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RESEARCH ARTICLE

A Morphological Comparison of the Caudal Rami of the Superior Temporal Sulcus in Humans, Chimpanzees, and Other Great Apes

Reyansh N. Sathishkumar[1] | Ethan H. Willbrand[2,3] | Priyanka Nanayakkara[4] | Willa I. Voorhies[5] | Yi-Heng Tsai[6] | Thomas Gagnant[7] | William D. Hopkins[8] | Chet C. Sherwood[9] | Kevin S. Weiner[10,11,12]

[1]Cognitive Science Program, University of California, Berkeley, Berkeley, California, USA | [2]Medical Scientist Training Program, School of Medicine and Public Health, University of Wisconsin–Madison, Madison, Wisconsin, USA | [3]Department of Radiology, School of Medicine and Public Health, University of Wisconsin–Madison, Madison, Wisconsin, USA | [4]Barnard College, Columbia University, New York, New York, USA | [5]Calbright College, Sacramento, California, USA | [6]Department of Psychology, University of North Carolina at Chapel Hill, Chapel Hill, North Carolina, USA | [7]Medical Science Faculty, University of Bordeaux, Bordeaux, France | [8]Department of Comparative Medicine, The University of Texas MD Anderson Cancer Center, Bastrop, Texas, USA | [9]Department of Anthropology and Center for the Advanced Study of Human Paleobiology, The George Washington University, Washington, DC, USA | [10]Department of Psychology, University of California, Berkeley, Berkeley, California, USA | [11]Helen Wills Neuroscience Institute, University of California, Berkeley, Berkeley, California, USA | [12]Department of Neuroscience, University of California, Berkeley, Berkeley, California, USA

Correspondence: Kevin S. Weiner (kweiner@berkeley.edu)

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ABSTRACT

For centuries, anatomists have charted the folding patterns of the sulci of the cerebral cortex in primates. Improvements in neuroimaging technologies over the past decades have led to advancements in the understanding of the sulcal organization of the human cerebral cortex, yet comparisons to chimpanzees, one of humans' closest extant phylogenetic relatives, remain to be performed in many regions, such as the caudal temporoparietal region (cTPR). For example, while several posterior branches, or rami, of the superior temporal sulcus (STS) have been identified within the cTPR in great apes since the late 1800s, no study has yet comprehensively identified and quantitatively compared these rami across species. To fill this gap in knowledge, in the present study, we defined the three caudal branches of the STS (cSTS) in 72 human and 29 chimpanzee brains (202 total hemispheres) and then extracted and compared the morphological (depth and surface area) properties of these sulci. We report three main findings. First, modern methods replicate classic findings that three rami of the posterior STS are unique to the hominid lineage (i.e., humans and great apes). Second, normalizing for brain size, the cSTS rami were relatively deeper in chimpanzees compared to humans. Third, the cSTS branches were relatively larger in surface area in humans compared to chimpanzees. Finally, we share probabilistic predictions of the cSTS to guide the identification of these sulci in future studies. Altogether, these findings bridge the gap between historic qualitative observations and modern quantitative measurements in a part of the brain that has expanded substantially throughout evolution and that is involved in human-specific aspects of cognition.

Reyansh N. Sathishkumar and Ethan H. Willbrand are co-first authors.

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1 | Introduction

Exploring the similarities and differences in brain structure among species is of major interest across neurobiological subdisciplines. For centuries, a central goal has been to determine which features of the central nervous system (CNS) are specific to humans. A feature of the CNS that offers unique utility to address this aim is the folding of the cerebral cortex (Zilles et al. 2013). For example, while species that are commonly used in neuroscientific studies (e.g., mice, rats, and marmosets) have relatively smooth (lissencephalic) cerebral cortices, 60%–70% of the human cerebral cortex is buried in sulci (Figure 1; Zilles et al. 1988; Van Essen 2007; Willbrand, Maboudian, et al. 2023; Ramos Benitez et al. 2024). There are also many other mammal species that have highly gyrified cortex, such as elephants, cetartiodactyls, carnivores, and others (Kazu et al. 2014; Lyras et al. 2016). Further, an array of recent studies has identified sulcal features that appear to occur exclusively in the cerebral cortex of hominid primates (i.e., humans and great apes—chimpanzees, bonobos, gorillas, and orangutans) from (i) smaller and shallower cortical indentations that are present in association cortices that are often functionally, behaviorally, and translationally relevant to (ii) deep sulcal points (Yücel et al. 2002; Bogart et al. 2012; Borst et al. 2014; Garrison et al. 2015; Leroy et al. 2015; Amiez et al. 2018; Lopez-Persem et al. 2019; Weiner 2019; Nakamura et al. 2020; Rollins et al. 2020; Ammons et al. 2021; Hopkins, Procyk, et al. 2021; Miller, Voorhies, et al. 2021; Voorhies et al. 2021; Harper et al. 2022; Willbrand, Voorhies, et al. 2022; Willbrand, Maboudian, et al. 2024; Yao et al. 2022; Parker et al. 2023; Maboudian et al. 2024). Here, we consider caudal branches, or rami, of the superior temporal sulcus (STS; caudal branches: cSTS) extending from the caudal superior temporal cortex (cSTC) into the inferior parietal lobule (IPL, which includes the supramarginal and angular gyri and associated sulci). Since this broad cortical location includes multiple gyri and sulci in different lobes, we refer to this neuroanatomical expanse as the caudal temporoparietal region (cTPR).

The cTPR represents a major associative expansion zone in humans compared to nonhuman primates. It is situated at the intersection of auditory, visual, and parietal association cortices, which positions it as a hub for multimodal integration (Goodale and Milner 1992; Konen and Kastner 2008; Harvey et al. 2013, 2015; Mackey et al. 2017; Schurz et al. 2017; Humphreys and Tibon 2023). Paleoanthropological and neuroimaging investigations show that the cTPR has expanded extensively throughout primate evolution (Segal and Petrides 2012; Zilles et al. 2013; Leroy et al. 2015; Bruner 2018; Van Essen et al. 2018; Petrides 2019; Bruner et al. 2023; Willbrand, Tsai, et al. 2023; Labra et al. 2024). Broadly, evolutionary expansion has been observed to be greater in association cortex compared to primary sensory areas, consistent with the evolutionary trend in humans toward enlarging heteromodal regions that integrate information across modalities (Avants et al. 2006; Van Essen and Dierker 2007; Hill et al. 2010; Chaplin et al. 2013; Rilling 2014; Bruner et al. 2017; Smaers et al. 2017; Bruner 2018; Donahue et al. 2018). For example, in the cTPR, this expansion is thought to support higher-order functions, including the processing of complex social signals, theory of mind, and the semantic and syntactic dimensions of language (Hein and Knight 2008; Redcay 2008; Deen et al. 2015; Basil et al. 2017; Schobert et al. 2018; Bukowski and Lamm 2020). Thus, evolutionary pressures may have reconfigured cTPR sulcal morphology to scaffold these, often uniquely human, forms of social communication and cognition.

Nevertheless, while the cSTS are specific to hominid brains (Figure 1) and have been consistently identified since the late 1800s across species (Kükenthal 1895; Bolk 1910; Shellshear 1927; Connolly 1950; Figure 2), the incidence and morphology of these branches have not been quantitatively compared between humans and great apes. Most recently, the STS has been referred to as having a "chaotic morphology," especially in the left hemisphere (Le Guen et al. 2018). This phrase captures the prominent variability in the sulcal organization of the STS across individuals. Such morphological "chaos" may indicate evolutionary change, reflecting the emergence of novel folding features (e.g., annectant gyri and tertiary sulci) and highly individualized folding patterns in association cortex (Bruner 2018; Miller and Weiner 2022). Investigating whether this "chaotic morphology" is shared with chimpanzees or is uniquely exaggerated in humans allows us to directly test whether such variability is a conserved or derived trait, and to link interindividual differences in morphology to evolutionary mechanisms of cortical expansion.

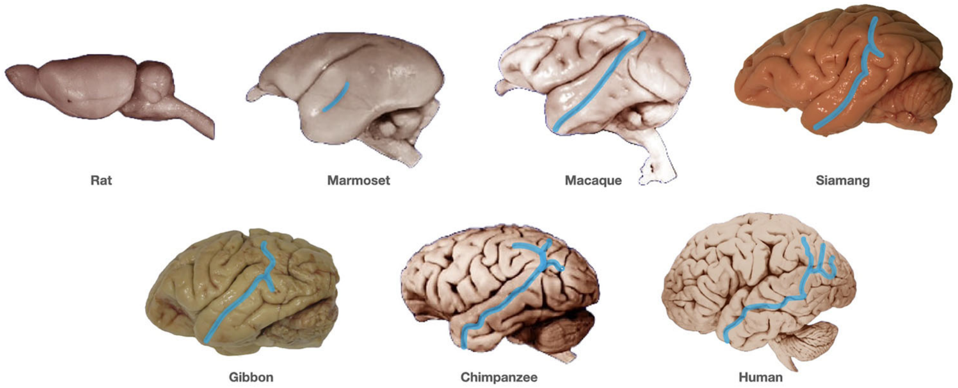

FIGURE 1 | Examples of the superior temporal sulcus across mammalian brains. As pictured, rats do not have a superior temporal sulcus (STS), while marmosets, macaques, chimpanzees, and humans do have an STS. The macaque STS is prominent, although there are no three caudal rami. In siamang and gibbon, there are two caudal rami. In chimpanzees and humans, three caudal rami are present. Brain images are from https://brainmuseum.org/Specimens/primates/index.html and the archives of authors W.D.H. and C.C.S. Images not to scale.

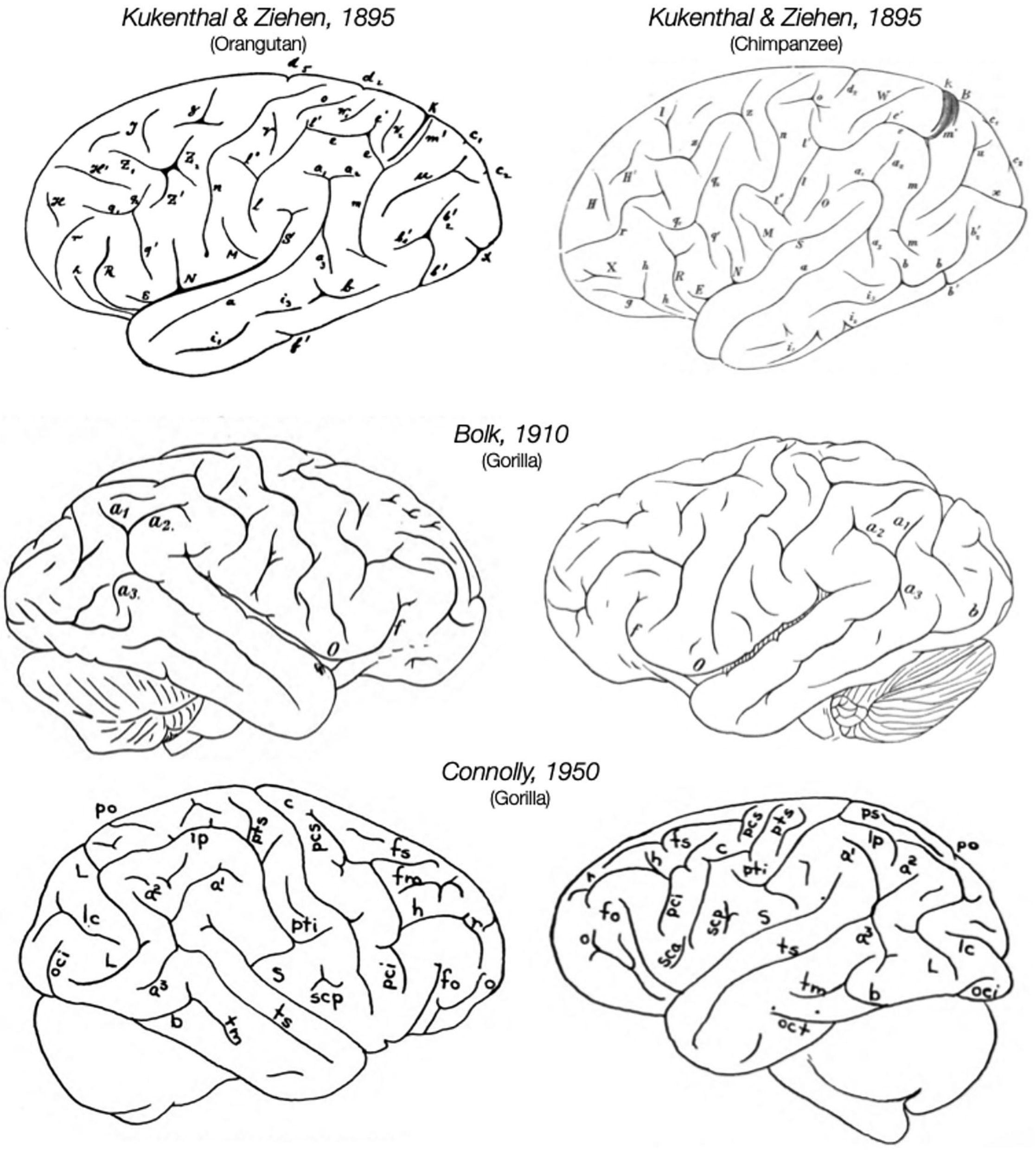

FIGURE 2 | The caudal rami of the superior temporal sulcus in an orangutan, gorilla, and chimpanzee as depicted in historical sources. Though many modern neuroanatomical atlases and neuroimaging software packages identify a single superior temporal sulcus (STS) in humans, neuroanatomists have labeled three caudal rami in great apes since the late 1800s. Historical labels of these rami (a1, a2, a3), anatomist, year, and species are included above in the images. Gustaf (1906) should also be considered, as he referenced the posterior rami of the STS (specifically termed the "Ramus posterior sulci tempor. sup."), which he identified as *ts'* (e.g., see tables XLIV, XLVII, XLVIII, L, and LI).

In the present study, beyond comparing the incidence of the cSTS between species, we also specifically examined the morphological features of these sulci, as in our prior work in other association cortices (Miller et al. 2020; Willbrand, Parker, et al. 2022; Willbrand, Maboudian, et al. 2023; Hathaway et al. 2023). The primary measure in the present study, sulcal depth, is a useful measure as it provides insight into both local folding mechanics and evolutionary cortical expansion. Increases in cortical sulcation (i.e., gyrencephalic brains) have been theorized to support increases in cortical surface area, and changes in sulcal depth have been theorized to reflect local increases in underlying neuronal organization (i.e., cytoarchitecture and myeloarchitecture) and white matter connectivity (Sanides 1962, 1964; Welker 1990; Vogt et al. 1995; Palomero-Gallagher et al. 2008; Van Essen et al. 2014; Reveley et al. 2015; Van Essen 2020; Amiez et al. 2021; Cachia et al. 2021; Cottaar et al. 2021; Miller, D'Esposito, et al. 2021). Indeed, long-range white matter fibers have been shown to have a gyral bias, while short-range white matter fibers have a sulcal bias, with some fibers projecting directly to the deepest points of a sulcus (Van Essen et al. 2014; Reveley et al. 2015; K. Schilling et al. 2018; K. G. Schilling et al. 2023; Cottaar et al. 2021). In humans, sulcal depth in multiple cortical regions has been shown to relate to cognition across various domains (e.g., memory, reasoning, and spatial orientation; Voorhies et al. 2021; Yao et al. 2022; Willbrand, Tsai, et al. 2023; Maboudian et al. 2024; Häkkinen et al. 2025). Therefore, comparative depth differences may reflect variation in both the magnitude and the organization of the underlying cortical architecture across species. In associative cortices, like the cTPR, these differences may highlight regions where evolutionary pressures have reshaped local circuitry to support emergent cognitive abilities.

Concomitantly, sulcal surface area provides a complementary measure of cortical expansion. Unlike depth, which likely reflects folding mechanics within a sulcus, surface area captures the areal extent of cortex allocated to a particular sulcal or gyral territory. Increased sulcal surface area in humans relative to chimpanzees and other great apes is thought to reflect both local cortical expansion and functional differentiation (Hill et al. 2010; Van Essen et al. 2018; Willbrand, Maboudian, et al. 2023). Within the cTPR, greater surface area may indicate the evolutionary enlargement of areas critical for complex audiovisual integration, speech perception, and social cognition—capacities that rely on broad networks spanning the temporal and parietal cortices (Hein and Knight 2008; Redcay 2008; Hecht et al. 2013; Deen et al. 2015; Caspers and Zilles 2018; Specht and Wigglesworth 2018; Bukowski and Lamm 2020; Bruner et al. 2023). Thus, by considering both depth and surface area of the cSTS, we can assess not only how the cTPR has folded differently but also how the amount of cortical real estate devoted to this region differs across species at a fine-grained level.

Accordingly, to quantitatively assess the cSTS between species, in the present study, we first sought to verify the occurrence of cSTS in great ape brains and to comprehensively compare the morphology (depth and surface area) of the cSTS between humans and chimpanzees, one of our species' closest extant phylogenetic relatives (Schrago and Voloch 2013). Given that features of the STS are cognitively and functionally relevant, comparing the cSTS between chimpanzees and humans will not only illuminate the comparative neuroanatomy of the STS between species but also provide a foundation to further understand the evolutionary emergence of structural–functional and structural–behavioral relationships in this complex cortical expanse (Hein and Knight 2008; Redcay 2008; Hecht et al. 2013; Deen et al. 2015; Basil et al. 2017; Bruner 2018; Schobert et al. 2018; Specht and Wigglesworth 2018; Bukowski and Lamm 2020; Rollins et al. 2020; Miller and Weiner 2022; Bruner et al. 2023; Lerosier et al. 2024). Altogether, the present study aims to bridge the gap between historic qualitative observations and modern quantitative measurements in a part of the brain that has expanded substantially throughout evolution and that is involved in human-specific aspects of cognition.

2 | Materials and Methods

2.1 | Participants

2.1.1 | Humans

Data from the young adult human cohort analyzed in the present study were from the Human Connectome Project (HCP) database (db.humanconnectome.org). Here, we used 72 participants (50% female; aged 22–36) who were also analyzed in several prior studies (Miller et al. 2020; Miller, Voorhies, et al. 2021; Willbrand, Parker, et al. 2022; Willbrand, Bunge, et al. 2023; Willbrand, Ferrer, et al. 2023; Willbrand, Maboudian, et al. 2023; Willbrand, Jackson, et al. 2024; Hathaway et al. 2023; Maboudian et al. 2024), including a prior investigation of the cTPR (Willbrand, Tsai, et al. 2023).

2.1.2 | Chimpanzees

Data from the adult chimpanzee cohort analyzed in the present study were from the National Chimpanzee Brain Resource (www.chimpanzeebrain.org). Here, our total sample consisted of 60 chimpanzees (*Pan troglodytes*; 63% female, aged 9–54) that were also analyzed in several prior studies (Miller et al. 2020; Willbrand, Parker, et al. 2022; Willbrand, Maboudian, et al. 2023; Hathaway et al. 2023). These were split into two groups. Thirty chimpanzees were used to create a species-specific average template and were not included in any other analyses. Of the remaining chimpanzees, 29 were included in the manual labeling and analyses, as one was excluded due to substantial issues in the cortical reconstruction pipeline. Chimpanzee MRIs were obtained from a data archive of scans collected prior to the 2015 implementation of US Fish and Wildlife Service and National Institutes of Health regulations governing research with chimpanzees.

2.1.3 | Bonobos, Gorillas, and Orangutans

Data from a cohort of nine adult or subadult great apes—three bonobos (*Pan paniscus*; two female), two gorillas (*Gorilla gorilla gorilla*; one female), and four orangutans (*Pongo pygmaeus*; one female)—were leveraged from prior work (Hopkins et al. 1998).

2.2 | Data Acquisition

2.2.1 | Humans

Anatomical T1-weighted MRI scans (0.8 mm voxel resolution) were obtained in native space from the HCP database, along with outputs from the HCP-modified FreeSurfer pipeline (Glasser et al. 2013).

2.2.2 | Chimpanzees

Detailed descriptions of the scanning parameters have been described in Keller et al. (2009), but we also describe the methods briefly here. Specifically, T1-weighted magnetization-prepared rapid-acquisition gradient echo (MPRAGE) MR images were obtained using a Siemens 3 T Trio MR system (TR = 2300 ms, TE = 4.4 ms, TI = 1100 ms, flip angle = 8, FOV = 200 mm) at the Emory National Primate Research Center (ENPRC) in Atlanta, Georgia. Before reconstructing the cortical surface, the T1 of each chimpanzee was scaled to the size of the human brain. As described in Hopkins et al. (2017), within FSL, (1) the BET function was used to automatically strip away the skull, (2) the FAST function was used to correct for intensity variations due to magnetic susceptibility artifacts and radiofrequency field inhomogeneities (i.e., bias field correction), and (3) the FLIRT function was used to normalize the isolated brain to the MNI152 template brain (Fonov et al. 2011) using a 7-degree-of-freedom transformation (i.e., three translations, three rotations, and one uniform scaling), which preserved the shape of individual brains. Next, each T1 was segmented using FreeSurfer. The fact that the brains are already isolated, both bias-field correction and size normalization, greatly assisted in segmenting the chimpanzee brain in FreeSurfer. Furthermore, the initial use of FSL also has the specific benefit, as mentioned above, of enabling the individual brains to be spatially normalized with preserved brain shape, and the values of this transformation matrix and the scaling factor were saved for later use.

2.2.3 | Bonobos, Gorillas, and Orangutans

Again, detailed descriptions of the scanning parameters have been described elsewhere (Hopkins et al. 1998), but we also describe the methods briefly here. All procedures were conducted in accordance with protocols approved by the ENPRC. Subjects were initially immobilized via intramuscular injection of ketamine hydrochloride (10 mg/kg), followed by maintenance anesthesia using a continuous infusion of propofol (2–6 mg/kg/h). Animals were transported under anesthesia by van to the MRI facility at Emory University Hospital and remained anesthetized throughout transport and imaging procedures, which lasted approximately 2 h in total. Postscan, subjects were temporarily housed in single cages for 6–12 h to allow recovery from anesthesia before being returned to their home enclosures and social groups. MRI scans were performed using two 1.5-Tesla Philips Model 51 scanners equipped with superconducting magnets. T1-weighted structural images were acquired in the transverse plane using a gradient echo protocol with the following parameters: repetition time = 19.0 ms, echo time = 8.5 ms, slice thickness = 1.2 mm, slice overlap = 0.6 mm, number of signal averages = 8, and matrix size = 256 × 256. These parameters were optimized based on preliminary studies and yielded high-resolution images suitable for morphometric analysis. Digital image data were archived onto optical diskettes and securely transferred for subsequent processing and analysis. Cortical reconstructions were generated from these T1 images in the same manner described above for chimpanzees.

2.3 | Manually Defining Caudal Rami of the STS in cTPR

2.3.1 | Humans

We first manually defined the cTPR sulci within each individual hemisphere using *tksurfer* tools in FreeSurfer as described in our prior work (Miller, Voorhies, et al. 2021). Manual lines were drawn on the inflated cortical surface based on the most recent schematics and studies of cTPR sulcal patterning (Segal and Petrides 2012; Petrides 2019; Willbrand, Tsai, et al. 2023), as well as on the pial and *smoothwm* surfaces of each individual. Using the inflated, pial, and *smoothwm* surfaces to inform our labeling allowed us to form a consensus across surfaces and clearly determine each sulcal boundary.

Sulci were manually defined using guidance from the most recent atlas by Petrides (2019), as well as recent empirical studies (Segal and Petrides 2012; Willbrand, Tsai, et al. 2023), which together offer a comprehensive definition of cerebral sulcal patterns, including evolutionarily new sulci. The cortical region of interest was bounded by the following sulci and gyri: (i) the postcentral sulcus (PoCS) served as the anterior boundary, (ii) the STS served as the inferior boundary, (iii) the intraparietal sulcus (IPS) served as the superior boundary, and (iv) the transverse occipital sulci (TOS) served as the posterior boundary. In the present study, we specifically examined the three different branches of the cSTS (posterior to anterior: cSTS 3, 2, and 1; Segal and Petrides 2012; Petrides 2019). The cSTS were identified as the set of posteriorly located sulcal branches that extend beyond the termination of the Sylvian (lateral) fissure and ascend into the IPL and the angular gyrus (criteria specified by Petrides 2019). For each hemisphere, the location of the three cSTS rami was confirmed by trained independent raters (E.H.W., Y.T., T.G.) and finalized by a neuroanatomist (K.S.W.). The morphological features of these sulci in humans have already been published (Willbrand, Tsai, et al. 2023), but have yet to be compared across species, which was the goal of the present study. See Figure 3A (right) for an example human hemisphere with the cSTS defined. All human cSTS sulcal definitions are in the Supporting Information of our prior work (Willbrand, Tsai, et al. 2023).

2.3.2 | Great Apes

For chimpanzees, bonobos, gorillas, and orangutans, sulci were manually labeled in the same manner as in humans, that is, on the inflated surface (informed by the pial and *smoothwm* surfaces) using the same *tksurfer* tools in FreeSurfer. The same sulci were also identified when present based on the most recent schematics and studies of cTPR sulcal patterning in humans (Segal and Petrides 2012; Petrides 2019; Willbrand, Tsai, et al. 2023) and historical sources in great apes (Figure 2). We began by identifying the sulcal borders: (i) PoCS, (ii) STS, (iii) IPS, and (iv) TOS. The three cSTS were subsequently defined within these boundaries. As with humans, for each hemisphere, the location of all sulci was confirmed by trained independent raters (R.N.S., W.I.V., P.N.) and finalized by a neuroanatomist (K.S.W.). See Figure 3A (left) for an example chimpanzee hemisphere with the cSTS defined. All chimpanzee cSTS sulcal definitions are in Figure 4. Given the smaller sample sizes of the bonobos, gorillas, and orangutans, we only quantified the incidence of the cSTS and did not include them in subsequent statistical analyses.

2.4 | Historical References to Caudal Rami of the STS

Below, we include text from previous neuroanatomical investigations identifying caudal branches of the STS (cSTS).

From Segal and Petrides (2012): "For example, schematic illustrations of the brain's lateral surface in both Duvernoy (1999) and Ono et al. (1990) represent two cSTS branches within the IPL. The schematic diagram in Duvernoy (1999, 7) labels two branches of the cSTS as the ascending and the horizontal posterior segments, while Ono et al. (1990, Chapter 2, page 16) identify two cSTS branches as the angular sulcus and the anterior occipital sulcus. At first, it may seem that the same two branches are represented in

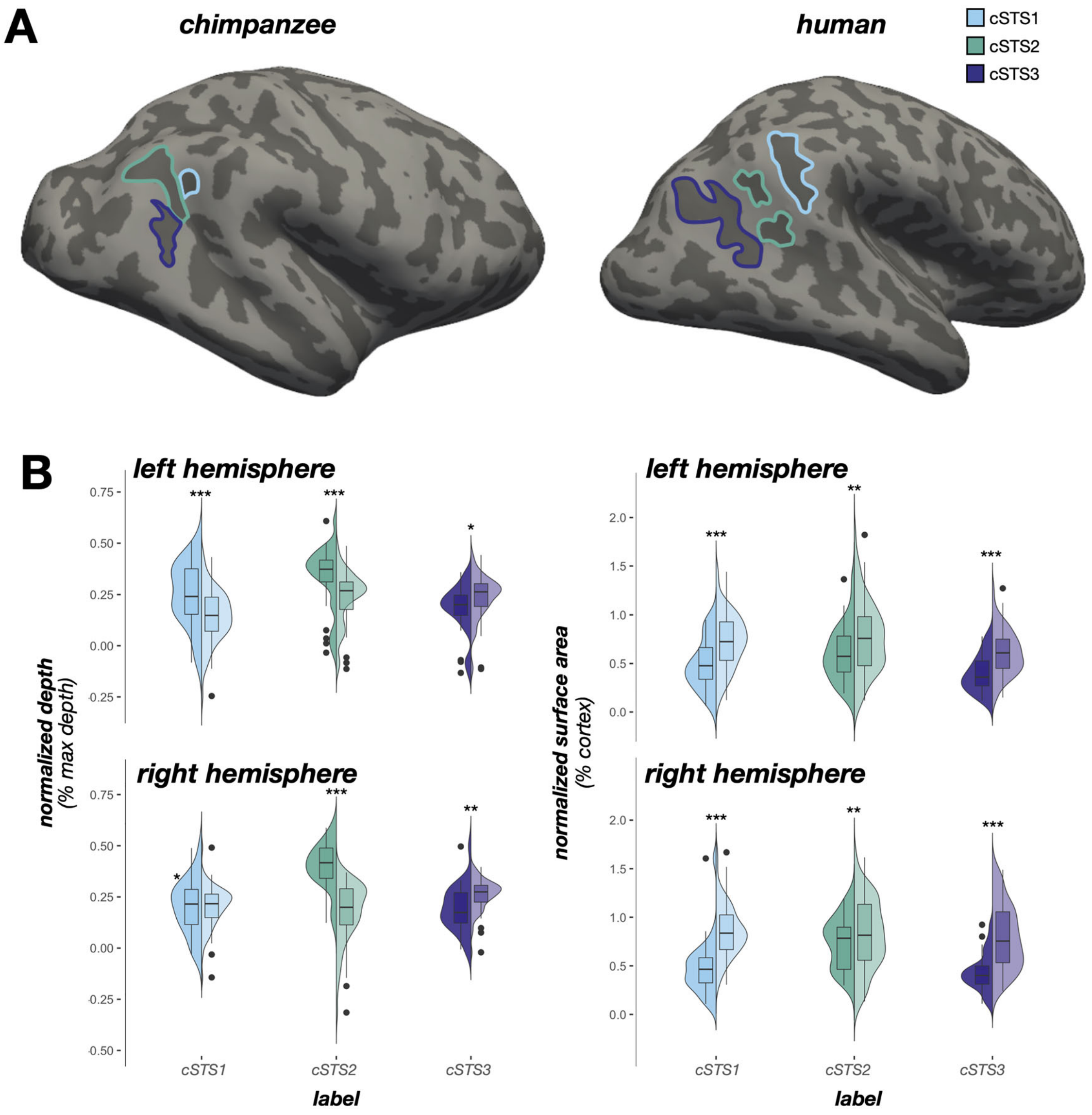

FIGURE 3 | The caudal rami of the superior temporal sulcus in chimpanzees. (A) Chimpanzee (left) and human (right) inflated cortical surface reconstructions with the three caudal rami of the superior temporal sulcus (cSTS) outlined on each surface (key). Sulci: dark gray; Gyri: light gray. (B) Left: Split violin plots (box plot and kernel density estimate) visualizing normalized sulcal depth (percent of max depth; percentage values are out of 100) as a function of sulcus (x-axis), species (lighter colors, right violin: human; darker colors, left violin: chimpanzee), and hemisphere (top: left hemisphere; bottom: right hemisphere). Significant differences between species (as a result of the species × sulcus × hemisphere interaction) are indicated with asterisks ($^*p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$). Right: Same as left, but for normalized surface area (percent of parietal surface area; percentage values are out of 100). Significant differences between species (as a result of the species × sulcus interaction) are indicated with asterisks ($^{**}p < 0.01$; $^{***}p < 0.001$).

these two atlases but under different names; closer examination indicates otherwise. The cSTS branch labeled as ascending by Duvernoy (1999) lies immediately behind the posterior ascending ramus of the Sylvian fissure (ascSF; see Duvernoy 1999; sagittal sections, pp. 258–259). However, in Ono et al. (1990) a similar sulcus found just behind the ascSF is treated as an infrequent configuration of the STS and called the double parallel-type termination (Chapter 10, page 77). The angular sulcus of Ono et al. (1990) now appears to refer to the horizontal posterior segment of Duvernoy. Thus, the above two atlases refer to two cSTS branches but they do not seem to identify the same two sulci."

From Shellshear (1927): "In Figure 9 the lower end of the sulcus occipitalis anterior is joined to a well developed sulcus temporalis medius. The usual description given in textbooks, originated without due regard to morphological facts, could be applied to this specimen. The sulcus temporalis superior is most commonly described as being the homolog of the parallel sulcus and ending in the angular gyrus. The middle temporal sulcus is diagrammatically represented as lying parallel with the sulcus temporalis superior and ending in the gyrus postparietalis. The detached portion of the superior parallel sulcus is disregarded or unrecognised. It is now clear that the STS so described is a complex sulcus consisting of the anterior temporal (related to the area temporalis polaris), the inferior parallel (related to areas 21 and 22), a portion of the superior parallel and the angular sulcus (related to area 39), with in some cases-depending upon the point of junction of the sulcus angularisthe sulcus annectans. Further,

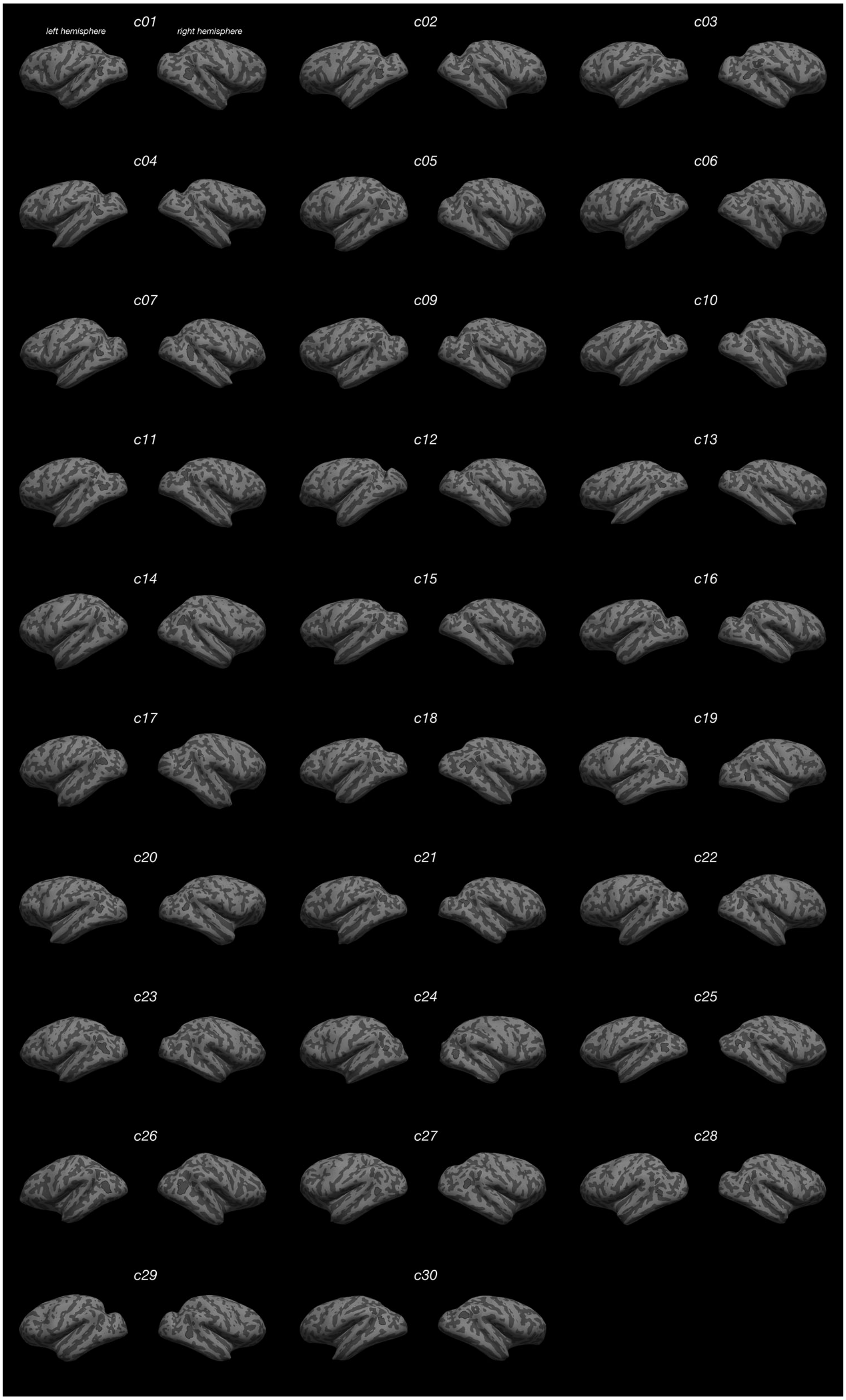

FIGURE 4 | The caudal rami of the superior temporal sulcus identified in every chimpanzee hemisphere. Each sulcus is displayed on the left and right hemisphere inflated cortical surfaces in FreeSurfer 6.0.0, with the label displayed as an outline according to the key at the top. This image is also available on this article's GitHub repository to ensure the brains are able to be viewed in optimal resolution (see Data Availability Statement).

when the angular sulcus is separate, the upper segment of the anterior occipital sulcus may be included. The middle temporal sulcus so described consists of a series of disconnected sulci (the proper middle temporal sulcus), occasionally joined together, connecting with the lower segment of the anterior occipital sulcus and thence continued to the postparietal lobule."

From Bailey et al. (1950): "*ts, the sulcus temporalis superior, sulcus parallelis*. With Shellshear (1927) the parallel sulcus can be divided into an anterior and a posterior part. The former, one of the oldest furrows of the primate brain, runs in the temporal lobe; the latter, changing profoundly from macaque to man, runs in the parietal lobe. Near the temporal pole, the anterior end may be in line with the rest of the sulcus or may be bent ventrad so that the temporal pole appears as a continuation of the superior temporal gyrus. Occasionally, as Blinkow (1938) observed, this anterior hook may be an independent sulcus and the temporopolar region may be opercularized. Submerged bridging convolutions within the anterior part have been described by Blinkow. Within the angular gyrus the posterior part generally breaks up into three rami. Connections with the sulci of both occipital lobe and IPL are frequent. Shellshear reports that an interruption of the parallel sulcus between anterior and posterior part is not infrequent. No anthropological observations about this sulcus were found by us."

From Tamraz and Comair (2006): "The posterior part is the angular sulcus which penetrates into the IPL and usually divides into three rami within the angular gyrus."

From Connolly (1950): "THE ANTERIOR OCCIPITAL of Wernicke (a3) separates the gyrus angularis from an area caudal to it and termed by Brodmann (1925) area praeoccipitalis (area 19). As the sulcus is not within the occipital lobe, the term used by Genna (1924) namely s. preoccipitalis seems more appropriate than anterior occipital. Eberstaller (1884) described a sulcus which is axial to the postparietal part of the IPL and viewed it as an ascending ramus of the temporal medius sulcus which is apparently identical with the anterior occipital sulcus of Wernicke. Kohlbrugge (1909) regarded the sulcus as independent of the midtemporal and a doubling of the STS. Shellshear (1927) gives a similar view. An upper and a lower part of the anterior occipital are, according to this view, both developed from the posterior wall of the superior parallel sulcus and at least in simply fissurated brains, are connected with it by the sulcus annectans. Wang and Kappers (1924) designate the anterior occipital or s. preoccipitalis as ascending ramus III, the superior parallel being the ascending ramus I and the s. angularis, the ascending ramus II. According to these authors the ascending branches are split off from ts."

2.5 | Analyzing Differences in Sulcal Incidence

All statistical analyses were implemented in R. We characterized the frequency of occurrence of each sulcus separately for the left and right hemispheres. In line with prior work (Amiez et al. 2019, 2021; Willbrand, Maboudian, et al. 2023), for any sulcus that was variably present in either species, we tested the influence of species and hemisphere on the probability of a sulcus being present with binomial logistic regression GLMs. For each statistical model, species (human, chimpanzee) and hemisphere (left, right), as well as their interaction, were included as factors for the presence (absent, present) of a sulcus. Analysis of variance (ANOVA) chi-squared (χ^2) tests were applied to each GLM, from which results were reported. GLMs were carried out with the glm function from the stats R package, and ANOVA χ^2 tests were carried out with the Anova function from the car R package.

2.6 | Extracting Sulcal Morphology

2.6.1 | Depth

As in our prior work (Voorhies et al. 2021), mean sulcal depth values (in standard FreeSurfer units) were computed in native space from the *.sulc* file generated in FreeSurfer (Dale et al. 1999) with custom Python code. Briefly, depth values are calculated based on how far removed a vertex is from what is referred to as a "mid-surface," which is determined computationally so that the mean of the displacements around this "mid-surface" is zero. Thus, generally, gyri have negative values, while sulci have positive values. To address scaling concerns between species, as in prior work (Miller et al. 2020; Hathaway et al. 2023; Willbrand, Maboudian, et al. 2023), each depth value was normalized by the deepest point in the given hemisphere (i.e., the insula).

2.6.2 | Surface Area

Surface area (mm^2) was generated for each sulcus from the *mris_anatomical_stats* function in FreeSurfer (Dale et al. 1999; Fischl et al. 1999). To address scaling concerns between species, as in prior work (Miller et al. 2020; Hathaway et al. 2023; Willbrand, Maboudian, et al. 2023), we report surface area relative to the total surface area of the respective lobe that these sulci primarily reside in, which is the parietal lobe (Figure 5).

2.7 | Morphological Comparisons

All morphological comparisons were conducted using linear mixed-effects models (LMEs). ANOVA *F*-tests were subsequently applied. For both depth and surface area analyses, model predictors included sulcus, hemisphere, and species, as well as their interaction terms. Species, hemisphere, and sulcus were considered fixed effects. Sulcus was nested within hemisphere, which was further nested within subjects. LMEs were implemented with the lme function from the nlme package. ANOVA *F*-tests were run with the aov function from the stats R package. Post hoc analyses were computed with the emmeans and contrast functions from the emmeans R package. Post hoc *p*-values were corrected with the Tukey multiplicity adjustment. In the present study, we focus on species-related effects given that the morphological comparisons between these sulci were already documented by our group in the human sample (Willbrand, Tsai, et al. 2023).

2.8 | Probability Maps

Sulcal probability maps were calculated to summarize those vertices that had the highest and lowest correspondence across individual chimpanzees. To generate these maps, each sulcal

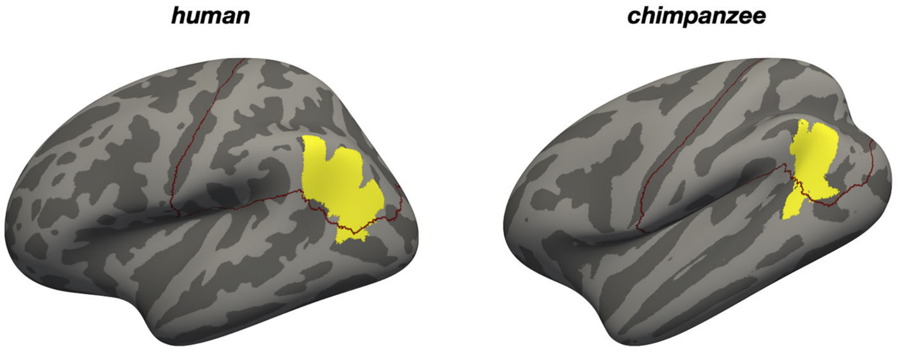

FIGURE 5 | Overlap between the caudal rami of the superior temporal sulcus and parietal lobe. Human (fsaverage surface; left) and chimpanzee (chimpanzee custom average template surface; Section 2; right) left hemisphere inflated cortical surface reconstructions with probability maps of the three caudal rami of the STS (cSTS) on each surface (in yellow). The human probability map is from our prior work (Willbrand et al. 2023); the chimpanzee is from the present work (Data Availability Statement; Figure 6). The parietal lobe FreeSurfer label is outlined in red. We normalized the surface area of the cSTS to the parietal lobe, given that the majority, if not all, of these sulci resided within the FreeSurfer parietal lobe label—as highlighted by this figure. Sulci: dark gray; Gyri: light gray.

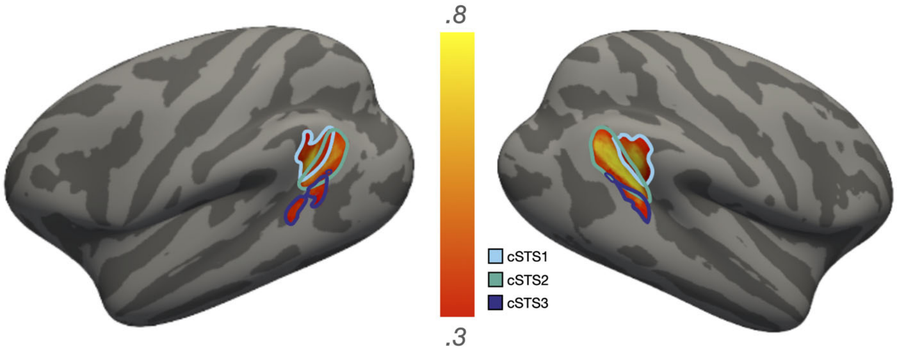

FIGURE 6 | Probability maps of the caudal rami of the superior temporal sulcus in chimpanzees. Probability maps for the three caudal rami of the superior temporal sulcus (cSTS) identified in the present work. To generate the maps, each label was transformed from each individual to a custom average template created from 30 additional chimpanzees that were not included in the original analysis. For each vertex, we calculated the proportion of chimpanzees for whom that vertex is labeled as the given sulcus (the warmer the color, the higher the overlap in each image). In the case of multiple labels for one vertex, the sulcus with the highest overlap across participants was assigned to a given vertex. To reduce spatial overlap for visualization purposes, these maps were thresholded to variable degrees of overlap across chimpanzees (scales).

label was transformed from the individual to a chimpanzee template surface from a held-out population of 30 chimpanzee brains that was made with the FreeSurfer *make_average_subject* function (Miller et al. 2020). Once transformed to this common template space, for each vertex, we calculated the proportion of chimpanzees for whom the vertex is labeled as the given sulcus. In the case of multiple labels, we employed a greedy, "winner-take-all" approach such that the sulcus with the highest overlap across participants was assigned to a given vertex. In addition to providing unthresholded maps, we also constrain these maps to maximum probability maps (MPMs) with 20% participant overlap (Figure 6), as MPMs help to avoid overlapping sulci and increase interpretability (Miller, Voorhies, et al. 2021). Human cTPR sulcal probability maps are available through our prior work (Willbrand, Tsai, et al. 2023).

3 | Results

We first sought to identify the three caudal rami of the STS (cSTS) in chimpanzees and then compare the incidence and morphology of these sulci to humans. Segal and Petrides (2012) have an excellent section in their article describing the variability of how these three branches have been referenced throughout the classic literature from Smith (1907), Economo and Koskinas (1925), Shellshear (1927), Cunningham (1931), Ono et al. (1990), and Duvernoy (1999; please refer to Segal and Petrides [2012] for full details and to Section 2 here for direct quotations from these authors). Nevertheless, those studies are largely restricted to the human cerebral cortex (though Shellshear [1927] focuses on comparative analyses across species), and due to the high incidence rates of these caudal rami in chimpanzees, we returned to classic neuroanatomical texts to explore if these three rami were identifiable in great apes by prior neuroanatomists. Several different neuroanatomists identified and labeled these three cSTS branches in orangutans, gorillas, and chimpanzees (Figure 2). This historical classification was replicated in our chimpanzee sample as the three cSTS rami were identifiable in all chimpanzee cortical surface reconstructions ($N = 29$, 58 hemispheres; exemplary hemisphere in Figure 3A; all hemispheres in Figure 4). We also found that the three cSTS rami were present in cortical surface reconstructions of other hominid species (bonobos, $N = 3$,

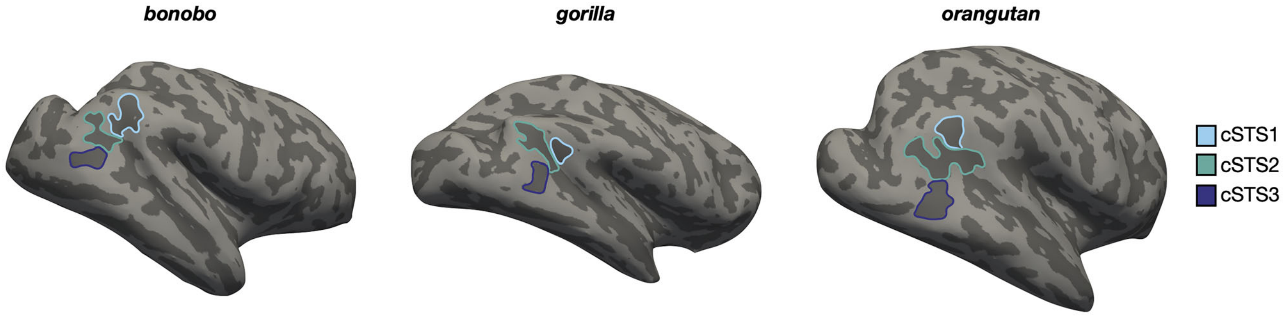

FIGURE 7 | The caudal rami of the superior temporal sulcus are present in three additional hominid species. Bonobo (left), gorilla (middle), and orangutan (right) inflated cortical surface reconstructions with the three caudal rami of the superior temporal sulcus (cSTS) outlined on each surface (key). Sulci: dark gray; Gyri: light gray.

six hemispheres; gorillas, $N = 2$, four hemispheres; orangutans, $N = 4$, eight hemispheres; see Figure 7 for example hemispheres) from previously published work (Hopkins et al. 1998). Finally, we found that the three cSTS rami were variably present in gibbon and siamang postmortem brains (Figure 8).

We next sought to examine if the three cSTS rami differed morphologically between humans and chimpanzees. In terms of depth (normalized to maximum hemispheric depth), an LME with predictors of sulcus, hemisphere, and species revealed three species-related findings. First, there was a main effect of species ($F(1, 593) = 23.26$, $p = 1.8 \times 10^{-6}$), such that the cSTS components were relatively deeper in chimpanzees (Figure 3B, left). Second, there was a species × sulcus interaction ($F(2, 593) = 36.65$, $p = 9.87 \times 10^{-16}$), which showed that cSTS1 and cSTS2 were relatively deeper in chimpanzees ($ps < 0.004$), whereas cSTS3 was relatively deeper in humans ($p = 0.001$; Figure 3B, left). Finally, there was a species × sulcus × hemisphere interaction ($F(2, 593) = 9.98$, $p = 5.45 \times 10^{-5}$). Post hoc pairwise comparisons revealed that (i) cSTS1 was relatively deeper in chimpanzees in the left ($p < 0.0001$), but not right ($p = 0.94$), hemisphere, (ii) cSTS2 was relatively deeper in chimpanzees in both hemispheres ($ps < 0.001$), and (iii) cSTS3 was relatively deeper in humans in both hemispheres ($ps < 0.05$; Figure 3B, left). In terms of surface area (normalized to hemispheric parietal lobe surface area), a similarly structured LME revealed two species-related findings. First, there was a main effect of species ($F(1, 593) = 83.97$, $p < 2 \times 10^{-16}$) such that the cSTS components were relatively larger in humans (Figure 3B, right). Second, there was a species × sulcus interaction ($F(2, 593) = 4.81$, $p = 0.008$) where post hoc pairwise comparisons identified that cSTS1 and cSTS3 exhibited larger differences in size between species ($ps < 0.0001$) than cSTS2 ($p = 0.006$; Figure 3B, right). There was no species × sulcus × hemisphere interaction ($p = 0.12$; Figure 3B, right).

To ensure that our results were not simply due to normalization, we also implemented the same analysis on the raw quantitative morphological metrics, which confirmed these findings. In terms of depth (mm), an LME with predictors of sulcus, hemisphere, and species revealed three species-related findings. First, there was a main effect of species ($F(1, 582) = 153.66$, $p = 2 \times 10\text{-}16$), such that the cSTS components were deeper in chimpanzees (Figure 9A). Second, there was a species × sulcus interaction ($F(2, 582) = 18.87$, $p = 1.14 \times 10\text{-}8$), which showed that all branches were deeper in chimpanzees ($ps < 0.0007$; Figure 9A). Finally, there was a species × sulcus × hemisphere interaction ($F(2, 582) = 6.542$, $p = 0.0015$), indicating similar relationships observed in the normalized results (Figure 9A). In terms of surface area (mm^2), a similarly structured LME revealed two species-related findings. First, there was a main effect of species ($F(1, 582) = 121.86$, $p < 2 \times 10\text{-}16$) such that the cSTS components were larger in humans (Figure 9B). Second, there was a species × sulcus interaction ($F(2, 582) = 3.95$, $p = 0.0019$) where post hoc pairwise comparisons showed that all three branches had a larger surface area in humans compared to chimpanzees ($ps < 0.0001$). There was no species × sulcus × hemisphere interaction ($p = 0.19$; Figure 9B).

4 | Discussion

By manually defining cTPR sulci in 144 human and 58 chimpanzee hemispheres, we show that the surface anatomy of this cortical expanse is both similar and different between these two closely related hominid species along three sulcal metrics: (i) incidence, (ii) depth, and (iii) surface area. These findings demonstrate several key similarities and differences that shed light on the evolutionary trajectory of cortical folding in this region.

First, we found that all three cSTS branches were identifiable in every chimpanzee hemisphere as well as the other great apes' brains we examined, mirroring the consistent presence previously documented in human populations (Segal and Petrides 2012; Willbrand, Tsai, et al. 2023). This high incidence rate across species *suggests* that these sulci are likely homologous and evolutionarily conserved features of hominid brains. Supporting this conclusion, we found similar anatomical positioning of these sulci in both humans and chimpanzees, consistent with classic schematics proposed by neuroanatomists over a century ago (e.g., Shellshear 1927; Connolly 1950; Figure 2; Section 2). These results contribute to a growing body of evidence (e.g., Amiez et al. 2019, 2021, 2023; Miller et al. 2020; Hopkins et al. 2022; Willbrand, Parker, et al. 2022; Willbrand, Maboudian, et al. 2023; Hathaway et al. 2023) showing that while some sulci may be evolutionarily novel in humans, others—even in association cortices—have evolutionary roots shared with great apes, with potential functional insights. For instance, previous work shows that particular branches of the human STS predict the location of functional regions involved in face processing that have a

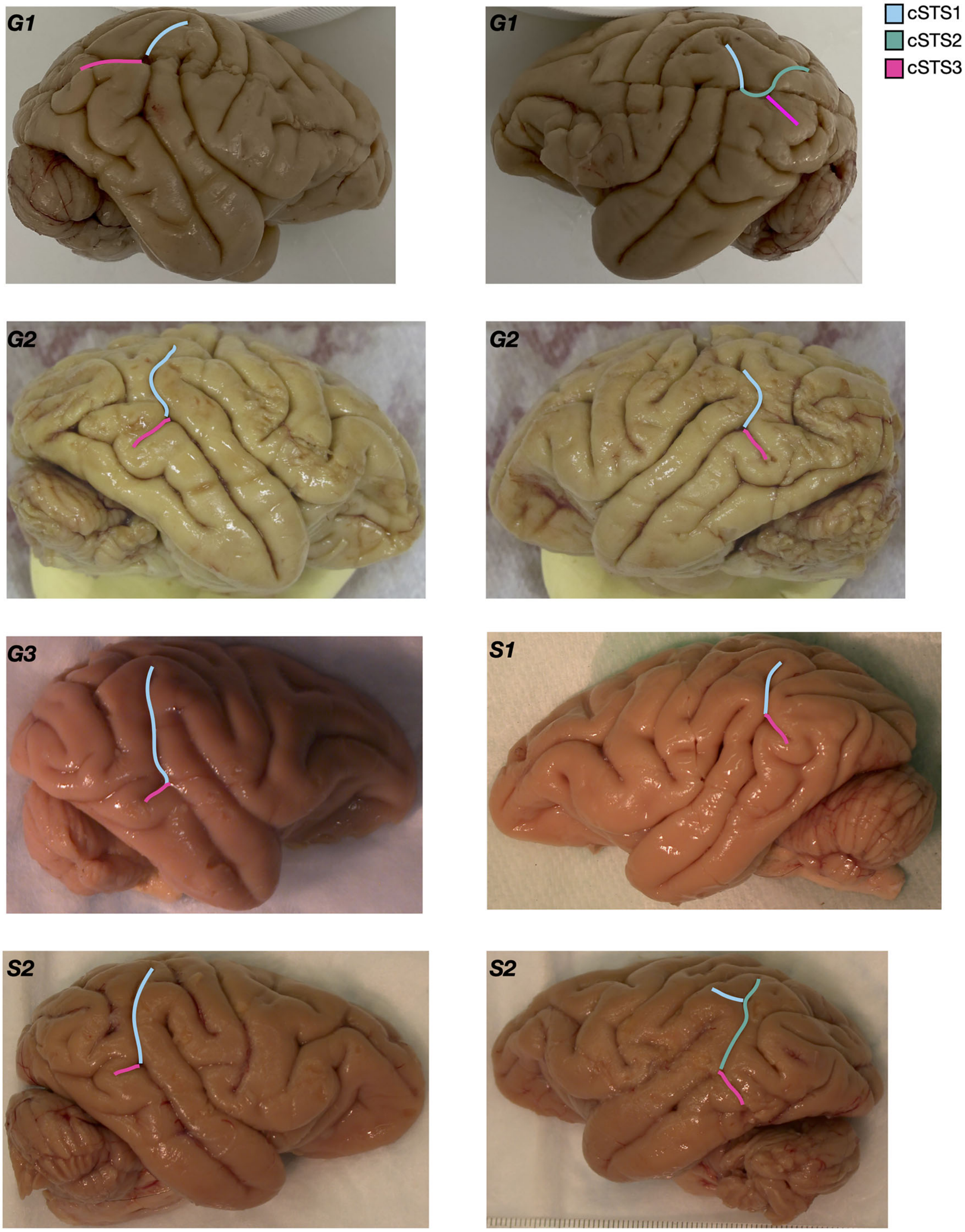

FIGURE 8 | The caudal rami of the STS are variably present in gibbon and siamang postmortem brain images. Gibbon (labeled G#) and siamang (labeled S#) postmortem brain images with the cSTS identified when present (key). Left hemispheres (LH) and right hemispheres (RH) are identified with their respective abbreviation. Brain images are from the archives of authors W.D.H. and C.C.S. Images not to scale.

consistent topological organization relative to functional regions selective for bodies and visual motion in a cortical expanse now referred to as the "lateral" visual stream (Weiner and Grill-Spector 2013; Gomez et al. 2019; Finzi et al. 2021; Pitcher and Ungerleider 2021; Weiner and Gomez 2021).

While we stress the lateral stream due to our focus on humans and nonhuman hominids in the present article (though a lateral stream has been proposed previously in nonhuman primates; Boussaoud et al. [1990], in this journal: "The diagram suggests that, in addition to the occipitotemporal (ventral) stream for object vision and the occipitoparietal (dorsal) stream for spatial vision, there may be a third processing stream which relays motion information from MST and FST forward into the cortex of the rostral superior temporal sulcus"), we also acknowledge the previous comparative anatomical and functional studies of

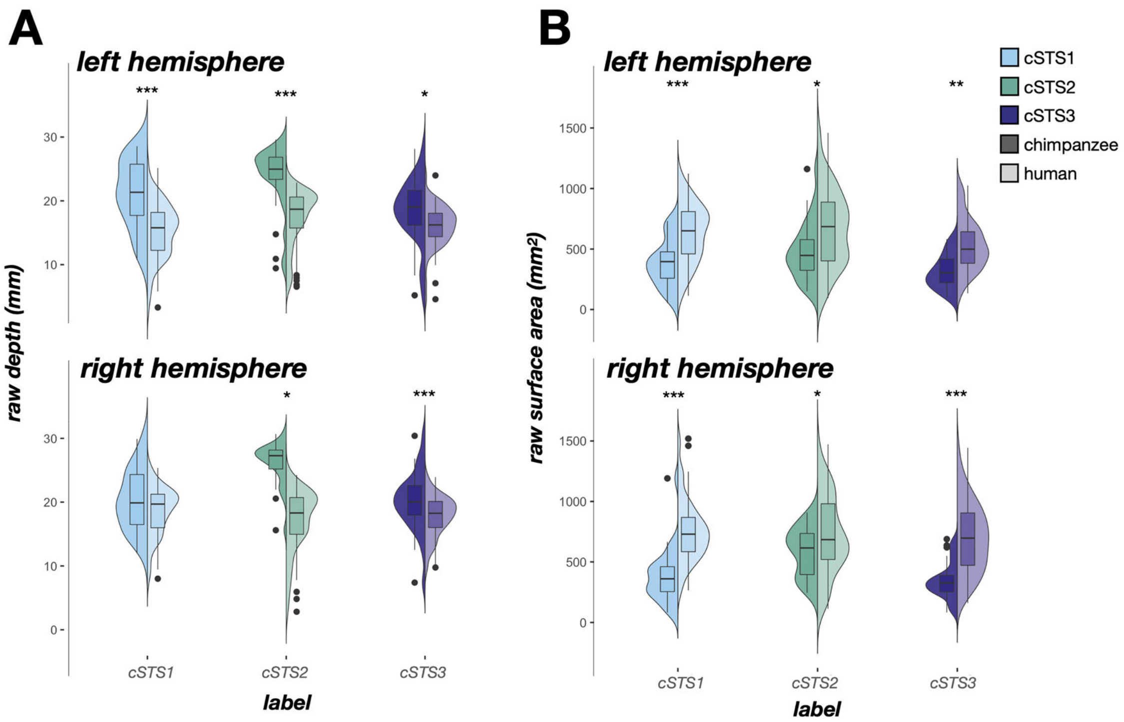

FIGURE 9 | Raw depth and surface area of the caudal rami of the superior temporal sulcus in humans and chimpanzees. (A) Split violin plots (box plot and kernel density estimate) visualizing raw sulcal depth (mm) as a function of sulcus (x-axis), species (darker colors, right violin: human; lighter colors, left violin: chimpanzee), and hemisphere (top: left hemisphere; bottom: right hemisphere). Significant differences between species (as a result of the species × sulcus × hemisphere interaction) are indicated with asterisks (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$). (B) Same as left, but for raw surface area (mm^2). Significant differences between species (as a result of the species × sulcus interaction) are indicated with asterisks (**$p < 0.01$, ***$p < 0.001$).

the STS between humans and macaques—including the potential homologies and analogies between species. For example, in macaques, the most posterior extent of the STS contains the "MT complex"—areas MT, MST, FSTd, and FSTv (with arguments about nomenclature, of course)—areas that can be defined based on postmortem anatomical measures, as well as in vivo functional measures (Orban et al. 2004; Sereno and Tootell 2005). However, in humans, the MT complex is shifted ventrally. Architectonically and functionally, the remainder of the STS has been parcellated differently across studies and species (Vogt and Vogt 1903, 1919; Brodmann 1908, 1909; Glasser et al. 2016; Huth et al. 2016; and Zachlod et al. 2020 are a few examples). Nevertheless, theories propose that the ventral portion of the macaque STS, extending into the inferotemporal gyrus, is the homolog of the ventral stream in humans (Desimone 1991; Harries and Perrett 1991; Gross and Sergent 1992; Tsao et al. 2003; Pinsk et al. 2009; Weiner and Grill-Spector 2013; Petrides 2023, among many other articles). For example, face patch ML, proposed to be the homolog of the fusiform face area, is located on the ventral lip of the STS in macaques (Tsao et al. 2006; Arcaro et al. 2020; Natu et al. 2021; Oishi et al. 2024). Future work is needed to better understand (i) homologous and analogous areas between macaques and humans in the cortical expanse studied here, as well as (ii) the benefit of three caudal rami in this cortical expanse spanning portions of the superior temporal and inferior parietal cortices in hominids compared to nonhuman primates. Recent reviews bring us closer to this goal (Caspers and Zilles 2018; Petrides 2023). And, an open question remains if there is a relationship between brain maps in this cortical expanse outside of face-selective regions and these caudal rami of the STS (Glasser et al. 2016; Gulban et al. 2020; Zachlod et al. 2020), which can be explored in future research. For instance, Steel et al. (2021, 2025) recently showed a transition from perception to memory near this cortical expanse.

Despite the consistent presence of these three caudal rami in both humans and chimpanzees, we did identify quantitative morphological differences. Specifically, the cSTS branches were relatively deeper in chimpanzees but had a greater surface area in humans. These evolutionary differences may reflect evolutionary pressures toward increased functional specialization in this part of the cortex, as depth and surface area are theorized to be linked to increased cortical surface available for local circuitry and potential expansion of specific functional features (Van Essen 2007; Miller and Weiner 2022). Indeed, neuroimaging studies have identified this region to be associated with complex higher-level cognitive functions (e.g., theory of mind, audiovisual integration, speech processing, and face processing)—functions thought to be associated with cortical areas that have expanded in humans relative to nonhuman primates (Hein and Knight 2008; Redcay 2008; Deen et al. 2015; Specht and Wigglesworth 2018; Bukowski and Lamm 2020). These differences may also reflect "compensatory" mechanisms. Specifically, Connolly's compensation theory of cortical folding proposes that the quantitative features of sulci are likely counterbalanced by those of their neighbors (Connolly 1940, 1950). In terms of the compensation theory, then, the decreased cSTS depth in humans may reflect the presence of an increased number of putative tertiary sulci apparently present in this cortical expanse in humans relative to chimpanzees (Willbrand, Tsai, et al. 2023; Häkkinen et al. 2025) and/or expansion of the cortical surface area both within and between the caudal branches (Van Essen 2007; Rakic 2009; Van Essen et al. 2018). Crucially, these possibilities are not mutually exclusive and can be directly tested in future studies.

Beyond macroanatomical comparisons, genetic and neurodevelopmental frameworks offer a critical context for interpreting species-specific sulcal morphology. For example, studies in both humans and chimpanzees have linked variation in cTPR morphology and function to polymorphisms in the *KIAA0319* gene, which is implicated in cortical development and associated with reading and language disorders in humans (Harold et al. 2006; Darki et al. 2012; Pinel et al. 2012; Jamadar et al. 2013; Hopkins, Staes, et al. 2021; Hopkins et al. 2023; Paniagua et al. 2022). Of direct relevance to the present study, one of these studies identified that the depth and surface area of the STS (especially in the central portion) were highly heritable and that polymorphisms in two genes (*KIAA0319* and *AVPR1A*) were associated with average STS depth and asymmetry (Hopkins et al. 2023). The presence of similar associations in chimpanzees and humans suggests a potentially conserved genetic influence on the organization of this region. Further, as the caudal rami of the STS examined in the present study are cortically distant from the most heritable portion of the STS identified by Hopkins et al. (2023; i.e., the central portion), this distance may partially explain the interspecies differences in the cSTS identified in the present study, given that strongly heritable sulci have been shown to be more evolutionarily conserved in humans and chimpanzees (Gómez-Robles et al. 2015; Amiez et al. 2018; Pizzagalli et al. 2020; Schmitt et al. 2021; Hopkins et al. 2023). Human studies have also shown that the left posterior STS is particularly susceptible to morphological variability, with features such as “pli-de-passage” (buried or annectant gyri) and sulcal fragmentation occurring more frequently in the left hemisphere and under moderate genetic control (Le Guen et al. 2018; Bodin et al. 2021). Such variability may then reflect both genetic constraints and experience-dependent changes in cortical development.

Together, these lines of evidence underscore that morphological evolution in the cTPR likely results from an interplay of conserved genetic architecture and species-specific neurodevelopmental trajectories, which may link variations in sulcal anatomy to the emergence of complex functional and cognitive features. Future studies should directly assess the role of genetic variations (such as polymorphisms in the *KIAA0319* gene) as well as that of other nongenetic factors (such as age) in the stability of and changes in the morphology of all cTPR sulci across hominid species, and whether these features have differing impacts on the morphology of the STS and the three cSTS rami specifically.

Furthermore, our results suggest that while the qualitative sulcal presence of the cSTS branches in the cTPR is conserved across humans and great apes, alterations have occurred at the quantitative level. These changes, which are especially striking compared to other species (Figure 1), parallel the cognitive and behavioral evolution of humans, particularly in visuospatial, attentional, and tool-use domains. These findings lay the groundwork for future investigations that link sulcal morphology in the cTPR to individual differences in cognition and behavior—both within and across species—and offer new insights into the neural basis of human-specific cognitive capacities.

4.1 | Limitations and Future Directions

There are several limitations to this work. First, while our chimpanzee ($N = 29$) sample is comparable to many nonhuman primate neuroimaging studies, this and our human ($N = 72$) samples are still modest compared to large N ($N > 1000$) human neuroimaging datasets (Gratton et al. 2022). Second, while we were able to compare sulcal incidence and morphology, we did not directly assess other relevant features (e.g., microanatomical, functional, or behavioral data) between species. For example, there is the potential relationship between the cSTS branches and the underlying cytoarchitectonic areas of the IPL. As noted by Segal and Petrides (2012), the central branch (cSTS2) lies in the middle of the angular gyrus and corresponds to Brodmann area 39 (or area PG identified by von Economo and Koskinas [1925]), and in more modern cytoarchitectonic mapping studies (Caspers et al. 2006, 2008), the cortex adjacent to cSTS1 aligns with area PFm, cSTS2 with area PGa, and cSTS3 with area PGp. Thus, the cSTS branches may provide important surface landmarks for differentiating subdivisions of the IPL, such as Brodmann areas 39 and 40, which are located dorsal to posterior temporal areas 21 and 22. Future analyses from multimodal data (e.g., including but not limited to cytoarchitectural, functional, and behavioral measures) in humans and chimpanzees could help clarify the extent to which sulcal landmarks correspond to neuroanatomical and functional representations within the cTPR and behavior (as has been done in the anterior cingulate cortex; Amiez et al. 2021; Hopkins, Procyk, et al. 2021). Additionally, developmental studies in both species could help determine whether differences in sulcal morphology arise from differences in developmental timing or rates of cortical expansion (Sakai et al. 2012). To aid the identification of these sulci in such future studies, we include chimpanzee probabilistic maps of these sulci (Data Availability Statement; Figure 6).

5 | Conclusion

This study provides the first (to our knowledge) direct quantitative comparative analysis of the three caudal rami of the STS between humans and chimpanzees. Our results reveal a shared sulcal framework with evidence of morphological differences in the human brain from that of chimpanzees. These findings illuminate both conserved and species-specific features of cortical organization that may advance our understanding of the structural foundations of human cognitive evolution.

Author Contributions

R.N.S., E.H.W., and K.S.W. designed the research. R.N.S., E.H.W., P.N., W.I.V., Y.T., T.G., W.D.H., C.C.S., and K.S.W. performed research. R.N.S., E.H.W., W.D.H., C.C.S., and K.S.W. wrote the article. All authors gave final approval to the article before submission.

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Ethics Statement

Human participants: HCP consortium data were previously acquired using protocols approved by the Washington University Institutional Review Board. Informed consent was obtained from all participants.

Chimpanzee participants: The chimpanzees were all members of the colony housed at the Emory National Primate Research Center (ENPRC). All methods were carried out in accordance with ENPRC and Emory University's Institutional Animal Care and Use Committee (IACUC) guidelines. Institutional approval was obtained prior to the onset of data collection.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data, code, analysis pipelines, and sulcal probability maps will be made publicly available on GitHub upon the publication of this article at https://github.com/cnl-berkeley/stable_projects.

Peer Review

The peer review history for this article is available at https://doi.org/10.1002/cne.70116.

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