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Publication Details
Journal of Human Evolution

Repository Citation

Hopkins, W. D., Phillips, K. A., Bania, A., Calcutt, S. E., Gardner, M., Russell, J., Schaeffer, J., ... Schapiro, S. J. (2011). Hand preferences for coordinated bimanual actions in 777 great apes: Implications for the evolution of handedness in Hominins. *Journal of Human Evolution, 60*(5), 605-611. doi: 10.1016/j.jhevol.2010.12.008

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J Hum Evol. Author manuscript; available in PMC 2012 May 1.

Published in final edited form as:
J Hum Evol. 2011 May ; 60(5): 605–611. doi:10.1016/j.jhevol.2010.12.008.

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Hand Preferences for Coordinated Bimanual Actions in 777 Great Apes: Implications for the Evolution of Handedness in Hominins

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Abstract

Whether or not nonhuman primates exhibit population-level handedness remains a topic of considerable scientific debate. Here, we examined handedness for coordinated bimanual actions in a sample of 777 great apes including chimpanzees, bonobos, gorillas, and orangutans. We found population-level right-handedness in chimpanzees, bonobos and gorillas, but left-handedness in orangutans. Directional biases in handedness were consistent across independent samples of apes within each genus. We suggest that, contrary to previous claims, population-level handedness is evident in great apes but differs among species as a result of ecological adaptations associated with posture and locomotion. We further suggest that historical views of nonhuman primate handedness have been too anthropocentric, and we advocate for a larger evolutionary framework for the consideration of handedness and other aspects of hemispheric specialization among primates.

Keywords

Great apes; handedness; asymmetry; laterality; language evolution

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Introduction

A universal trait of the human species is population-level right-handedness (see also Perelle et al., 1981; Perelle and Ehrman, 1994;Raymond et al., 1996;Raymond and Pontier, 2004). Though there are cultural differences in the percentage of left-handedness in every human culture studied to date, a significant majority of individuals prefer to use the right hand for motor actions (Porac and Coren, 1981). Archeological evidence dates the existence of population-level handedness to at least 2 Ma(Cashmore, 2009; Uomini, 2009). Furthermore, handedness is associated with hemispheric specialization for language: 96% of self-reported right-handed individuals show left hemisphere dominance for language, whereas only 70% of left-handed individuals show the same left hemisphere dominance (Rasmussen and Milner, 1977; Knecht et al., 2000). The association between lateralization for handedness and language lateralization, though not terribly strong, has led many to hypothesize that the evolution of language and right-handedness are linked in fundamental ways (Corballis, 1992, 2002;Annett, 2002;McManus, 2002).

Many historical as well as some contemporary views of behavioral lateralization, including handedness, have claimed that population-level asymmetries are uniquely human (Corballis, 1992; Crow, 2004). Specifically, it has been well documented that individual animals may show limb or hand preferences for certain tasks (Warren, 1980; Lehman, 1993;), but the extent to which a significant majority show the same preference for a given task has been the topic of significant debate, particularly within the past 20 years (MacNeilage et al., 1987; Marchant and McGrew, 1991; McGrew and Marchant, 1997; Hopkins, 1999; Palmer, 2002; Hopkins and Cantalupo, 2005; Papademetriou et al., 2005; Cashmore et al., 2008; Cashmore, 2009; Uomini, 2009). Recent studies in a variety of vertebrate species have documented evidence of population-level behavioral asymmetries (Rogers and Andrew, 2002; Vallortigara and Rogers, 2005). For example, we now know that chicks and several bird species show significant eye preference asymmetries during visual discrimination for different classes of visual stimuli (Andrew, 1991; Andrew et al., 2000). Several species of toad prefer to right themselves when lying upside down in water by turning rightward (Bisazza et al., 1996). Studies in these so-called lower vertebrates clearly challenge the historical and contemporary views of the uniqueness of hemispheric specialization to humans. However, the issue of non-human primate handedness and population-level asymmetry continues to be a point of considerable contention and debate (Tommasi, 2009).

The first aim of this study was to assess handedness in four great ape species. Hopkins and colleagues(2003) previously examined hand preferences or a task requiring coordinated bimanual actions, referred to as the TUBE task, in a sample of chimpanzees (*Pan troglodytes*), gorillas (*Gorilla gorilla*) and orangutans (*Pongo pygmaeus*) and reported population-level right handedness for chimpanzees and left-handedness for orangutans(Rogers and Kaplan, 1995). Gorillas showed a non-significant trend toward right-handedness. In theirstudy, the sample sizes for the gorillas (n = 30) and orangutans (n = 19) were relatively small and therefore the lack of population-level handedness in gorillas could be attributable tolow statistical power, though admittedly the orangutans showed a population-bias with an even smaller sample. Furthermore, the population-level left handedness found in orangutans was unexpected because they deviated directionally from the two other great ape species, but sampling bias could not be ruled out as an explanation for the results in this species. Thus, in this study, we evaluated whether or not the previously reported left-hand bias in orangutans and the lack of population-level handedness in gorillas were spurious results by measuring a new, independent sample of gorillas and orangutans. We compared the data from the new cohort with the previous findings reported by Hopkins et al. (2003) to assess consistency in directional biases in handedness in great apes between samples.

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In addition to expanding the previous study on handedness in great apes, the second aim of this study was to include data from bonobos for comparison to the other great apes. There have been relatively few studies of handedness in bonobos compared to other great apes (Hopkins and De Waal, 1995; Shafer, 1997; Harrison and Nystrom, 2008), and recent reports of hand preference in bonobos using the TUBE task have failed to detect population-level biases in this species (Chapelain and Hogervorst, 2009; Chapelain et al., in press). Thus, we aimed to obtain a new set of handedness data for comparison to these recent reports. The inclusion of the bonobo data allows for a more comprehensive assessment of handedness in hominid apes and potentially provides data that would speak to ecological or social factors that might influence the expression of handedness in great apes and thereby contribute to our understanding of the evolutionary history of manual lateralization in great apes.

Lastly, even though published data on individual handedness for the TUBE task in chimpanzees are quite large in comparison to other great apes (n> 450 individuals), in this study we report additional data on the TUBE task in a new cohort of chimpanzees. The collection of the additional chimpanzee data served two purposes. First, it provided a novel set of data for comparison to the handedness data from the other great apes. Second, the new data from chimpanzees allowed us to assess the consistency of handedness in chimpanzees from different captive settings. Despite data to the contrary, some researchers argue that handedness assessments in monkeys and apes is unreliable, inconsistent across settings, and potentially influenced by observer bias (Crow, 2004; Cashmore et al., 2008; Cashmore, 2009; Uomini, 2009). With the inclusion of data from this study, there are now handedness data for the TUBE task in 4 different samples of captive chimpanzees residing in different US laboratories including, a) the Yerkes National Primate Research Center (n = 207); b) the Alamogordo Primate Facility (n = 144); c) the University of Texas M. D. Anderson Center (n = 125); and d) the Primate Foundation of Arizona (n = 52). This later data setrepresents the novel data in this report, along with a small sample of chimpanzees housed at the Honolulu Zoo (n = 9). In a separate analysis, we compared the handedness of chimpanzees from these 4 different cohorts as a means of assessing consistency in handedness across settings in chimpanzees. If handedness is inconsistent and unreliable, as suggested by some, then significant differences in handedness should be found between these different cohorts.

Materials and methods

Subjects

In total, handedness data were collected in 774 great apes including 536 chimpanzees, 76 gorillas, 118 bonobos and 47 orangutans. Within this total sample, there were two cohorts, including those apes previously studied (n = 581) and those apes that were new to this study (n = 193). Listed in Table 1 are the age and sex composition of the total sample as well as whether they represent the new or old cohort of subjects. In this study, new data are being presented on 28 orangutans (*Pongo pygmaeus;* 19 males, 9 females), 45 gorillas (*Gorilla gorilla;* 23 males, 22 females), 83 chimpanzees (*Pan troglodytes;*41 males, 42 females) and 41 bonobos (*Pan paniscus;*19 males, 21 females). The great apes of this study reside at zoological gardens or research facilities located in North America. Specifically, handedness data for the orangutans were obtained from individuals housed at the National Zoo, Cleveland Zoo, Columbus Zoo, Honolulu Zoo, Toledo Zoo and Great Ape Trust of Iowa. The gorilla data were obtained from individuals housed at the National Zoo, Milwaukee County Zoo, Lincoln Park Zoo, Columbus Zoo and Jacksonville Zoo. Bonobo handedness data for this study were obtained from apes housed at the Jacksonville Zoo, Columbus Zoo, Milwaukee County Zoo and Great Ape Trust of Iowa. Lastly, data for most of the chimpanzees were obtained from individuals originally housed at the Primate Foundation of Arizona (PFA) that recently relocated to the University of Texas M.D. Anderson Cancer

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Center (BASTROP). A small set of handedness data were obtained from the chimpanzees housed at the Honolulu Zoo and from other chimpanzees at the University of Texas M.D. Anderson Cancer Center. Data from all of the apes were obtained only after administrative approval in the care and use of animals was obtained at each institution.

Procedures

Following procedures described elsewhere, handedness was assessed for a task measuring coordinated bimanual actions referred to as the TUBE task (Hopkins, 1995). We selected this measure because previous studies in chimpanzees have linked variation on this task with neuroanatomical asymmetries in the motor-hand area of the precentral gyrus (Hopkins and Cantalupo, 2004; Dadda et al., 2006), which some speculateis the neural substrate for handedness in humans (Hammond, 2002). Moreover, hand preference for the TUBE task has been shown to be reliable and consistent during test-retest assessments separated by as long as 6 years (Hopkins et al., 2001). Lastly, because the TUBE task requires coordinated bimanual actions, individual hand preferences are less subject to situational factors, such as food position, that can influence hand use during unimanual tasks (see Lehman, 1993 for review).

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 that the subjects cannot lick the contents completely off with their mouths but rather must use one hand to hold the tube and the other hand to remove the substrate (see Figure 1). The hand of the finger used to extract the peanut butter was recorded as either right or left by the experimenter. Each subject was tested on at least two,and as many as four, occasions so that a minimum of 30 responses were obtained from each subject. As much as possible, the subjects were tested while temporarily separated from other members of their social group; however, when this was not possible, the apes were tested in groups ranging from 2 to 9 individuals. If tested in a group, all members of the group were provided with tubes in order to minimize competition for the food. Focal sampling in the frequency of hand use was collected on the subject of interest during these tests. Individual hand preferences were classified on the basis of *z*-scores computed on the frequency of right and left hand use for the TUBE task. Subjects with *z*-scores of 1.96 or higher were classified as right-handed whereas subjects with *z*-scores < 1.96 were classified as left-handed. All other subjects were classified as ambiguously-handed. In addition, we computed a handedness index score (HI) for each subject following the formula [$HI = (R - L)/(R+L)$] where R and L reflect the frequency in left and right hand use. Positive HI values reflected right hand preferences while negative values indicated left hand preferences.

Results

Descriptive data

In the initial analysis, we compared the HI between each species and cohort using an analysis of variance. A significant main effect for species was found $F_{(3, 769)} = 6.721$, $p<0.001$ (correct subsequent) . The mean HIscores for each species and cohort can be seen in Figure 2. Post-hoc analysis using Tukey's HSD indicated that orangutans had significantly lower HI scores than chimpanzees and gorillas but not bonobos. Gorillas had significantly higher HI scores than all other species. No other significant differences were found. We also performed one-sample *t*-tests on the HIscores within each species. Chimpanzees $t_{(534)}=5.35$, $p<0.001$ and gorillas $t_{(75)} = 3.27$, $p<0.01$ both showed significant population-level right handedness whereas orangutans $t_{(46)} = -2.88$, $p<0.04$ showed significant left handedness. Bonobos failed to show population-level handedness $t_{(117)}=0.791$, n.s.

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We next considered species differences in handedness based on the hand preference classification data. A chi-square test of independence revealed a significant association between species and handedness X^2=(6, n = 774) = 31.88, $p<0.001$. The distribution of handedness for each species is shown in Table 2. We subsequently compared the number of right- and left-handed apes within each species using a chi-square goodness-of-fit test. There were significantly more right- than left-handed chimpanzees X^2=(1, N = 421) = 29.27, $p<0.001$ and gorillas X^2=(1, N = 58) = 9.93, $p<0.002$ and significant more left-compared to right-handed orangutans X^2=(1, N = 35) = 10.31, $p<0.005$. There was no significant difference in the number of right- and left-handed bonobos. Thus, analysis of the classification data based on *z*-scores confirmed the previous findings based on the HI scores.

Age and sex differences within each species

We next considered the potential influence of age and sex on handedness within each species. The effect of sex and age on handedness was analyzed separately for each species because of both differences in the sample sizes between the species and the fact that significant differences in directional biases in handedness were evident between species. To increase statistical power within each species for this analysis, we combined the juvenile and adolescent age groups into a single group (sub-adult) for comparison to the adult subjects. For the gorillas, chimpanzees and orangutans, neither age, sex nor the interaction between these variables were significant. However, a significant main effect for age was found in the bonobos $F_{(1,114)}=4.663$, $p<0.01$. The mean HI scores were significantly higher in adults compared to sub-adult individuals. The mean HI scores for each age group and species are shown in Figure 3. Because significant age effects were found for the bonobos, we re-ran the one sample *t*-tests on all 4 species to assess whether population-level handedness was evident when considering only the adult apes. Gorillas $t_{(39)} = 3.89$, $p< 0.001$ and chimpanzees $t_{(323)}=4.63$, $p< 0.001$ both showed significant population-level right handedness while the adult orangutans showed population-level left handedness$t_{(26)}=-2.35$, $p< 0.05$. The bonobos showed a borderline trend toward population-level right handedness $t_{(51)}=1.93$, $p< 0.06$.

Consistency in handedness across settings in chimpanzees

We next analyzed the consistency in handedness among the different chimpanzee samples by comparing the mean HI scores collected from 4 cohorts including chimpanzees from the Yerkes National Primate Research Center (YERKES), University of Texas M.D. Anderson Cancer Center (BASTROP), Alamogordo Primate Foundation (APF) and Primate foundation of Arizona (PFA) (see Figure 4). There was no significant difference in HI scores between the four chimpanzee samples. One sample *t*-tests within each sample revealed significant population-level right handedness for each cohort. For comparison, we have also provided the mean HI scores for a sample of 114 chimpanzees housed in Mona Centre de Recuperacio de Primates sanctuary in Spain and Chimfunshi (MONA), located in Chingola, Zambia, that were tested on the TUBE task by Llorente et al. (2010) (see Figure 4). The results reported by Llorente et al. are also consistent with the data reported in captive apes living in laboratories within the USA.

Discussion

The results of this study are relatively straightforward. For coordinated bimanual actions, species differences in handedness are evident among great apespecies. These results apply across independent samples of apes,suggesting that the results are repeatable. Second, within great ape species, little evidence of sex differences in handedness were found, but age proved to be an important factor, particularly in bonobos and to a lesser extent in gorillas.

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Lastly, in chimpanzees, there was absolutely no evidence that different settings influence the expression of handedness.

With respect to the species difference in handedness, adult chimpanzees, and gorillas showed population-level right handedness, whereas orangutans showed left handedness. Bonobos showed a borderline significant trend toward population-level right handedness. With the exception of gorillas, these results are largely consistent with previous reports on bonobos, chimpanzees and orangutans(Chapelain et al., in press). Gorillas analyzed by Hopkins et al. (2003) failed to show population-level handedness, but this is likely a consequence ofa limited number of subjects. The inclusion of 46 additional gorillas in this study provided for a large enough sample to detect population-level handedness in this species. Thus, the lack of population-level handedness in the gorillas studied by Hopkins et al. (2003) was probably an artifact of the small sample size and this observation reinforces previous arguments that the lack of evidence for population-level handedness in many studies in captive and wild apes may reflect the relatively small sample sizes in these reports (Hopkins, 2006). In fact, the Cohen's d effect sizes for the gorilla, orangutan and chimpanzee handedness values based on the one sample *t*-tests in this sample were 0.358, 0.386 and 0.217, respectively. These are considered small to moderate effect sizes and this observation supports the notion that relatively large sample sizes are needed in nonhuman primate samples to detect population-level handedness, even under ideal experimental and observational conditions.

The species differences in handedness among great apes reported here also directly challenge claims that raising apes in captivity in a human right-handed environment induces right-handedness in these species(McGrew and Marchant, 1997; Cashmore et al., 2008; Cashmore, 2009; Uomini, 2009). Specifically, many of the apes in this study were captive born and this was true among all 4 great ape species. For instance, when we compared the proportion of individuals who were captive or wild born in orangutans, gorillas, chimpanzees and bonobos, the percentage of captive born apes were 90%, 73%, 80% and 45%, respectively. Thus, the highest proportion of captive born individuals was within the orangutan sample but they were theleast right-handed of all the apes. Assuming that the same human rearing forces are determining handedness in all captive apes, then there is no reason to predict or find species differences in captive great apes. In short, if population-level right handedness in great apes was simply and uniformly determined by human rearing, then all captive born apes should be right-handed, which is not what was found in this study.

Why great apes differ with respect to their directional biases in handedness is unclear, but we offer three possible explanations. First, inherent differences in positional behavior and patterns of locomotion differ in these species, with orangutans being the most arboreal of the apes and gorillas the most terrestrial. Bonobos and chimpanzees are both terrestrial and arboreal, and therefore represent a somewhat intermediate pattern. MacNeilage et al. (1987) proposed the postural origins (PO) theory of handedness. The PO theory proposes that more arboreal species show left-handedness due to postural support principally being performed by the right arm and side of the body. According to the PO theory, with the evolution of more terrestrial lifestyles, the left hand subsequently became the subordinate hand, which allowed the right hand to serve the function of manipulation. The results reported here are entirely consistent with the predictions of the PO hypothesis. Specifically, the most terrestrial species of the great ape is the gorilla and they showed the most robust expression of right-handedness compared to the chimpanzees, bonobos and orangutans.

Alternatively, it may be that great apes divide the roles of the subordinate and dominant hand differently and this manifests itself in how they interact and perform the TUBE task.

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Chimpanzees, bonobos and gorillas all could assign the subordinate role of holding the PVC pipe to the left hand and actively manipulate the food with the right hand, whereas the orangutans engage in the opposite role assignment. Of course, this explanation begs the question as to why the orangutans would assign different roles to the hands and this is entirely unclear. Lastly, it could be argued that population-level right handedness for coordinated bimanual actions is a recent evolutionary event that occurred after gorillas and chimpanzees split from the orangutans. Thus, the antecedents to human right handedness developed in African apes, after they split from the common ancestor with orangutans.

At least one of the more interesting patterns to emerge from these data is the ratio ofright-to-left handedness (or left-to-right handedness in the orangutans) within each species (see Table 2). Specifically, if we focus on the results from adults in each species, there are roughly twice as many individuals who show the dominant to non-dominant hand preference, with the exception of gorillas which had a slightly higher ratio (3.28:1). These ratiosare far lower than the typically reported 8:1 or 9:1 for humans. Some of these differences likely reflect measurement variability between humans and nonhuman primates. Notably, most studies of handedness in humans use questionnaire data with ordinal scales of measurement which do not translate well when comparing the measurement and quantification of nonhuman primate handedness. However, other factors that may account for these differences remain unclear,although morphological, genetic, sociological and cultural factors have all been proposed. For example, Hopkins (2006) has argued that the 2:1 ratio in right-to-left handedness observed in chimpanzees may reflect the inherent biological and genetic basis for manual asymmetries in humans and great apes; however, in human evolution after the split from the common ancestor with chimpanzees, there has been increasing selection for cultural influences on hand use and this has resulted in an even greater expression of right-handedness in modern humans compared to great apes. Support for this view comes from the observation that heritability in hand preferences in chimpanzees and humans are quite similar based on family studies. That is to say, there is a significantly higher proportion of right-handed offspring born to two right-handed parents compared to two left-handed or mixed-handed parents in both humans and chimpanzees. Nonetheless, humans show a higher proportion of right-handedness among all parental pairings which is likely attributable to cultural influences.

Likewise, Hopkins (2004) has argued that inherent species differences in early social experiences, such as maternal cradling biases, may explain phylogenetic variation in handedness, For instance, species differences in maternal cradling biases have been reported in great apes (Manning et al., 1994) with orangutans tending to hold their offspring on the right side whereas gorillas and chimpanzees prefer to cradle on the left side. In chimpanzees, it has been reported that cradling preferences of the female are inversely related to the hand preferences of the offspring (Hopkins et al., 1993). Thus, females who cradle their offspring on the left side tend to have right-handed offspring and vice versa. If the association between individual differences in maternal cradling biases and offspring handedness similarly applies to phylogenetic variation in handedness, then the results reported here are consistent with the alleged differences in maternal cradling biases reported in great apes. Clearly, further research on this topic is warranted in order to determine which, if any, of these factors playsan important role in the evolution and development of handedness(Hopkins, 2004, 2006).

Even in the face of evidence of population-level right handedness in great apes, the fact that the ratio of dominant to non-dominant individuals is lower in apes compared to humans, suggeststo some that there are qualitative differences in handedness between human and nonhuman primates. Indeed, Cashmore (2009) has suggested that the word “population-level” handedness be restricted to those populations in which 90% or more of the individuals

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exhibit the same hand preference, which she considers to be uniquely human. We disagree with this view for several reasons. First, the fact that cultural factors influence handedness in modern humans suggests that handedness is a somewhat malleable trait and, in fact, many non-traditional westernized societies do not show 90% or higher levels of right-handedness. Second, this is a highly anthropocentric claim and has a *scalanaturae* perspective that is counterintuitive to evolutionary theory. It suggests that the standard for defining handedness is the human pattern and that all other species must conform to their pattern of expression for any evolutionary homologies to be drawn, and leaves no room for the possibility that natural selection may act to influence handedness differently from one species to another based on a myriad of factors. We are in no way suggesting that the expression of handedness in great apes is the “same” as in humans based on the results of this study. Instead, we are suggesting that apes do show population-level handedness but that the magnitude of expression is lower than that reported in humans and handedness varies in direction between ape species. To us, this raises the interesting question about the role of specific human adaptations that may have played an important role in shaping human handedness, such as tool use, bipedalism or spoken language, to name just a few theories that have been advanced (Bradshaw and Rogers, 1993; Steele and Uomini, 2009; Braccini et al., 2010).

Another significant finding from this study was the consistency in handedness between the different samples of chimpanzees (see Figure 4). Though there were differences in the magnitude of handedness between the different cohorts, none were statistically significant from each other and in every population, a small but significant degree of right-handedness was found in the chimpanzees. If one combines all the published data on the TUBE task in the literature, hand preference data are now available in more than 600 chimpanzees and this, without doubt, constitutes the single largest sample of handedness data in nonhuman primates. We believe the data unequivocally demonstrate evidence of population-level right handedness in captive chimpanzees for coordinated bimanual actions and suggest that it may representa species-specific trait. We certainly recognize that these data do not directly address the issue of potential differences in handedness between captive and wild chimpanzees, for which additional data are clearly needed but the consistency of results between captive housed apes and sanctuary living individuals suggests that rearing effects are negligible. There is also a growing body of evidence suggesting population-level handedness in wild chimpanzees for such actions as termite fishing, ant-dipping, leaf sponging and some aspects of pestle-pounding (Boesch, 1991;Biro et al., 2003,2006; ; Lonsdorf and Hopkins, 2005;Hopkins, 2006,2007a;Humle and Matsuzawa, 2009;Marchant and McGrew, 2007). One significant and persistent limitation in the comparison in handedness findings between captive and wild apes is the fact that the measures differ substantially between settings. Studies in wild chimpanzees have focused on tool use,whereas captive studies have focused on other dimensions of behavior, and we believe it is difficult to make comparisons between wild and captive apes for this reason. Until the issue of measurement gets resolved, there will continue to be problems in the interpretation of handedness results between wild and captive chimpanzees.

Interestingly, in cases where common measures have been reported in captive and wild apes, some similar results have emerged. For instance, there are reports of population-level right-handedness for bimanual feeding in wild gorillas and chimpanzees (to a lesser extent) (Byrne and Byrne, 1991; Marchant and McGrew, 1991; Corp and Byrne, 2004)and this has similarly been reported in captive gorillas and chimpanzees(Hopkins, 1994; Meguerditchian et al., 2010). In chimpanzees, population-level left handedness has been reported for termite fishing(Lonsdorf and Hopkins, 2005) and there is at least one report of left-handedness for simulated termite fishing in captive chimpanzees(Hopkins et al., 2009). Finally, handedness data for grooming have been reported in both captive and wild chimpanzees and similar patterns of results were obtained between the two cohorts, with both showing small but

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significant right hand preferences (Hopkins et al., 2007) Thus, continued efforts to assess handedness on common measures between captive and wild apes would greatly facilitate the interpretation of results between settings.

In summary, the results reported here indicate significant species differences in handedness among great apes. When considering adult apes, gorillas, chimpanzees and bonobos showed small but significant population-level right handedness whereas orangutans showed population-level left handedness. Similar differences in handedness have been reported in closely related primates, such as between macaque species, suggesting that different life history, social or ecological factors may contribute to phylogenetic variation in primate handedness (Hopkins, 2007b). These factors have been relatively unexplored in relation to the development and evolution of handedness, or other dimensions of behavioral lateralization, and should be the focus of future studies of primates, including humans (Raymond et al., 1996).

Acknowledgments

This research was supported in part by NIH grants NS-42867, HD-60563, and HD-56232 as well as NIH grant U42 to the M. D. Anderson Cancer Center. American Psychological Association guidelines for the ethical treatment of animals were adhered to during all aspects of this study. We are grateful to the entire animal care and intern staff at the Regenstein Center for African Apes at Lincoln Park Zoo, especially Maureen Leahy, the keepers from the Milwaukee County Zoo, notably Ms. Barbara Bell and Ms. TracyFenn from the Jacksonville Zoo. We also thank Dr. Heidi Lyn for assistance in some data collection at Great Ape Trust of Iowa.

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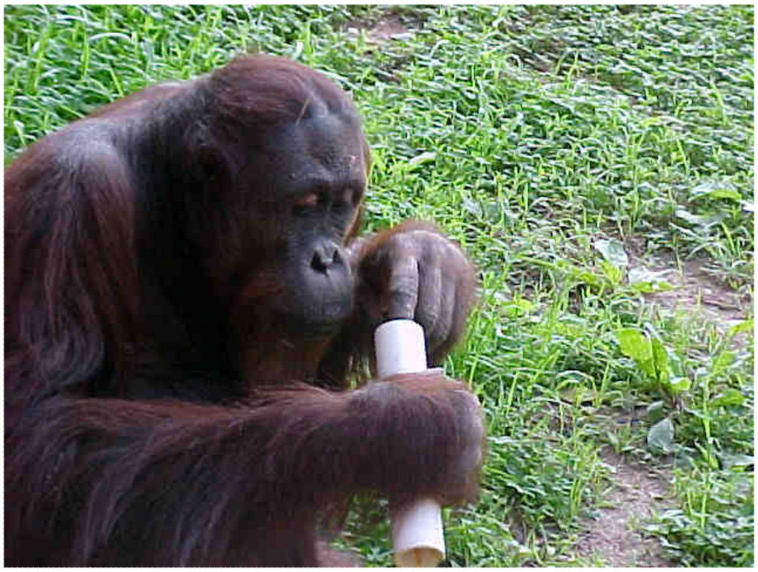

Figure 1.
Photographshowing an orangutanengaged in the TUBE task.

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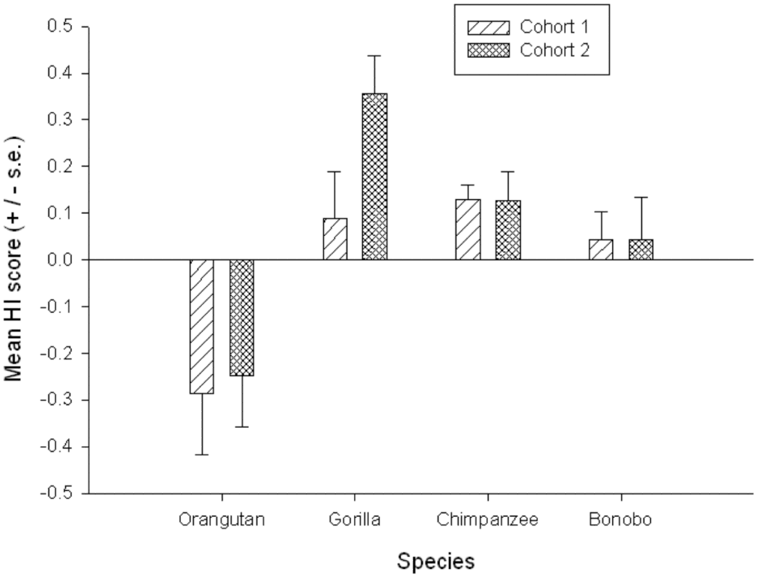

Figure 2.

Mean HI scores (+/− s.e.) for each species and cohort on the TUBE task. Cohort 1 are those apes tested by Hopkins et al. (2003) while cohort 2 represents those new individuals tested in this study.

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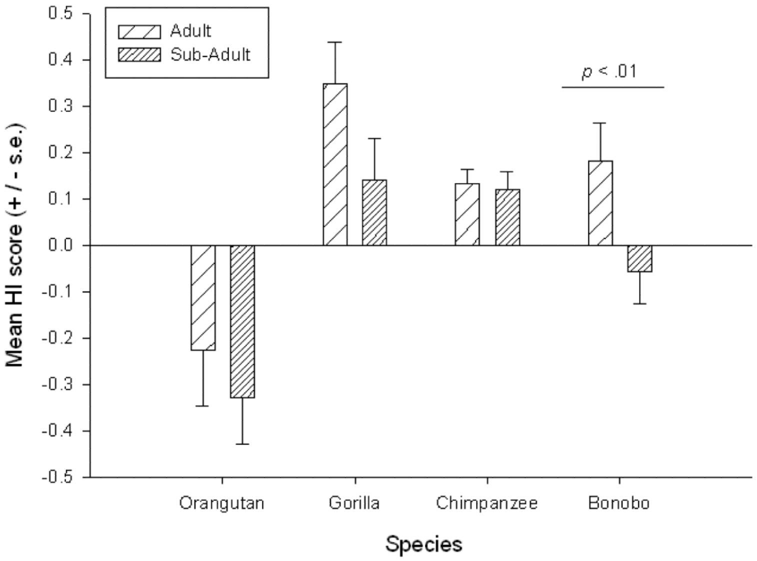

Figure 3.

Mean HI scores (+/− s.e.) for each age class within each species on the TUBE task

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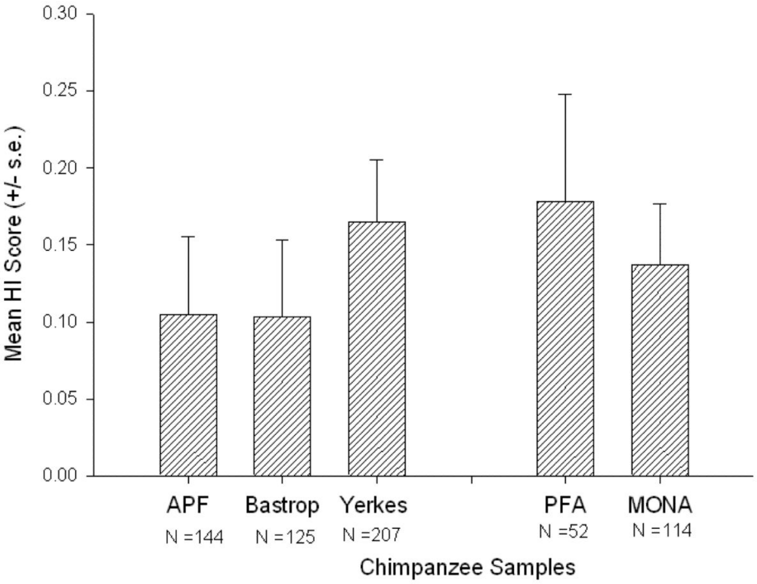

Figure 4.

Mean HI scores (+/− s.e.) for each sample of chimpanzees on the TUBE task.

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Table 1

Demographic information of great ape sample

	Cohort		Total		Total		
	New	**Old**	**#M**	**#F**	**Juvenile**	**Adolescent**	**Adult**
Pongo	28	19	21	26	6	12	29
Gorilla	45	31	35	41	22	14	40
Chimpanzees	83	453	240	296	86	126	324
Bonobo	40	78	54	64	42	24	52

M = male, F = female.

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Table 2

Handedness distribution for each great ape species

	Adults			Sub-Adults			Adults Only
	#L	**#A**	**#R**	**#L**	**#A**	**#R**	**R:L Ratio**
Orangutan	16	6	7	11	5	2	0.38
Gorilla	7	10	23	10	8	18	3.28
Chimpanzees	95	66	163	60	49	103	1.72
Bonobo	20	4	28	30	13	23	1.40

#L = number of left-handed, #A = number of ambiguously-handed, #R = number of right-handed