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Chimpanzees (*Pan troglodytes*) Are Predominantly Right-Handed: Replication in Three Populations of Apes

William D. Hopkins,
Division of Psychobiology, Yerkes National Primate Research Center, Atlanta, Georgia, and Department of Psychology, Berry College

Michael J. Wesley,
Division of Psychobiology, Yerkes National Primate Research Center

M. Kay Izard,
Alamogordo Primate Facility, Alamogordo, New Mexico

Michelle Hook, and
Department of Psychology, Texas A&M University

Steven J. Schapiro
Department of Psychology, Southwestern University, and Department of Veterinary Sciences, The University of Texas M. D. Anderson Cancer Center

Abstract

Population-level right-handedness has historically been considered a hallmark of human evolution. Even though recent studies in chimpanzees (*Pan troglodytes*) have demonstrated population-level right-handedness for certain behaviors, some have questioned the validity and consistency of these findings by arguing that reported laterality effects are specific to certain colonies of apes and to those chimpanzees reared by humans. The authors report evidence of population-level right-handedness in 3 separate colonies of chimpanzees. Moreover, handedness in the 3 colonies was unrelated to the proportion of subjects that were raised by humans. This is the strongest evidence to date that population-level handedness is evident in chimpanzees and is not an artifact of human rearing.

One of the most robust manifestations of hemispheric specialization in humans is right-handedness and left-hemisphere specialization for language function (Annett, 1985;McManus, 2002;Yeo, Thoma, & Gangestad, 2002). Although some variation exists between cultures, right-handedness has been uniformly reported in extant human populations (Porac & Coren, 1981), and the archeological record points to the existence of right-handedness in early hominids (Bradshaw & Rogers, 1993;Corballis, 1997). Many have argued that population-level right-handedness is unique to human evolution and related to the emergence of gestural language, speech, tool use, and other higher cognitive functions (Bradshaw & Rogers, 1993;Corballis, 2002). However, recent studies in captive chimpanzees have reported evidence of population-level right-handedness for certain manual actions, including throwing, gestural communication, and coordinated bimanual actions (Colell, Segarra, & Sabater-Pi, 1995;Hopkins, 1995;Hopkins, Bard, Jones, & Bales, 1993;Hopkins & Cantalupo, 2003;Hopkins et al., 2001;Hopkins & Leavens, 1998;Wesley et al., 2002). These results challenge the long-held belief in the uniqueness of human right-handedness. Notwithstanding, several authors have been critical of the existing findings, and there are at least three issues that have been raised in the context of previous findings. First, Palmer (2002) has noted that

Correspondence concerning this article should be addressed to William D. Hopkins, Division of Psychobiology, Emory University, Yerkes National Primate Research Center, 954 Gatewood Road, Atlanta, GA 30322. E-mail: lrcbh@rmy.emory.edu or whopkins@berry.edu

nearly all of the evidence of population-level right-handedness in chimpanzees has come from studies conducted at the Yerkes National Primate Research Center and suggests that observer bias might explain this effect. Second, both Palmer (2003) and McGrew and Marchant (1997) have suggested that perseveration in responding in recordings of hand-use frequency may explain the observed pattern of right-handedness reported in the Yerkes chimpanzees. Last, McGrew and Marchant (1997) have argued that evidence of population-level right-handedness is restricted to captive chimpanzees and is an artifact of being raised by humans in a right-handed environment. The principal argument in support of this interpretation is that data from wild chimpanzees do not indicate population-level handedness, and this difference in findings has been attributed to the fact that captive apes would be extensively exposed to humans and have lived in a human, right-handed world, thereby causing them to develop right-handed preferences. However, the types of measures and the methods of data collection differ substantially between wild and captive settings, and, arguably, the differences in findings might reflect these factors rather than rearing per se (for discussion, see Hopkins, 1999;Hopkins & Cantalupo, in press).

The purpose of this study was threefold. First, we present data on hand preference for a task requiring coordinated bimanual actions in three colonies of chimpanzees housed in North America. If handedness is restricted to chimpanzees housed at the Yerkes National Primate Research Center, then right-handedness should be more prevalent in these chimpanzees compared with those at other facilities. Second, if the previously reported evidence of population-level right-handedness in chimpanzees is restricted to those individuals raised by humans, then human-reared chimpanzees should be significantly more right-handed than chimpanzees reared in other conditions, and in particular those that are wild-caught. Moreover, colonies of chimpanzees with a higher proportion of human-raised chimpanzees should have significantly more right-handed chimpanzees than colonies with fewer human-reared chimpanzees. To test this hypothesis, we compared handedness across three colonies of chimpanzees that differed significantly with respect to the number of human-reared subjects. If the previously reported evidence of right-handedness in captive chimpanzees is due to human-rearing, then right-handedness should be most evident in the colony of apes with the largest proportion of human-reared subjects. Third, to address the issue of handedness measurement, we recorded the total frequency of hand use and noted the hand used in making the very first response. By recording the subjects' first responses, we were able to evaluate hand use without the influence of previous responses on subsequent hand use within a given test. If recording frequency of hand use biases the results toward increased classification of right- versus left-handed subjects, as suggested by others (McGrew & Marchant, 1997;Palmer, 2003), then a significantly higher proportion of right-handed subjects should be found on the basis of this classification criteria compared with the subjects' first response.

Method

Subjects

Handedness data were collected in a total of 467 chimpanzees (*Pan troglodytes*) from three captive populations, including the Alamogordo Primate Facility in Alamogordo, New Mexico (APF; $n = 148$); The University of Texas M. D. Anderson Cancer Center (Bastrop; $n = 117$); and the Yerkes National Primate Research Center in Atlanta, Georgia (Yerkes; $n = 202$). The data from the Yerkes and Bastrop groups have been previously reported (Hopkins, Hook, Braccini, & Schapiro, 2003), but the APF data are new to this article. For the combined data, there were 204 males and 263 females, ranging in age from 4 to 57 years. In terms of rearing histories of the subjects, there were 144 mother-reared, 227 human-reared, and 96 wild-caught chimpanzees in the APF, Bastrop, and Yerkes colonies, respectively. Human-reared chimpanzees were subjects that were born in captivity and had been removed and raised by

humans before the age of 30 days. Mother-reared chimpanzees were subjects that were born in captivity but raised by their mothers. Wild-caught chimpanzees were subjects captured in Africa before 1973 and raised in captivity since that time.

Procedure

Hand preference was assessed with a task designed to elicit coordinated bimanual actions, referred to as the *tube task* (see Figure 1). The procedure for this task has been described in detail elsewhere (Hopkins, 1995). Briefly, peanut butter was smeared on the inside edge of polyvinyl chloride (PVC) tubes approximately 15.0 cm in length and 2.5 cm in diameter. The peanut butter was placed on both ends of the PVC pipe and was positioned far enough inside the tube that the chimpanzees could not lick the contents completely out with their mouths but rather had to use their fingers to remove the substrate. The PVC tubes were handed to the subjects in their home cages, and a focal sampling was used to collect individual data from each subject. The hand and finger used to extract the peanut butter was recorded as either right or left by the experimenter. Data were collected until the subjects either dropped the tube, stopped extracting peanut butter for a period of 10 s, or returned the PVC pipe back to the experimenter. The 10-s limit did not include instances in which the subjects were locomoting with the PVC pipe. Rather, this time limit was specific to instances in which they had the PVC in hand, were stationary in positional behavior, and were not attempting to feed (usually because of the absence of any remaining peanut butter).

Each subject was tested on at least two occasions, and a minimum of 20 responses was obtained from each subject. Previous research in chimpanzees (Hopkins et al., 2001) has shown the test-retest reliability for the tube task, even after 6 years between tests, to be positive and significant ($r > .60$, $p < .01$). Although the procedures for data collection were identical between the different chimpanzee populations, different observers recorded the data in each colony in order to maximize objectivity in the recording of hand use.

Data Analysis

For each subject, individual handedness was determined in two ways. First, a handedness index (HI) was derived according to the formula HI = (number right − number left) ÷ (number right + number left), with positive values reflecting right-hand bias and negative values reflecting left-hand bias. Second, as has been done previously (Hopkins & Pearson, 2000), subjects with HI values more than three standard errors below or above a value of zero were classified as left- and right-handed, respectively. All other subjects were classified as ambiguously handed. Lastly, for each subject, the hand used to make the very first response was characterized as right or left. Because these data were nominal, they were analyzed by means of nonparametric statistics. For all analyses, alpha was set to $p < .05$.

Results

Initially, one-sample *t* tests were performed on the HI scores within each colony to evaluate whether the values differed from zero, as would be predicted if the distributions were bimodally or normally distributed rather than skewed. Population-level right-handedness was found for the APF, $t(147) = 2.14$, $p < .03$, Bastrop, $t(116) = 2.32$, $p < .02$, and Yerkes, $t(202) = 4.76$, $p < .01$, colonies. A one-way analysis of variance was performed on the HI scores, with colony serving as the independent variable, and no significant difference was found. The mean HI scores for the APF, Bastrop, and Yerkes colonies were .108, .123, and .164, respectively. To test for the effect of rearing history and sex on handedness, we used analysis of variance to compare the HI scores, with sex and rearing history serving as between-group variables. No significant main effects or interactions were found.

Results were similar for the hand-preference classification data. A chi-square goodness-of-fit test indicated that the distribution of hand preference differed significantly from a random distribution, $\chi^2(2, N = 467) = 183.86$, $p < .01$. The number of right-handed subjects ($n = 272$) was significantly higher than the number of left-handed subjects ($n = 162$), $\chi^2(1, N = 434) = 27.88$, $p < .01$, and ambiguously handed subjects ($n = 33$), $\chi^2(1, N = 305) = 187.28$, $p < .01$. Chi-square tests of independence failed to reveal significant interactions between colony and rearing history on the distribution of hand preference.

A chi-square test of independence did reveal a significant association between rearing history and colony, $\chi^2(2, N = 467) = 81.98$, $p < .01$. The proportion of human-reared chimpanzees was significantly higher in the APF population compared with the Bastrop, $\chi^2(2, N = 266) = 75.53$, $p < .01$, and Yerkes, $\chi^2(2, N = 350) = 14.00$, $p < .01$, colonies (see Figure 2). In addition, the proportion of captive-born, human-reared chimpanzees was significantly higher in the Yerkes colony compared with the Bastrop colony, $\chi^2(2, N = 320) = 41.86$, $p < .01$ (Figure 2). Thus, despite significant differences in the proportion of human-raised chimpanzees in the three colonies, the mean HI and proportion of right-handed subjects were nearly identical between them.

On the basis of first-response data in the 452 chimpanzees for which these data were available, there were 269 right-handed and 183 left-handed subjects, a distribution that differs significantly, $\chi^2(1, N = 452) = 16.36$, $p < .01$. Chi-square tests of independence indicated no significant interactions between rearing history or sex on the hand-preference distribution. A phi-coefficient between the handedness classifications based on the first response compared with the HI scores was positive and significant ($\varphi = .508$, $df = 450$, $p < .01$).

Discussion

This is the single largest study on handedness ever reported in chimpanzees or any other nonhuman primate. The results clearly indicate population-level right-handedness in this species, are consistent across colonies of apes, and are unrelated to their individual rearing history. Both first-response and cumulative frequency data reveal right-handedness, and therefore any explanation of this effect as being due to perseveration in responding seems very unlikely. The collective results also challenge previous claims that handedness is restricted to certain colonies of apes and to those reared by humans (McGrew & Marchant, 1997;Palmer, 2002), and strongly suggest that handedness is an endogenous trait inherent to chimpanzees.

These results do not resolve discrepancies in handedness findings between wild and captive chimpanzees (Hopkins, 1999;McGrew & Marchant, 1997). To date, evidence of population-level handedness in wild chimpanzees has been weak, at best (Boesch, 1991;Corp & Byrne, 2004;Marchant & McGrew, 1996;McGrew & Marchant, 1992,2001;McGrew, Marchant, Wrangham, & Klein, 1999;Sugiyama, 1995;Sugiyama, Fushimi, Sakura, & Matsuzawa, 1993). We believe these differences largely reflect methodological or procedural differences in handedness assessment (Hopkins & Cantalupo, in press), rather than the influence of human rearing on the expression of hand preference in chimpanzees. Furthermore, relatively small sample sizes in wild chimpanzees preclude having enough statistical power to detect population-level effects, compared with the larger sample sizes typically obtained with captive chimpanzees (for discussion, see Hopkins, 1999). In fact, the relative proportion of right- to left-handed subjects is comparable in wild and captive chimpanzees for some measures, and larger sample sizes of wild chimpanzees would yield statistically significant effects (see Hopkins & Cantalupo, in press).

Our results further indicate that captive chimpanzees are less right-handed than humans, with an approximate 2:1 ratio of right-to left-handed individuals, compared with much higher ratios

in human populations (8:1). The origin of this difference is unclear, with some researchers suggesting genetic explanations (Corballis, 1997;Warren, 1980), and others offering nongenetic explanations, including issues of measurement and social or cultural differences (Hopkins, 1999;Hopkins, Dahl, & Pilcher, 2000). Heritability of hand preferences has been reported in chimpanzees (Hopkins, Dahl, & Pilcher, 2001;Matsuzawa et al., 2001), and the degree of heritability is comparable to values reported in humans. However, data from either species do not directly speak to possible genetic differences in the expression of handedness because no gene or set of genes has yet been linked to handedness. Further genetic and behavioral research should serve to clarify the cause of, and differences in, the expression of handedness in chimpanzees and humans.

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Figure 1.
A chimpanzee demonstrating the coordinated bimanual handedness task.

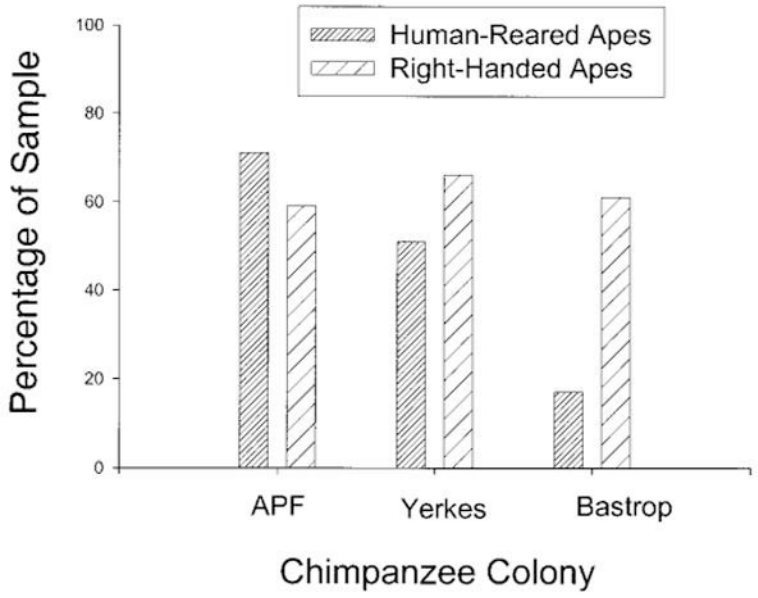

Figure 2.
The percentage of the sample of subjects that were right-handed and human-reared in each colony of chimpanzees. APF = Alamogordo Primate Facility; Yerkes = Yerkes National Primate Research Center; Bastrop = The University of Texas M. D. Anderson Cancer Center.