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A lateralized brain network for visuospatial attention

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Right hemisphere dominance for visuospatial attention is characteristic of most humans, but its anatomical basis remains unknown. We report the first evidence in humans for a larger parieto-frontal network in the right than left hemisphere, and a significant correlation between the degree of anatomical lateralization and asymmetry of performance on visuospatial tasks. Our results suggest that hemispheric specialization is associated with an unbalanced speed of visuospatial processing.

Clinical studies in patients with brain lesions and decades of neuropsychological testing in split-brain patients have led to the assumption that visuospatial attention is a function of the right hemisphere[1,2]. Nevertheless, right visuospatial neglect is a frequent finding in patients with left hemisphere damage[3] suggesting that visuospatial attention is probably a bilateral function, with right hemisphere dominance in most, but not all, humans[4]. The anatomical basis of the hemispheric dominance for visuospatial attention is largely unknown.

In the monkey brain, the activity of neurons dedicated to visuospatial attention has been recorded simultaneously using multiple electrodes implanted in the parietal and frontal cortices[5]. Axonal tracing studies have shown that these neurons are directly linked through a system of connections running longitudinally in the dorsolateral regions of the brain[6]. Recent structural[7] and functional[8] imaging studies provide indirect evidence of a similar system in the human brain. However, the hemispheric lateralization of the parieto-frontal connections in the human brain and its correlation with visuospatial performances has never to our knowledge been demonstrated.

In this study, we performed virtual *in vivo* dissections of the parieto-frontal connections in 20 right-handed subjects (11 males, 9 females) using diffusion imaging tractography based on spherical deconvolution[9]. A comparison between our human tractography dissections and the corresponding reconstructions from a monkey atlas[6] that we modified is illustrated in **Figure 1**. Overall, parieto-frontal connections of the human and the monkey brain are similarly organized in three longitudinal parieto-frontal tracts separated into a dorsal superior longitudinal fasciculus (SLF) I, middle SLF II and ventral SLF III. These findings were confirmed with post-mortem dissections in one human

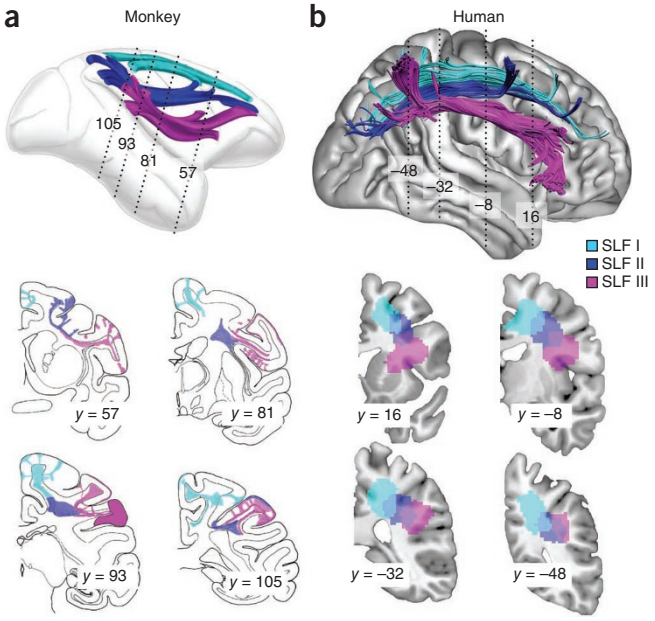

Figure 1 The three branches of the superior longitudinal fasciculus (SLF I, II and III). (**a**,**b**) Comparison between axonal tracing in monkey[6,10] (**a**) and *in vivo* spherical deconvolution (SD) tractography in humans (**b**). Three-dimensional reconstructions are displayed at the top of each panel, and coronal sections at the indicated *y* planes are at the bottom.

right hemisphere (**Supplementary Methods**, **Supplementary Results**, **Supplementary Note**, **Supplementary Figs. 1**–**7** and **Supplementary Tables 1** and **2**)[10].

By measuring the volumes of the tracts in both hemispheres we were able to show a dorsal to ventral gradient of lateralization of the SLF (**Fig. 2a**). The SLF I is symmetrically distributed between left and right hemispheres ($t_{19} < 1$); the SLF II shows a trend of right lateralization ($t_{19} = 1.141$; $P = 0.268$) and the SLF III is right lateralized ($t_{19} = 6.083$; $P < 0.001$).

To test whether this lateralization was related to the attentional bias for one visual hemifield, we asked the participants to perform a line bisection test[11]. In the general population, a small left deviation in the line bisection test is observed and referred to as the 'pseudoneglect effect'[11]. Consistent with previous studies[12], our participants deviated toward the left at a group level (-1.53 ± 2.02 mm; $t_{19} = 3.148$; $P = 0.005$). In most participants, the correlation analysis indicates that larger SLF II volumes on the right hemisphere corresponded to a greater deviation to the left in the line bisection ($r = -0.734$; $P < 0.001$) (**Fig. 2b**). Notably, the three subjects deviating to the right showed

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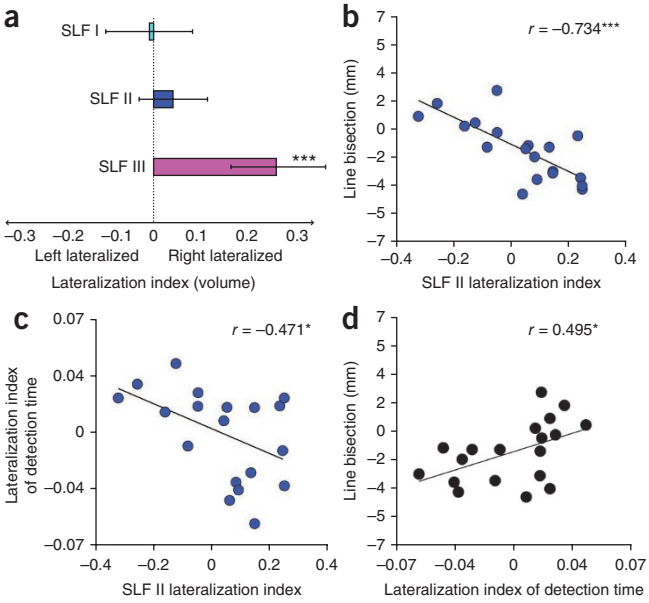

Figure 2 Correlations between anatomical and behavioral lateralizations. (**a**) Hemispheric lateralization of the three SLF branches, with 95% confidence intervals. (**b**,**c**) Correlations between the lateralization of the SLF II and both the deviation on the line bisection task (**b**) and the lateralization of the detection time (**c**). (**d**) Correlation between the deviation on the line bisection task and the detection time. $^{*}P < 0.05$ and $^{***}P < 0.001$.

an opposite pattern of lateralization (that is, larger volume of the left SLF II; see **Supplementary Table 1**). Correlations with the SLF I ($r = 0.258$; $P = 0.286$) and the SLF III ($r = -0.295$; $P = 0.220$) were not statistically significant.

It is unknown how differences between the two hemispheres in SLF II volume can lead to asymmetrical processing of visual scenes. A larger tract in the right hemisphere could depend on several factors, including greater fiber myelination, more axons and larger axonal diameter, that are correlated with conduction speed[13,14]. In light of this previous work, we suggest that the left deviation in the line bisection we observed in most subjects may result from unbalanced speed of visuospatial processing between the two hemispheres along the SLF II. To test this hypothesis, we asked subjects to complete a modified Posner paradigm[15] in which they detected as quickly as possible targets that appeared either in their left or right hemifield. In most subjects, the correlation analysis indicated that larger SLF II volumes in the right hemisphere corresponded to faster detection times in the left hemifield ($r = -0.471$; $P = 0.042$) (**Fig. 2c**). Correlations with SLF I ($r = 0.271$; $P = 0.262$) or SLF III ($r = -0.271$; $P = 0.262$) were not statistically significant. Moreover, larger deviation toward the left in the line bisection corresponded to faster detection times in the left hemifield ($r = 0.495$; $P = 0.031$) (**Fig. 2d**).

The correlations between the lateralization of the SLF II, the deviation observed in the line bisection and the detection times represent the first demonstration, to our knowledge, that anatomical asymmetry of the parieto-frontal connections predicts behavioral performance on visuospatial attention tasks. These findings may help to interpret the neuroanatomical basis of models of visuospatial attention based on functional imaging and studies of individuals who show clinical neglect. The cortical projections of the SLF I overlap with the dorsal network activated during the voluntary orienting of spatial attention toward visual targets, and the SLF III overlaps with the ventral network that is activated during the automatic capture of spatial attention by visual targets[8] and damaged in people with visuospatial neglect (**Supplementary Fig. 8**). In contrast, the SLF II overlaps with the parietal component of the ventral network and the prefrontal component of the dorsal network. Thus, our findings suggest that the SLF II represents a direct communication between the dorsal and ventral networks. This communication may act as a modulator for the dorsal network, redirecting goal-directed attention mediated by the SLF I to events identified as salient by the SLF III[8].

In conclusion, we report the existence of a bilateral parieto-frontal network, previously described only in monkey, whose hemispheric lateralization predicts the degree of specialization of the right hemisphere for visuospatial attention. Our results also suggest that this hemispheric specialization is associated with an unbalanced speed of visuospatial processing along the SLF II. This lateralization may be predictive of visuospatial recovery in patients with lesions of parieto-frontal networks.

Note: Supplementary information is available on the Nature Neuroscience website.

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AUTHOR CONTRIBUTIONS

M.T.d.S. conceived and coordinated the study, reviewed and collected neuropsychological data, performed the tractography dissections, helped with the post-mortem dissections and wrote the manuscript. F.D. developed the spherical deconvolution algorithm, collected and preprocessed the neuroimaging data before the dissections and helped drafting the manuscript. S.J.F. helped collecting neuropsychological data and drafting the manuscript. A.S. and D.G.M.M. provided funding for the neuroimaging data and helped to draft the manuscript. F.V. helped drafting the manuscript and performed the post-mortem dissections. M.C. helped to conceive and coordinate the study. M.C. also wrote the manuscript and performed the post-mortem dissections.

COMPETING FINANCIAL INTERESTS

The authors declare no competing financial interests.

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Erratum: A lateralized brain network for visuospatial attention

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In the version of this article initially published, the institute identifier was omitted from the INSERM affiliation of author Michel Thiebaut de Schotten. The correct affiliation should read Unité Mixte de Recherche (UMR) S 975. The error has been corrected in the HTML and PDF versions of the article.