

Sex and Handedness Effects on Corpus Callosum Morphology in Chimpanzees (*Pan troglodytes*)

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Findings suggest that in humans, sex and hand preference may be associated with the size of the corpus callosum (CC). The authors measured CC morphology from MRIs in 67 chimpanzees (*Pan troglodytes*) to see whether similar effects were present in this species. Hand preference was assessed by performance on 4 tasks, and chimpanzees were classified as left-handed, right-handed, or ambidextrous. In a subsequent analysis, the chimpanzees were reclassified into 2 groups: right-handed and left-handed. The results revealed no sex difference in CC area, but significant effects of hand preference were found for several CC regions (rostrum body, anterior midbody, posterior midbody, isthmus, and splenium) and for overall CC size, with left-handed chimpanzees exhibiting significantly smaller CC measurements than right-handed chimpanzees. The results indicate that lateralized hand use in chimpanzees, as in humans, is associated with variation in CC size.

Keywords: *Pan troglodytes*, corpus callosum, handedness

The corpus callosum (CC) is the major set of fibers connecting homologous and heterologous cortical regions in the left and right cerebral hemispheres as well as some subcortical structures of the brain (Bermudez & Zatorre, 2001; Gazzaniga, 2000). Its presence allows for interhemispheric communication of sensory and motor functions within the brain. Previous research has shown that projections through the CC proceed on an anterior-to-posterior gradient that roughly connects cortical regions from the frontal to occipital lobe (Witelson, 1989). The morphology of the CC has been the topic of considerable debate, particularly as it relates to sex differences and lateralization (Byne, Bleier, & Houston, 1988; Denenberg, Kertesz, & Cowell, 1991; Driesen & Raz, 1995; Habib et al., 1991; Jancke & Steinmetz, 1998; Peters et al., 2002; Westershausen et al., 2003).

The presence of a sexual dimorphism in the human CC was first reported by de Lacoste-Utamsing and Holloway (1982). In their study, de Lacoste-Utamsing and Holloway found that women had a larger and more bulbous splenium (posterior fifth of the CC) than did men. Furthermore, de Lacoste-Utamsing and Holloway found that when brain weight was accounted for, women had a larger

overall CC. Significant findings of a dimorphism favoring a larger total CC area or regional CC area in female humans have been reported in subsequent studies on cadaver specimens as well as from in vivo imaging studies (Achiron, Lipitz, & Achiron, 2001; Bermudez & Zatorre, 2001; Burke & Yeo, 1994; Clarke, Kraftsik, Van Der Loos, & Innocenti, 1989; Witelson, 1989); however, several studies have found no evidence of sex differences in the size of the CC (Bishop & Wahlsten, 1997; Driesen & Raz, 1995; Habib et al., 1991; Horton, Crawford, Harrington, & Downs, 2004; Witelson, 1985).

In addition to sex differences in CC morphology, the relationship between handedness and CC morphology has also been considered. In one of the earliest studies, Witelson (1985) found that mixed-handed individuals (those who did not consistently use their right hand for specific items on a questionnaire) had a larger overall CC than did those who always preferred their right hand. A meta-analysis by Driesen and Raz (1995) also found that left-handed individuals had a larger CC area measurement than did right-handed individuals across the 43 studies included in their analysis. Habib et al. (1991) reported that non-right-handed participants had larger CC area measurements, especially in the anterior half of the CC. Evidence suggests that left-handed or mixed-handed individuals tend to exhibit a lesser degree of overall lateralization than those who prefer their right hand (Burke & Yeo, 1994; Driesen & Raz, 1995; Sheehan & Smith, 1986). Witelson (1989) hypothesized that the CC was larger in non-right-handed people as a function of the decreased lateralization. Sex by handedness interactions have also been reported in studies by Witelson (1989) and Habib et al. (1991). In both of these studies, non-right-handed or mixed-handed males had larger overall CC areas than right-handed males. The present study also considers the effect, if any, of strength of hand preference on CC size. A study conducted by Habib et al. (1991) suggested that individuals with a strong hand preference tended to exhibit a smaller CC. This was true for both strongly right- and strongly left-handed participants.

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Although the effects of sex and hand preference on CC size have been frequently studied in humans, few studies have examined whether sex or handedness is related to differences in CC morphology in the brains of nonhuman primates. Some have suggested that behavioral and brain asymmetries evolved as a consequence of decreasing interhemispheric connectivity, and therefore, comparative data are particularly important for testing these theories (Aboitiz, Lopez, & Montiel, 2003; Ringo, Doty, Demeter, & Simard, 1994; Rosen, 1996). In one study, de Lacoste and Woodward (1988) reported a sexual dimorphism within the family *Pongidae*, the family of primates including great apes (*Pan*, *Pongo*, and *Gorilla*), with females within this taxonomic group having a larger overall CC area than males, after accounting for differences in brain volume. This study was limited, however, to a group of only 15 subjects representing three genera. As far as we know, no studies to date have examined the relationship between handedness and CC morphology in nonhuman primates.

The purpose of the present study was to evaluate the relationship between sex, handedness, and CC morphology in a sample of captive chimpanzees. Chimpanzees represent an important species for these comparative studies for several reasons, including (a) their close genetic relationship to humans (The Chimpanzee Sequencing and Analysis Consortium, 2005); (b) like humans, they are not strongly dimorphic in terms of body size; and (c) recent studies have documented population-level handedness in both captive and wild chimpanzees (Hopkins, Wesley, Izard, Hook, & Schapiro, 2004; Lonsdorf & Hopkins, 2005). Assuming that common biological mechanisms influence the expression of CC morphology in humans and chimpanzees, we hypothesized that female chimpanzees would show a larger CC than male chimpanzees. Furthermore, we hypothesized that left-handed or ambidextrous chimpanzees would have larger CC areas than right-handed chimpanzees. Last, in this study, we examined the relationship between strength of hand use and CC morphology in a way typically not used in studies with human subjects. In the previous studies on CC morphology and handedness in humans, mixed-handed or inconsistently handed subjects were made up of both left-handed and ambidextrous individuals. However, in principle, subjects can be consistently left- or right-handed with all other subjects being inconsistently handed. In this study, we evaluated consistently and inconsistently handed chimpanzees as a means of assessing the role of strength compared with directional biases in hand use on CC morphology.

Method

Subjects

MRIs were collected in a sample of 67 chimpanzees (*Pan troglodytes*) including 37 females and 30 males with an average age of 21.87 years ($SE = 2.06$ years). All of the chimpanzees are or were members of a captive colony housed at the Yerkes National Primate Research Center (YNPRC) in Atlanta, Georgia. Thirteen of the brains were scanned post-mortem, whereas the other 54 chimpanzees were alive and healthy at the time of the scan.

Image Collection and Procedure

The cadaver specimens were stored in a solution of water and 10% formaldehyde for intervals ranging from 1 week to 5 years. The cadaver

brains were scanned with a 4.7 Tesla magnet (Bruker, BioSpec, Bartlesville, OK). T1-weighted images were collected in the transverse plane through the use of a fast spin 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).

For the in vivo scans, subjects were first immobilized by ketamine injection (10 mg/kg) and subsequently anesthetized with propofol (40–60 mg/(kg/hr)) following standard procedures at the YNPRC. Subjects were then transported to the MRI facility. They 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 = approximately 2 hr). 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 majority of the subjects were scanned with a 1.5 Tesla scanner (Model 51, Phillips, The Netherlands). The remaining chimpanzees were scanned with a 3.0 Tesla scanner (Siemens Trio, Milwaukee, Wisconsin) located at the YNPRC.

For all subjects scanned with the 1.5 Tesla machine, T1-weighted images were collected in the transverse plane by using a gradient echo protocol (pulse repetition = 19.0 ms, echo time = 8.5 ms, number of signals averaged = 8, and a 256×256 matrix). These scan parameters were developed in previous studies (Hopkins, Marino, Rilling, & MacGregor, 1998) and provided excellent resolution of the brain areas of interest to this study. For those subjects scanned with a 3.0 Tesla scanner, T1-weighted images were collected by using a 3-D gradient echo sequence (pulse repetition = 2,300 ms, echo time = 4.4 ms, number of signals averaged = 3, matrix size = 320×320).

After the MRI procedures were completed, the subjects were returned to the YNPRC and temporarily housed in a single cage for 6–12 hr 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 postimage processing.

MRI Analysis

CC area measurements were taken from the midsagittal slice by using a method similar to that described by Witelson (1989). The method divides the CC into seven segments that are roughly associated with different sets of fiber projections to various cortical regions of the brain (Pandya, Karol, & Heilbronn, 1971; Witelson, 1989). Witelson's (1989) study was conducted on postmortem brain tissue; therefore, the method was adapted for use with MRI scans and computer analysis (see Figure 1). ANALYZE 6.0, an MRI analysis software program distributed by the Mayo Clinic, was used to divide and measure the CC. Using the region of interest function within ANALYZE, the CC was first divided into thirds. The anterior third was then subdivided into three regions by inserting a vertical line through the point where the anterior CC begins to curve back slightly. This delineated Regions 1, 2, and 3, which are congruent to Witelson's (1989) rostrum, genu, and rostrum body. The region of the middle third was subdivided into two equal sections, creating Regions 4 and 5, referred to as the anterior and posterior midbodies. The posterior third was further subdivided into two sections, the isthmus and splenium. Witelson (1989) defined the splenium as occupying the posterior one fifth of the total CC length. To delineate this region, a total CC length measurement, from the most anterior point to the most posterior point of the CC, was taken. On the basis of the length measurement, a vertical line was drawn through the CC to define the posterior one fifth as the splenium. The remaining section, just anterior to the splenium, was congruent to Witelson's (1989) isthmus. Using the tracing tool, the area (in mm^2) of the CC lying within each outlined region was measured in each individual.

Brain volumes were also determined for each chimpanzee by using an automated thresholding function within ANALYZE. Brain volumes included white and gray matter and ventricles but excluded the cerebellum and brainstem structures.

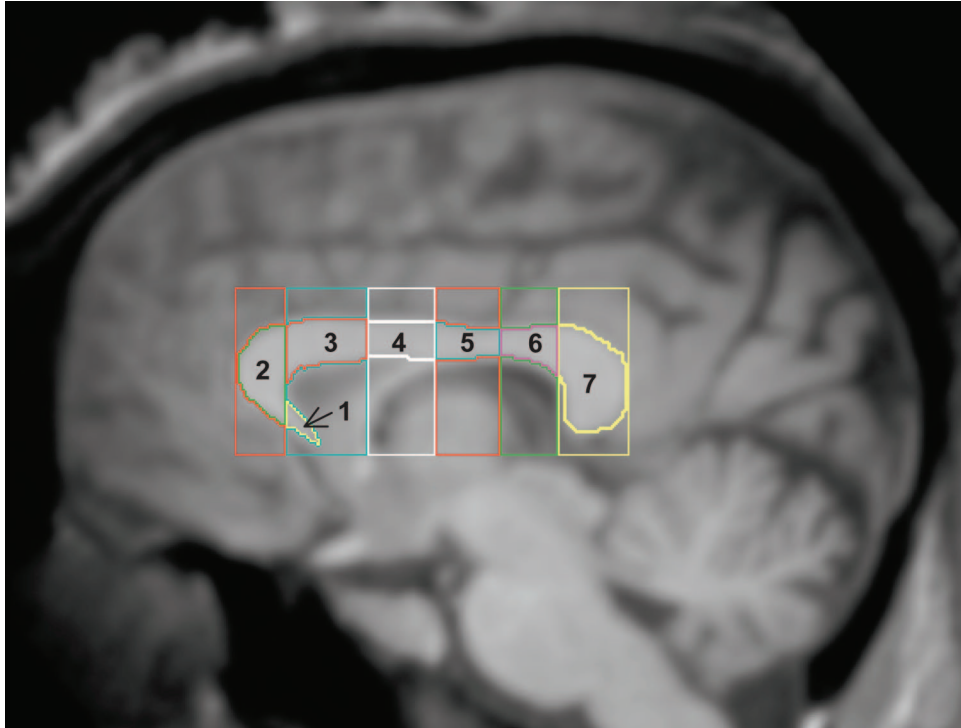


Figure 1. Midsagittal view of the chimpanzee corpus callosum. The seven subdivisions used for measurement are depicted here as numbers 1–7: 1 = rostrum, 2 = genu, 3 = rostrum body, 4 = anterior midbody, 5 = posterior midbody, 6 = isthmus, and 7 = splenium.

Handedness Measurement

Hand preferences were assessed for four measures including manual gestures (Hopkins et al., 2005), simple reaching (Hopkins, Cantalupo, Wesley, Hostetter, & Pilcher, 2002), bimanual feeding (Hopkins, 1994), and a task measuring coordinated bimanual actions, referred to as the TUBE task (Hopkins, 1995). These four measures were selected on which to derive a single measure of handedness because (a) they were uncorrelated with each other (see Hopkins, in press), (b) they each elicit consistent hand preferences in the chimpanzees, and (c) these measures were available in the largest cohort of subjects. A brief description of each measure is provided below.

Bimanual feeding. Each afternoon, the primates housed at the YNPRC receive fruits and vegetables as part of their daily diet. Each subject usually receives two oranges, one banana, some celery stalks, and/or carrots. Upon retrieving the food, the subjects typically move to a seating place and consume the food. The chimpanzees generally hold the extra pieces of food with one hand and feed with the opposite hand. Hand use was recorded when the chimpanzees were feeding with one hand for a minimum duration of 3 s and the nonfeeding hand was holding the remaining portions of food. The dominant hand was recorded as the one feeding.

Coordinated bimanual actions (TUBE). The second handedness measure was a task requiring bimanual coordinated actions, referred to as the TUBE task (Hopkins, 1995). For the TUBE task, peanut butter is smeared on the inside edges of polyvinyl chloride (PVC) tubes approximately 15 cm in length and 2.5 cm in diameter. Peanut butter is smeared on both ends of the PVC pipe and is placed far enough down the tube such that the subjects cannot completely lick off the contents with their mouths but rather must use their fingers to remove the substrate. The PVC tubes were handed to the subjects in their home cages, and a focal sampling technique was used to collect individual data from each subject. The hand of the finger used to extract the peanut butter was recorded as either right or left by the

experimenter. Each time the subjects reached into the tube with their finger, extracted peanut butter, and brought it to their mouth, the hand used was recorded as left or right.

Manual gestures. At the onset of each trial, an experimenter would approach the chimpanzee's home cage and center himself or herself in front of the chimpanzee at a distance of approximately 1.0–1.5 m. If the chimpanzee was not already positioned in front of the experimenter at the onset of the trial, the chimpanzee would immediately move toward the front of the cage when the experimenter arrived with the food. The experimenter then called the chimpanzee's name and offered a piece of food until the chimpanzee produced a manual gesture. Only responses in which the chimpanzee unimanually extended the digit(s) through the cage mesh to request the food were considered a response. Other possible manual responses such as cage banging or clapping were not counted as a gesture. Two-handed gestures, although rare, were not scored as were gestures that were produced by the chimpanzee prior to the experimenter arriving in front of the chimpanzee's home cage.

Simple reaching. On each trial, a raisin was thrown into the chimpanzee's home cage. The raisin was thrown by the experimenter to a location at least 3 m from the focal subject so that the chimpanzees had to locomote to position to the raisin, pick up the raisin, and bring it to their mouth for consumption. When the chimpanzee acquired the raisin, the experimenter recorded the hand used as left or right. One, and only one, reaching response was recorded on each trial to assure independence of data points (see Hopkins, 1999, and McGrew & Marchant, 1997, for contrasting views). Thus, raisins were not randomly scattered in home cages, but rather an individual raisin was thrown into cages and subjects retrieved the raisin before another was thrown into the cages. Subjects were required to locomote at least three strides between reaching responses to maintain postural readjustment between trials.

All of the chimpanzees were tested in the outdoor portion of their home cages. The number of responses obtained from each chimpanzee differed within and between tasks. Notwithstanding, a minimum of 30 responses were obtained for each chimpanzee for each task. Individuals recording the hand use data were blind to the brain asymmetries of the subjects, the size of the CC, and the hypothesis of the study.

Hand Preference Classification

Hand preferences were characterized in several ways. Initially, a handedness index (HI) for each measure was derived following the formula $[(HI = (\#R - \#L)/(\#R + \#L))]$. The four resulting HI scores were then averaged, and subjects were classified as right- or left-handed on the basis of the sign of their average HI score. Subjects with positive average HI values were classified as right-handed ($n = 42$), and subjects with negative average HI values were classified as left-handed ($n = 25$). In addition, we adopted a psychometric approach to handedness classification in our sample. The mean average HI score for the sample was .113 with a standard error of .034. On the basis of this descriptive information, subjects with average HI scores that were greater than $(HI > .12; n = 31)$ or less than $(HI < -.12; n = 12)$ three standard errors from zero were classified as either right- or left-handed. The remaining subjects were classified as ambidextrous ($n = 24$).

Data Analysis

The best way to analyze differences in CC morphology is a matter of some debate (Smith, 2005). The principal issue is the confounding relationship between CC size and overall brain volume. To address this issue, in this study, brain volume was regressed on the total CC area as well as the area measures for each of the seven CC regions. The individual unstandardized residuals were saved from these analyses, and these served as subsequent dependent variables in evaluating the influence of hand and sex on CC morphology. The residuals represent the degree of deviation in the size of the CC area of each individual as predicted from his or her brain size. Thus, positive values represent individuals that have larger CC areas for an organism of their brain volume, whereas negative values represent individuals that have smaller CC areas for their individual brain volume.

Results

The data were initially screened for any outliers, and none were found. Descriptive statistics on the residual values for each CC region were normally distributed and had comparable variances, therefore meeting the assumptions for inferential statistics. The subsequent data were submitted to a multivariate analysis of covariance (MANCOVA). Age was treated as a covariate, whereas sex and hand preference were considered as independent variables of interest. Alpha was set to $p < .05$, and all post hoc tests were performed using Tukey's honestly significant difference test.

Effects of Handedness and Sex on Residual CC Morphology

In the initial analysis, the residual of the overall CC and each region of the CC served as dependent variables in a between-groups MANCOVA. Sex (male, female) and handedness (right, left) served as independent variables, whereas age served as a covariate. The MANCOVA indicated an overall significant effect for handedness, $F(8, 55) = 2.75, p < .02$. The subsequent univariate F tests indicated a significant main effect for handedness for the overall CC, $F(1, 62) = 10.52, p < .01$; rostrum body, $F(1,$

$62) = 13.30, p < .01$; anterior midbody, $F(1, 62) = 4.40, p < .04$; posterior midbody, $F(1, 62) = 12.32, p < .01$; isthmus, $F(1, 62) = 8.10, p < .02$; and splenium, $F(1, 62) = 5.26, p < .03$. For every region of the CC, left-handed individuals had significantly smaller total CC residual values than did right-handed individuals. There was no main effect for sex for any of the CC regions. The mean CC residual for each handedness group can be seen in Figure 2.

Effect of Ambidexterity, Right-, and Left-Handedness on CC Morphology

To facilitate comparisons with existing studies on the relationship between handedness and CC morphology in humans, we performed the same analysis as previously described but used the classification criteria that derived a right-handed, left-handed, and ambidextrous group. The MANCOVA results indicated a significant effect for handedness, $F(8, 54) = 2.14, p < .05$.

Subsequent univariate F tests indicated significant differences for the overall CC, $F(1, 62) = 3.41, p < .04$; rostrum body, $F(1, 62) = 5.81, p < .04$; posterior midbody, $F(1, 62) = 3.96, p < .05$; and splenium, $F(1, 62) = 3.36, p < .05$. Post hoc analysis using Tukey's honestly significant difference test indicated that left-handed chimpanzees had significantly lower residual CC values than right-handed chimpanzees for all regions. No differences were found when left- and right-handed chimpanzees were compared with ambidextrous chimpanzees. The mean CC residuals for the overall CC and each CC region are shown in Table 1.

Analysis of Strength of Hand Preference and Sex on Residual CC Morphology

Consistent with the study by Habib et al. (1991) in humans, we also evaluated strength of handedness and sex on CC morphology. In this analysis, rather than evaluate the effect of directional biases in hand use on CC morphology, we classified hand preference in the chimpanzees as consistent or inconsistent. Subjects that were previously classified as left- or right-handed were combined to form one group referred to as consistently handed ($n = 43$). Subjects that were previously classified as ambidextrous were recoded as inconsistently handed ($n = 24$). The overall and regional differences in CC size were compared as a function of hand strength (consistently handed, inconsistently handed) and sex by using MANCOVA. As with the previous analyses, age served as the covariate. No significant main effects or interactions were found for either the MANCOVA or univariate F tests.

Correlations Between Mean Hand Use and CC Morphology

As an alternative means of assessing the relation between CC morphology and handedness, we performed several initial analyses. Specifically, there is some debate over whether handedness represents a qualitative trait made up of discrete groups of right- and left-handed individuals or whether handedness lies on a continuum from strongly left- to strongly right-handed individuals (e.g., Brown, Roy, Rohr, & Bryden, 2006; Corey, Hurley, & Foundas, 2001). To address this potential issue, we correlated the average HI score with each of the seven CC regions and the overall CC residual. Significant positive correlations were found between

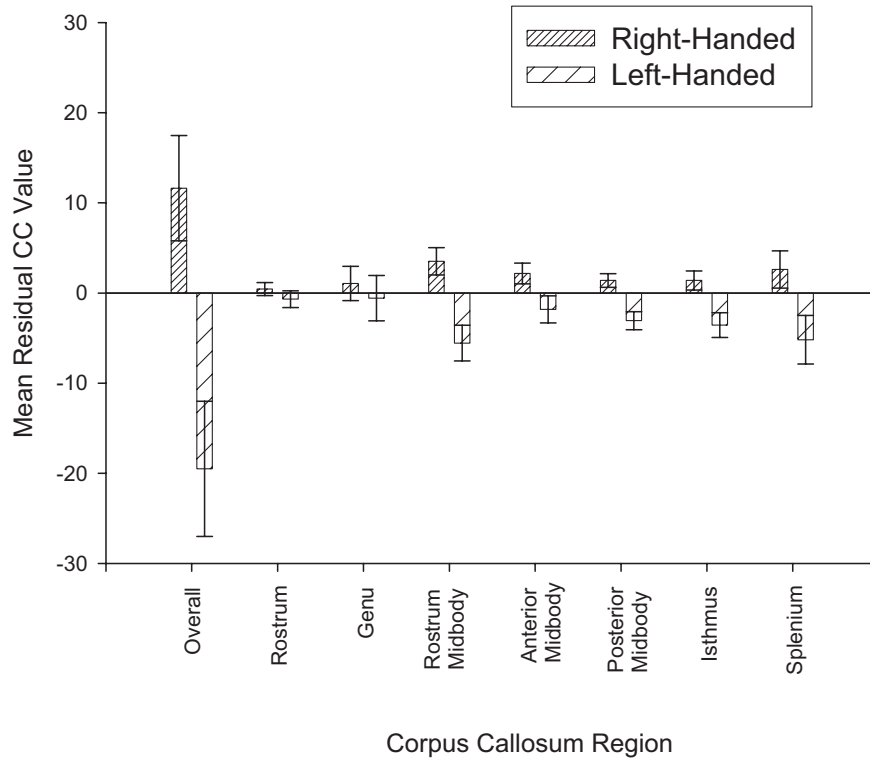


Figure 2. Mean (\pm SE) residual total corpus callosum (CC) values as a function of handedness.

the mean HI and the overall CC ($r = .292, df = 65, p < .02$), rostrum body ($r = .398, df = 65, p < .01$), and posterior midbody ($r = .351, df = 65, p < .01$). We also correlated strength in handedness based on a continuous scale by taking the absolute value of the average HI score and correlating this value with the overall CC and region-specific residual values. Significant positive correlations were found between the absolute value of the mean HI and the rostrum body ($r = .264, df = 65, p < .04$) and isthmus ($r = .292, df = 65, p < .05$).

Task Analysis

Last, our initial analyses were based on hand preference classification for four separate tasks. To evaluate whether the pattern of results was explained more by one specific measure than another, we individually correlated the HI scores for manual gestures, reaching, feeding, and the TUBE task with the overall and region-specific residual CC scores. The results of this analysis are shown in Table 2. In general, the associations were consistent between the four measures, although none of the associations were particularly strong. This suggests that the combined measure of hand use was better associated with variation in the CC than any specific measure.

Discussion

Two significant findings emerged from this study. First, when subjects were classified as left- or right-handed or handedness was considered on a continuous scale of measurement, significant associations were found between lateralized hand use and CC size

in chimpanzees. Second, handedness was associated with region-specific variation in CC morphology.

With respect to regional variation in CC morphology (overall CC area, rostrum body, anterior midbody, posterior midbody, isthmus, and splenium), left-handed chimpanzees had smaller CCs than right-handed chimpanzees. Similarly, when subjects were classified as right-, ambidextrous, or left-handed, left-handed chimpanzees had significantly smaller regional CC measurements (overall CC area, rostrum body, posterior midbody, and splenium) than right-handed chimpanzees. Left-handed chimpanzees did not differ significantly from the ambidextrous chimpanzees. The majority of literature on humans reports the opposite trend, with right-handed individuals typically having smaller CCs than non-right-handed individuals (Driesen & Raz, 1995; Habib et al., 1991; Witelson, 1989; but see Jancke & Steinmetz, 1998). Notwithstanding, our results do correspond well with other work in nonhuman animals. For instance, one study using dogs found that the posterior sections (posterior midbody, isthmus, and splenium in our study) were significantly larger in right-pawed as opposed to left-pawed animals (Aydınlioğlu et al., 2000). Similarly, several studies on mice with callosal agenesis or surgical transection of the CC (resulting in smaller CC measurements) have shown that these mice are overwhelmingly left-pawed (Manhães et al., 2003; Manhães, Schmidt, & Filgueiras, 2005). The explanation for the species differences is not readily apparent, but several hypotheses can be posited. First, the species differences may reflect the manner in which hand preferences are assessed and classified in humans as compared with chimpanzees. Human handedness is typically assessed by questionnaire, and different investigators have used

Table 1
Mean Residual Corpus Callosum (CC) Values for Each Sex and Handedness Group of Chimpanzees

CC region	Male			Female		
	Left-handed	Ambidextrous	Right-handed	Left-handed	Ambidextrous	Right-handed
Rostrum						
<i>M</i>	-2.13	-0.97	0.09	-0.71	1.22	1.14
<i>SE</i>	2.25	1.29	1.43	1.79	1.53	1.08
Genu						
<i>M</i>	-2.27	0.90	-0.35	-2.20	4.12	0.53
<i>SE</i>	5.98	3.44	3.81	4.78	4.06	2.86
Rostrum body						
<i>M</i>	-6.86	-1.15	5.18	-5.22	-4.02	4.00
<i>SE</i>	4.78	2.75	3.04	3.81	3.24	2.29
Anterior midbody						
<i>M</i>	-2.17	-0.09	3.77	-0.60	0.53	0.73
<i>SE</i>	3.68	2.11	2.34	2.93	2.50	1.76
Posterior midbody						
<i>M</i>	-2.41	-1.58	1.72	-3.41	-0.98	1.64
<i>SE</i>	2.46	1.41	1.57	1.96	1.67	1.18
Isthmus						
<i>M</i>	0.10	-1.70	4.13	-2.26	-3.45	-0.52
<i>SE</i>	3.37	1.93	2.14	2.68	2.29	1.61
Splenium						
<i>M</i>	-17.63	0.18	1.32	-2.00	1.61	3.28
<i>SE</i>	6.36	3.65	4.05	5.07	4.31	3.04
Overall CC						
<i>M</i>	-33.72	-3.11	16.54	-14.87	0.64	7.22
<i>SE</i>	18.81	10.80	11.96	14.98	12.76	8.99

different response criteria for classifying subjects as mixed- or non-right-handed. In contrast, chimpanzees' handedness was assessed by observation of only four behaviors, and the classification of right-handed, left-handed, or ambidextrous chimpanzees was based on the average HI values for the four measures. Consistent criteria for the assessment of handedness in human and nonhuman primates are needed to facilitate comparative analyses between studies and between species. Alternatively, humans and chimpanzees may differ with respect to the neural organization of the CC. Unfortunately, presently, there are few data on CC organization with respect to fiber density and distribution in different primate species (but see Broadfield, 2001), but such data would be important for interpreting the differences reported here.

When considering the correlation between mean hand use and regional variation in CC morphology, we found a significant positive relationship between average HI score and CC size. In addition, significant positive correlations were found for two CC regions (rostrum body and posterior midbody). For all regions, as the average HI score increased (indicating a greater degree of right-handedness), so too did the size of the CC, results consistent with other analyses. A significant positive correlation was also found between regional CC size (rostrum body and isthmus) and strength in handedness. When considering the absolute value of the mean HI score, we found that as the absolute HI value increased (indicating a stronger degree of hand preference), the size of the rostrum body and isthmus also increased. When the corresponding analysis of strength of hand preference was completed using a discrete scale (inconsistently handed and consistently handed groups), no significant differences were found. These results suggest that the scale of measurement used to characterize hand

preference can influence the statistical analysis and interpretation of the association between handedness and CC size.

In summary, the results of this study indicate that both direction and strength of handedness are significantly associated with both overall and regional variation in CC size in chimpanzees. We believe this is the first evidence of an association between handedness and CC size in nonhuman primates. Our results suggest that right-handed chimpanzees have a larger CC than left-handed chimpanzees. This pattern of results differs from previous reports in humans, and the origin of these differences remains unclear. We found no evidence of sex differences in CC morphology in chimpanzees, and this finding does not support biological interpreta-

Table 2
Correlation Coefficients Between Handedness Index Scores for the FEED and TUBE Tasks and Each Corpus Callosum (CC) Region in Chimpanzees

CC region	FEED	TUBE	GESTURE	REACH
Rostrum	.024	.048	.097	.134
Genu	-.026	-.032	.026	-.019
Rostrum body	.228	.257*	.327**	.190
Anterior midbody	-.015	.181	.142	.367*
Posterior midbody	.245*	.373**	.112	.133
Isthmus	.290*	.140	.105	-.056
Splenium	-.050	.195	.294*	.091
Overall CC	.168	.207	.227	.130

Note. FEED = bimanual feeding; TUBE = coordinated bimanual actions; GESTURE = manual gestures; REACH = simple reaching.
 * $p < .05$. ** $p < .01$.

tions for gender differences reported in humans. The lack of sex difference in CC morphology in the chimpanzees might alternatively suggest that gender differences seen in modern humans reflect a unique adaptation of the genus *Homo*, as has been suggested by some (Broadfield, 2001).

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