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Handedness for tool use in captive chimpanzees (*Pan troglodytes*): Sex differences, performance, heritability and comparison to the wild

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Abstract

There is continued debate over the factors influencing handedness in captive and wild primates, notably chimpanzees. Previous studies in wild chimpanzees have revealed population-level left handedness for termite fishing. Here we examined hand preferences and performance on a tool use task designed to simulate termite fishing in a sample of 190 captive chimpanzees to evaluate whether patterns of hand use in captive chimpanzees differed from those observed for wild apes. No population-level handedness was found for this task; however, significant sex differences in preference and performance were found, with males showing greater left handedness and poorer performance compared to females. We also found that the hand preferences of offspring were significantly positively correlated with the hand preferences of their mothers. Lastly, older females performed more slowly on the task compared to younger individuals. The overall results neither confirm nor reject previous hypotheses claiming that raising chimpanzees in captivity induces right-handedness, but rather suggest that other factors may account for differences in hand preferences for tool use seen in wild and captive chimpanzees.

Keywords

chimpanzee; *Pan troglodytes*; handedness; sex differences; tool use

In the past 20 years, there has been a plethora of studies on hand preferences and other behavioral manifestations of lateralization in human and nonhuman animals (Bradshaw & Rogers, 1993; Ward & Hopkins, 1993; Hook-Costigan & Rogers, 1997; Rogers & Andrew, 2002; Papademetriou et al., 2005; Hopkins, 2006; Hopkins, 2007). With specific reference to handedness, comparative studies of laterality in nonhuman primates are of interest to scientists because a) it has been claimed that population-level handedness is a uniquely human adaptation (Corballis, 1992; Crow, 2004) and b) some have suggested that handedness is an indirect marker of lateralization for language (Leask & Crow, 2001; Annett, 2002). In support of this latter claim is the finding that left hemisphere lateralization for speech is significantly higher among individuals who self-report being right-handed compared to those who report being left-handed (Rasmussen & Milner, 1977; Knecht et al., 2000; MacNeilage, 2008).

The renewed interest in the study of handedness in nonhuman primates was stimulated by the review article by MacNeilage et al. (1987) who argued that there was some evidence of population-level handedness in nonhuman primates, a view that was at odds with the extant view at that time. Subsequently, handedness data have been reported in a variety of nonhuman primate species, yet there are conflicting opinions as to whether nonhuman primates exhibit population-level handedness. Several review articles on the topic have come to different conclusions (McGrew & Marchant, 1997; Hopkins & Cantalupo, 2005; Papademetriou et al., 2005), but one common theme is that hand preferences in nonhuman primates are influenced by the different cognitive and motor demands of the tasks. In addition, contextual, postural and situational factors can also influence hand preference (MacNeilage et al., 1987; Olson et al., 1990; Lehman, 1993; De Vleeschouwer et al., 1995). Collectively, these findings indicate that the question of handedness in nonhuman primates, as it relates to both the measurement and expression of handedness in humans is a complex issue with no simple answer.

The primary aim of the current study was to address the specific question of whether handedness for tool use differs between captive and wild populations of chimpanzees. There is some disagreement about whether evidence of population-level handedness is specific to captive populations or represents a species-specific trait. McGrew and Marchant (1997) have argued that evidence of population-level handedness is unique to captive populations due to the fact that the apes are being raised in a human, right-handed world. To further support their argument, McGrew and Marchant (1997) point out that there is a lack of evidence of population-level handedness in wild chimpanzees. In contrast, Hopkins and Cantalupo (2005) have argued that there is no evidence that rearing histories of chimpanzees influence their handedness and that there is some evidence of population-level handedness in wild chimpanzees, including measures of tool use. For instance, Lonsdorf and Hopkins (2005) reported population-level left handedness for termite fishing in the Gombe chimpanzees. When combining the data on leaf sponging in wild chimpanzees from Bossou (Biro et al., 2006) and the Tai forest (Boesch, 1991), wild chimpanzees show population-level right-handedness. Lastly, wild chimpanzees from both Mahale and Bossou appear to prefer the right hand for ant-dipping, even though ecological and postural demands of this behavior differ between these two communities (Marchant & McGrew, 2007; Humle & Matsuzawa, in press). Hopkins and Cantalupo (2005) further argue that it is difficult to compare handedness in wild and captive chimpanzees because there are so few tasks or measures that have been systematically assessed across the two populations. Most studies of handedness in wild chimpanzees have focused on tool use, while very few studies in captive apes have measured these types of behaviors.

In the current study, we examined hand preferences and performance for a tool use task that was designed to simulate the termite fishing behaviors seen in wild chimpanzees. As noted above, previous studies in wild chimpanzees from Gombe have reported population-level left handedness for termite fishing (McGrew & Marchant, 1992; McGrew & Marchant, 1996; Lonsdorf & Hopkins, 2005) and we sought to evaluate whether a similar pattern of results was evident in captive chimpanzees. There are several studies on hand use for simulated termite fishing in captive chimpanzees and these data seem to support the results seen in the wild (Steiner, 1990; Morris et al., 1993; Morange, 1994; Hopkins, 1999b; Fletcher & Weghorst, 2005). However, these reports utilized only small samples and did not provide an adequate means of comparing results from the two settings. Here we examined hand preferences for a task requiring the chimpanzees to insert a stick into a small hole in order to gain access to a preferred food substance. If handedness for tool use is influenced by human rearing and modeling, then it was hypothesized that captive chimpanzees should be right-handed for this task. In contrast, if handedness is not influenced by rearing and is consistent across behavioral settings, then it was hypothesized that, like wild chimpanzees, captive chimpanzees would show a significant left hand preference for this task.

A second aim of the current study was to explore other, non-rearing factors that may influence handedness for tool use in chimpanzees including differences in performance across sex and age as well as heritability of handedness for the simulated termite fishing task. First, we examined performance on the tool use task to assess potential sex differences. In the human neuropsychological literature, it is commonly held that females do better than males on tasks that require fine motor skill (Kimura, 1999). Whether nonhuman primates show sex differences in motor skill has not been frequently studied but there is some evidence suggesting that female macaques do better on some fine motor tasks than males (Lacreuse et al., 2005). In wild chimpanzees, Lonsdorf et al. (2004) found that females acquire termite fishing skills at a younger age than males and McGrew (1977) reported that females engage in more object manipulation than males. In the current study, we explicitly tested this hypothesis, based on these reports, that females may perform better on tool use tasks.

Second, we examined the association between hand preference and performance. Although it would seem logical that individuals would prefer to perform a task using the hand that performed with greater efficiency, the evidence for a strong relationship between preference and performance asymmetries in human and nonhuman primates is not that convincing. For example, in humans, correlations between preference and performance are far from perfect suggesting that preference and performance are somewhat dissociable motor processes (Porac & Coren, 1981). In nonhuman primates, performance differences between hands have been reported for grasping in chimpanzees and capuchin monkeys, however these data did not correlate strongly with hand preferences (Hopkins et al., 2002; Hopkins & Russell, 2004; Spinozzi et al., 2004). In macaques, differences in performance on a psychomotor task were also found to be unrelated to preference (Andrews & Rosenblum, 2001).

Lastly, because some of the chimpanzees were related in this study, we assessed the association between offspring and maternal hand preferences for a subset of the sample. Lonsdorf and Hopkins (2005) found a significant positive correlation between maternal and offspring handedness in their study of wild chimpanzees and we sought to assess whether a similar relationship for a comparable handedness task might exist in this sample. Previous studies in captive chimpanzees have reported heritability in hand preference for a non-tool-use task involving the use of coordinated bimanual actions (Hopkins, 1999a; Hopkins et al., 2006) and also for throwing (Hopkins et al., 2005a) and we hypothesized that a similar significant association would be found in this study.

METHODS

Subjects

A total of 190 captive chimpanzees were observed, including 108 females and 82 males. The chimpanzees were housed at two facilities, including the Yerkes National Primate Research Center (YNPRC) of Emory University ($n = 78$) and the Michael E. Keeling Center for Comparative Medicine and Research of The University of Texas M. D. Anderson Cancer Center (UTMDACC) ($n = 112$). Between the two facilities, the chimpanzees ranged in age from 5 to 49 years ($\text{Mean} = 23.32$ years, $\text{s.d.} = 10.13$). Prior to testing, all the chimpanzees had been exposed to a simulated termite fishing tool use task similar to that described in this study. This form of tool use is used as an enrichment device for the apes at both facilities. However, prior to the study, no systematic data on hand use had been collected for this tool use task. Identical materials and procedures were used at the two facilities.

Materials

Although reports of tool and mound specifications for termite fishing in the wild vary greatly from site to site, the most comprehensive report of this behavior to date were made in the

Goualougo Triangle, Republic of Congo (Sanz & Morgan, 2007). Chimpanzees there use stems measuring approximately 43.1 cm (s.d.=12.9cm) in length and 4.5 mm (s.d.=1.33mm) in diameter to probe for termites in both subterranean and elevated nests. The motor and cognitive requirements of termite fishing were simulated using threaded poly-vinyl-chloride PVC pipes (approx. 4 cm in diameter and approx. 20 cm in length) attached to threaded (PVC) bases that were affixed to the subjects' home enclosures at multiple locations approximately 60 to 80 cm above the ground or floor. The pipes were fitted with a disc in one end with a 7 mm hole cut out to greatly reduce the size of the opening available for tool insertion, thus increasing the motor demands of the task. The other end was closed with a removable screw on cap. The pipes were filled with a preferred food substance that would adhere to the tool, such as mustard, yogurt, syrup, or applesauce, before being screwed into the bases. The chimpanzees were provided with flexible, thin 'lollipop' sticks (approx. 11 cm in length and 4 mm in diameter, like those used to make large lollipops), made out of tightly rolled, thin paper. The animals use the lollipop sticks to dip into the small hole of the pipe and retrieve the food (See Fig. 1).

Procedure

Subjects were tested in their home enclosures. Subjects were either sub-divided into smaller social groups in order to reduce competition for each device or multiple devices were made available so that subjects had unimpeded access to the device during data collection. Each PVC pipe was filled with a preferred food substance and then screwed onto a base. After placing the device on the enclosure, each subject was supplied with a tool by either handing it to them directly or by dropping it near them. If the tool became unusable, a new tool was offered to the subject. The experimenter recorded the hand used by the subject (left or right) each time they successfully inserted the tool into the pipe. If the subject changed hands during an attempt, the hand used when the tool was successfully inserted was recorded. Occasionally a subject would insert the stick with one hand and withdraw it with the other. In this circumstance, the hand used to insert the stick was recorded since it is the insertion that requires the most fine motor skill, motor planning, and hand to eye coordination. In addition to hand use, the experimenter recorded the time required to insert the stick into the hole during each attempted probe. Time per dip was measured from the time the subject initiated an attempt to insert the tool with one hand and ended when the chimpanzee successfully inserted the tool, stopped attempting to use the tool, or switched the tool to their mouth or other hand. A minimum of 50 successful tool insertions were recorded for each subject. However, the time per dip included all time when the subject was attempting to insert the tool with a given hand, regardless of whether they were successful during that particular bout. Testing sessions were conducted on separate days for each subject until a minimum of 50 successful responses were obtained from each subject. The number of days of testing needed to obtain 50 responses varied from 1 to 11 (Mean = 2.13 days, s.d. = 1.11).

Data Analysis

Hand preferences were characterized in several ways. First, for each subject and measure, a handedness index was derived following the formula $HI = [(R - L) / (R + L)]$. Positive HI values reflected right hand biases and negative values reflected left hand biases. The absolute value of the handedness score reflected the magnitude of hand preference. Second, based on the total left and right hand frequencies, *z*-scores were used to evaluate whether the hand preferences of individual subjects deviated significantly from chance. This is the procedure most frequently used in the non-human primate literature (see Hopkins, 1999). Subjects with *z*-scores greater than 1.96 or less than - 1.96 were classified as right- and left-handed, respectively. All other subjects were classified as ambiguously-handed. For all analyses, alpha was set at $p < .05$ and all post-hoc tests were conducted using Tukey's Honestly Significance Difference (HSD) test. The average time per successful dip for each hand was calculated using

the following formula: Average Left Time = Total Left Time/Left Frequency and Average Right Time = Total Right Time/ Right Frequency.

RESULTS

Hand Preferences

The distribution of hand preferences are shown in Table 1. Initially, a one sample *t*-test was performed on the HI values and no significant population-level handedness was found. A chi-square goodness-of-fit test comparison also indicated no significant difference in the distribution of hand preferences based on the individual *z*-scores.

We next compared the HI scores as a function of sex and colony using an analysis of covariance. The HI score was the dependent measure while sex (male, female) and colony (YNPRC, UTMDACC) served as the between group variables. Age served as a covariate. A significant main effect for sex was found $F(1,185)=5.11, p < .03$. Males had significantly lower HI values than females (see Fig. 2). Subsequent one sample *t*-tests on the HI values within the male and female groups revealed significant leftward asymmetries for the males $t(81) = -2.368, p < .03$ but not the females $t(108) = 0.107, n.s.$.

Performance Measures

For each subject, the latency to dip for the left and right hands was calculated by averaging the scores across all trials. Overall performance was calculated by averaging the performance of the two hands. We examined the effect of sex and colony on overall performance using an ANCOVA with sex and colony serving as between group factors while age was the covariate. Significant main effects for colony $F(1,185)=49.06, p < .001$ and sex $F(1,185)=9.82, p < .01$ were found. Post-hoc analysis indicated that males (Mean = 7.10 sec) were significantly slower than females (Mean = 6.24 sec) and the YERKES chimpanzees (Mean = 9.12 sec) were significantly slower than the UTMDACC (Mean = 4.90 sec) chimpanzees.

The differences in performance found between the cohorts of chimpanzees likely reflects the duration and experience using the tool use device as this is a relatively new enrichment device for the YERKES apes while this form of enrichment has been in place at the UTMDACC facility for a much longer period of time. Presumably the longer exposure to tool using tasks would have a facilitative effect on performance. Because of the differences in performance between colonies, we were somewhat concerned with the potential problem that male chimpanzees from YERKES were having a disproportionately significant influence on the observed sex difference in performance. To address this issue, we converted the latency values to standardized *z*-scores within the two colonies so that individual performances were normalized within each cohort. Subsequently, we ran the same analyses as previously described, but used the standardized *z*-scores as the dependent measure, rather than the average time per dip. The main effect for sex remained significant $F(1,85)=8.48, p < .001$ with males having higher standardized *z*-scores than females (see Fig. 3).

Hand Preference and Performance

In this analysis, we compared overall and lateralized performance on the tool use task in the chimpanzees as a function of their handedness. For this analysis, a mixed model ANCOVA was performed with hand use (left, right) serving as a repeated measure while hand preference (left, ambiguous, right) was the between group factor. Age served as the covariate. A significant two-way interaction was found between hand use time per dip and hand preference $F(2, 173) = 23.34, p < .001$. Post-hoc analysis indicated that left-handed and ambiguously-handed chimpanzees performed the tool use task significantly faster with their left compared to right

hand. In contrast, right-handed subjects performed the task significantly faster with their right compared to their left hand (see Fig. 4a).

The previous analysis utilized all the available data but arguably, because differences in frequency of hand use may have strongly biased the performance data, we ran the same analysis again but restricted it to those subjects that made at least six or more responses with each hand ($n = 150$). As with the previous analysis, a significant two-way interaction was found between hand use time per dip and hand preference $F(2,143) = 16.95, p < .001$. Post-hoc analysis indicated that left-handed and ambiguously-handed chimpanzees performed the tool use task significantly faster with their left compared to right hand. In contrast, right-handed subjects performed the task significantly faster with their right compared to left hand (see Fig. 4b). Thus, even using a more statistically conservative approach, the pattern of results was similar. Lastly, rather than treat handedness as a between group factor, we used the HI values for each chimpanzee based on their hand preferences and correlated them with the difference in average time per dip scores for the left and right hands. A significant association was found ($r = .380, df = 188, p < .001$). Chimpanzees that more strongly preferred their right hand performed a successful dip more quickly with the right compared to left hand.

Age Effects on Hand Preference and Performance

Age varied considerably in our sample; on the whole, males were significantly younger than females $F(1, 185) = 5.21, p < .03$. Thus, we correlated age with the HI values as well as the standardized time per dip scores to assess whether variation in age was associated with either of these measures. The results are shown in Table 2. Overall, no significant associations were found between age and either the HI or standardized performance values; however, when considering each sex separately, a significant positive association was found between age and the standardized performance values in the females. Older females had increasingly longer times per successful dip compared to younger individuals.

Maternal and Offspring Handedness

Handedness data for both maternal and offspring handedness were available in 56 pairs of individuals. A Pearson product moment correlation between maternal and offspring HI scores was positive and significant ($r = .266, df = 54, p < .05$). More strongly right-handed females had more strongly right-handed offspring. Within the chimpanzee sample, not all females raised their offspring; therefore, we ran separate correlations between offspring and maternal handedness for those offspring who were ($n = 44$) or were not ($n = 12$) raised by their biological mother. The correlation coefficients were comparable (both $r \geq .29$) and did not differ significantly from each other. Lastly, in cases where the females had multiple offspring, the sample could be arguably inflated due to repeated representation of the same individuals. To address this issue, we calculated a mean HI value for all offspring born to a single female and correlated these values with the maternal HI values. Despite the reduced sample size, the correlation coefficient was still positive and significant ($r = .373, df = 27, p < .05$).

Comparison with Previous Studies in Captive and Wild Chimpanzees

As noted above, there are previously published data on hand use for simulated termite fishing tasks in captive chimpanzees ($n = 27$ individuals) (Steiner, 1990; Morange, 1994; Hopkins, 1999b; Fletcher & Weghorst, 2005) as well as data on hand preferences for termite fishing in wild chimpanzees ($n = 53$ animals) (McGrew & Marchant, 1992; McGrew & Marchant, 1996; Lonsdorf & Hopkins, 2005). The frequencies in left and right-hand use were available for all the subjects in the captive and wild samples, allowing individual HI scores to be derived for each individual. Thus, we directly compared our results with the previously published captive data as well as those in wild chimpanzees using an analysis of variance. Sex (male, female) and cohort (this study, previous captive studies, and wild studies) served as between

group factors. No significant main effects or interactions were found from this analysis. Thus, when directly comparing the data from wild chimpanzees with those from our study and those from previous studies in captive chimpanzees, no significant differences in HI values were found. Shown in Table 3 are the mean HI values as well as hand preference distributions from the wild and previous studies in captivity. We also compared these three cohorts on strength of handedness. For this analysis, we took the absolute value of the HI scores. Values ranged from 0 (no hand preference) to 1.0 (complete unilateral hand preference) and compared them between the group. A significant main effect for rearing was found $F(2, 256)=10.53, p < .001$. Post-hoc analysis using Tukey's HSD indicated that wild chimpanzees were more lateralized than the previously reported captive data and the data reported in this study (See Table 3). No significant difference was found between the previous captive results and those reported here.

DISCUSSION

There were six main findings in this study. First, no significant population-level hand preference for tool use was found for this particular tool use task. Second, significant sex differences in hand preference for a tool use task were found in a sample of captive chimpanzees. Third, sex differences were also found in performance on the tool use task with males performing less successfully than females. Fourth, performance differences in hand skill conformed well to hand preference, with chimpanzees having shorter times per dip on the tool task when using their dominant compared to their non-dominant hand. Fifth, older female chimpanzees performed more slowly on the tool use task than younger females. Lastly, maternal and offspring handedness were positively correlated with each other suggesting that hand preferences for tool use may be heritable.

The current study provides important information regarding the factors that may influence handedness for tool use in chimpanzees. First, although no population-level hand preference for tool use was found in this population, there were significant differences in hand use between males and females. This significant, albeit not robust sex difference in handedness was not anticipated and it is unclear why the males appear to be more left-handed than the females. There is no evidence of sex differences in handedness for tool use in wild chimpanzees, though it has been reported that male chimpanzees are significantly more left-handed for bimanual feeding than are females (Corp & Byrne, 2004). There is also evidence in humans that non-right-handedness is more prevalent in males than females (Papadatou-Pastou et al., 2008). Thus, in one sense, the results reported here are consistent with some previous results; however, it should be emphasized that sex differences have not been previously found for other measures within this population of chimpanzees. These measures include simple reaching, coordinated bimanual actions and manual gestures (Hopkins et al., 2004; Hopkins et al., 2005b; Hopkins et al., 2005c). Thus, whether sex differences in handedness are specific to tool use in captive chimpanzees remains unclear.

Among females but not males, older individuals did more poorly on this motor task than younger ones. Relatively little research has been conducted in chimpanzees, and indeed in nonhuman primates on the whole, on age-related changes in motor functions. Age-related changes in motor functions have been reported in rhesus monkeys and some have found sex differences, with aged males performing worse than females (Lacreuse et al., 2005). The pattern of results reported here is the opposite of the pattern reported in rhesus monkeys, suggesting a possible species difference in age-related changes in motor function. However, it should be noted that the male population of chimpanzees in this study was significantly younger (Mean = 21.13 years) than the female population (Mean = 24.66 years). Indeed, there were only 3 males over 40 years of age compared to 14 females. Thus, by virtue of incidentally sampling an older group of females, we may have biased the results toward revealing age-related changes in motor performance in this cohort. Moreover, because the age-related

comparisons are cross-sectional rather than longitudinal, a potential cohort effect cannot be ruled out. In short, the question of potential sex differences in age-related changes in motor skill will require additional analyses.

Using time per dip as a measure of performance on the tool use task, males performed more slowly than females and this finding is consistent with at least some reports of sex differences in wild chimpanzees for the acquisition of tool use (Lonsdorf et al., 2005) and in terms of propensity to manipulate objects (McGrew, 1977). The results are also consistent with previous reports of sex differences in grasping skill between male and female chimpanzees (Hopkins et al., 2002; Hopkins & Russell, 2004); females typically make fewer errors than males, even after adjusting for differences in body size. One possible explanation for the comparatively poor performance by males in this study is that they used a different grasping and foraging strategy with the tool. Specifically, the grip adopted by the chimpanzees in holding the stick varied considerably across subjects. Though we did not record grip type in our data collection, it may be that the males used more of a power grip than the females and therefore used less precise motor actions when inserting the stick into the hole. The use of the power grip may have afforded less execution of the fine motor adjustments needed to guide the 4 mm stick into the 7 mm hole. Alternatively, the males may have made more calculated insertion movements that required more time aligning the stick and the hole than did the females. Thus, they performed more slowly because they invested more effort in correctly inserting the stick into the hole each time.

One consistent finding between our results and those of Lonsdorf and Hopkins (2005) is in heritability of hand use. Both in captive and wild chimpanzees, handedness seems to run in families. In wild chimpanzees, it is difficult to isolate the role of social learning from early rearing or situational effects; however, in captivity, because some apes are human-raised and some are raised by their conspecific mothers, it is possible to isolate social learning from rearing effects. Our results suggest that social learning does not seem to be the main mechanism for the development of handedness. The association between maternal and offspring handedness was comparable between individuals raised with or apart from their biological mothers, suggesting that factors other than human or conspecific rearing, may govern the development of hand use. This pattern of results is also consistent with previous studies reporting no effect of early rearing on heritability of hand preference in captive chimpanzees (Hopkins, 1999a; Hopkins et al., 2001; Hopkins, 2006; Hopkins et al., 2006)

The results from the present study provide important insight into the question of whether rearing has a significant effect on handedness. Given that the human population is strongly right-handed, the lack of population-level handedness in our sample refutes the hypothesis that human rearing has a significant influence on hand preferences for tool use in captive chimpanzees. In addition, the lack of a significant difference in HI values between wild and captive chimpanzees supports the claim that these two categories of animals do not differ in their hand use patterns. One challenge in this type of comparison is that within the captive populations studied by us and by others, there are groups of animals that have been reared differently, including animals that were a) wild caught ($n = 37$), b) captive-born and raised by conspecifics ($n = 96$), and c) captive born and raised by humans ($n = 57$). A comparison of HI values among these three cohorts revealed no significant differences, but the most pronounced left-handed animals were the wild caught individuals ($\text{Mean} = -.187$) compared to the conspecific- ($\text{Mean} = -.028$) and human-reared individuals ($\text{Mean} = -.058$). Indeed, the mean HI values for the wild caught chimpanzees is similar to the value reported by Lonsdorf and Hopkins (2005) in wild chimpanzees ($\text{Mean} = -.188$). Thus, when comparing the wild chimpanzee data with data from individuals with the most comparable early rearing experiences (wild caught), the differences are minimal. It is critical to point out that age is confounded with the aforementioned rearing variable. The United States stopped importing

wild chimpanzees in 1973, thus the oldest chimpanzees in our sample are, in large part, wild caught individuals. It could be argued that the oldest cohort in our sample, rather than the wild caught individuals per se, are the chimpanzees whose hand use patterns most resemble the results from the wild. However, given that no relationship was found between HI and age in our sample, it is more likely that rearing rather than age explains this finding.

A word of caution is warranted in comparing the handedness results on tool use in captive and wild chimpanzees. We are assuming that the task used in this study simulates the perceptual, cognitive and motor demands of termite fishing in wild chimpanzees. Termite fishing has large sensory and haptic components, since the chimpanzees must feel when the stick has accumulated a sufficient number of termites before extracting it from the mound and then take care not to lose termites by bumping the stick during extraction. The level of haptic discrimination needed for the task used in the present study may not adequately simulate that of termite fishing since unlike in actual termite fishing, in the simulated task only the insertion requires a great deal of fine motor skill and the success rate of actually extracting reward is quite high once the tool is inside the device. This difference in haptic and sensory requirements during insertion and extraction may influence how the subjects use their hands.

In addition, the extent to which termite-fishing elicits hand preference in wild chimpanzees differs from the extent to which the current task elicited handedness in captive chimpanzees (see Table 3). For example, in wild chimpanzees, 50% of individuals that termite fish show exclusive hand use (McGrew & Marchant, 1997) whereas only 8% of our sample showed exclusive hand use for this tool use task. Thus, termite fishing seems to elicit strong preferences at the individual level in wild chimpanzees whereas the task used here and in other captive populations did less so in captive chimpanzees. The basis for this difference is not clear and could be related to differences in experience or learning. Alternatively, it may reflect differences in the sensitivity of the task to induce behavioral asymmetries.

Strength of handedness may also explain, in part, the difference in overall handedness in our sample compared to wild chimpanzees. Though not significant, our chimpanzees showed a trend toward population-level left handedness but they also do not show pronounced individual hand preferences for our task. In contrast, wild chimpanzees show population-level left handedness and are also highly lateralized for the task. Thus, if a simulated termite fishing task in captivity elicited the same degree of hand preference as seen in wild chimpanzees, comparable results might be evident. Indeed, when we restrict our analysis of the hand preference data to those chimpanzees that had ABS-HI values equal to or greater than the average ABS-HI value reported for wild chimpanzees ($N = 53$), the mean HI was $-.161$, a value not all that different from the reported average HI for wild chimpanzees (see Table 3). Clearly more research in both captive and wild chimpanzees is needed to explore the various variables and parameters of tool use and their relation with handedness.

In summary, the results presented here indicate that rearing chimpanzees in a captive environment appears to have little effect on handedness for tool use. In contrast, sex does seem to influence hand preference and performance, with males being more left-handed and performing less proficiently than females. These differences, though significant, are not extremely robust. Similarly, maternal handedness also appears to influence the handedness of the offspring, although again, not exceptionally strongly. In our view, continued study of behaviors that elicit strong hand preferences at the individual level in both captive and wild chimpanzees are needed to shed further light on the factors that influence the expression of handedness in chimpanzees and other primates.

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Figure 1.
Picture of a chimpanzee using the simulated termite fishing device.

Figure 2.
Mean HI values ($\pm$ s.e.) for male and female chimpanzees in each colony of chimpanzees.

Figure 3.
Mean standardized z-scores on the latencies measures as a function of sex and colony.

Figure 4. Mean latency in performance ($\pm$ s.e.) by the left and right hands for left-, ambiguously- and right-handed chimpanzees.

Table 1

Distribution of Hand Preference and Mean HI Values for Male and Female Chimpanzees

	#L	#A	#R	Mean HI	s.e.	t
Males	34	25	23	-.141	.059	-2.368*
Females	40	27	41	.005	.055	0.107
Overall	74	52	63	-.057	.040	-.1416

*
p < .03

Table 2

Correlation Coefficients Between Age, Handedness and Standardized Performance Scores

	Age + HI	Age + Performance Z-Score
Overall	-.112	.100
Females	-.135	.200*
Males	-.127	-.051

* indicates $p < .05$

Mean HI Scores and Hand Preference Distributions for Results from this Study Compared to Previous Studies in Captive and Wild Chimpanzees

Table 3

	#L	#A	#R	Mean HI	Mean ABS-HI
Wild	30	7	16	-.215 (.084)	.694 (.044)
Previous Captive	16	4	8	-.177 (.132)	.480 (.069)
This study	74	52	64	-.073 (.084)	.467 (.024)

See text for reference to the data sets making up each cohort.