Published in final edited form as:

Neuroscience. 2009 March 31; 159(3): 1119–1125. doi:10.1016/j.neuroscience.2009.01.061.

A COMPARATIVE STUDY OF CORPUS CALLOSUM SIZE AND SIGNAL INTENSITY IN CAPUCHIN MONKEYS (*CEBUS apella*) AND CHIMPANZEES (*PAN troglodytes*)

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Abstract

The evolution of corpus callosum (CC) was integral to the development of higher cognitive processes and hemispheric specialization. An examination of CC morphology and organization across different primate species will further our understanding of the evolution of these specified functions. Using magnetic resonance imaging (MRI) as a non-invasive technique to measure CC size and to approximate the degree of myelination in the corpus callosum, we report differences in CC morphology and organization in capuchin monkeys and chimpanzees, two divergent primate species that have independently evolved several behavioral and anatomical characteristics. Species differences in CC morphology were detected, with chimpanzees having a larger overall CC compared to capuchin monkeys. Additionally, chimpanzees had the genu as the largest subdivision; in capuchin monkeys, the genu and splenium were the largest subdivisions. Sex differences in signal intensity were detected; capuchin monkey males had higher signal intensity values whereas chimpanzee females had higher signal intensity values. Thus, while capuchin monkeys and chimpanzees show some similarity in patterns of CC morphology, these species differ significantly in the regional organization of the CC.

Keywords

corpus callosum morphology; corpus callosum organization; capuchin monkey; chimpanzee; magnetic resonance imaging; signal intensity

The corpus callosum (CC) is the largest white matter tract providing inter-hemispheric communication, with axons of various sizes connecting homotopic and heterotopic regions of the cerebral cortex (Tomasch, 1954). The importance of the CC for various motor, perceptual and cognitive functions has been highlighted in the studies of “split-brain” human patients (Gazzaniga, 2000) and rhesus macaques (Hamilton, 1977; Hamilton and Vermeire, 1988) 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 (Sperry, 1984). Others have suggested that the CC was critical to the development and evolution of lateralized structures and functions of the cerebral cortex (Witelson, 1985; Rosen et al., 1989; Rilling and Insel, 1999b; Dorion et al., 2000; Hopkins and

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Rilling, 2000). For instance, in comparative studies of the CC in relation to brain size in mammals, as brain size increased the CC did not keep pace, such that mammals more closely related to humans have a relatively smaller CC after adjusting for brain size than species more distantly related (Oliveras et al., 2001). Similar associations have been reported within the primate order. After adjusting for brain size differences, the primates 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 (Rilling and Insel, 1999a). As brain size increased during primate evolution, the two cerebral hemispheres became increasingly isolated or “split” (Hopkins and Cantalupo, 2008). As such, these evolutionary conditions allowed for the emergence of separate, specialized functions within each hemisphere.

One limitation of the existing data on CC morphology in relation to brain size in primates is that comparisons have largely been made between species from different taxa that vary considerably in their ecological, social and behavioral repertoires. For instance, great apes include chimpanzees, gorillas and orangutans for which there are well-known differences in locomotor adaptation, social organization and motor functions (Tuttle, 1986). Similarly, in the study by Rilling and Insel (1999a), New World monkeys consisted of capuchin and squirrel monkeys, two species that drastically differ in their ecological niches, social organization and cognitive and motor abilities (Costello and Frigaszy, 1988; Christel, 1994). Thus, in these initial studies, species differences in ecology, social organization and cognitive abilities were not considered within the larger framework of potential factors that might influence the development of the CC (and related brain structures).

One aim of the current study was to compare CC morphology in two divergent species that share some common social and cognitive abilities—capuchin monkeys and chimpanzees. Though these two species differ significantly in terms of brain and body size, they have independently evolved several behavioral and anatomical characteristics in common—including complex manipulative abilities, use of tools in the wild (Phillips, 1998; Frigaszy et al., 2004), and the use of precision grips (Costello and Frigaszy, 1988; Spinozzi et al., 2004)—making them ideal species for comparisons of brain morphology and organization. Moreover, both capuchins and chimpanzees have relatively large brains for primates of their body size (Rilling and Insel, 1999b), suggesting that CC size should be comparable between them assuming that relative brain size is the driving mechanism influencing CC size.

An additional aim of this paper was to evaluate whether these species display differences in CC organization. Specifically, we sought to indirectly measure the degree of white matter connectivity that was expressed in the CC of capuchin monkeys and chimpanzees. In humans, analysis of postmortem brain tissue 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 (Witelson, 1989; Highley et al., 1999). Furthermore, increased density of axons is found toward the posterior midbody and posterior pole of the CC (Aboitiz et al., 1992). Macaques also have higher density of fibers in the midbody than other callosal regions (Lamantia and Rakic, 1990) suggesting similarities between humans and macaque monkeys.

In vivo visualization of axon density and diameter within the CC is impossible at the moment but more indirect measures of CC white matter integrity have begun to emerge using magnetic resonance imaging (MRI) technologies in the form of both signal intensity measures and diffusion tensor imaging (DTI) (Hofer and Frahm, 2006). With structural MRI scans, neurons with greater myelination are expressed as higher voxel intensity values whereas gray matter has lower intensity values. Thus, within the CC, the average intensity of the signal from selective regions may indirectly reflect the level of myelinated axons traversing the CC at any

point along the anterior–posterior gradient. A recent study in humans quantified the CC signal intensity and found it to differ between different clinical populations with hypothesized differences in CC organization (Brambilla et al., 2004). Thus, CC signal intensity measures may be a reliable measure of myelination (Reinartz et al., 1988).

Lastly, we sought to test for sex differences in CC morphology and signal intensity. In humans, females have been reported to have a relatively larger CC and relatively larger posterior portions of the CC than males (Kertesz et al., 1987; Clarke et al., 1989; Witelson, 1989; Clarke and Zaidel, 1994). Histological examination of fiber composition of callosal subdivisions in human postmortem tissue has not revealed significant sex differences (Aboitiz et al., 1992), but this may be due to low power associated with relatively small sample sizes employed, as males were found to have more small fibers, and females more large fibers. A histological examination of axon density in the splenium of long tailed macaques and chimpanzees likewise found no sex differences in either species (Broadfield, 2001). However, splenia from only four macaques (two males, two females) and two chimpanzees (one male, one female) were examined, thus leaving in doubt whether or not sex differences exist in axonal composition of the splenium.

Sex differences in CC:brain ratio have been documented in capuchins and rhesus macaques with males having smaller ratios than females (Franklin et al., 2000; Phillips et al., 2007), though not all investigators have found sex differences (Holloway and Heilbronner, 1991; Pierre et al., 2008). The sex differences in the morphology of the capuchin CC appear to persist throughout development (Phillips and Sherwood, 2008). Dunham and Hopkins (2006) did not detect sex differences in CC morphology in chimpanzees. The third aim of this study was to further test for sex differences in capuchin monkeys and chimpanzees in not only CC size, but also signal intensity values within the CC of each species.

EXPERIMENTAL PROCEDURES

Subjects

MRI were collected in a sample of 29 adult chimpanzees (*Pan troglodytes*) including 18 females and 11 males (mean age 22.76, SD = 11.92 years; range 12–51 years) and 27 adult capuchin monkeys (*Cebus apella*) composed of 13 males and 14 females (mean age 8.20, SD = 4.09 years; range 3–20 years). All the chimpanzees were members of a captive colony housed at Yerkes National Primate Research Center (YNPRC) in Atlanta, GA, USA. Capuchins were housed at Hiram College (Hiram, OH, USA), Northeastern Ohio Universities College of Medicine (Rootstown, OH, USA), the College of Wooster (Wooster, OH, USA), or the University of Pittsburgh (Pittsburgh, PA, USA). All experimental procedures conformed to the guidelines of the National Institutes of Health, United States Public Health Service policy, and the United States Department of Agriculture on the ethical care and use of animals. Additionally, efforts were undertaken to minimize the number of subjects used and to minimize subjects' suffering in this study.

Image collection and procedure

Chimpanzee subjects were first immobilized by ketamine injection (10 mg/kg) and subsequently anaesthetized with propofol (40–60 mg/(kg/h)) following standard procedures at the YNPRC. Subjects were then transported to the MRI facility. The subjects remained anesthetized for the duration of the scans as well as the time needed to transport them between their home cage and the imaging facility (total time ~2 h). Subjects were placed in the scanner chamber in a supine position with their head fitted inside the human-head coil. Scan duration ranged between 40 and 80 min as a function of brain size. The chimpanzees were scanned using a 3.0 T scanner (Siemens Trio, Malvern, Pennsylvania, USA) located at YNPRC. T1-weighted

images were collected using a 3D gradient echo sequence (pulse repetition = 2300 ms, echo time = 4.4 ms, number of signals averaged = 3, matrix size = 320×320). After completing MRI procedures, the subjects were returned to the YNPRC and temporarily housed in a single cage for 6–12 h to allow the effects of the anesthesia to wear off, after which they were returned to their home cage. The archived MRI data were stored on optical diskettes and transported to an Easy Vision workstation for post-image processing.

Capuchins were transported to the Brain Imaging Research Center in Pittsburgh, PA, USA, for the MR procedure. Once at the facility, subjects were initially immobilized with one of two drug cocktails: (a) ketamine (7 mg/kg) injection i.m., medetomidine (0.06 mg/kg) injection i.m. and atropine (0.05 mg/kg) injection SQ, or (b) ketamine (25 mg/kg) injection i.m., acetylpromazine (1 mg/kg) injection i.m., and atropine (0.05 mg/kg) injection SQ. All subjects were subsequently anaesthetized with propofol (250–350 μ g/kg/min) to maintain anesthesia. Subjects were placed into the scanner chamber and their heads were fitted inside a 16 cm or 12 cm head coil. At the cessation of the scan, subjects receiving drug cocktail “a” received atipamazole (0.06 mg/kg) injection i.m. Subjects were allowed to recover from the effects of anesthesia before return transport.

All capuchin monkeys were scanned on the same Siemens 3 T Allegra Scanner (Malvern, Pennsylvania, USA). T1-weighted images were acquired (TR = 1500 ms, Te = 3.04 ms, no echo-train, number of signals averaged = 3, matrix size = 256×256). Scan acquisition time was approximately 30 min. Prior to morphometric analysis, data were converted into the Analyze 3D volume file format to facilitate re-slicing into orthogonal planes. Computer files for individual monkeys were numerically coded prior to measurement to prevent observer bias.

MRI analysis

CC area and signal intensity—CC area measurements were taken from the midsagittal slice using a method similar to that described by Sanchez et al. (1998) and others (Phillips et al., 2007; Pierre et al., 2008) in nonhuman primates. The method divides the CC into five segments which are roughly associated with different sets of fiber projections to various cortical regions of the brain (Pandya et al., 1971; Witelson, 1989) (see Fig. 1). Analyze 7.0 (Overland Park, Kansas, USA), an MRI analysis software program distributed by the Mayo Clinic, was used to divide and measure the CC. Using the region of interest function (ROI) within Analyze, the CC was first divided into five equally spaced sections and included the genu, anterior-midbody, central-midbody, posterior-midbody and splenium. Using the tracing tool, the area (in mm²) of the CC lying within each outlined region was measured in each individual. The five regions were summed to derive an area measure for the entire CC. With respect to the signal intensity, within each of the five regions of the CC, a small 2×2 mm box was placed randomly within the region (see Fig. 1). The mean intensity of the MRI voxels within the 2×2 mm region was then calculated for each region and subject. Higher values indicated greater signal strength that would presumably represent the relative amount of white matter within that region of the CC.

Lastly, brain volumes were also determined for each subject. For the chimpanzees, this was accomplished using an automated thresholding function within Analyze. Brain volumes included white and gray matter and ventricles as well as the cerebellum but not brain stem structures. For the capuchins, total brain volume was determined by measuring every 8th slice from the parasagittal series. This yielded, on average, 12.1 slices that were measured per individual to calculate total brain volume. In each slice, voxels representing gray matter, white matter, and ventricular space were identified and separated from the skull using manual segmentation. The entirety of the cerebral hemispheres, cerebellum, midbrain, brainstem, and ventricles was included in the measurement of brain volume, following protocols described in a previous study of nonhuman primate brains (Sherwood et al., 2004). The volume

corresponding to these voxels was calculated for each slice and multiplied by the interslice distance to obtain the whole brain volume. The brain volumes were calculated so that size of the CC could be adjusted for individual and species differences in the CC.

Data analysis

To adjust for individual and species differences in the CC, following the procedure of Smith (2005), the square root of each of the CC areas was divided by the cube root of the brain volume to create a ratio (CC ratio) for each individual subject. This appropriately scaled the linear measure of area of the CC to the cubic volume of the whole brain in both species.

In addition, within the capuchin monkeys and chimpanzee samples, the signal intensities of each region of the CC were standardized around the mean signal intensity within each species for the entire CC. Each subject's SI value for each region was subtracted from the mean SI value and divided by the standard deviation. This was done because we were not explicitly interested in species differences in the signal density per se but rather in sex differences in the signal intensities. By standardizing the scores, it removed potential differences that might be present between species due to different scanning parameters, field noise, or other extraneous variables. All analyses were performed using inferential statistics at $P < 0.05$ and any necessary post hoc tests were conducted using Tukey's honestly significant difference (HSD) test.

RESULTS

CC morphology

We initially compared the two species on the regional variation in size of the CC after adjusting for difference in brain size using a mixed model analysis of variance (ANOVA). The CC-ratios for the five CC regions served as the repeated measure while species (chimpanzees, capuchin) and sex (male, female) served as the grouping variables. There was a significant main effect for sex $F(1,46) = 14.28$, $P < 0.001$ and significant two-way interaction was found between species and CC region $F(4,184) = 41.33$, $P < 0.001$ and a borderline significant two-way interaction between species and sex $F(1,46) = 73.87$, $P = 0.055$. There was no significant three-way interaction between sex, species and CC region. The mean CC-ratio for each region and species is shown in Fig. 2. Post hoc analysis indicated that chimpanzees had relatively larger corpus callosi for all five regions compared to capuchins. Within the chimpanzees, the relative size of the genu and splenium was significantly larger than the rostral, central and posterior mid-bodies. Moreover, the size of the genu was significantly larger than the splenium. Within the three central CC regions, the central midbody was significantly smaller than the anterior midbody but did not differ from the posterior midbody. Within the capuchin monkey sample, the relative size of the genu and splenium was significantly larger than the three remaining central regions. However, unlike in the chimpanzees, the genu did not differ significantly from the splenium. In addition, the anterior mid-body did not differ in size compared to the central midbody. For the sex difference, in chimpanzees and capuchin monkeys, females had relatively larger CC ratios compared to males. The mean CC ratio for male and female capuchins and chimpanzees is shown in Table 1.

CC signal intensity

We next considered species and sex differences in the CC signal intensity values for the five CC regions. For this analysis, the five standardized z-score intensity values served as repeated measures in a mixed model analysis of variance. Species (chimpanzee, capuchin) and sex (male, female) served as between group factors. Significant two-way interactions were found between species by CC region $F(4,208) = 6.45$, $P < 0.001$ and between species and sex $F(1,52) = 10.17$, $P < 0.001$. With respect to the species by sex interaction, the mean CC-intensity for male and female capuchins and chimpanzees are shown in Fig. 3. Post hoc analysis indicated

that in capuchin monkeys, the mean CC-intensity values in males were significantly higher compared to females. In contrast, in chimpanzees, males had relatively lower CC-intensity values compared to females.

For the species by CC region interaction, the mean standardized z -scores for each CC region and species are shown in Fig. 4. Post hoc analysis indicated that within the chimpanzees, the standard z -scores for region 3 were significantly lower than all other regions. None of the other means differed significantly within the chimpanzee sample. For the capuchin monkeys, the mean z -scores for regions 1 and 2 were significantly lower than regions 3 and 4 but not region 5. None of the other regions differed significantly from each other. As can be seen in Fig. 4, the pattern of CC intensity across the CC differed between chimpanzees and capuchin monkeys. The lowest values were the central regions within the chimpanzees whereas the lowest values were in the anterior regions for the capuchin monkeys.

DISCUSSION

There were two main findings in this study. First, species and sex differences were evident in both CC morphology and CC intensity values. Second, there were regional differences in both the CC size and signal intensity values between chimpanzees and capuchins that might reflect differences in CC organization between these two species.

Species differences

With respect to morphology, chimpanzees had a larger CC compared to capuchins, after adjusting for differences in brain size. However, for the most part, relative size differences were consistent across all regions of the CC. In the chimpanzees, the relative sizes of each CC region differed significantly from each other, with the genu the largest region followed by the splenium. Capuchins showed similar differences in the relative sizes, with the genu and splenium as the largest subregions. One interspecific difference with respect to CC region variability concerned relative size of the midbody regions, with chimpanzees showing differences and capuchin monkeys not. These findings might suggest that, in chimpanzees and capuchins, there are similar expansions of regions in the CC that are related to higher order association areas of the frontal lobe. However, the signal intensity results indicate differences within the organization of the CC between chimpanzees and capuchins. For all CC regions, the mean signal intensity values, presumably reflecting increased myelination, were significantly higher in chimpanzees compared to capuchin monkeys. This finding is consistent with evidence of greater white matter volumes in frontal lobes of apes compared to Old and New World monkeys (Rilling and Insel, 1999b; Schoenemann et al., 2005).

More pronounced species differences were detected in the regional variation in intensity values across the CC. For chimpanzees, the higher signal intensity values were found in the genu and splenium while the lowest values were in the central midbody. This may indicate regions of densely distributed axons of small diameter found in regions of the CC that connect association cortex compared to primary motor or somatosensory regions. In contrast to chimpanzees, capuchin monkeys showed a different pattern of distribution in signal intensity values. The highest signal intensity values were found in the central regions of the CC, connecting premotor and supplementary motor areas, whereas the smallest values were found in the genu and splenium. This suggests that in capuchins, fiber tracts connecting premotor and supplementary motor cortical regions are more densely myelinated, whereas in chimpanzees, fiber tracts connecting prefrontal cortical regions (higher association areas) are more densely myelinated. Thus, what seems to emerge from this analysis is a different potential topography of connectivity between cortical regions in capuchin monkeys compared to chimpanzees, particularly as it relates to connection between association areas of the cortex.

One possible explanation is that the organization and cortical connectivity of the capuchin monkey brain differ from that of chimpanzees. This cannot be evaluated with existing data from either this study or the published literature because the data are not available at present. Notwithstanding, other imaging technologies could be employed to address this question, notably DTI. DTI would allow for the application of tractography to myelinated fibers traversing the CC in the capuchin brain and provide a means for further evaluating CC tract projections. Recently, Hofer et al. (2007) used DTI to compare the tractography of the CC in humans and rhesus monkeys; they found considerable homology in the cortical projections of fibers running through the CC in these two species. In addition, in the rhesus monkey sample ($n=4$), the highest fractional anisotropic (FA) values were in the genu and splenium and lowest in the central regions of the CC. As FA values reflect the degree of white matter integrity within the region of interest, the results in the rhesus monkeys using DTI are similar to those results reported here for the chimpanzees. Thus, if we assume that similar mechanisms broadly govern the calculation of FA values in DTI and the signal intensity values as measured here, it appears that rhesus and chimpanzees show similar topography compared to the capuchin monkeys.

Sex differences

Significant sex differences were found in CC size and signal intensity in both the capuchin monkeys and chimpanzees. For CC size, in both chimpanzees and capuchin monkeys, females had relatively larger values compared to males. This observation is consistent with previous reports in human subjects (Lacoste-Utamsing and Holloway, 1982; Holloway and Lacoste, 1986; Driesen and Raz, 1995) and suggests that similar mechanisms might be determining sexual dimorphism in the CC size. The likely explanation for the observed similarities between humans, chimpanzees and capuchin monkeys is brain size. Males have larger brains than females, and if brain size is inversely associated with CC size as some have suggested (Jäncke et al., 1997; Rilling and Insel, 1999a), this would explain why males have a relatively smaller CC than females in these difference species.

The sex differences in signal intensity are more difficult to explain because the capuchin monkeys and chimpanzees showed the opposite pattern of results. Overall CC signal intensity values were significantly higher in females compared to males in chimpanzees and significantly higher in males compared to females in capuchin monkeys. The potential explanations for this result are not immediately evident but again suggest that profound differences exist within the organization and connectivity of the CC of capuchin monkeys and chimpanzees. Histological data are necessary to examine whether there are corollary differences in the packing densities of small and large diameter fibers and the branching patterns of callosal axons.

Limitations and statistical issues

One limitation of this study is the working assumption that the signal intensity values indirectly reflect the degree of myelination of axons traversing the CC. The process of myelination corresponds to decreases in brain tissue water content, gliosis, and cellular lipid accumulation. These changes result in a decrease in relaxation time of T1-weighted images and an increase in MR signal intensity (Inder and Huppi, 2000; Paus et al., 2001). The use of signal intensity to evaluate differences in CC organization in clinical populations has been employed in previous studies with humans (Brambilla et al., 2004; Diwadkar et al., 2004) but there are no direct empiric data showing that these measures are associated with the level of myelination at the neuronal level. Furthermore, the relationship between myelination, axonal size, and MR signal intensity is not fully understood. Increases in axonal size and width should be accompanied by an increase in brain tissue water content which would result in a decrease in MR signal intensity. We would predict then that CC regions composed of larger diameter fibers should show lower signal intensities; this pattern was found in the chimpanzee sample but not the capuchins. An analysis of fiber composition of CC regional areas in both chimpanzees and

capuchin monkeys is needed. Such an analysis would also further our understanding of the pattern of observed sex differences in CC signal intensity.

It should also be noted that the relative size of the CC was significantly higher in the chimpanzees compared to the capuchin monkeys. These results run counter to previous reports in mammals, and specifically primates of smaller CC values relative to increasing brain size (Rilling and Insel, 1999a). This may be an artifact of how the size of the CC is configured to adjust for differences in brain size as it relates to (a) sex differences and (b) comparative differences. Multiple approaches are used including statistical co-varying brain volume, dividing the CC area by brain volume or using logged CC areas and logged brain volumes (see Smith, 2005). As rightly pointed out by Smith (2005), a straight ratio of CC area divided by brain volume is problematic because the scales of measurement differ; hence, our use of the square root of the CC divided by the cube root of the brain volume. However, in previous comparative studies of the relative CC size, most have used logged CC and brain volume values. Thus, the estimate of the CC size is very sensitive to the procedure used to adjust for brain volume at both the individual and species levels of analyses.

CONCLUSIONS

While capuchin monkeys and chimpanzees show similarity in some aspects of their behavior, ecology, and neuroanatomy, our results indicate profound differences exist in the organization of the CC. These differences may underlie more pronounced differences in interhemispheric and intrahemispheric connectivity and certainly warrant further investigation. For example, although the evidence suggests that both capuchin monkeys and chimpanzees engage in nut-cracking tool use, an analysis of the complimentary or independent nature of hand use in nut-cracking might prove fruitful in explaining differences in CC morphology. Thus, both species use tools but how the two hemispheres, as expressed in the complimentary use of the hands, are employed in the same tool using behavior might provide insight into what cognitive and neurological differences explain the expression of tool using behavior in relation to inherent differences on cortical organization.

Acknowledgements

This research was supported in part by NIH grants NS-36605, NS-42867, HD-38051, and HD-56232 and the Howard Hughes Medical Institute. The Yerkes Center is fully accredited by the American Association for Accreditation of Laboratory Animal Care.

Abbreviations

CC	corpus callosum
DTI	diffusion tensor imaging
FA	fractional anisotropic
MRI	magnetic resonance imaging
YNPRC	Yerkes National Primate Research Center

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Fig. 1. Anatomical subdivision of the CC in a capuchin monkey and chimpanzee MRI sagittal view. The total midsagittal area was divided into five equally spaced subdivisions: 1, genu; 2, anterior midbody; 3, central midbody; 4, posterior midbody; and 5, splenium.

Fig. 2.

Mean ($\pm$ SE) CC: brain ratio for each subdivision in capuchin monkeys and chimpanzees. ANT-MB, anterior midbody; Central-MB, central midbody; Posterior-MB, posterior midbody.

Fig. 3. Mean ($\pm$ SE) standardized signal intensity values of the CC in male and female capuchin monkeys and chimpanzees.

Fig. 4. Mean ($\pm$ SE) standardized signal intensity values of CC subdivisions in capuchin monkeys and chimpanzees. ANT-MB, anterior midbody; Central-MB, central midbody; Posterior-MB, posterior mid-body.

Table 1
Mean ratio in CC size to brain volume in male and female capuchin monkeys and chimpanzees

	CC region				
	Genu	Ant-MB	Central-MB	Posterior-MB	Splenium
Capuchin monkeys					
Males	0.922 (0.076)	0.794 (0.062)	0.789 (0.085)	0.735 (0.064)	0.899 (0.079)
Females	0.975 (0.078)	0.911 (0.074)	0.924 (0.066)	0.867 (0.056)	1.014 (0.065)
Chimpanzees					
Males	1.38 (0.118)	1.083 (0.097)	0.995 (0.099)	1.05 (0.084)	1.246 (0.078)
Females	1.408 (0.114)	1.112 (0.078)	1.042 (0.080)	1.040 (0.091)	1.326 (0.075)

Values represent mean ratio values (SD in the parentheses).