Journal of Comparative Psychology
2005, Vol. 119, No. 4, 363–370

0735-7036/05/$12.00 DOI: 10.1037/0735-7036.119.4.363

Factors Influencing the Prevalence and Handedness for Throwing in Captive Chimpanzees (*Pan troglodytes*)

William D. Hopkins
Yerkes National Primate Research Center and Berry College

Jamie L. Russell
Yerkes National Primate Research Center

Claudio Cantalupo
Clemson University

Hani Freeman
Yerkes National Primate Research Center

Steven J. Schapiro
University of Texas M. D. Anderson Cancer Center

Humans throw right-handed, and it has been suggested that the neurophysiological demands of aimed throwing may have served as a precursor to the evolution of left hemisphere specialization for linguistic functions. Although there are descriptions of throwing by wild and captive chimpanzees (*Pan troglodytes*), systematic observations of aimed throwing and handedness have not been reported. In this article, evidence of population-level right-handedness for throwing is reported in 2 samples of captive chimpanzees. It is further reported that right-handed throwing is more pronounced than other measures of handedness in captive chimpanzees. The implications of these findings are discussed in the context of theories relating throwing to the evolution of lateralization for language functions.

Hemispheric specialization refers to perceptual, motor, and cognitive processes that are differentially represented in the left and right cerebral hemispheres. Right-handedness and left hemisphere dominance for language functions are two of the most pronounced manifestations of hemispheric specialization in humans, and many researchers have suggested that these two traits are unique to hominid evolution (Corballis, 1992). Recent studies in a host of vertebrates have documented population-level behavioral and neuroanatomical asymmetries, indicating that language is not a necessary condition for the expression of hemispheric specialization, but rather that hemispheric specialization may be widespread in the animal kingdom (Rogers & Andrew, 2002).

Less clear from the existing literature on hemispheric specialization in animals is how it relates to the evolution of right-handedness and left hemisphere dominance for language in humans. Some have suggested that right-handedness evolved in the context of increasing motor and cognitive demands associated with tool use (for review, see Bradshaw & Rogers, 1993), but evidence of population-level handedness for tool use in captive and wild chimpanzees is not very compelling (Biro et al., 2003; Boesch, 1991; McGrew & Marchant, 1992, 1996; but see Hopkins, in press; Lonsdorf & Hopkins, 2005). Others have suggested that right-handedness evolved from extant left hemisphere lateralization for motor functions associated not with tool use but instead with vocalizations and possibly manual communicative functions (Corballis, 2002). In primates, there is little to no evidence of left hemisphere specialization in the production of vocalizations (Fernandez-Carriba, Loeches, Moricello, & Hopkins, 2002; Hauser, 1993; Hook-Costigan & Rogers, 1998), although there is evidence of population-level right-handedness for manual gestures (Hopkins, Russell, Freeman, et al., 2005). Thus, not all the assumptions of this theory are met from the extant literature.

Calvin (1983) proposed that right-handedness and left hemisphere dominance for language evolved in the context of increasing neurophysiological, motor, and cognitive demands associated with throwing. Calvin argued from a neurophysiological standpoint that throwing requires that subjects acquire very precise timing windows with respect to the distance, movements, and trajectory of the thrown object toward the target. According to Calvin, no single neuron can accomplish this goal alone; therefore, for throwing to have evolved, there had to be an increased demand on the number of neurons applied to the task. Moreover, the increasing neurons had to be synchronized or to operate in parallel either through spatial or temporal summation mechanisms. According to Calvin, timing and sequencing specialization associated with throwing overlap considerably with linguistic functions asso-

William D. Hopkins, Division of Psychobiology, Yerkes National Primate Research Center, and Department of Psychology, Berry College; Jamie L. Russell and Hani Freeman, Division of Psychobiology, Yerkes National Primate Research Center; Claudio Cantalupo, Department of Psychology, Clemson University; Steven J. Schapiro, Department of Veterinary Sciences, University of Texas M. D. Anderson Cancer Center.

This work was supported in part by National Institutes of Health Grants RR-00165, U42-RR-15090, NS-42867, NS-36605, and HD-38051. The Yerkes National Primate Research Center and University of Texas M. D. Anderson Cancer Center facilities are accredited by the American Association of Laboratory Animal Care. American Psychological Association guidelines for the care and use of animals were adhered to during all aspects of this study. We thank the care staff from each facility for assistance in data collection.

Correspondence concerning this article should be addressed to William D. Hopkins, Division of Psychobiology, Yerkes National Primate Research Center, 954 Gatewood Road, Emory University, Atlanta, Georgia 30322. Email: lrcbh@rmy.emory.edu

ciated with speech perception and production, functions well known to be lateralized to the left hemisphere (e.g., Zatorre, Belin, & Penhun, 2002). Thus, right-handed throwing may have been a preadaptation for the eventual emergence of left hemisphere specialization for speech in humans.

In the current study, we evaluated handedness in chimpanzees for throwing. It has been proposed that throwing evolved in humans in response to selection for hunting and predator defense (Watson, 2001). Throwing allowed for adequate defense from predators and reduced mortality from wounds inflicted from prey by increasing the distance between the thrower and either its prey or its predator. Throwing may also have been an effective means of capturing the attention of an otherwise inattentive social audience when channels of vocal communication were limited, either structurally or contextually (see Hostetter, Cantero, & Hopkins, 2001). Throwing is relatively uncommon in nonhuman primates, and although there are reports of throwing in wild and captive chimpanzees and other apes (Colell, Segarra, & Sabater-Pi, 1995; Goodall, 1986; Hopkins, Bard, Jones, & Bales, 1993; Marchant, 1983; Shafer, 1993), no systematic and long-term observations on throwing in a relatively large sample of chimpanzees have been conducted to date. In this study, we evaluated the role of subject variables on the prevalence and handedness of throwing in two samples of captive chimpanzees. With respect to handedness, our hypothesis was that if right-handedness in humans evolved in the context of throwing, as proposed by Calvin (1983), then chimpanzees should be right-handed for this behavior.

Method

Subjects

Data were collected from two captive colonies of chimpanzees (*Pan troglodytes*): the Yerkes National Primate Research Center (Yerkes) and the University of Texas M. D. Anderson Cancer Center (UTMDACC). Between the two facilities, 140 animals (58 males, 82 females) were observed to throw at least once. Analyses related to handedness were done with all 140 animals as well as with a subset of animals with six or more observations of throwing. There were a total of 89 chimpanzees that threw on six or more occasions, including 55 females and 34 males. Six observations were selected because this is the minimum needed to evaluate individual hand preferences by using binomial z scores. Of these 89 chimpanzees, there were 40 mother-reared, 45 nursery-reared, and 4 wild-caught individuals.

Procedure

Throwing in chimpanzees is a spontaneous and somewhat unpredictable behavior; therefore, our methods of data collection were very flexible. The authors worked with the chimpanzees at the two facilities on a daily basis in a variety of situations. The experimenters were involved with the animals in purely observational experiments as well as more controlled and interactive studies. In addition, animals not actively being tested were also often in visual proximity to the experimenters. Subjects were never encouraged to throw for the purpose of this study, but instead observations were made on the occasions when throwing occurred in these varied contexts. Most observations were made while subjects were in the outdoor portions of their home cages. At Yerkes and UTMDACC, the chimpanzees are housed in either pairs, small social groups of 3 to 12 individuals, or larger groups (13 to 22 individuals) living in compounds (for a description of housing conditions, see Hopkins, Wesley, Izard, Hook, & Schapiro, 2004).

Although the social context was not recorded for each throwing event observed here, in our extensive experience with captive chimpanzees, we have observed that they throw substrates in three social contexts. First, the chimpanzees are often observed to throw at unfamiliar humans who are in proximity or approaching their home cages. Although the chimpanzee's motivation for throwing at humans is not clear, the behavior appears to be largely defensive and transient because most chimpanzees stop throwing at the individual with increasing familiarity with him or her. Second, throwing is observed during agonistic encounters between individuals living in the same groups or in adjacent cages. The third social context is when throwing is used to capture the attention of an otherwise inattentive chimpanzee or human, as has been described in previous studies (e.g., Hostetter, Cantero, & Hopkins, 2001). In all three contexts, the chimpanzees are generally throwing at an individual who is within 2 to 8 feet (0.61–2.4 m) of them and on relatively the same vertical plane. When throwing was seen in these three contexts, observers noted whether the chimpanzees threw with their right or left hand and whether they threw overhand or underhand. To some extent, posture was confounded with the throwing preference with nearly all subjects who threw overhand maintaining an erect posture (see Figure 1). In contrast, nearly all instances of underhand throwing were recorded when chimpanzees threw from a tripedal posture. At Yerkes, data were collected between 1990 and 2004. At the UTMDACC, data were collected between 2003 and 2004.

Data Analysis

Each chimpanzee currently living at Yerkes and UTMDACC was categorized as a thrower or nonthrower on the basis of the total number of observed throws. Chimpanzees that were observed to throw at least once were categorized as throwers, and those that were never observed to throw were categorized as nonthrowers. For each subject, a handedness index (HI) was derived following the formula $HI = (\#R - \#L)/(\#R + \#L)$, where #R and #L are the number of right-handed and left-handed responses, respectively. The resulting HI value ranged from -1.0 to 1.0, with the sign of the value indicating direction in hand use and the absolute value indicating the strength of hand use. In addition, binomial z scores were calculated for each subject. Subjects with z scores exceeding -1.96 or 1.96

Figure 1. Four sequential frames demonstrating a chimpanzee throwing a polyvinyl chloride (PVC) pipe toward a human in a tower above the subject. The chimpanzee stands bipedally, brings the PVC pipe back, and then throws the object. Note that the force of the chimpanzee's throw causes him to leave the ground.

were classified as left- and right-handed, respectively. All others subjects were classified as ambiguously handed.

Results

Prevalence of Throwing

Overall, throwing was recorded on 2,455 occasions from 140 different chimpanzees from both facilities. The number of times the chimpanzees were observed to throw ranged from 1 to 137 responses. As noted above, observations of throwing at Yerkes began in 1993, whereas observations at UTMDACC did not start until 2003. Therefore, to more accurately evaluate the factors that influence throwing in captive chimpanzees, we compared the distribution of throwing and nonthrowing chimpanzees from the living UTMDACC and Yerkes colonies from 2003 to present. This restricted our analysis to a possible 262 chimpanzees between the two colonies.

Table 1 shows the distribution of throwers and nonthrowers across rearing history, sex, and colony. A chi-square test of independence revealed a significant association between rearing history and whether the chimpanzees were observed to throw, $\chi^2(2, N = 262) = 35.10$, $p < .001$. Post hoc analysis revealed no difference in the distribution of mother- and nursery-reared chimpanzees. However, there were significantly more mother- and nursery-reared throwers than wild-caught throwers, $\chi^2(1, N = 180) = 29.04$, $p < .001$, and $\chi^2(1, N = 134) = 31.88$, $p < .001$, respectively. In addition, Yerkes chimpanzees were significantly more likely to be observed to throw than UTMDACC animals, $\chi^2(1, N = 262) = 22.53$, $p < .001$. No significant difference was found in the distribution of male and female chimpanzees that threw. An independent-samples t test with age as the dependent measure and classification as a thrower or nonthrower as the grouping variable revealed that the mean age of throwers ($M = 16.81$, $SD = 16.81$) was significantly younger than the mean age of nonthrowers ($M = 23.56$, $SD = 11.73$), $t(260) = 5.26$, $p < .001$.

Population Handedness Effects for Throwing

First, we carried out analyses of handedness that included the entire population of chimpanzees that were ever observed to throw.

Table 1
Number of Chimpanzees Categorized as Throwers and Nonthrowers on the Basis of Rearing History, Sex, and Colony

Variable	Throwers	Nonthrowers
Rearing history		
Mother-reared	65	63
Nursery-reared	46	36
Wild-caught	4	48
Sex		
Females	71	80
Males	44	67
Colony		
Yerkes	77	55
UTMDACC	38	92
Total	115	147

Note. UTMDACC = University of Texas M. D. Anderson Cancer Center.

A one-sample t test on the HI scores revealed significant population-level right-handedness for throwing ($M = .321$), $t(139) = 4.96$, $p < .001$. For a more conservative measure, we then repeated analyses by including only subjects with six or more separate observations of throwing. Again, a one-sample t test on the HI scores revealed significant population-level right-handedness ($M = .299$), $t(88) = 3.81$, $p < 001$. On the basis of individual z scores of the 89 subjects with six or more observations, there were 50 right-, 23 left-, and 16 ambiguously handed chimpanzees, a distribution that differs significantly from chance, $\chi^2(2, N = 89) = 21.33$, $p < .001$. The number of right-handed chimpanzees was significantly greater than the number of left-handed subjects ($z = 6.60$, $p < .001$) and ambiguously handed subjects ($z = 8.09$, $p < .001$). Chi-square tests of independence indicated that neither sex nor rearing history of the subjects had a significant influence on handedness. We correlated the age of the subjects with their HI scores and found no association between these two variables.

Some researchers have suggested that different sample sizes can potentially influence the distribution of handedness in primates (e.g., Palmer, 2002) and that funnel plots more accurately reflect potential biases than do standard statistical approaches, such as correlation. Given the disparate sample sizes in our data, we have provided a funnel plot of the distribution of handedness in relation to sample size in Figure 2. The presence of relatively uniform data points inside the funnel across the distribution indicates that sample size did not influence our results.

Many of the chimpanzees were related in our sample. As an alternative means of assessing population-level handedness from a genetically independent group, we isolated 50 individuals that represented unique genetic data points and evaluated the mean HI scores for this cohort by using a one-sample t test. This population of animals showed population-level right-handedness ($M = 26$), $t(49) = 2.76$, $p < .01$.

Posture and Handedness for Throwing

The influence of throwing style on handedness for throwing was robust. For each subject that threw on six or more occasions ($n = 89$), the percentage of overhand throws was calculated, and on the basis of these percentages, we classified subjects as being an underhand thrower ($n = 25$; ≤10% overhand throws), mixed-posture thrower ($n = 27$; >10% and <90% overhand throws), or overhand thrower ($n = 38$; ≥90% overhand throws). HI scores were compared as a function of their sex and throwing style classification by using an analysis of variance. There was a significant main effect for throwing style, $F(2, 83) = 6.21$, $p < .001$. Post hoc analysis indicated than the mean HI score for overhand throwers was significantly higher ($M = .60$) compared with underhand throwers ($M = .01$) and mixed-posture throwers ($M = .15$). No other significant main effects or interactions were found.

Behavioral–Genetic Analysis of Throwing

To evaluate whether either prevalence or handedness of throwing was acquired through genetic or social learning mechanisms, we took advantage of the pedigree information available at the Yerkes and UTMDACC colonies to test these hypotheses. There were very few data on throwing in the sires in relation to the dams;

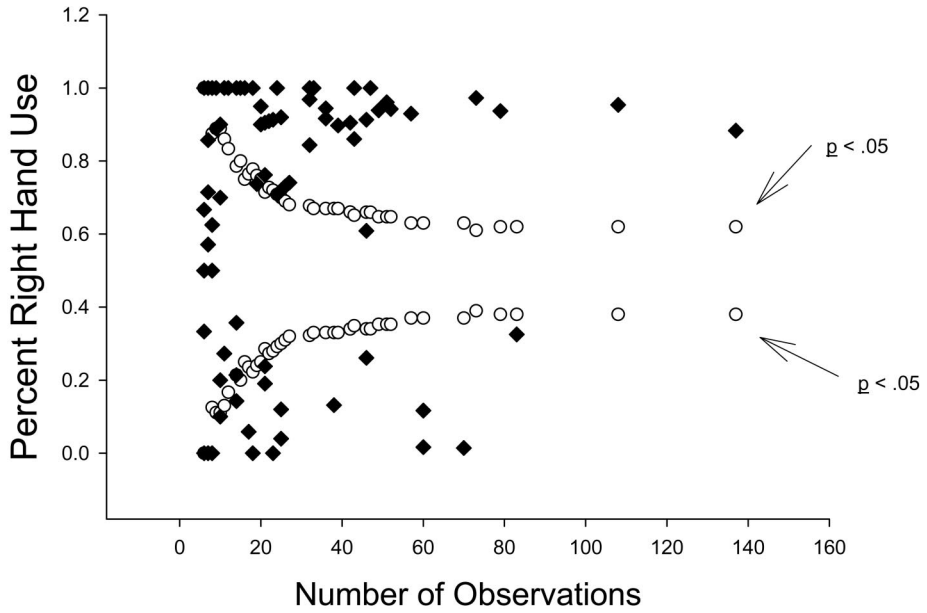

Figure 2. Funnel plot of the distribution of percentage of right-hand use (represented by black diamonds) for each subject in relation to the number of observed throwing events. The values represented by the white circles indicate the percentage of right- or left-hand use needed to be classified as left- or right-handed. Black diamonds falling in the middle of the funnel represent subjects with no hand preference. Black diamonds falling outside the funnel indicate subjects with significant left- or right-hand preference on the basis of *z* scores.

therefore, we largely restricted our analyses to comparison between offspring and dams.

Prevalence

In total, pedigree information on throwing was available in 171 mother–offspring dyads. On the basis of the throwing classification data, we compared the distribution of throwing behavior of offspring relative to mothers and found no significant association (see Table 2). We also separated offspring on the basis of their rearing history (mother, nursery) and performed separate chi-square analyses. No significant associations were found for either mother- or nursery-reared subjects. Thus, there was no evidence that the prevalence of throwing was heritable.

Handedness

Mother–offspring. Throwing data were available in 32 mother–infant dyads. Shown in Table 3 is the distribution of right- and left-handed offspring as a function of the handedness of the mother. No significant association was found between offspring and maternal handedness; however, the odds ratios are of note. Offspring born to right-handed females were 3.5 times more likely to be right-handed. In contrast, offspring born to a left-handed female were no more likely to be right- or left-handed. This pattern of results was consistent whether or not the female raised or did not raise her offspring.

Sibling concordance. To assess whether the concordance percentages were statistically significant, we derived expected prob-

Table 2
Distribution of Offspring That Throw as Function of Rearing History and Maternal Throwing

	Offspring	
Dam	Nonthrower (*n*)	Thrower (*n*)
Mother-reared		
Nonthrower	34	30
Thrower	6	8
Nursery-reared		
Nonthrower	10	7
Thrower	47	29
Total		
Thrower	44	37
Nonthrower	53	37

Table 3
Distribution of Offspring Handedness for Throwing as a Function of Rearing History and Maternal Handedness

	Offspring handedness		
Dam handedness	Left	Right	Right:Left odds
Mother-reared			
Left	4	2	0.40
Right	3	8	2.67
Nursery-reared			
Left	3	5	1.67
Right	1	6	6.00
Total			
Left	7	7	0.00
Right	4	14	3.50

abilities of concordance and disconcordance on the basis of the distribution of hand preferences for the entire sample. To increase statistical power, we combined the left- and ambiguously handed subjects into one group referred to as non-right-handed. The probability of being right-handed or non-right-handed was .56 (50/89) and .44 (39/89), respectively. The probability of any 2 subjects both being right-handed was (.56 × .56 =) .31 or of being non-right-handed was (.44 × .44 =) .19. The probability of any 2 subjects being mixed handed (one right-handed, one non-right-handed) was [2 × (.44 × .56) =] .49. These probabilities were then applied to the entire sample of full and maternal half-siblings ($N = 60$) to derive chance-expected values for a chi-square goodness-of-fit test for comparison with the observed concordance rates. The observed and expected distribution of hand preference for full and maternal half-siblings is shown in Figure 3. The chi-square goodness-of-fit indicated that the observed concordance rates in hand use differed significantly from a chance distribution, $\chi^2(2, N = 60) = 14.15$, $p < .01$. We also evaluated whether the observed frequency differed from the expected within each phenotype. There were significantly more right-handed offspring than was predicted ($z = 3.60$, $p < .01$) but not for the mixed- or left-handed offspring.

Comparison With Other Handedness Measures

Throwing elicited strong asymmetries in hand use for the chimpanzees. In the UTMDACC and Yerkes chimpanzees, we have previously reported population-level right-handedness for simple reaching (Hopkins, Russell, Hook, Braccini, & Schapiro, 2005), coordinated bimanual actions (Hopkins, Hook, Braccini, & Schapiro, 2003), and manual gestures (Hopkins, Russell, Freeman, et al., 2005). Shown in Figure 4 are the mean handedness indices for each of these three measures for comparison with the throwing data. As can be seen, with the exception of manual gestures, the chimpanzees were significantly more right-handed for throwing compared with simple reaching and coordinated bimanual actions.

Discussion

The overall results contribute to our understanding of the evolution of handedness and its possible relationship with the origins of left hemisphere specialization for language in several important ways. First, assuming that right-handed throwing reflects left hemisphere specialization in motor skill, our findings support the theory by Calvin (1983) that the neurophysiological, cognitive, and motor demands of throwing may have been the precursor to the evolution of right-handedness in humans. As far as we know, there are no systematic reports on handedness for throwing in wild chimpanzees, but on the basis of our findings, these data would be important for comparison with our results.

Second, the acquisition and maintenance of throwing by the chimpanzees was observed in largely agonistic social contexts. Some researchers have suggested that individual hand preferences in nonhuman primates are acquired by incidental learning, with food being the primary reinforcer for the development of hand use (e.g., Warren, 1980). The chimpanzees at both facilities were not food rewarded for throwing at people or other chimpanzees, and this implies that the contingencies of reinforcement that exerted stimulus control of this behavior were social, not nutritive. The lack of overt nutritive reinforcement for hand use in throwing suggests that the contingencies of reinforcement were self-regulated (i.e., reactions of the respondents were reinforcing) and

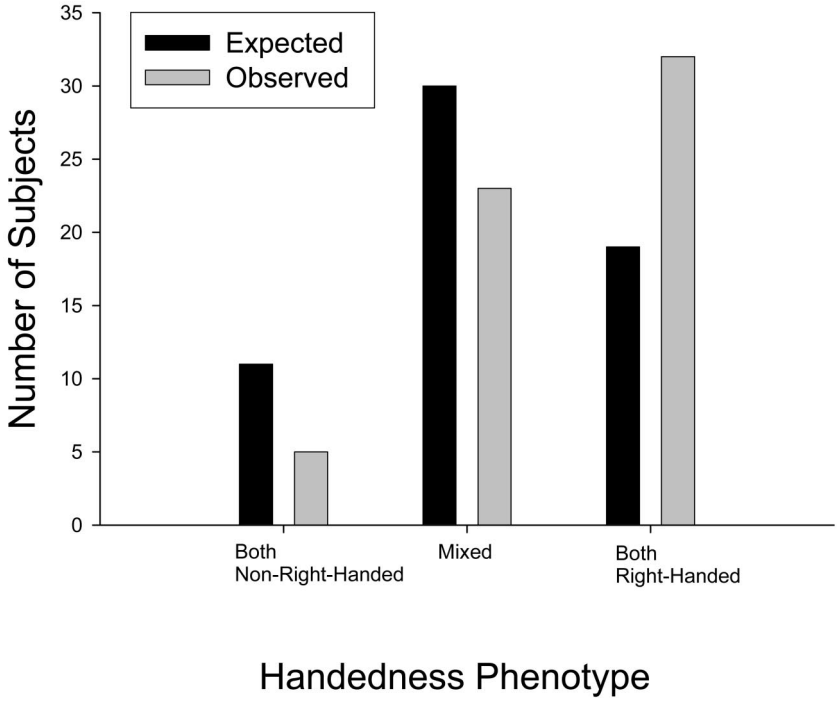

Figure 3. The observed and expected frequencies of concordance in hand preference between siblings.

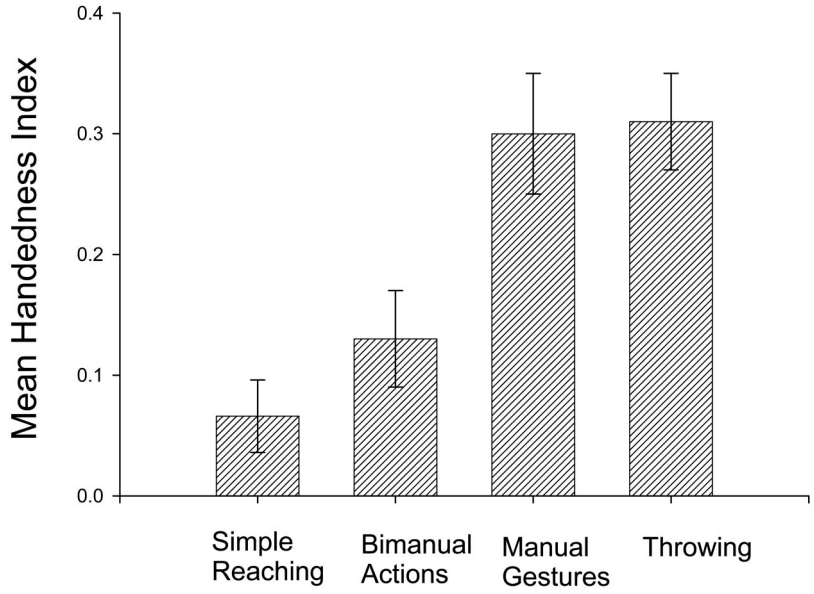

Figure 4. Mean handedness indices for four different behavioral measures of handedness in the University of Texas M. D. Anderson Cancer Center and Yerkes chimpanzees. Handedness indices (HI) were calculated following the formula HI = [(#R − #L)/(#R + #L)], where #R and #L are the number of right-handed and left-handed responses, respectively.

likely reflects an inherent bias or specialization in motor skill by the left hemisphere in chimpanzees. The observed handedness findings cannot be attributed to a lack of independence of data points. Some researchers have suggested that a lack of independence in data points can skew handedness data toward the occurrence of population-level effects (e.g., McGrew & Marchant, 1997; Palmer, 2003). This is not a possible explanation for our results as each throwing response was independent of the other because subjects often threw only once in a bout or, if the chimpanzees threw repeatedly, they had to reposition between responses to retrieve additional substrates.

Third, posture and handedness were related to a higher proportion of right-handedness associated with overhand throwing. This distinction speaks directly to the function of throwing along the dimension of aimed versus incorporated throwing in chimpanzees. Although we did not attempt to quantify the intentionality of the chimpanzees' actions, our observations indicate that overhand throwing was a very deliberate behavior and was not typically observed when the chimpanzees were displaying or engaging in otherwise overt aggressive behaviors toward humans or conspecifics. Indeed, many chimpanzees would wait patiently for another chimpanzee or human to approach them before throwing. In contrast, underhand throwing was much more frequently observed when the chimpanzees were displaying at a human or conspecific. The distinction in posture and throwing style seems critical for explaining the prevalence of right-handedness observed in these two samples of chimpanzees compared with other reports of laterality and throwing in captive apes (Marchant, 1983) and monkeys (Westergaard, Liv, Haynie, & Suomi, 2000) where there is little evidence of population-level handedness.

Why these two postures elicit different biases in hand use is unclear, but one suggestion might be that when chimpanzees are throwing underhand in the context of their displays, they are running toward the target while carrying the item to be thrown in their left hand, which keeps their right hand free for locomotion. Previous studies in captive apes have reported evidence of right-leading limb biases (Heestand, 1986; but see Marchant & McGrew, 1996), and therefore, left-handed throwing from this posture may be a consequence of the use of the right limb for locomotion. In contrast, when throwing overhand, most subjects were sitting or standing upright, which allowed for both hands to be free, and this may have facilitated greater use of the right hand (see MacNeilage, Studdert-Kennedy, & Lindblom, 1987). Previous studies in apes have reported greater preferential use of the right hand when reaching from an upright posture (Hopkins, 1993; Olson, Ellis, & Nadler, 1990), and therefore, this hand may similarly be used for throwing from the upright posture.

With respect to the prevalence of throwing, nearly 50% of the apes were not observed to throw, and our analyses indicated that this cohort largely consisted of wild-caught individuals. It is important to emphasize that rearing history is confounded with age in the chimpanzees. Because importation of wild chimpanzees stopped around 1972, most wild-caught individuals are also the oldest individuals in the colonies. Thus, it is not clear whether age or rearing history per se is the more important factor contributing to this effect. If the wild-caught chimpanzees are excluded, significant differences are still found in the age of subjects observed to throw (M = 16.29 years) and not throw (M = 19.18 years), $t(208) = 2.17$, $p < .05$. This finding suggests that age, rather than rearing history, is probably the more important factor. Older chimpanzees may throw less often because these animals are generally less excitable and energetic or because their long history of captivity has caused them to be less threatened by strangers. It is unclear what causes such individual variability, but throwing does

not appear to be heritable; therefore, it is reasonable to assume that it may be a combination of individual temperament, social learning, and previous (though unintentional) social reinforcement of this behavior.

Last, there was some evidence of heritability in hand preferences for throwing, although in many ways the analyses were limited because of the lack of statistical power. Given that paternal information was limited and there was not a large sample of females and offspring that both threw, the generalizability of these results is very limited. Notwithstanding this limit, the evidence that concordance rates in hand preferences of siblings were greater than would be predicted by chance is consistent with previous reports of heritability in hand preferences for chimpanzees (Hopkins, 1999; Hopkins, Dahl, & Pilcher, 2001). Many have suggested that human handedness is under genetic control, whereas nonhuman primate handedness is determined by random chance factors (Annett, 2002; Warren, 1980), and these results appear to challenge this perspective. Additional data from a larger sample of apes would be particularly useful for evaluating the role of genetic and nongenetic factors on the expression of handedness in chimpanzees and other primates.

In conclusion, the findings reported here support the theory that right-handedness may have evolved in the context of the increasing cognitive, postural, and motor demands associated with throwing. The social role of throwing should not be minimized as a potentially important element to the emergence of left hemisphere specialization in motor skill and language. If throwing is conceived of as a social form of tool use, then it could be argued that neural recruitment and adaptation of lateralization for communication systems from existing motor systems involved in social contexts (i.e., throwing) would have been selected for rather than motor systems adapted for nonsocial functions, such as tool use associated solely with the procurement of food (see Vallortigara & Rogers, 2005).

References

Annett, M. (2002). *Handedness and brain asymmetry: The right shift theory*. Philadelphia, PA: Psychology Press.

Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C., & Matsuzawa, T. (2003). Cultural innovation and transmission of tool use in wild chimpanzees: Evidence from field experiments. *Animal Cognition, 6,* 213–223.

Boesch, C. (1991). Handedness in wild chimpanzees. *International Journal of Primatology, 6,* 541–558.

Bradshaw, J., & Rogers, L. J. (1993). *The evolution of lateral asymmetries, language, tool use and intellect*. San Diego, CA: Academic Press.

Calvin, W. (1983). *The throwing Madonna*. New York: Bantam Books.

Colell, M., Segarra, M. D., & Sabater-Pi, J. (1995). Hand preferences in chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*) and orangutans (*Pongo pygmaeus*) in food-reaching and other daily activities. *International Journal of Primatology, 16,* 413–434.

Corballis, M. C. (1992). *The lopsided brain: Evolution of the generative mind*. New York: Oxford University Press.

Corballis, M. C. (2002). *From hand to mouth: The origins of language*. Princeton, NJ: Princeton University Press.

Fernandez-Carriba, S., Loeches, A., Morcillo, A., & Hopkins, W. D. (2002). Asymmetry of facial expression of emotions by chimpanzees. *Neuropsychologia, 40,* 1523–1533.

Goodall, J. (1986). *The chimpanzees of Gombe: Patterns in adaptation*. Cambridge, MA: Harvard University Press.

Hauser, M. D. (1993, July 23). Right hemisphere dominance in the production of facial expression in monkeys. *Science, 261,* 475–477.

Heestand, J. (1986). *Behavioral lateralization in four species of ape*. Unpublished doctoral dissertation, University of Washington, Seattle.

Hook-Costigan, M. A., & Rogers, L. J. (1998). Lateralized use of the mouth in production of vocalizations by marmosets. *Neuropsychologia, 36,* 1265–1273.

Hopkins, W. D. (1993). Posture and reaching in chimpanzees (*Pan troglodytes*) and orangutans (*Pongo pygmaeus*). *Journal of Comparative Psychology, 17,* 162–168.

Hopkins, W. D. (1999). Heritability of hand preference in chimpanzees: Evidence from a partial interspecies cross-fostering study. *Journal of Comparative Psychology, 113,* 1–7.

Hopkins, W. D. (in press). Comparative and familial analysis of handedness in great apes. *Psychological Bulletin*.

Hopkins, W. D., Bard, K. A., Jones, A., & Bales, S. (1993). Chimpanzee hand preference for throwing and infant cradling: Implications for the origin of human handedness. *Current Anthropology, 34,* 786–790.

Hopkins, W. D., Dahl, J. F., & Pilcher, D. (2001). Genetic influence on the expression of hand preferences in chimpanzees (*Pan troglodytes*): Evidence in support of the right shift theory and developmental instability. *Psychological Science, 12,* 299–303.

Hopkins, W. D., Hook, M., Braccini, S., & Schapiro, S. J. (2003). Population-level right handedness for a coordinated bimanual task in chimpanzees (*Pan troglodytes*): Replication and extension in a second colony of apes. *International Journal of Primatology, 24,* 677–689.

Hopkins, W. D., Russell, J., Freeman, H., Buehler, N., Reynolds, E., & Schapiro, S. J. (2005). The distribution and development of handedness for manual gestures in captive chimpanzees (*Pan troglodytes*). *Psychological Science, 16,* 487–493.

Hopkins, W. D., Russell, J., Hook, M., Braccini, S., & Schapiro, S. (2005). Simple reaching is not so simple: Association between hand use and grip preferences in captive chimpanzees. *International Journal of Primatology, 26,* 259–277.

Hopkins, W. D., Wesley, M. J., Izard, K., Hook, M., & Schapiro, S. J. (2004). Chimpanzees are predominantly right-handed: Replication in three colonies of apes. *Behavioral Neuroscience, 118,* 659–663.

Hostetter, A., Cantero, M., & Hopkins, W. D. (2001). Differential use of vocal and gestural communication in chimpanzees in response to the attentional status of a human audience. *Journal of Comparative Psychology, 115,* 337–343.

Lonsdorf, E. V., & Hopkins, W. D. (2005). Wild chimpanzees show population-level handedness for tool use. *Proceedings of the National Academy of Sciences, USA, 102,* 12634–12638.

MacNeilage, P. F., Studdert-Kennedy, M. G., & Lindblom, B. (1987). Primate handedness reconsidered. *Behavioral and Brain Sciences, 10,* 247–303.

Marchant, L. F. (1983). *Hand preferences among captive island groups of chimpanzees*. Unpublished doctoral dissertation, Rutgers, The State University of New Jersey, New Brunswick.

Marchant, L. F., & McGrew, W. C. (1996). Laterality of limb function in wild chimpanzees of Gombe National Park: Comprehensive study of spontaneous activities. *Journal of Human Evolution, 30,* 427–443.

McGrew, W. C., & Marchant, L. F. (1992). Chimpanzees, tools, and termites: Hand preference or handedness? *Current Anthropology, 33,* 114–119.

McGrew, W. C., & Marchant, L. F. (1996). In W. C. McGrew, L. F. Marchant, & T. Nishida (Eds.), *Great ape societies* (pp. 255–272). Cambridge, England: Cambridge University Press.

McGrew, W. C., & Marchant, L. F. (1997). On the other hand: Current issues in and meta-analysis of the behavioral laterality of hand function in nonhuman primates. *Yearbook of Physical Anthropology, 40,* 201–232.

Olson, D. A., Ellis, J. E., & Nadler, R. D. (1990). Hand preferences in captive gorillas, orangu-tans, and gibbons. *American Journal of Primatology, 20,* 83–94.

Palmer, A. R. (2002). Chimpanzee right-handedness reconsidered: Evaluating the evidence with funnel plots. *American Journal of Physical Anthropology, 118,* 191–199.

Palmer, A. R. (2003). Reply to Hopkins and Cantalupo: Chimpanzee right-handedness reconsidered: Sampling issues and data presentation. *American Journal of Physical Anthropology, 121,* 382–384.

Rogers, L. J., & Andrew, J. R. (2002). *Comparative vertebrate lateralization*. Cambridge, England: Cambridge University Press.

Shafer, D. D. (1993). Patterns of hand preference in gorillas and children. In J. P. Ward & W. D. Hopkins (Eds.), *Primate laterality: Current behavioral evidence of primate asymmetries* (pp. 267–283). New York: Springer-Verlag

Vallortigara, G., & Rogers, L. J. (2005). Survival with an asymmetrical brain: Advantages and disadvantages of cerebral lateralization. *Behavioral and Brain Sciences, 28,* 575–589.

Warren, J. M. (1980). Handedness and laterality in humans and other animals. *Physiological Psychology, 8,* 351–359.

Watson, N. V. (2001). Sex differences in throwing: Monkeys have a fling. *Trends in Cognitive Science, 5,* 98–99.

Westergaard, G. C., Liv, C., Haynie, M. K., & Suomi, S. J. (2000). A comparative study of aimed throwing by monkeys and humans. *Neuropsychologia, 38,* 1511–1517.

Zatorre, R. J., Belin, P., & Penhune, V. B. (2002). Structure and function of auditory cortex: Music and speech. *Trends in Cognitive Sciences, 6,* 37–46.

Received September 8, 2004
Revision received March 2, 2005
Accepted March 4, 2005 ■

New Editors Appointed, 2007–2012

The Publications and Communications (P&C) Board of the American Psychological Association announces the appointment of three new editors for 6-year terms beginning in 2007. As of January 1, 2006, manuscripts should be directed as follows:

- *Journal of Experimental Psychology: Learning, Memory, and Cognition* (www.apa.org/journals/xlm.html), **Randi C. Martin, PhD,** Department of Psychology, MS-25, Rice University, P.O. Box 1892, Houston, TX 77251.

- *Professional Psychology: Research and Practice* (www.apa.org/journals/pro.html), **Michael C. Roberts, PhD,** 2009 Dole Human Development Center, Clinical Child Psychology Program, Department of Applied Behavioral Science, Department of Psychology, 1000 Sunnyside Avenue, The University of Kansas, Lawrence, KS 66045.

- *Psychology, Public Policy, and Law* (www.apa.org/journals/law.html), **Steven Penrod, PhD,** John Jay College of Criminal Justice, 445 West 59th Street N2131, New York, NY 10019-1199.

Electronic manuscript submission. As of January 1, 2006, manuscripts should be submitted electronically through the journal's Manuscript Submission Portal (see the Web site listed above with each journal title).

Manuscript submission patterns make the precise date of completion of the 2006 volumes uncertain. Current editors, Michael E. J. Masson, PhD, Mary Beth Kenkel, PhD, and Jane Goodman-Delahunty, PhD, JD, respectively, will receive and consider manuscripts through December 31, 2005. Should 2006 volumes be completed before that date, manuscripts will be redirected to the new editors for consideration in 2007 volumes.

In addition, the P&C Board announces the appointment of **Thomas E. Joiner, PhD** (Department of Psychology, Florida State University, One University Way, Tallahassee, FL 32306-1270), as editor of the *Clinician's Research Digest* newsletter for 2007–2012.