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Planum Temporale Asymmetries Correlate with Corpus Callosum Axon Fiber Density in Chimpanzees (*Pan troglodytes*)

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Abstract

The corpus callosum (CC) is the major white matter tract that connects the two cerebral hemispheres. Some have theorized that individual differences in behavioral and brain asymmetries are linked to variation in the density of axon fibers that traverse different sections of the CC. In this study, we examined whether variation in axon fiber density in the CC was associated with variation in asymmetries in the planum temporale (PT) in a sample of 20 post-mortem chimpanzee brains. We further tested for sex differences in small and large CC fiber proportions and density in the chimpanzees. We found that the distribution of small and large fibers within the CC of chimpanzees follows a similar pattern to those reported in humans. We also found that chimpanzees with larger asymmetries in the PT had fewer large fibers in the posterior portion of the CC, particularly among females. As has been reported in human brains, the findings reported here indicate that individual differences in brain asymmetries are associated with variation in interhemispheric connectivity as manifest in axon fiber density and size.

Keywords

Chimpanzees; brain asymmetry; corpus callosum; axon fiber density; planum temporale

The corpus callosum (CC) is the largest brain white matter tract in the brain providing interhemispheric communication [1]. The importance of the CC for various motor, perceptual, and cognitive functions have been highlighted in the studies of “split-brain”

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human patients [2] and rhesus macaques [3] and some have suggested that the evolution of the CC was fundamentally important to the emergence of higher order cognitive functions in modern humans, including a unified consciousness [4]. Others have suggested that the CC was critical to the development and evolution of lateralized structures and functions of the cerebral cortex. For instance, in comparative studies of the CC in relation to brain size in mammals, it has been demonstrated that as brain size increases, the cross-sectional area of the CC does not keep pace, such that mammals with larger brain size have a relatively smaller CC [5]. Similar associations have also been reported in analyses restricted to the primate Order. After adjusting for brain size differences, the primates with the largest brains and most closely related to humans, the great apes, have a relatively smaller CC compared to more distantly related primate taxa including Old and New World monkeys [6]. Thus, as brain size increased during primate evolution, the two cerebral hemispheres became increasingly isolated or “split” [7]. As such, these evolutionary conditions allowed for the emergence of separate, specialized functions within each hemisphere.

Studies of within-species variation among human subjects have reported that differences in relative size of the CC are found between sexes, with females having relatively larger CC than males, though not all studies have found this effect [8–11]. It has also been reported that left-handed individuals have relatively larger CC than right-handed individuals [12, 13], although this finding has been difficult to replicate [8]. In studies that have reported sex or handedness differences in the CC size, the larger CC size in females and left-handed subjects has been attributed to these individuals having greater interhemispheric connectivity, which might translate into their brain’s being less lateralized and having more bilateral representation of motor and cognitive functions [12, 13].

One significant limitation of the comparative studies in relative CC size is that they have measured the midsagittal area from either cadaver specimens or from *in vivo* structural MRI scans; however, it is quite possible that size itself does entirely explain the within- and the between-species variability in behavioral or brain asymmetries. Specifically, within the CC, there is variation in both axon fiber density and the proportion of differentially myelinated fibers from different regions. For example, data from postmortem human brains indicates that small diameter ($< 2 \mu\text{m}$), lightly myelinated fibers are found mainly in the genu and splenium and connect higher-association areas, whereas large diameter fibers ($> 2 \mu\text{m}$) are predominant in the body and isthmus and connect primarily motor and somatosensory areas [13, 14]. Furthermore, increased density of axons is found toward the posterior mid-body and posterior pole of the CC [15]. In one of the only post-mortem studies in nonhuman primates, macaques were found to also have a higher density of fibers in the mid-body than other callosal regions [16] suggesting similarities between humans and macaque monkeys. In contrast, two recent comparative studies of fiber diameters in the CC of humans, chimpanzees and macaques reported that, like humans, larger diameter fibers are found in more posterior regions of the CC in humans and chimpanzees but not in macaques [17]. For example, Innocenti et al. [18] quantified the fiber diameters of axons within the sector of the CC where the planum temporale (PT) is connected between hemispheres in humans, chimpanzees and macaque monkeys and found that the a higher proportion of small diameter axons were evident in macaques compared to humans and chimpanzees. The PT is a region of particular interest because it is one of the most consistent leftward anatomical asymmetries in the human brain [19].

The extent to which differences in either fiber density and/or fiber composition explain species and individual differences in lateralization is unclear and has been relatively unexplored to date in nonhuman animals. In humans, there is some evidence in support of an inverse association between CC fiber density and asymmetries in the planum temporale (PT) and sylvian fissure (SF) length. For example, Aboitiz, Scheibel, Fisher and Zaidel [15]

measured the fiber density and composition of the CC in humans and correlated these measures with the direction and strength of asymmetry in SF length in a sample of 10 male and 10 female brains. Aboitiz *et al.* (1992) found that the number of larger diameter fibers (those between 1 and 3 μm) in the isthmus (for males) and anterior splenium (for females) was negatively associated with the magnitude of SF asymmetries. Thus, subjects with larger SF asymmetries had fewer larger diameter fibers in the posterior regions of the CC. More recently, Chance *et al.* [20] correlated asymmetries in primary and posterior auditory cortex volume and minicolumn organization with CC axon fiber numbers in 17 adult human brains. These authors found that asymmetries in minicolumn organization within the posterior auditory region were significantly correlated with asymmetries in the PT (Chance *et al.* 2006), but they did not distinguish between direction and strength of asymmetry.

The goals of this study were three-fold. First, we sought to quantify axon fiber densities in the corpus callosum of chimpanzees. Although several recent studies have quantified fiber composition and axon diameters in a small sample of chimpanzees ($n = 3$), as far as we know, there are no studies on CC fiber density in chimpanzees. Data on a primate species so closely related to humans are critical for reconstructing the evolution of cortical organization in our lineage. Second, we further sought to test for sex differences in fiber density in chimpanzees. There are some reports of sex differences in the size of the CC in humans with females having a relatively larger CC than males, after adjusting for overall differences in brain size. There are also reports of sex differences in CC fiber composition and density with females having a higher density than males [14]. In chimpanzees and other nonhuman primates, there are few if any reports of sex differences in the relative size of the CC [21–24]. Thus, at an anatomical level, human and nonhuman primates differ with respect to size differences in the CC. Here, we tested whether sex differences might be evident in axon fiber density in chimpanzees.

Finally, following the approach adopted by Aboitiz *et al.* [25], we tested the hypothesis that PT asymmetries are associated with variation in fiber proportions and density within the CC in chimpanzees. We selected the PT as the brain region of interest because several studies have reported that chimpanzees show a population-level leftward asymmetry for this region, as has been repeatedly found in human brains [26–28]. Because all the ape brains were scanned prior to dissection of the CC, we were able to quantify morphological asymmetries in the PT. If brain asymmetries are associated with fewer interhemispheric connecting fibers, then we predict that subjects with more lateralized PT values (i.e., values further from zero) should have relatively fewer CC fibers, particularly in the posterior regions where presumably the fibers that connect these regions are located.

Methods

Subjects

Post-mortem tissue was available from 20 adult chimpanzees including 10 females and 10 males. The chimpanzees were all adults and had died from natural causes. The corpora callosa were dissected out from the brains of these individuals and placed in formalin fixative prior to fiber counting. Necropsies and extraction of the brains for each subject were obtained with 10 hours of death.

Tissue preparation and fiber counting

Corpus callosum recovery, fixation and subdivision—At death, the whole brains were extracted and were initially stored in formalin, then transferred to a solution of 0.1% sodium azide in PBS at 4° C. Each brain was scanned post-mortem with a Bruker 7 T scanner. T2-weighted images were collected in the transverse plane using a gradient echo

protocol (pulse repetition = 22.0 s, echo time = 78.0 ms, number of signals averaged = 8–12, and a 256×192 matrix reconstructed to 256×256). The whole brains were divided along the mid-sagittal plane and the medial plane of each CC dissection was photographed and the anterior-posterior axis was measured. A 2 mm-thick parasagittal slice along the medial surface of the CC was removed and then cut into seven regions following the regional definitions used by Witelson [12, 13]. To subdivide the CC into 7 regions, the entire length of the CC was first measured, then divided into thirds (see Fig. 1). The anterior third was further divided into three regions by tracing a vertical line through the point where the anterior CC began to curve back slightly. This resulted in three subdivisions: rostrum (1), genu (2), and the anterior mid-body (3). The middle third of the overall CC was subdivided into equal sections, resulting in the central mid-body (4) and posterior mid-body (5). Finally, the posterior third of the overall CC was subdivided into the isthmus (6) and splenium (7). The splenium was defined as the posterior fifth of the entire CC; the remaining area within the posterior third was defined as the isthmus. To calculate the area for each of the 7 CC regions, the MRI scans were realigned in the sagittal plane and imported in the post-image analysis software ANALYZE 7.0. Using the tracing tool, the area (in mm^2) of the CC lying within each outlined region was measured in each individual.

Histological preparation—Tissue samples were dehydrated through an alcohol series, transferred through xylene and embedded in paraffin. Parasagittal plane sections were cut at 5–7 μm thickness and fixed to slides. Sectioned tissues were stained using the Palmgren method for nerve fibers [29, 30] and incorporating modifications recommended by the Neuropathology Department, University Hospital of Wales, Cardiff (the “Cardiff Modification,” version 4, available upon request). This modification eliminates the alcoholic aniline intensifier, the oxalic acid and the toning with gold chloride. Following staining, the slides were dehydrated through an alcohol series and a cover slip was mounted.

Determining fiber density and number—Stained sections from each region of each subject’s corpus callosum were observed with a Leica DM-RE microscope fitted with a Leica PL Fluotar 100x objective and an ocular grid with a hundred $10 \times 10 \mu\text{m}$ squares (total area counted = $1500 \mu\text{m}^2$). Large and small nerve fibers were counted directly from the microscope in 15 randomly designated counting frames in each region of the corpus callosum. Small fibers were those measuring $\sim 1 \mu\text{m}$ diameter and large fibers were those between 2 and 4 μm diameter (see Fig. 2). The large and small fiber densities for each CC region were calculated by averaging the number of fibers counted in the 15 counting frames for each subject. To estimate the fiber numbers in each CC region, we multiplied the mean density for fibers in each CC region by its area (scaled in μm) to yield an estimate of the number of fibers within the region. This was done separately for large and small fibers and the two measures were summed to calculate a measure of the total fiber density within each region. The individuals counting the fibers were blind to both the sex and brain asymmetries of each specimen. Inter-rater reliability between the two individuals counting the fibers was established prior to the onset of counting (intraclass r value $> .80$).

Planum temporale

Prior to measurement, the raw T2-weighted MRI scans were aligned in the axial, coronal and sagittal planes along the AC-PC line. Prior to data collection, two raters blind to the hemisphere and handedness of the chimpanzees independently measured the PT in 10 specimens. Inter-rater correlations between the two tracers were positive and significant for both the right ($r = 0.91$, $p < 0.01$) and left hemispheres ($r = 0.97$, $p < 0.01$). The surface area of the PT was measured following the procedures described by Cantalupo and colleagues [31]. The PT was traced in the coronal plane and the anterior border was defined by the most frontal slice showing Heschl’s gyrus (HG). The posterior border was defined by the most

caudal slice showing the SF. Once the anterior and posterior border was delineated, the depth of SF (i.e., width of PT) on each slice was measured from the superolateral margin of the superior temporal gyrus. Depth measures were taken up to the lateral ridge of HG in all the slices where HG was present (normally, HG was no longer present in slices proximal to the posterior border of PT). PT area was measured to the closest 0.1 mm using a mouse-driven computer-guided cursor available in ANALYZE 7.0. Following a well established procedure in the human literature [19], an estimate of the PT surface areas (in mm²) was computed as the sum of the cumulative PT depth measures for each slice within a hemisphere multiplied by the slice thickness (1 mm). An asymmetry quotient (PT_AQ) was derived following the formula $[PT_AQ = (R - L) / ((R + L) * 0.5)]$ where R and L represents the right and left hemispheres area measures. Positive PT_AQ values indicated a rightward asymmetry and negative values indicated a leftward asymmetry. We also computed a measure of the magnitude of PT asymmetry (ABS_PT_AQ), independent of direction, by taking the absolute value of the PT_AQ. Higher ABS_PT_AQ values indicated larger asymmetries in the PT.

Results

Corpus callosum fiber density and relative distribution

The density of large and small fibers in each CC region and sex is shown in Table 1. We initially examined regional variation in fiber density as a function of sex using repeated measures analysis of variance (ANOVA) based on the total fiber densities within each CC region. CC regional fiber density was the repeated measure while sex was the between groups factor. For this and all subsequent analyses, we excluded data from CC region 1 (the rostrum) was limited because we could only obtain a reasonable count in 11 chimpanzees and therefore including this region would have significantly reduced our sample size. Thus, for all analyses, we only included the genu, anterior mid-body, central mid-body, posterior mid-body, isthmus and splenium. Analysis of the fiber density data revealed a significant main effect for CC region ($F_{(5, 70)} = 4.55, p < 0.001$). The mean fiber densities for each CC region are shown Figure 3. Post-hoc analysis indicated the fiber densities of the genu and splenium were significantly higher than all other CC regions. The fiber densities of the genu and splenium did not differ significantly from each other.

In the next analyses, we examined the effect of sex and CC region on fiber density for the small and large fibers when considered separately. Thus, we performed two ANOVAs, one for the density of large and one for the density of small fibers. For each analysis, CC region was the repeated measure while sex was the between group factor. For the small but not the large fibers, a significant main effect for CC region was found ($F_{(5, 70)} = 4.08, p < 0.002$). Post-hoc analysis of the small fiber results indicated that the mean density of small fibers in the genu was significantly higher than in the central mid-body and posterior mid-body. None of the means from the remaining CC regions differed significantly from each other. For both small and large fibers, there were no significant sex differences in the density of fibers nor were there any significant interactions between sex and CC region.

We also calculated the relative distribution of the small and large fibers across the different regions of the CC. For this analysis, the density of small and large fibers were calculated for each CC region and subject and divided by the total density of small and large fibers, then multiplied by 100. Therefore, these values represented the percentage of total small and large fibers found in each CC region after adjusting for the total number of small and large fibers within each subject. Analyses of variance revealed significant main effects for CC region in the percentage of both the small ($F_{(5, 70)} = 4.18, p < 0.002$) and large ($F_{(5, 70)} = 3.13, p < 0.02$) fibers. The mean percentage of small and large fibers within each CC region is shown in Figure 4. Post-hoc analysis revealed that the percentage of small fibers in the

genu was significantly higher than in the anterior mid-body, central mid-body, posterior mid-body and isthmus. Furthermore, the percentage of small fibers in the splenium was significantly higher than in the isthmus and posterior mid-body. Post-hoc analysis of the large fiber results indicated that percentage of axons in the posterior mid-body was significantly greater than in the genu, anterior mid-body and splenium. Neither the main effect for sex nor the interaction between sex and CC region were significant in these analyses.

Corpus callosum fiber number

We next examined regional variation in fiber number as a function of sex using repeated measures analysis of variance (ANOVA). Three analyses were performed, one on the total number of fibers, and one each on the number of small and large fibers. For each analysis, CC region was the repeated measure while sex was the between group factor. The mean number of fibers for male and female chimpanzees can be found in Table 2 (though excluded from the analysis, we have included the descriptive statistics for the rostrum). For the number of small ($F_{(5, 70)} = 35.07, p < 0.001$), large ($F_{(5, 70)} = 3.16, p < 0.02$) and total fibers ($F_{(5, 70)} = 34.59, p < 0.001$), significant main effects for CC region were found. For the number of small and total fibers, the post-hoc results were identical. For both measures, the number of fibers in the genu and splenium were significantly higher than in the other four CC regions. Furthermore, the number of fibers in the anterior mid-body was significantly higher than in the central mid-body, posterior mid-body and isthmus. Post-hoc analysis of the density of large fibers indicated that the density of the isthmus was significantly higher than in the central mid-body. No significant main effects for sex were found nor were there any significant interactions between sex and CC region.

Planum temporale (PT)

We compared the PT_AQ and ABS_PT_AQ scores between males (Mean PT_AQ = -0.133, SE = 0.05; Mean ABS_PT_AQ = 0.169, SE = 0.04) and females (Mean PT_AQ = -0.098, SE = 0.04, Mean ABS_PT_AQ = 0.124, SE = 0.03) and found no significant differences. A one-sample *t*-test on the PT_AQ values showed a significant population-level leftward asymmetry ($t_{(19)} = 3.243, p < 0.01$). Based on the sign of the PT_AQ values, 14 subjects had a left hemisphere bias and 6 had a right bias.

Association between PT asymmetries in CC fiber density

We next considered the associations between the PT_AQ and ABS_PT_AQ scores and fibers numbers within the seven CC regions. Recall that the chimpanzees showed a leftward asymmetry in the PT and there is a significant negative correlation ($r = -.814, p < .001$) between the PT_AQ and ABS_PT_AQ. This reflects the sample fact that the less lateralized subjects more rightward or higher PT_AQ scores. Thus, because the distribution of scores is skewed rather than normally distributed, the two measures are somewhat redundant when considering how they might be related to variation in fiber density within the CC. For this reason, we focused the correlation analyses on the ABS_PT_AQ scores in relation to total fiber density (see Table 3). We initially correlated the ABS_PT_AQ scores with the total fiber density for CC region and found no significant associations. We subsequently ran separate correlations between ABS_PT_AQ scores and the total fiber densities for each CC region within the males and females. For females, we found a significant positive association between the ABS_PT_AQ scores and the isthmus ($r = .750, p < .03$). In contrast, among males, we found a significant negative correlation between the ABS_PT_AQ scores and the isthmus ($r = -.717, p < .04$). A comparison of these two correlation coefficients found that they significantly differed from each other ($z = 3.25, p < .003$) (see Table 3).

Discussion

One aim of this study was to quantify axon fiber number and densities of the CC in chimpanzees and to test for sex differences. As has been reported in humans [14], the number of fibers is higher in the genu and isthmus/splenium regions of the CC compared to the central portions of the CC. Specifically, in terms of fiber density, we found that significantly higher densities of small fibers are in the genu and splenium whereas relatively higher densities of large fibers are found in the central portions of the chimpanzee CC (see Figure 3). This pattern of fiber density distribution is consistent with reports in humans and the notion that the presence of larger, more myelinated fibers in the central portion of the CC are needed for rapid interhemispheric transmission of sensory and motor information between hemispheres [32]. In short, variation in fiber number and density across different CC regions in the chimpanzee are consistent with findings in humans [33].

We failed to find sex differences in the CC axon fiber number and density in chimpanzees, a finding consistent with results on CC size in chimpanzees as measured from magnetic resonance images [34]. The lack of sex differences in CC size, CC fiber number and density are inconsistent with at least some reports in humans. In a study that used similar methods as those employed in this report in a population of schizophrenic and control subjects, Highley *et al.* [14] reported that control females had significantly higher CC fiber number and density than control males. Rabi *et al.* [35] failed to find overall sex differences in CC fiber numbers in humans but did report that females had significantly more small diameter fibers in the genu than males whereas males had more large diameter fibers in the mid-body and splenium. In this and other studies of CC fiber density in males and females, sample sizes are generally small and statistical power is low, so we would caution against making too strong of a conclusion regarding sex differences in the CC in humans and chimpanzees. These observations notwithstanding, based on current results, sex differences in CC fiber density and number may be evident in humans but absent in chimpanzees and therefore reflect a unique adaptation of our species.

Another finding from this study was the mediating effect of sex on the correlation between fiber density and the magnitude of asymmetries in the PT. Males with larger PT asymmetries had fewer fibers in the isthmus. In contrast, females with larger PT asymmetries had more fibers in the isthmus. The results reported here are consistent with a previous report of a correlation between PT asymmetry and isthmus CC fiber density in humans [25] and suggest that similar mechanisms may underlie individual differences in PT asymmetry in humans and chimpanzees. Samples sizes are relatively small in this study and we would therefore recommend some caution in the interpretation of these results. More generally, the findings are consistent with the hypothesis that behavioral and neuroanatomical asymmetries are correlated with interhemispheric connectivity at both the individual and potentially the species levels [6, 32, 36], though these effect may differ between males and females. It should be noted that association between PT asymmetry and fiber density was specifically within the isthmus, the region of the CC that many believe possess the homotopic fibers connecting the left and right superior temporal gyrus [13]. Using diffusion tensor imaging, Phillips and Hopkins [37] have shown that the cortical topographic projections through the chimpanzee CC are similar to those of humans. This observation in relation to the findings reported here reinforces the view that there is considerable homology in the human and chimpanzee CC organization.

One limitation of this study was that we did not directly quantify axon fiber diameter but rather made qualitative judgments of the large and small fibers. Measuring axon diameters within the CC requires a different set of procedures in terms of tissue preservation as well as quantification techniques that were not readily useable for this study. Additional studies that

focus on direct quantification of axon diameters should be conducted in the future. Though we found a significant association between the PT asymmetry and fiber density in the posterior mid-body, it is not clear that this region is where the fibers that connect the PT are located within the CC. This study did not attempt to track fibers between hemispheres in regions corresponding to the PT but based on our findings, we would predict that this is where those connecting fibers are located within the CC. With recent advent of *in vivo* imaging techniques, such as diffusion tensor imaging, testing this hypothesis is now feasible and should be pursued.

In summary, the pattern of variation in axon fiber number and density within the CC of chimpanzees appears similar to reports in the human brain. Furthermore, individual differences in asymmetries in the PT were associated with fewer large fibers in the isthmus of the CC, but the direction of the associations differed between males and females. The evidence of sex-dependent associations between PT asymmetry and CC fiber density is consistent with some reports in humans and suggest that similar, as yet unknown, factors may influence the cortical organization and potential lateralization of the nervous system of apes and humans.

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Figure 1. Midsagittal view of the 7 CC regions displayed on a MRI scans. 1, rostrum; 2, genu; 3, anterior mid-body; 4, central mid-body; 5, posterior mid-body; 6, isthmus; and 7, splenium. Area measures from each region were calculated for each subject in order to estimate the number of small and large fibers in each region.

Figure 2.
Light micrograph of 7 μm thick section from corpus callosum of *Pan troglodytes* stained to show nerve fibers. Single open arrow head, small fiber; double open arrow head, large fiber; solid arrow head, glial cell nucleus. Scale bar = 4 μm .

Figure 3.
Mean fiber density ($\pm$ SE) found in each region of the CC, excluding the rostrum.

Figure 4.

Mean percentage of small and large fibers ($\pm$ SE) found in each region of the CC, excluding the rostrum. For each CC region, the percentage of small or large fibers was computed by dividing the regional value by either the total number of small or large fibers.

Table 1

Mean density of fibers ($\pm$ SE) in male and female chimpanzees

	Rostrum	Genu	Anterior mid-body	Central mid-body	Posterior mid-body	Isthmus	Splenium
<i>Small fibers</i>							
Females	16.53 (3.01)	18.78 (2.19)	15.93 (1.21)	14.59 (1.81)	13.59 (1.29)	15.77 (1.28)	19.23 (2.50)
Males	21.88 (4.91)	22.12 (2.21)	17.83 (1.74)	14.53 (0.74)	14.76 (0.79)	16.21 (1.95)	18.12 (2.07)
<i>Large fibers</i>							
Females	0.36 (0.34)	0.73 (0.39)	0.63 (0.21)	0.77 (0.20)	0.59 (0.13)	0.64 (.23)	0.65 (0.23)
Males	0.28 (0.11)	0.58 (0.15)	0.75 (0.26)	0.74 (0.16)	0.76 (0.16)	0.45 (0.11)	1.00 (0.41)

Values represent average number of fibers counted in 15 of the 1500 μm^2 sampling regions.

Table 2

Mean number of callosal fibers per region ($\pm$ SE) in male and female chimpanzees

	Rostrum	Genu	Anterior mid-body	Central mid-body	Posterior mid-body	Isthmus	Splenium
<i>Small fibers</i>							
Females	1,122,410 (367,133)	9,323,448 (1,648,175)	8,283,616 (846,736)	5,187,176 (651,938)	4,081,220 (383,041)	4,984,698 (398,589)	15,860,414 (2,036,329)
Males	1,565,440 (263,970)	12,738,023 (1,260,785)	9,499,548 (712,644)	5,196,922 (382,932)	4,533,790 (354,854)	4,273,031 (693,120)	12,507,135 (1,108,645)
<i>Large fibers</i>							
Females	23,424 (21,254)	482,642 (319,049)	309,429 (109,930)	258,812 (62,876)	183,371 (44,920)	185,178 (54,810)	546,800 (193,740)
Males	20,871 (12,965)	332,491 (104,654)	431,412 (150,128)	251,068 (56,907)	233,554 (64,147)	96,967 (20,829)	780,850 (316,422)
<i>Total fibers</i>							
Females	1,145,834 (370,688)	9,806,091 (1,845,063)	8,593,045 (815,637)	5,443,989 (652,843)	4,264,592 (407,546)	5,169,887 (386,614)	16,407,214 (2,090,133)
Males	1,586,311 (273,385)	13,070,515 (1,256,316)	9,930,960 (717,084)	5,447,990 (410,972)	4,767,344 (398,196)	4,369,998 (688,365)	13,287,986 (1,277,975)

Table 3

Correlation coefficients between fiber number and ABS_PT_AQ scores in chimpanzees

	Rostrum	Genu	Anterior mid-body	Central mid-body	Posterior mid-body	Isthmus	Splenium
<i>Total</i>							
ABS_PT_AQ	-0.452	-0.181	-0.354	-0.509	-0.221	-0.413	0.121
<i>Females</i>							
ABS_PT_AQ	-0.600	0.333	0.133	0.300	-0.190	0.750	0.017
<i>Males</i>							
ABS_PT_AQ	-0.314	-0.527	-0.176	-0.212	-0.333	-0.717	-0.217

Bolded coefficients were significant at $p < .05$