Continuity, divergence, and the evolution of brain language pathways

James K. Rilling1,2,3,4*, Matthew F. Glasser5, Saad Jbabdi6, Jesper Andersson6 and Todd M. Preuss3,2,8

1 Department of Anthropology, Emory University, Atlanta, GA, USA
2 Department of Psychiatry and Behavioral Sciences, Emory University, Atlanta, GA, USA
3 Center for Translational Social Neuroscience, Emory University, Atlanta, GA, USA
4 Yerkes National Primate Research Center, Emory University, Atlanta, GA, USA
5 Department of Anatomy and Neurobiology, Washington University, St. Louis, MO, USA
6 Centre for Functional Magnetic Resonance Imaging of the Brain, University of Oxford, Oxford, UK
7 Division of Neuropsychopharmacology and Neurologic Diseases, Yerkes National Primate Research Center, Emory University, Atlanta, GA, USA
8 Department of Pathology and Laboratory Medicine, Emory University School of Medicine, Atlanta, GA, USA

Published: 03 January 2012

Keywords: language, evolution, brain, chimpanzee, arcuate fasciculus, extreme capsule

INTRODUCTION

Language is one of the fundamental evolutionary innovations of the human lineage. Our closest relatives, chimpanzees and bonobos, can learn signs, but do not produce grammatical expressions (Wallman, 1992; Rivas, 2005; Premack, 2007). How did evolution transform a non-linguistic ancestral primate brain into a linguistic human brain? The fossil record provides few clues about this transformation: we know that brain volume increased dramatically (about threefold) after the human lineage separated from the chimpanzee lineage about six to eight million years ago, but soft tissues like the brain are not preserved during fossilization, so there is no record of the changes in the brain's internal organization related to language. To understand language evolution we must employ the comparative method, using information about the shared characteristics of living species to infer ancestral states (e.g., Sherwood et al., 2008; Preuss, 2011). In particular, we need to compare humans to the primates with which we are most closely related, namely apes and Old World monkeys, the latter including the familiar macaque monkeys. The scale of research done on the connections and functions of macaque brains makes them an especially valuable source of information.

NON-HUMAN PRIMATE BRAIN COMMUNICATION SYSTEMS

Intuitively, uniquely human functions would seem to require uniquely human brain structures, so some neuroscientists have maintained that the classic language areas of Broca and Wernicke must be unique to humans (e.g., Brodmann, 1909; Crick and Jones, 1993). The work of evolution, however, more commonly involves the modification of existing anatomical structures to serve different functions than the addition of new structures. There is, in fact, considerable evidence that homologs of Broca’s and Wernicke’s areas exist in apes and monkeys, based on similarities in architectonics, common position within the cortical mantle relative to other areas, and shared non-linguistic functions (e.g., Bonin, 1944; Galaburda and Pandya, 1982; Rizzolatti and Arbib, 1998; Preuss, 2000, 2011; Arbib, 2007). Yet, presumably, there was something about the non-human homologs of the classic language areas that made them suitable to be “recruited” (Bonin, 1944; Arbib, 2007) into the evolving language system.

Perhaps language evolved from brain systems that perform related functions in non-human primates, such as the production and perception of communicative calls and facial expressions. Area F5, the macaque homolog of the posterior part of Broca’s area (area 44), is involved in the production of orofacial expressions (Petrides et al., 2005), and mirror neurons in F5 respond to communicative mouth gestures, presumably using motor simulation to form a natural link between sender and receiver that facilitates communication (Rizzolatti and Fogassi, 2007). Calls and vocalizations are processed in the ventral auditory pathway that links anterior and middle STG, STS, and inferotemporal cortex (IT) with areas 45 and 47/12 (the likely homologs of the anterior and orbital parts of Broca’s area in humans) via the extreme capsule (Petrides and Pandya, 2009). This pathway is involved in auditory object identification. Although not specific for calls, both nodes
Although the human language system likely recruited components pare the human brain with that of our closest living relative, the human–macaque comparisons alone, as macaques are relatively human primate brains that endow us with this special ability. We functional and anatomical differences between human and non-pose human primates but with the differences. That is, since humans possess language and other primates do not, there must be critical present in non-human primates, the key to understanding the human left hemisphere (Schmahman present in chimpanzees or macaques, it is reasonable to assume that the trait uniquely evolved in humans after we diverged from chimpanzees six to eight million years ago.

HUMAN BRAIN LANGUAGE SPECIALIZATIONS

Given the traditionally accepted importance of Wernicke’s and Broca’s areas in language, were there changes in the temporal and frontal cortices that contain these regions? Here, we will focus on temporal cortex. Early functional MRI studies of the human visual system noted differences in the location of human and macaque visual areas (Ungerleider et al., 1998). Whereas macaque visual cortex spanned the lateral IT, human visual cortex was in a more ventral and posterior position. This prompted the suggestion that an evolutionary expansion of human language cortex in the lateral temporal lobe displaced human visual cortex to its present location. Although the visual system has not been mapped in the chimpanzee brain, the chimpanzee lunate sulcus, which marks the anterior border of V1, is in a macaque-like rather than a human-like location (Holloway et al., 2008), suggesting that chimpanzees largely preserve macaque-like visual cortical organization.

If human visual cortex was displaced by expanded temporal lobe language cortex, where specifically in the temporal lobe did this expansion take place? Lesion (Damasio et al., 1996; Dronkers et al., 2004), fMRI (Binder et al., 2009; Price, 2010), and structural and functional connectivity (Glasser and Rilling, 2008; Turken and Dronkers, 2011) data implicate the left MTG as a neural epicenter for lexical–semantic processing in the human brain (Turken and Dronkers, 2011). Functional MRI studies additionally implicate the adjacent STS as a core region involved in syntax (Grodzinsky and Friederici, 2006). If one assumes evolutionary continuity, one might reasonably hypothesize that this cortex (STS/MTG) is connected to ventrolateral prefrontal cortex via the ventral auditory pathway that was inherited from non-linguistic non-human primates. Further, this ventral pathway should mediate lexical–semantic retrieval and syntax. Given the expansion of cortical surface area (Van Essen and Dierker, 2007), we would also predict a corresponding expansion in the ventral extreme capsule pathway relative to the dorsal arcuate fasciculus pathway in linguistic humans vs. non-linguistic chimpanzees if the continuity hypothesis is correct. Furthermore, we might expect the pathway to be leftwardly asymmetric, given that lexical–semantics and syntax extend to be left-lateralized (Nucifora et al., 2005; Parker et al., 2005; Glasser and Rilling, 2008). We can test this prediction directly with comparative diffusion tractography (DT), which can estimate the extent and route of connections between cortical regions.

RESULTS AND DISCUSSION

Contrary to the hypothesis that expanded temporal lobe language cortex is most strongly connected to Broca’s area via the ventral extreme capsule pathway, we previously found a qualitatively stronger connection via the dorsal arcuate fasciculus pathway (Rilling et al., 2008). These data suggest that the dorsal arcuate fasciculus pathway may have been the focus of language-related change in human evolution. To quantitatively evaluate this claim, we here compare a rough measure of connection strength of the dorsal and ventral pathways in a sample of 26 human brains with the homologous pathways in 26 chimpanzee brains. If the dorsal...
pathway was augmented in human evolution, then it should be stronger relative to the ventral pathway in humans vs. chimpanzees, and this is what was found. Although present in both hemispheres, the effect is more pronounced in the left hemisphere, where humans have a particularly strong dorsal pathway. Nevertheless, the dorsal pathway was leftwardly asymmetric in both species, a finding consistent with previously reported leftward asymmetries in the planum temporale, a portion of Wernicke’s area (Gannon et al., 1998; Hopkins et al., 1998, 2008), and in peri-sylvian white matter volume (Cantalupo et al., 2009). These findings suggest that the anatomical substrates for lateralization of communicative functions may have been present in the common ancestor of humans and chimpanzees (Cantalupo et al., 2009). In contrast to the dorsal pathway, the ventral pathway is not asymmetric in either humans or chimpanzees. We would expect a pathway that mediates syntax and lexical–semantic retrieval to be leftwardly asymmetric, like the human arcuate, rather than symmetric, like the human extreme capsule (Table 1; Figure 1).

Finally, as reported previously (Rilling et al., 2008), in humans the arcuate projections into the temporal cortex are concentrated in STS and MTG, ventral to classic Wernicke’s area, whereas in chimpanzees they are concentrated in STG. On the other hand, extreme capsule projections to temporal cortex are concentrated in STS and cortex ventral to it in both species. Thus, in terms of both pathway strength and pattern of cortical connectivity, the dorsal arcuate fasciculus seems to have undergone more evolutionary change than the ventral extreme capsule pathway.

Did the expanded arcuate fasciculus pathway displace the ventral visual stream in the human brain, as suggested above? Tracking the ventral visual stream (the inferior longitudinal fasciculus, ILF) in both species revealed that the arcuate abuts the ILF in humans but not chimps and does appear to have replaced ILF in a ventromedial direction (Figure 2).

CONCLUSION
Comparative DT data suggest that the specialized, derived features of human language (syntax and lexical–semantics) are likely to be mediated by the arcuate fasciculus pathway. The most cited evidence to the contrary is from a paper by Saur et al. (2010) who used fMRI to identify frontal and temporal cortical regions involved in processing word meaning and then used DT to track between these functional ROIs. They found stronger connectivity between frontal and temporal semantic ROIs via the ventral extreme capsule pathway as opposed to the dorsal arcuate fasciculus pathway. Critically, however, despite widespread activation across the MTG, they limited their tractography seeds to activation peaks in the anterior and posterior extremes of the MTG. That is, they did not track from the core lexical–semantic and syntactical areas in mid MTG and STS respectively (Vigneau et al., 2006; Glasser and Rilling, 2008; Turken and Dronkers, 2011). Furthermore, they used tensor-based single fiber tractography, which is unable to follow non-dominant pathways and gives less accurate estimates of fiber orientations (Behrens et al., 2007). Here we show extreme capsule pathway versus the ventral arcuate fasciculus.

Table 1 | Diffusion tractography normalized streamline counts and asymmetry indices (AIs) in chimpanzees and humans.

<table>
<thead>
<tr>
<th></th>
<th>Left dorsal</th>
<th>Right dorsal</th>
<th>Left ventral</th>
<th>Right ventral</th>
<th>Left D/V Al</th>
<th>Right D/V Al</th>
<th>Dorsal L/R Al</th>
<th>Ventral L/R Al</th>
</tr>
</thead>
<tbody>
<tr>
<td>Human</td>
<td>116073</td>
<td>53214</td>
<td>27947</td>
<td>34753</td>
<td>0.61 ± 0.06**</td>
<td>0.00 ± 0.13</td>
<td>0.42 ± 0.11**</td>
<td>−0.17 ± 0.09</td>
</tr>
<tr>
<td>Chimpanzee</td>
<td>2865</td>
<td>379</td>
<td>23761</td>
<td>18942</td>
<td>−0.84 ± 0.08**</td>
<td>−0.08 ± 0.08**</td>
<td>0.66 ± 0.07**</td>
<td>0.08 ± 0.10</td>
</tr>
<tr>
<td>Human–Chimpanzee</td>
<td>1.14 ± 0.10**</td>
<td>0.89 ± 0.15**</td>
<td>−0.24 ± 0.13</td>
<td>−0.24 ± 0.13</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Streamline counts were normalized to remove variance in ROI size (after deformation from standard ROIs to individuals) and for differences in trackability across subjects within a species. The assumption was made that the total number of streamlines counted across all four pathways should be the same across individuals within a species, as we are only interested in relative differences between the pathways across subjects and want the average normalized streamline counts to reflect equal contributions from all subjects. D, dorsal; V, ventral; L, Left; R, right; AI, Asymmetry Index \(AI_{LR} = (W_L - W_R)/(W_L + W_R)\) or \(AI_{DV} = (W_D - W_V)/(W_D + W_V)\).

\(* p < 0.05, ** p < 0.01\)
that tracking from mid MTG/STS with crossing-fiber tractography yields stronger connectivity via a dorsal compared with a ventral route. This is not to say that the extreme capsule pathway has no role in human language. Indeed, there is evidence that electrical stimulation of the extreme/external capsule (EC) induces semantic role in human language. Indeed, there is evidence that electrical stimulation of the extreme/external capsule (EC) induces semantic retrieval and syntax, occurred in the arcuate fasciculus. Therefore, that study.

TRACTOGRAPHY METHODS

Our goal was to track between Broca’s region (i.e., area 44, 45, and 47l) and association cortex in the posterior two-thirds of the lateral temporal cortex lying dorsal and anterior to visual association cortex and ventral to early auditory cortex. Frontal and temporal surface ROIs (white outlines in Figures 1A–D, G–I) were used together with volumetric fascicle selection ROIs (translucent white on coronal slice in Figures 1E,J) that required streamlines to travel via either a dorsal or ventral route. ROIs were drawn on group average templates and then warped into individual subjects’ diffusion space for tractography.

Surface ROIs were defined as follows: Fiber pathways of interest were initially localized by tracking from white matter ROIs in the superior longitudinal fasciculus (SLF) and EC. The surface terminations from this tractography defined an outer bound on the possible connections between frontal and temporal regions, and, within this area, myelin maps and probabilistic cytoarchitecture were used to define homologous frontal and temporal surface ROIs across hemispheres and species. The frontal surface ROI was defined in humans using surface-based probabilistic cytoarchitectonic areas 44, 45, and 47l (Amunts et al., 1999; Ongür et al., 2003; Fischl et al., 2008; Van Essen et al., 2011) and was located in
a region of lightly myelinated cortex posterior/superior to heavily myelinated area 47 on the inferior frontal gyrus. In chimpanzees, volume-based probabilistic areas 44 and 45 (Schenker et al., 2010) together with cortical myelination were used to define a homologous region. Single ROI tractography from this region was used in both species to further refine the localization of temporal terminations. The lightly myelinated posterior two-thirds of the lateral temporal cortex in the STG, STS, and MTG including probabilistic areas TE 3.0 (Morosan et al., 2005) in humans and 22 (Spoer et al., 2010) in chimps that was bordered superiorly by more myelinated auditory belt cortex, posteriorly by more myelinated MT+ cortex, and ventrally by more myelinated ventral visual cortex formed the temporal surface ROI. These ROIs were constrained to include only those vertices that also received surface terminations in the localizer tractography.

The resulting surface ROIs were largely the same shape and size across hemispheres, but differed across species. As has been previously suspected for macaque monkeys (Ungerleider et al., 1998; Van Essen and Dierker, 2007), temporal cortical areas have undergone significant shifts relative to the cortical anatomy in humans relative to chimpanzees (Glasser et al., 2011), and geographically corresponding ROIs (i.e., ROIs of the same shape and size) would not have spanned homologous cortex. The availability of human and chimpanzee surface templates with rich probabilistic post-mortem and in vivo architectonic data is unprecedented for a non-invasive connectivity study.

The final probabilistic tractography was constrained to run symmetrically via either the dorsal or ventral route between the surface ROIs and streamlines were displayed on the surface (terminations) and in the volume (fascicles). 150,000 streamlines were sent out from each vertex/voxel in proportion to the fiber volume fraction in voxels with more than one fiber modeled and streamlines were stopped when they attempted to exit the white matter surface. The total number of streamlines that successfully traced the required route (the “waytotal”) was recorded during tractography. Within a subject, these waytotals are proportional to the probability that the streamlines reach their target ROIs, and provide a rough metric of pathway strength when compared to another pathway seeded from ROIs of the same size. To compare across individuals, however, it is necessary to normalize these waytotals by the size of the ROIs used as seeds and the total number of streamlines counted across all four pathways. This normalization accounts for differences in ROI size after deforming standard ROIs to individuals and for global differences in trackability between individuals (e.g., motion, SNR, brain size) within a species. AIs were used (see Table 1 for values and definitions), and the surface terminations and volume probabilistic fascicles were also normalized by the sum of each subject’s waytotals so each contributed equally to the group average (Figure 1). A one-sample t-test (two tailed) was used to test if each AI was significantly different from zero (no asymmetry), and a two-sample t-test (two tailed) was used to test if the AIs were different between humans and chimpanzees.

The ILF (Figure 2) was defined using two volume ROIs orthogonal to the pathway one-third of the way back from the temporal pole and in the deep occipital white matter. The atlas brain was rotated 45˚ around the x-axis so that a coronal section cut the ILF orthogonally in the anterior temporal lobe. An ROI was drawn within the entire white matter on this slice, and single ROI tractography was done to identify occipital projections. A second ROI was drawn to select these projections, and the result in Figure 2 was produced with symmetric two ROI tractography between these ROIs.

ACKNOWLEDGMENTS
We thank Ashley DeMarco, Longchuan Li, Govind Bhagavatheeshwaran, Bhargav Errangi, Xiaodong Zhang, and Xiaoping Hu for assistance with various aspects of this study. Matthew F. Glasser was supported by a National Research Science Award – Medical Scientist NIH T32 GM007200. Mark Jenkinson provided a preview version of boundary-based registration in FSLIRT for T2w to T1w registration. Bill Hopkins provided probabilistic cytoarchitectonic areas for the chimpanzees. Some computations were performed using facilities of the Washington University Center for High Performance Computing, partially supported by Grant NCRR 1S10RR022984-01. Funding was provided by NIMH Grant R01 MH084068-01A1, NIA Grant 5P01 AG026423-03, and the Yerkes Base Grant: NIH RR-00165. The contents of this article are solely the responsibility of the authors and do not necessarily represent the official views of the NIH.

REFERENCES

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 31 October 2011; paper pending publication: 26 November 2011; accepted: 12 December 2011; published online: 03 January 2012.


Copyright © 2012 Rilling, Glasser, Jbabdi, Andersson and Preuss. This is an open-access article distributed under the terms of the Creative Commons Attribution Non Commercial License, which permits non-commercial use, distribution, and reproduction in other forums, provided the original authors and source are credited.