



Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Q3 Virtual dissection and comparative connectivity of the superior longitudinal fasciculus in chimpanzees and humans

Q4 Erin E. Hecht ^{a,*}, David A. Gutman ^b, Bruce A. Bradley ^c, Todd M. Preuss ^d, Dietrich Stout ^a

Q5 ^a Department of Anthropology, Emory University, 1557 Dickey Drive, Rm 114, Atlanta, GA 30322, USA

^b Department of Biomedical Informatics, Emory University School of Medicine, 36 Eagle Row, PAIS Building, 5th Floor South, Atlanta, GA 30322, USA

^c Department of Archaeology, University of Exeter, Laver Building, North Park Road, Exeter EX4 4QE, UK

^d Yerkes National Primate Research Center, Div. Neuropharmacology & Neurologic Diseases & Center for Translational Social Neuroscience, Emory University, 954 Gatewood Rd., Atlanta, GA 30329, USA

9 A R T I C L E I N F O

10 Article history:
11 Accepted 8 December 2014
12 Available online xxxxx

13 Keywords:
14 Laterality
15 Cerebral asymmetry
16 Evolution
17 White matter
18 Diffusion tensor imaging
19 Tractography

A B S T R A C T

Many of the behavioral capacities that distinguish humans from other primates rely on fronto-parietal circuits. The superior longitudinal fasciculus (SLF) is the primary white matter tract connecting lateral frontal with lateral parietal regions; it is distinct from the arcuate fasciculus, which interconnects the frontal and temporal lobes. Here we report a direct, quantitative comparison of SLF connectivity using virtual *in vivo* dissection of the SLF in chimpanzees and humans. SLF I, the superior-most branch of the SLF, showed similar patterns of connectivity between humans and chimpanzees, and was proportionally volumetrically larger in chimpanzees. SLF II, the middle branch, and SLF III, the inferior-most branch, showed species differences in frontal connectivity. In humans, SLF II showed greater connectivity with dorsolateral prefrontal cortex, whereas in chimps SLF II showed greater connectivity with the inferior frontal gyrus. SLF III was right-lateralized and proportionally volumetrically larger in humans, and human SLF III showed relatively reduced connectivity with dorsal premotor cortex and greater extension into the anterior inferior frontal gyrus, especially in the right hemisphere. These results have implications for the evolution of fronto-parietal functions including spatial attention to observed actions, social learning, and tool use, and are in line with previous research suggesting a unique role for the right anterior inferior frontal gyrus in the evolution of human fronto-parietal network architecture.

© 2014 Elsevier Inc. All rights reserved.

36 Introduction

Many of the behaviors that distinguish humans from other primates – including social learning and tool use – rely on activation of, and communication between, frontal and parietal cortical regions (Johnson-Frey, 2004; Fabbri-Destro and Rizzolatti, 2008; Peeters et al., 2009; Caspers et al., 2010). Evidence for human specializations in these circuits is accumulating from a growing number of comparative studies. For example, action observation involves inferior frontal and inferior parietal regions in macaques, chimpanzees, and humans (Fabbri-Destro and Rizzolatti, 2008; Caspers et al., 2010; Rilling and Stout, 2014), but the type of detailed, methods-oriented social learning that is uniquely developed in humans may be related to increased activation and connectivity in inferior fronto-parietal cortex (Hecht et al., 2013a,b). Similarly, tool use involves homologous inferior frontal and inferior parietal regions in monkeys and humans (Johnson-Frey,

2004; Ferrari et al., 2005; Hihara et al., 2006; Obayashi et al., 2007; Quallo et al., 2009; Orban and Rizzolatti, 2012), but a region of human anterior inferior parietal cortex has unique response properties that may support uniquely human capacities for causal understanding (Peeters et al., 2009; Orban and Rizzolatti, 2012). More generally, there is evidence for organizational changes and expansion of gray and white matter in the frontal lobes (Smaers et al., 2010; Preuss, 2011; Passingham and Smaers, 2014), changes in frontal and parietal white and gray matter asymmetry (Schenker et al., 2010; Gilissen and Hopkins, 2013; Hopkins and Avants, 2013; Van Essen and Glasser, 2014) and emergence of new functional response properties in inferior frontal (Neubert et al., 2014) and parietal cortex (Peeters et al., 2009). Together, these studies suggest that fronto-parietal circuits were a likely locus of structural-functional adaptation in human brain evolution. Here we report a direct, quantitative comparison between humans and chimpanzees in the superior longitudinal fasciculus (SLF), the primary white matter tract connecting lateral frontal with lateral parietal regions.

The SLF is an antero-posteriorly oriented tract located in the lateral aspect of the cerebral white matter. The label “superior longitudinal fasciculus” is sometimes used interchangeably with “arcuate fasciculus,” but distinct bundles of fronto-parietal and fronto-temporal fibers can be

* Corresponding author at: Department of Psychology, Center for Behavioral Neuroscience, Georgia State University, P.O. Box 5010, Atlanta, GA 30302, USA.

E-mail addresses: ehecht@emory.edu, ehecht@gsu.edu (E.E. Hecht), dgutman@emory.edu (D.A. Gutman), B.A.Bradley@exeter.ac.uk (B.A. Bradley), tpreuss@emory.edu (T.M. Preuss), dwestout@emory.edu (D. Stout).

76 recognized in both macaques and humans (Makris et al., 2005; Q7
77 Fernandez-Miranda et al., 2008; Gharabaghi et al., 2009; Petrides Q8
78 and Pandya, 2009; Thiebaut de Schotten et al., 2011a; Martino and Marco Q9
79 de Lucas, in press). Here we use the term “SLF” to refer specifically to Q10
80 direct fronto-parietal connections and consider the arcuate to consist Q11
81 of fronto-temporal connections (see the Comparison to previous Q12
82 studies section for a more extensive discussion of terminology). Studies Q13
83 in humans (Makris et al., 2005; Thiebaut de Schotten et al., 2011a) and Q14
84 macaques (Petrides and Pandya, 1984, 2002; Schmahmann et al., 2007; Q15
85 Thiebaut de Schotten et al., 2012) have identified 3 sub-tracts within the Q16
86 SLF. The superior-most branch is SLF I, which links the superior parietal Q17
87 lobule with the supplementary motor area, posterior dorsolateral Q18
88 prefrontal cortex, dorsal premotor cortex, and the rostral part of primary Q19
89 motor cortex. SLF II is located inferior and lateral to SLF I and links Q20
90 posterior inferior parietal cortex with dorsal premotor cortex and Q21
91 dorsolateral prefrontal cortex. SLF III is the inferior- and lateral-most Q22
92 of these tracts, traveling in the opercular white matter. It connects the Q23
93 posterior inferior prefrontal and ventral premotor cortex with anterior Q24
94 inferior parietal cortex. Functionally, SLF has been linked with motor Q25
95 planning and visuospatial processing in humans and monkeys Q26
96 (Petrides and Pandya, 2002; Thiebaut de Schotten et al., 2011a) and is Q27
97 thus one likely locus of evolutionary changes supporting uniquely Q28
98 human capacities for tool-use and social learning of observed actions. Q29

99 Although macaques and chimpanzees are capable of simple tool-use, Q30
100 humans are distinguished by the complexity of their tool-use and tool- Q31
101 making, including the use of tools to make other tools, the construction Q32
102 of multi-component tools, and the accumulation of complexity in tool Q33
103 design through social learning (Johnson-Frey, 2003; Frey, 2007). In Q34
104 humans, tool use involves a distributed network of interconnected Q35
105 frontal, parietal, and occipitotemporal regions (Johnson-Frey, 2004; Q36
106 Ramayya et al., 2010; Rilling and Stout, 2014). This network overlaps Q37
107 with an evolutionarily ancient fronto-parietal network for object- Q38
108 directed grasping (Rizzolatti and Fadiga, 1998) but human tool-use Q39
109 networks are undoubtedly more complex than macaque object-grasping Q40
110 networks. It has been proposed that use of “complex” tools (those that Q41
111 alter the functional properties of the hand) requires additional causal Q42
112 understanding resulting from an integration of dorsal (“how”) and Q43
113 ventral (“what”) processing streams in a left-lateralized network of Q44
114 temporal, frontal and parietal areas (Frey, 2007). This capacity may be Q45
115 supported by the evolution of new functional response properties in Q46
116 left anterior inferior parietal cortex (Peeters et al., 2009) and by the Q47
117 expansion of gray matter and extension of white matter in lateral Q48
118 temporal cortex, particularly the middle temporal gyrus, which plays Q49
119 an important role in semantic representation (Orban et al., 2004; Q50
120 Rilling et al., 2008; Hecht et al., 2013a).

121 Beyond tool-use, actual tool-making involves longer action chains Q51
122 with more complex, abstract goals. There has been relatively little Q52
123 study of such multi-step technological actions, but lesion (Hartmann Q53
124 et al., 2005) and neuroimaging (Frey and Gerry, 2006; Hamilton and Q54
125 Grafton, 2008) evidence implicate right frontoparietal cortex in the Q55
126 representation of action sequences and goals. Experimental studies of Q56
127 stone tool-making, a behavior practiced by human ancestors for more Q57
128 than 2.5 million years, have reported left anterior inferior parietal-ventral Q58
129 premotor activation during simple tool-making and increased right Q59
130 inferior parietal-inferior frontal (ventral premotor, *pars triangularis* of Q60
131 the inferior frontal gyrus) during more complex tool-making. A longitudinal Q61
132 study of stone tool-making skill acquisition identified training- Q62
133 related changes (increased fractional anisotropy) in white matter Q63
134 underlying these fronto-parietal cortical regions, including right *pars* Q64
135 *triangularis* (Hecht et al., in press). A “mirror-system” or “simulation” Q65
136 account of action understanding suggests that similar neural systems Q66
137 would be involved in the social learning of tool-making methods, and Q67
138 this has been supported by an fMRI study of stone tool-making action Q68
139 observation (Stout et al., 2011).

140 Comparative evidence relevant to understanding the anatomy and Q69
141 evolution of these left and right fronto-parietal circuits is limited. In a

142 previous comparative DTI study, we used probabilistic tractography to Q70
143 compare frontal-parietal-temporal connectivity in macaques, Q71
144 chimpanzees, and humans and found a gradient in the pattern of net- Q72
145 work organization (Hecht et al., 2013a). In macaques, frontal-temporal Q73
146 connections via the extreme and/or external capsules dominated this Q74
147 network, while in humans, frontal-parietal-temporal connections via Q75
148 the superior and middle longitudinal fasciculi were more prominent; Q76
149 chimpanzees were intermediate. Thiebaut de Schotten et al. (2012) Q77
150 employed a “virtual dissection” approach to obtain more detailed Q78
151 anatomical reconstructions. They not only concluded that SLF is “highly Q79
152 conserved” between humans and macaques but also reported apparent Q80
153 differences, including more anterior frontal terminations of SLF III in Q81
154 humans. The chimpanzee condition is unknown. Human SLF III is right Q82
155 lateralized (Thiebaut de Schotten et al., 2011a,b), but the symmetry/ Q83
156 asymmetry of SLF branches in both macaques and chimpanzees is Q84
157 again unknown. Ramayya et al. (2010) used deterministic tractography Q85
158 to examine asymmetries of a putative human tool-use network, not Q86
159 only confirming the presence of leftwardly-asymmetric connections Q87
160 between the middle temporal gyrus, anterior inferior parietal lobe and Q88
161 inferior frontal cortex but also finding a strongly rightwardly asymmetric Q89
162 pathway between the posterior inferior parietal and frontal cortex. It is Q90
163 tempting to conclude that these patterns of asymmetry and enhanced Q91
164 fronto-parietal connectivity reflect uniquely human adaptations for the Q92
165 execution and social transmission of tool-use and tool-making, but Q93
166 more detailed information on comparative anatomy is needed, particu- Q94
167 larly from our closest living relative, the chimpanzee. We thus conducted Q95
168 a virtual dissection study of humans and chimpanzees to assess the Q96
169 presence/absence of differences in the relative size, lateralization, and Q97
170 connections of SLF I, II, and III.

171 Materials and methods

172 Subjects and data acquisition

173 Chimpanzees

174 The current study analyzed archived chimpanzee datasets from Q98
175 previous studies. Chimpanzee subjects were 2 males and 47 females Q99
176 housed at the Yerkes National Primate Research Center. The scans ana- Q100
177 lyzed in the current study were acquired at the Yerkes National Primate Q101
178 Research Center under propofol anesthesia (10 mg/kg/h) using previ- Q102
179 ously described procedures (Chen et al., 2013; Hecht et al., 2013b). All Q103
180 procedures were carried out in accordance with protocols approved Q104
181 by YNPRC and the Emory University Institutional Animal Care and Use Q105
182 Committee (approval no. YER-2001206). 60-direction DTI images with Q106
183 isotropic 1.8 mm³ voxels were acquired on a Siemens Trio 3.0 T scanner Q107
184 (TR: 5900 ms; TE: 86 ms; 41 slices). 5 B0 volumes were acquired Q108
185 with no diffusion weighting. T1-weighted images were acquired on Q109
186 the same scanner with isotropic 0.8 mm³ voxels (TR: 2600 ms; TE: Q110
187 3.06 ms; slice thickness: 0.8 mm).

188 Humans

189 One group of human subjects consisted of 5 males and 1 female Q111
190 recruited from the undergraduate and graduate programs at the Univer- Q112
191 sity of Exeter, all right-handed by self-report, with no neurological or Q113
192 psychiatric illness. Scans were acquired at the Wellcome Department Q114
193 of Imaging Neuroscience at University College London. All subjects Q115
194 provided written consent. The National Hospital for Neurology and Q116
195 Neurosurgery and Institute of Neurology Joint Research Ethics Commit- Q117
196 tee approved the study. 61-direction DTI images with isotropic 1.7 mm³ Q118
197 voxels were acquired on a Siemens Trio 3.0 T scanner (TR: 1820 ms; Q119
198 TE: 102 ms; 80 slices). 6 B0 volumes were acquired with no diffusion Q120
199 weighting. T1-weighted images were acquired on the same scanner Q121
200 with isotropic 1 mm³ voxels (TR: 1820 ms; TE: 102 ms; 80 slices).

201 A second group of human subjects consisted of 58 females, 2 left- Q122
202 handed and the rest right-handed by self-report, with no known neuro- Q123
203 logical or psychiatric illness. Scans were acquired at the Yerkes National

Download English Version:

<https://daneshyari.com/en/article/6025854>

Download Persian Version:

<https://daneshyari.com/article/6025854>

[Daneshyari.com](https://daneshyari.com)