach, we related these findings to the underlying white matter association bundles that form the main frontoparietal and frontotemporal connections (Barrett et al., 2020; Fernández-Miranda et al., 2015; Thiebaut de Schotten et al., 2011). By estimating the cortical projections of the SLF to the FEF and IFJ, we showed that bilaterally, the SLF1 streamlines terminated within the FEF ALE cluster, whereas the SLF3 streamlines terminated within the IFJ ALE cluster. These two branches of the SLF could underlie the connectivity patterns we have reported of the FEF to the medial and superior parietal cortex on the one hand, and the connectivity patterns of the IFJ to the lateral inferior parietal cortex on the other. The SLF2 instead seemed to project to the FEF and IFJ to the same degree, possibly representing a shared pathway mediating their communications with the posterior parietal cortex and its associated functions (Marshall et al., 2015; Parlatini et al., 2017; Thiebaut de Schotten et al., 2011). The connections of the IFJ with the ventral visual stream could be mediated by the arcuate fasciculus based on our virtual dissection results (see the Supplementary Information, Fig. S8 for example results and some caveats).

Our probabilistic tractography pipeline was carefully modeled on the methods reported in Donahue et al. (2016), a study assessing the relationship between different tractography approaches and retrograde tracer injections taken as a ‘silver standard’ (Sarwar et al., 2021). We relied on the excellent quality and spatial resolution of HCP's 3 T dMRI data (Van Essen, Smith, et al., 2013), Van Essen, Ugurbil, & Behrens, 2013nd we performed all our analyses at the individual subject level, thus preserving as much as possible the detailed anatomy of each brain. We parcellated the cortex according to the MMP1 (Glasser et al., 2016), one of the most comprehensive brain atlases available to date, mapping it to the individual white matter segmentation using surface-based methods, thus exploiting its high parcel resolution, which is often deteriorated in studies using volumetric techniques (Coalson et al., 2018). Our approach

was also designed to include as many anatomically plausible constraints as possible based on our hypothesis to optimize the reconstruction of long-range cortico-cortical connections (Jbabdi et al., 2015) and to mitigate some of the biases and common pitfalls of dMRI tractography (Jeurissen et al., 2019; Sotiropoulos & Zalesky, 2017). First, using a pial termination mask allows for discarding streamlines that would incorrectly propagate between adjacent gyri (Hernandez-Fernandez et al., 2019). Second, we chose to seed the streamlines from the WM/GM boundary as several studies show that it is beneficial in alleviating the gyral bias (Girard et al., 2014; Schilling et al., 2018; Van Essen et al., 2014), as well as in reducing partial volume effects (Cottaar et al., 2021; Kleinnijenhuis et al., 2015) and length biases (Girard et al., 2014). Third, several 'avoid' masks, which included the segmentations of subcortical nuclei, the corpus callosum, and the cerebellum, were added to discard invalid streamlines that would have potentially resulted in increasing false positive connections (Hernandez-Fernandez et al., 2019). Finally, by mapping the MMP1 onto the white matter surface, we endeavored to improve the assignment of streamline terminations to the appropriate cortical target (St-Onge et al., 2021; Yeh et al., 2019). While this parcellation matches the scale and cortical features we were interested in (in particular, the topographic organization of the dorsal visual stream) and allowed us to formulate predictions regarding the connectivity patterns (Revell et al., 2022), the reliance on a single parcellation limits the generalizability of our results. Follow-up studies should test our hypotheses with alternative parcellation schemes, including a random parcellation to assess the robustness of the structural connectivity differences we reported.

Our findings highlight that the two visual stream architecture may extend into the PFC, as was first proposed in the macaque model (Romanski, 2004; Wilson et al., 1993; Yeterian et al., 2012; see Martinez-Trujillo, 2022, for a recent review). These findings also provide converging evidence for the functional specialization of the FEF and IFJ in spatial versus non-spatial processing in attention and working memory functions (Bedini & Baldauf, 2021; O'Reilly, 2010; see Bichot et al., 2015, 2019, for comparative evidence), which need to be further substantiated by functional connectivity evidence (see Soyuhos & Baldauf, 2023 for MEG evidence; Rolls, 2024, for a revised proposal of the organization of 'what' and 'where' streams in relation to the MMP1). Based on its set of input and output connections, the FEF is optimally placed within the visual processing hierarchy to efficiently bias spatial selection and working memory in posterior visual regions (Felleman & Van Essen, 1991; Liu & Hou, 2013; Yeo et al., 2011). Similarly, the IFJ receives inputs and sends feedback signals to regions across the ventral stream to efficiently bias non-spatial (feature- and object-based) attention and working memory (Baldauf & Desimone, 2014; Bedini, 2025; Liu & Hou, 2013; Zanto et al., 2011; Zhang et al., 2018). These multimodal connectivity patterns suggest that the attention networks may be organized in a domain-specific manner. In the spatial domain, it is well established that spatial information is encoded by each region at the neural population level forming topographic maps along the visual hierarchy, culminating in the PFC where they overlap with the FEF (Mackey et al., 2017; Wang et al., 2015). Corresponding topographic representations of the visual field are structurally and functionally wired across adjacent regions in the visual, parietal, and ventral cortex (Finzi et al., 2021; Greenberg et al., 2012; Heinzle et al., 2011; Movahevedian Attar et al., 2020). Recently, preferential topographic patterns of connectivity (both structural and functional, resting-state and task-based) were also uncovered between frontal regions and V1 (Griffis et al., 2015; Knapen, 2021; Sims et al., 2021; Yeo et al., 2011). These patterns of preferential connectivity may provide a computationally efficient architecture for top-down spatial selection (Jbabdi, Sotiropoulos, & Behrens, 2013). In the case of non-spatial domains, it is arguably more difficult to pinpoint an architecture of this kind. Comparative studies have, however, begun to elucidate the organization of the ventrolateral PFC in the form of feature and object-selective cortical patches (Haile et al., 2019; Tsao et al., 2008). We suggest that, in principle, this form of organization could provide a similar basis for preferential topographical connectivity across different processing domains (Xu et al., 2022). Our study ties into this framework by highlighting the white matter pathways associated with different forms of top-down control and opens the possibility of fractionating the attention networks based on the representational content encoded (Bedini & Baldauf, 2021; Liu & Hou, 2013; Osher et al., 2019; Parlatini et al., 2017; Rajan et al., 2021; Soyuhos & Baldauf, 2023).

5. Conclusion

Here, by combining an ALE fMRI meta-analysis with probabilistic tractography, we uncovered the structural connectivity of the FEF and the IFJ with the dorsal and ventral visual streams. Our surface-based approach, informed by the MMP1 parcellation and analysis in the native subject space of a large sample from the HCP dataset, allowed us to provide evidence supporting the view that the two visual streams essentially extend into the human PFC. Our study suggests that the functions of the FEF and IFJ, namely spatial and non-spatial top-down control (Bedini & Baldauf, 2021), may be ultimately grounded in their structural connectivity fingerprints (Osher et al., 2016; Passingham & Lau, 2022; Saygin et al., 2012).

CRediT authorship contribution statement

Marco Bedini: Writing – original draft, Writing – review & editing, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Emanuele Olivetti:** Supervision, Methodology. **Paolo Avesani:** Writing – review & editing, Supervision, Methodology. **Daniel Baldauf:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Data availability

Raw and processed ALE meta-analysis data are available in figshare: https://figshare.com/articles/preprint/Surface-based_Tractography_uncovers_What_and_Where_Pathways_in_Prefrontal_Cortex_-_ALE_meta-analysis_data/31795573. The

structural and diffusion MRI data released by the HCP were downloaded from: https://db.humanconnectome.org. The HCP pipelines can be found at: https://github.com/Washington-University/HCPpipelines. The command-line tools from the FSL FDT toolbox are available at: https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FSL. The binaries of probtrackX GPU implementation were downloaded from: https://users.fmrib.ox.ac.uk/~moisesf/Probtrackx_GPU/Installation.html. Our example probtrackx command can be found here: https://github.com/mbedini/app-fsl-probtrackx. The code for mapping the MMP1 atlas to the native structural space can be found at: https://figshare.com/articles/dataset/HCP-MMP1_0_volumetric_NIfTI_masks_in_native_structural_space/4249400.

Declaration of competing interest

The authors declare no competing interests.

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Scientific transparency statement

DATA: Some raw and processed data supporting this research are publicly available, while some are subject to restrictions: https://balsa.wustl.edu/project?project=HCP_YA, https://doi.org/10.6084/m9.figshare.31795573, https://github.com/mbedini/app-fsl-probtrackx, https://github.com/jasp-stats.

MATERIALS: This research did not make use of any materials to generate or acquire data.

DESIGN: This article reports, for all studies, how the author(s) determined all sample sizes, all data exclusions, all data inclusion and exclusion criteria, and whether inclusion and exclusion criteria were established prior to data analysis.

PRE-REGISTRATION: No part of the study procedures was pre-registered in a time-stamped, institutional registry prior to the research being conducted. No part of the analysis plans was pre-registered in a time-stamped, institutional registry prior to the research being conducted.

For full details, see the *Scientific Transparency Report* in the supplementary data to the online version of this article.

Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cortex.2026.03.016.

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