

Handedness in Chimpanzees (*Pan troglodytes*) Is Associated With Asymmetries of the Primary Motor Cortex but Not With Homologous Language Areas

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The neurobiology of hand preferences in nonhuman primates is poorly understood. In this study, the authors report the 1st evidence of an association between hand preference and precentral gyrus morphology in chimpanzees (*Pan troglodytes*). Hand preferences did not significantly correlate with other asymmetric brain regions associated with language functions in humans including the planum temporale and frontal operculum. The overall results suggest that homologous regions of the motor cortex control hand preferences in humans and apes and that these functions evolved independently of left-hemisphere specialization for language and speech.

The study of the neurobiological basis of handedness has a long history in neuroscience. Historically, in humans handedness has been predominantly linked to the presence of neuroanatomical asymmetries associated with language functions. For example, early studies that used the sodium amytal test indicated that 96% of right-handed subjects showed arrest in speech when the left but not right hemisphere was temporarily anesthetized. In contrast, only 70% of left-handed subjects showed speech arrest when the left hemisphere was anesthetized (Rasmussen & Milner, 1977). More recently, studies that used functional magnetic resonance imaging (fMRI) and Doppler sonography have confirmed the previous sodium amytal results showing greater left hemisphere involvement in speech and language tasks in right-handed compared with left-handed individuals (Knecht et al., 2000; Szaflarski et al., 2002). These collective findings are often taken as evidence that handedness and language are related and evolved uniquely in the human brain; however, studies that have focused on the association between handedness and asymmetries in cerebral morphology for language areas such as the planum temporale, pars oper-

cularis, and par triangularis have yielded mixed results (Beaton, 1997; Foundas, Leonard, & Heilman, 1995).

In contrast to the historical focus on the association between handedness and neuroanatomical asymmetries associated with language areas of the brain, recent studies in humans have shown that asymmetries in regions of the primary motor cortex are associated with handedness (Amunts et al., 1996; White, Lucas, Richards, & Purves, 1994). For example, functional imaging studies (i.e., positron-emission tomography and fMRI) have localized single digit movements and thumb–index finger oppositions to a specific region in the dorsal primary motor cortex in the hemisphere contralateral to the active hand (Pizzella, Tecchio, Romani, & Rossini, 1999). Transcranial magnetic stimulation studies indicate that movement thresholds for the fingers are lower in the hemisphere contralateral to the preferred hand, which in most cases is the right hand (Boroojerdi et al., 1999; Triggs, Subramaniam, & Rossi, 1999). Finally, neuroanatomical studies in humans have identified a morphological landmark in the precentral gyrus, referred to as the *knob*, that corresponds to the area where the contralateral hand and fingers are represented on the motor strip (Hlustik, Solodkin, Gullapalli, Noll, & Small, 2001; Maldjian, Gottschalk, Patel, Detre, & Alsop, 1999; Yousry et al., 1997). Collectively, these data suggest that the neurobiological basis for control of the hand and hand preference is localized to the dorsal area of the primary motor cortex and lateralized to the left hemisphere.

The neurobiology and evolution of hand preference in nonhuman primates is poorly understood (Bradshaw & Rogers, 1993). Although neurophysiological correlates of hand preference have been occasionally reported in some monkey species (Nudo, Jenkins, Merzenich, Prejean, & Grenda, 1992), historical attempts to link hand preference to specific regions of the brain in monkeys have not produced reliable results (Ettlinger, 1988; Warren, 1980). The difficulty in linking functional asymmetries associated with hand preference to specific neuroanatomical regions in nonhuman primates has led some to suggest that the mechanisms controlling

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the expression of hand preferences in humans are fundamentally different than those in other primates (Warren, 1980). In addition, the historical lack of evidence for population-level right handedness in nonhuman primates has reinforced the view that different neural systems and mechanisms are involved in the expression of human and nonhuman primate handedness (Corballis, 1992; Warren, 1980). To date, there are no published studies on the neurobiological basis of hand preference in great apes. This is unfortunate because recent studies in captive and, to a lesser extent, wild great apes have shown evidence of population-level right handedness for some motor tasks (Bradshaw & Rogers, 1993; Byrne & Byrne, 1991; Corp & Byrne, 2004; Hopkins & Cantalupo, in press; McGrew & Marchant, 1997; Ward & Hopkins, 1993). Moreover, great apes exhibit population-level left-hemisphere neuroanatomical asymmetries in the inferior frontal gyrus (Cantalupo & Hopkins, 2001), the planum temporale (Gannon, Holloway, Broadfield, & Braun, 1998; Hopkins, Marino, Rilling, & MacGregor, 1998), and the precentral gyrus (Hopkins & Pilcher, 2001). The evidence of population-level right handedness and neuroanatomical asymmetries in homologous language areas as well as primary motor cortex in great apes suggest that the neural basis for hand preference for humans may predate hominoid evolution. However, to date, no studies have directly linked handedness to neuroanatomical asymmetries in nonhuman primates, notably chimpanzees.

In the current study, we report a new set of data on neuroanatomical asymmetries in three cortical regions of chimpanzees including the planum temporale (PT), fronto-orbital (FO) sulcus, and the motor hand area (knob). Previous data have been reported for the PT and the knob in a subset of the subjects in this study (see Hopkins & Pilcher, 2001; Hopkins et al., 1998). Here we report data on a much larger set of subjects, and we restricted our analyses to chimpanzees rather than to a heterogeneous group of ape species.

In addition to providing a descriptive analysis of neuroanatomical asymmetries in a larger sample of apes, in this article we correlate neuroanatomical asymmetries with three measures of handedness including simple reaching, bimanual feeding, and a measure of coordinated bimanual actions. These three behaviors were selected for theoretical and pragmatic reasons. Pragmatically, both magnetic resonance imaging (MRI) scans and behavioral data were available on a reasonable number of subjects for each measure. In addition, the three handedness measures were uncorrelated and had different motor requirements. Simple reaching was the least demanding and required only that the subjects produce a unimanual grasp of a stationary food item. Bimanual feeding was motorically more demanding than was simple reaching because it required independent, manipulative whole actions of the two hands. In addition, bimanual coordination was motorically the most complex because it required coordinated actions of the two hands and the use of a single digit in extracting the food items.

We further selected these three measures of hand use because they have been found to elicit comparable degrees of handedness in different colonies of chimpanzees and show significant test-retest reliability within the same samples of apes (see Hopkins, 1994; Hopkins & Cantalupo, 2003b; Hopkins et al., 2001; Hopkins et al., in press; Hopkins, Hook, Braccini, & Schapiro, 2003; Hopkins, Wesley, Izard, Hook, & Schapiro, 2004). Thus, these three measures have considerable internal and external validity

because they elicit consistent hand preferences at the individual level and generalize across different colonies of chimpanzees.

Method

Subjects

MRIs were collected in a sample of 66 chimpanzees (*Pan troglodytes*) including 37 females and 29 males ranging in age from 8 to 49 years ($M = 22.07$, $SD = 11.63$). All the chimpanzees were members of a captive colony housed at Yerkes National Primate Research Center (YNPRC) in Atlanta, Georgia. Fourteen apes were wild caught, 16 were raised by their conspecific mother, and the remaining 36 were raised by a human. Nineteen of the brains were scanned postmortem, whereas the other 47 subjects were alive and healthy at the time of the scan. For the postmortem brains, ages ranged from 8 to 47 years ($M = 20.20$ years, $SD = 10.88$), and for the in vivo scans ages ranged from 11 to 48 years ($M = 26.60$ years, $SD = 12.34$).

Image Collection and Procedure

Prior to scanning, the subjects were immobilized with ketamine injections (2–6 mg/kg) and were subsequently anesthetized with propofol (10 mg/kg/hr) following standard veterinary procedures used at the YNPRC. The subjects remained sedated for the duration of the scans as well as the time needed for transport between YNPRC and the scanner location (total time approximately 1 hr). After completing the MRI scan, the nonhuman primate subjects were returned to Yerkes and were temporarily housed in a single cage for 6 to 12 hr to allow the effects of the anesthesia to wear off before being returned to their home cage and cage mates.

At the MRI facility, the animals were placed in the scanner chamber and their heads were fitted inside the head coil. The cadaver brains were placed inside the human knee coil with the dorsal side up. Scan duration ranged from 40 to 80 min as a function of brain size. This project involved the use of two MRI machines (Model NT; Phillips, Bothell, WA), each of which with 1.5-Tesla superconducting magnets. For all subjects, T1-weighted images were collected in the axial plane by means of a gradient echo protocol (pulse repetition = 19.0 ms, echo time = 8.5 ms, slice thickness 1.2 mm, slice overlap = .6 mm, number of signals averaged = 8, matrix = 256×256). These scan parameters were based on preliminary studies and provided excellent resolution of the brain areas of interest. The raw images were reformatted into the different planes with ANALYZE multiplanar formatting software (ANALYZE, Lenexa, KS).

Brain Regions of Interest

Neuroanatomical asymmetries were derived from three regions of the brain including the motor hand area referred to as the *knob*, the PT, and a portion of the inferior frontal gyrus containing part of Broca's area. The methods of measurement for some of these brain regions have been described in detail elsewhere (Cantalupo & Hopkins, 2001; Hopkins et al., 1998; Hopkins & Pilcher, 2001), and here we provide a brief description of the areas of interest that were quantified from MRI. By measuring multiple brain regions, we sought to evaluate which regions, if any, best explained individual differences in the hand use of chimpanzees.

Motor hand area (knob). The knob was localized in serial 1-mm slices in the axial plane following procedures previously used in human and ape brain specimens (Hopkins & Pilcher, 2001; Yousry et al., 1997). The horizontal epsilon or inverted omega that projected into the postcentral gyrus was traced on each image (see Figure 1). The dorsal and ventral edges of the knob served as the markers for defining the boundaries of the area. For each slice and hemisphere, an area measurement of the region was calculated through the use of a mouse-driven pointer that traced the omega shaped region of interest. The total areas from all slices in which the

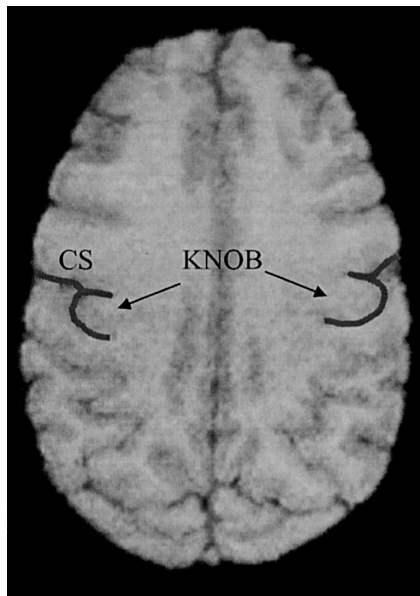


Figure 1. Lines indicate the tracing of the central sulcus (CS) in the axial plane. The horizontal epsilon or inverted omega that projects into the postcentral gyrus was traced on each image. The dorsal and ventral edges of the knob served as the markers for defining the boundaries of the area.

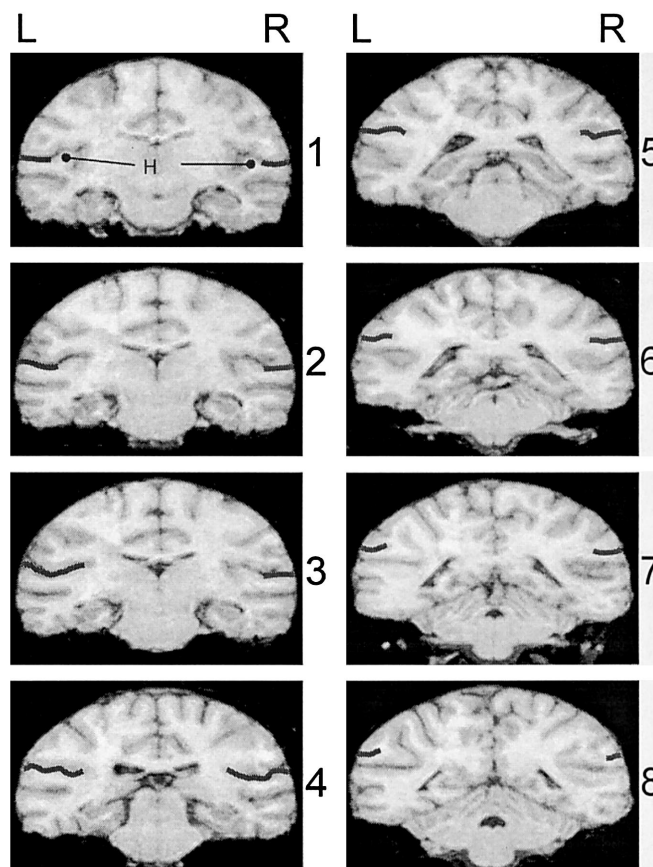
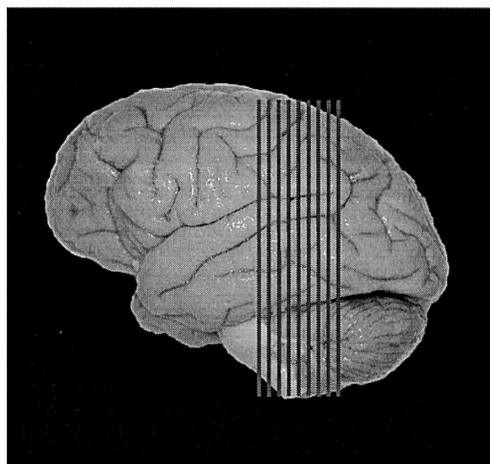


Figure 2. Procedure for tracing of the planum temporale (PT) in serial 1-mm slices in the coronal plane. Lines indicate the measurement of the depth of the sylvian fossa from the lateral portion of the brain to the insular region. H = Heschel's gyrus.

knob was present were summed and used to derive a volume of the knob for each hemisphere (ranging from 5 to 13 slices in the sample).

PT. For the PT, the MRI scans were aligned in the coronal planes and cut into 1-mm slices. The anterior border of PT was defined by the most frontal slice showing Heschl's gyrus (HG). The posterior border was defined by the most caudal slice showing sylvian fissure (SF). Once the anterior and posterior borders were delineated, the depth of SF (i.e., width of PT) on each slice was measured from the superolateral margin of the superior temporal gyrus (Cantalupo, Pilcher, & Hopkins, 2003; see present Figure 2). The respective depths of the SFs were summed across all slices for each hemisphere to derive a total area measure for each hemisphere.

FO. Finally, a portion of the inferior frontal gyrus (IFG) in which part of Broca's area is located was measured by tracing the length of the FO sulcus, a prominent landmark of the opercular portion of the IFG (see Figure 3). FO could be clearly seen in parasagittal (1 mm thick) MRI slices, and its length was traced from the first lateral slice where it was present up to the slice immediately preceding the opening of the insula. Rather than quantify the entire frontal operculum, as has been done previously (Cantalupo & Hopkins, 2001), we focused on FO because there is less variability in this sulcus compared with other borders used to demark the frontal operculum.

Some have suggested that there is too much variability in IFG sulci, particularly in the inferior precentral sulcus (PCI), which comprises the landmarks of the frontal operculum in great apes, to obtain a reliable assessment of asymmetry in this region (Sherwood, Broadfield, Holloway, Gannon, & Hof, 2003). Although variability is observed in the sulci that

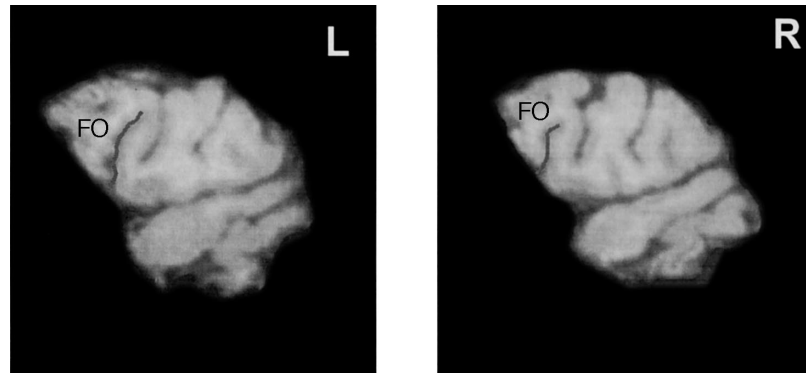


Figure 3. Lines indicate the length of the fronto-orbital (FO) sulcus in the left and right hemispheres in the sagittal plane.

comprise the frontal operculum of apes, we believe consistent criteria can be applied to this region to obtain reliable measurements. Specifically, the majority of cases of PCI bifurcation we have observed in our sample of chimpanzee brains follows a typical pattern in which the posterior ramus of the bifurcation both (a) terminates at a more dorsal level than does the anterior one, and (b) tends to run more horizontally than does the anterior ramus, which in turn runs more vertically and parallel to the central sulcus. It should also be noted that Sherwood and colleagues gave a similar account for the usual pattern of PCI bifurcation in their cadaver specimens. Thus, in our opinion, most instances of PCI bifurcation do not present any serious ambiguity as to the determination of the posterior boundary of the pars opercularis. Because PCI is usually seen as running vertically and roughly parallel to the central sulcus in the common sulcal pattern of the IFG of great apes, and because, in many instances, it is likely that the posterior ramus of a PCI bifurcation is, in fact, the subcentral anterior sulcus joining PCI (as also pointed out by Sherwood and colleagues), one can consistently adopt the criterion of choosing the anterior ramus of a PCI bifurcation as the posterior boundary for the pars opercularis. In fact, this criterion was consistently used in the Cantalupo and Hopkins (2001) report of a population-level leftward asymmetry of the pars opercularis in great apes. Sherwood et al. (2003) also questioned whether the cytoarchitectonic map of the inferior frontal gyrus mapped entirely as Brodmann's area 44 cells or whether other cells were found in this region, notably Brodmann's area 45 and 46 cells. In the Cantalupo and Hopkins (2001) article, we used the map outlined by Bailey, von Bonin, and McCulloch (1950) and, at the time, no new data were available and we welcomed the new data presented by Sherwood et al. Notwithstanding, the evidence of other cell types present in the inferior frontal gyrus does not directly address the methods used to quantify the gross morphology of this brain region and, because we used the same landmarks in the left and right hemispheres, this does not affect the measurement of asymmetry. In addition, FO length is strongly correlated ($r = .627, n = 56, p < .01$) with other measures of Broca's area asymmetry reported elsewhere (Cantalupo & Hopkins, 2001). Moreover, the incidence of FO bifurcation is moderate in both our sample and that of Sherwood et al. (2003; about 11% of specimens). Thus, FO constitutes a reliable estimate of asymmetries of the frontal operculum, as defined by the landmarks used by Cantalupo and Hopkins (2001).

Behavioral Measures

Simple reaching (reach task). Simple reaching was measured by throwing a raisin into the subject's home cage (see Hopkins, Cantalupo, Wesley, Hostetter, & Pilcher, 2002 for description). The subjects had to move to a spot near the food, reach for and pick up the food. Hand use was recorded as right or left. Fifty responses were recorded from each subject. To assure that hand choice on each trial was not influenced by the hand

used on the previous trial (McGrew & Marchant, 1997), subjects had to reposition themselves between trials. All subjects were tested in the outdoor portion of their home cage.

Bimanual feeding (feed task). 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. Once retrieving the food, the subjects typically move to a seating place and consume the food. The chimpanzees typically hold the extra pieces of food with one hand and feed with the opposite hand. Hand use was recorded when the subjects 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. A minimum of 50 responses was obtained from each subject.

Coordinated bimanual actions (tube task). 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 lick the contents completely off with their mouths but must use their fingers to remove the substrate. Experimenters handed the PVC tubes to the subjects in their home cages and used a focal sampling technique to collect individual data from each subject. The hand of the finger the subjects 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.

Data Analysis

For the three brain regions, left-right asymmetries were calculated with the formula $(R - L) \div ([R + L] \times 0.5)$. Positive values indicated right-hemisphere biases and negative values reflected left-hemisphere biases. In terms of classifying subjects' brain asymmetries, individuals with asymmetry quotient (AQ) scores greater than .025 or less than $-.025$ were categorized as left- and right-hemisphere dominant. All other subjects were categorized as exhibiting no bias. The cutoff points for classifying subjects' brain asymmetries were based on previous values used in humans and apes (see Cantalupo et al., 2003).

For the three handedness tasks, binomial z scores were calculated for each subject on the basis of the frequency of left- and right-hand use for all assessments of hand use. Subjects with z scores greater than 1.95 or less than -1.95 were classified as right and left handed. Subjects with z scores between -1.96 and 1.96 were classified as nonpreferent. In addition, a handedness index (HI) was derived for each subject and task by subtracting the number of right-hand responses from the number of left-hand responses

and dividing by the total number of responses, $HI = (R - L) \div (R + L)$. Positive values reflected right-hand preferences and negative values reflected left-hand preferences. All analyses adopted an alpha of $p < .05$ as the level of significance. We conducted post hoc tests, when necessary, using Tukey's honestly significant difference (HSD) with $p < .05$.

Results

Descriptive Statistics

The distribution of left-right brain asymmetries and mean asymmetry coefficients for each brain region are shown in Table 1. To assess population-level asymmetries for each brain area, single-sample t tests were performed on the asymmetry coefficients. Significant leftward asymmetries were found for the PT, $t(60) = 4.82, p < .001$; and for the FO, $t(59) = 3.37, p < .001$; but not for the knob, $t(62) = 0.48, ns$. We compared the AQ scores for each brain region that have been reported previously with the AQ scores that were new to this set of analyses by means of an independent samples t test. No significant differences were found for any of the brain regions.

With respect to the handedness measures, borderline significant population-level right handedness was found for the tube, $t(62) = 1.78, p < .08$; feed, $t(58) = 1.75, p < .09$; and reach tasks, $t(56) = 1.88, p < .07$. For all three measures, the mean HI values were comparable with previously published reports in much larger samples of subjects (Hopkins, 1994; Hopkins et al., 2001, 2002). The mean HI scores for the tube, feed, and reach tasks were .12, .10, and .09, respectively.

We compared males and females on each of the brain regions to assess the effect of sex on brain asymmetry. No significant differences were found, a result that contradicts at least some recent reports in humans (Good et al., 2001). Similarly, because at least one recent study in wild chimpanzees found sex differences in handedness (Corp & Byrne, 2004), we evaluated the effect of sex on the three handedness measures. No significant differences were found.

Handedness and Sex Effects

In this initial analysis, we compared left-, ambiguously, and right-handed subjects for each behavioral measure on each of the three brain regions with analyses of variance (ANOVA). For these analyses, sex and handedness served as between groups factors, whereas the AQ scores from the brain region served as the dependent variable. The mean AQ score for each brain region in left-, ambiguously, and right-handed chimpanzees is shown in Table 2.

Table 1
Asymmetry Quotient (AQ) Scores (Mean and Standard Error)
and Distribution of Asymmetry Classifications for Each Brain
Region

| Brain region | Hand use | | | AQ | |
|-----------------------|----------|-------|---------|----------|-----------|
| | Left | Right | No bias | <i>M</i> | <i>SE</i> |
| Planum temporale | 44 | 9 | 8 | -.122 | .025 |
| Fronto-orbital sulcus | 35 | 22 | 3 | -.146 | .043 |
| Motor hand area | 33 | 25 | 5 | .031 | .065 |

Table 2
Mean Asymmetry Quotient Score (and Standard Error) for Each
Brain Region as a Function of Hand Use

| Task and brain region | Left | | Ambiguous | | Right | |
|--------------------------|----------|-----------|-----------|-----------|----------|-----------|
| | <i>M</i> | <i>SE</i> | <i>M</i> | <i>SE</i> | <i>M</i> | <i>SE</i> |
| Tube | | | | | | |
| PT | -.183 | .02 | .035 | .06 | -.069 | .02 |
| FO | -.240 | .08 | -.059 | .14 | -.109 | .06 |
| Knob | .257 | .11 | -.028 | .20 | -.110 | .09 |
| Feed | | | | | | |
| PT | -.085 | .03 | -.130 | .03 | -.114 | .03 |
| FO | -.157 | .08 | -.198 | .10 | -.166 | .07 |
| Knob | .235 | .12 | .170 | .14 | -.114 | .11 |
| Reach | | | | | | |
| PT | -.143 | .04 | -.118 | .03 | -.091 | .03 |
| FO | -.156 | .11 | -.148 | .07 | -.069 | .07 |
| Knob | .07 | .11 | .10 | .11 | .07 | .12 |

Note. PT = Planum temporale; FO = fronto-orbital; Knob = motor hand area.

Tube. The ANOVA revealed a significant main effect of handedness on the PT, $F(2, 55) = 7.10, p < .01$; and knob, $F(2, 58) = 3.24, p < .05$; but not on the FO. For the PT, left-handed chimpanzees had significantly lower AQ scores than did right-handed subjects but not ambiguously handed subjects. In contrast, for the knob, right-handed subjects had significantly lower AQ scores than did left-handed subjects but not ambiguously handed subjects.

Feed. With respect to the knob, a borderline significant main effect for handedness was found, $F(2, 53) = 2.77, p < .07$. Left-handed subjects had significantly higher AQ scores than did right-handed subjects. No significant main effects or interactions were found for the PT and FO.

Reach. No significant main effects or interactions were found for any of the brain regions.

Correlations Between Handedness and Brain Asymmetry

In the previous analyses, hand preferences were treated as dichotomous variables and analyzed separately on each brain structure of interest. As an alternative approach to analyzing the association between structural asymmetries and handedness, we correlated the AQ scores for each brain region with the HI scores for each behavioral measure of handedness. These results are shown in Table 3. Significant positive correlations were found between the HI scores for the tube task and the PT and FO AQ scores. A significant negative correlation was found between HI scores for the tube and the knob AQ values. No other correlation coefficients were significant.

Association Between Age and Brain Asymmetry

Finally, we correlated the age of the subjects with the AQ scores for each brain region and found no significant associations. We also compared the AQ scores for each brain region in relation to whether the measurements were taken from cadaver brains compared with in vivo scans, and no significant differences were found.

Table 3
Pearson Correlation Coefficients for Each Brain Region With
the Three Measures of Hand Use Task

| Brain region | Task | | |
|--------------|---------|--------|-------|
| | Tube | Feed | Reach |
| PT | .430** | -.131 | .151 |
| FO | .280* | -.061 | .081 |
| Knob | -.328** | -.230† | -.014 |

Note. PT = planum temporale; FO = fronto-orbital sulcus; Knob = motor hand area.

† $p < .10$. * $p < .05$. ** $p < .01$.

Discussion

The results of this study are relatively straightforward. Chimpanzees show population-level left-hemisphere asymmetries in the planum temporale and fronto-orbital sulcus, and these findings are consistent with previously reported findings in apes and humans (Hopkins, Pilcher, & Cantalupo, 2003). In addition, the results of this study indicate that asymmetries in different brain regions are associated with handedness for bimanual coordinated actions in chimpanzees. Specifically, right- and left-handed subjects differed with respect to asymmetries in the planum temporale and the precentral gyrus. As far as we know, this is the first evidence of an association between functional asymmetries associated with hand preference and a specific neuroanatomical substrate in chimpanzees.

With respect to the tube task, the differences between right- and left-handed subjects in relation to the PT and knob can best be characterized as quantitative versus qualitative differences. For the PT, left-handed subjects had lower AQ scores (indicative of left-hemisphere asymmetry) than did right-handed subjects; however, it is important to point out that both left- and right-handed subjects showed left-hemisphere asymmetries. Thus, left- and right-handed subjects differed in the magnitude of the left-hemisphere asymmetry. In contrast, for the knob, the AQ scores were in opposite directions with left-handed subjects showing right-hemisphere asymmetries and right-handed subjects showing left-hemisphere asymmetries. This reflects a qualitative difference in the direction of brain asymmetry in relation to hand use.

Associations between handedness and neuroanatomical asymmetries were evident only for the tube task and not for the feed and reach tasks, although the feed task approached conventional levels of statistical significance and were in the same direction as the tube results. We believe that the most parsimonious explanation for this finding is due to the sensitivity of each handedness measure. The three measures differed significantly in their sensitivity in eliciting individual hand preferences as reflected in the absolute value of the HI scores obtained for each measure and in the proportion of ambiguously handed individuals. Comparisons of the absolute values of the HI scores among the three measures revealed that the tube task ($M = .46$, $SE = .035$), had significantly higher values than did the feed ($M = .37$, $SE = .029$), $t(58) = 1.93$, $p < .05$; and reach tasks ($M = .30$, $SE = .031$), $t(58) = 2.99$, $p < .01$. Higher absolute HI values indicate that subjects are closer to using one hand exclusively (left or right) for the task. Similarly, the percent-

age of individuals that were ambiguously handed for the tube, feed, and reach tasks were 14%, 28%, and 42%, respectively. Thus, the tube task elicited more pronounced hand preferences at the individual level compared with the feed and reach tasks. The greater sensitivity of the tube (and to a lesser extent the feed) task in assessing hand preferences likely reflects its sensitivity to underlying brain asymmetries, and this was manifest in the significant findings found for this measure compared with the others. As has been suggested elsewhere (Hopkins, Hook, et al., 2003), the sensitivity of the tube task for evaluating individual handedness likely is due to the fact that the hands have to work in a coordinated manner to perform the task. The bimanual requirement of the task removes the potential influence of situational factors on hand use to which feed and reach are more prone because they do not require coordinated actions.

The significant association between the knob and handedness for the tube task but not the reach and feed tasks has significant implications for the study of handedness in nonhuman primates. In particular, simple reaching and feeding have historically been and continue to be some of the primary measures of handedness used with nonhuman primates, with the assumption being that hand use for reaching reflects an underlying neurological asymmetry (see Lehman, 1993; Papademetriou, Sheu, & Michel, in press). The goal of many handedness studies is to evaluate whether population-level handedness exists for the species, and most studies have yielded negative results. On the basis of the results of this study feeding and, particularly, simple reaching do not seem to correlate with neuroanatomical asymmetries. This finding raises questions about the usefulness of measuring handedness for simple reaching and inferring something about population-level handedness from this measure in nonhuman primates. Our results suggest that investigators need measures of handedness that elicit strong preferences at the individual level if they hope to link these behaviors with underlying neuroanatomical asymmetries.

The results of this study also raise some questions regarding the link between handedness and neuroanatomical asymmetries in humans. In particular, our results did not find an association between handedness and the classic "language" areas, a result that is consistent with some recent reports with human subjects (e.g., Good et al., 2001) but not others (see Beaton, 1997). Our results are also consistent with recent findings showing an association between handedness and regions of the primary motor cortex (Amunts et al., 1996). One question that arises from our findings is whether different measures of handedness in humans correlate more or less strongly with different brain regions. As far as we know, there are no studies that have directly examined whether some measures are more or less sensitive to predicting variation in brain asymmetries. Typically, only one single measure or one composite measure of handedness is used to correlate with various brain regions. This would be an important question in the context of different theories on the origin of handedness and its alleged link to the emergence of language and speech.

Of course, the present data do not speak to the issue of a causal association between brain and behavioral asymmetries in chimpanzees. Thus, whether chimpanzees are right or left handed because of an inherent asymmetry in the brain remains unclear. The fact that chimpanzees show behavioral asymmetries as early as 30 days of life, such as in grasping duration (Fagot & Bard, 1995), thumb sucking (Hopkins & Bard, 1993), head orientation

during sleep (Hopkins & Bard, 1995), and leading limb locomotion (Hopkins, Bard, & Griner, 1997) all suggest that learning or early rearing effects are unlikely explanations for the adult forms of handedness. What are needed are measures of brain asymmetries in young or neonatal chimpanzees. With the advent of noninvasive imaging techniques, such as MRI, these data should be obtainable in the not too distant future.

The results of this study have a twofold implication for theories addressing the origin of handedness. First, the evidence presented here challenges the long held belief that the neurobiological substrates for handedness are unique to humans. Recent studies in human subjects have also found an association between hand preference and central sulcus morphology (Amunts et al., 1996), and the results in the great apes are remarkably similar. Second, asymmetry in language area homologs (PT and FO) does not predict asymmetry in hand use in chimpanzees. This result is consistent with recent reports that the association between handedness and asymmetry in language-related cortical areas in humans is much less robust than was traditionally assumed (Beaton, 1997; Lieberman, 2003). The fact that both FO and PT show significant leftward asymmetries in chimpanzees that do not correlate with handedness suggests that they might be associated with behavioral asymmetries in perception, cognition, or other motor functions. We believe candidate behaviors would include gestural communication (see Hopkins & Cantalupo, 2003a), oro-facial asymmetries associated with facial expressions (Fernandez-Carriba, Loeches, Morcillo, & Hopkins, 2002), or the perception of species-specific vocalizations. Additional research should shed light on this important line of investigation.

In summary, the collective results of this study indicate that individual variation in the handedness of chimpanzees is associated with variation in primary motor regions of the brain rather than areas typically defined as "language" regions in the human brain. This pattern of results suggests that the neurobiological basis for handedness evolved as early as 5 million years ago and emerged independent of systems associated with language and speech, as some have proposed (see Bradshaw & Rogers, 1993; Corballis, 2002; Rogers & Andrew, 2002).

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