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Chimpanzee Hand Preference in Throwing and Infant Cradling: Implications for the Origin of Human Handedness[1]

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Calvin (1983) has hypothesized that the neurophysiological, perceptual, and cognitive demands of throwing may have served as important evolutionary precursors to a variety of traits (e.g., handedness, tool use, and language processing) in early hominids. Eighty-eight percent of humans throw with their right hands (Healey, Liederman, and Geschwind 1986), and Calvin has argued that this right-handed throwing evolved as a result of a left-hemisphere specialization for planned sequential movements. He has further suggested that right-handed throwing would have been more prevalent in females than in males because females predominantly carried infants on the left arm, leaving the right hand available for other actions. Infant carrying has also been hypothesized as a major selective feature in the evolution of bipedalism in hominids (Leakey 1976).

Whether nonhuman primates exhibit population-level hand preference for any behavior is a topic of considerable recent debate (Corballis 1992, Fagot and Vauclair 1991, MacNeilage 1991, MacNeilage, Studdert-Kennedy, and Lindblom 1987, Marchant and McGrew 1992, Warren 1980, Ward and Hopkins 1993). Population-level hand preferences have been reported for carrying, object manipulation, and bimanual activities in great apes (see Hopkins and Morris 1993 for review), but some researchers question the applicability of nonhuman primate findings to considerations of human handedness (Byrne and Byrne 1991, Corballis 1992). Feral as well as captive chimpanzees have been observed to throw objects at potential predators, during aggression, and in displays (Goodall 1986:550–59; Marchant 1983). In feral chimpanzees there are clear gender differences in the frequency and persistence of throwing: males exhibit higher levels than females. In addition, in most instances, the throwing is goal-directed (Goodall 1986). There are, however, few experimental reports or observational studies of hand use in throwing in nonhuman primates (Marchant 1983, Morris, Hopkins, and Bolser Gilmore 1993). Chimpanzees housed at the Yerkes Regional Primate Research Center (YRPRC) throw objects at unfamiliar humans visiting or working near the housing facility. Systematic data were collected on this throwing in an effort to examine Calvin's model with respect to hand use in aimed throwing.

There are some reports of a significant population-level left-side carrying bias in both great apes and monkeys (Hatta and Koike 1991, Lackard 1984, Manning and Chamberlain 1990), but the definitions of carrying and the nature of the object being carried vary. Lateral bias in carrying is operationally defined in some studies as head position of the infant (Manning 1991, Manning and Chamberlain 1990, Manning, Chamberlain, and Heaton 1992, Hatta and Koike 1991) and in other studies as the hand used to hold an object (e.g., Hopkins et al. n.d.). In at least one study, a left-side bias was found for carrying of objects other than infants, and therefore the role of infants per se in the lateralization of carrying can be questioned (Hopkins et al. n.d.). In other studies, no significant left-side bias was found (Morris, Hopkins, and Bolser Gilmore 1993, Marchant 1983). Recent studies suggest that infant head position may be influenced by nipple preference rather than asymmetric maternal carrying (e.g., Nishida 1993). Finally, it is not clear from the previous studies whether the bias is due to the mothers' carrying bias or to some lateral bias in the infants' behavior (e.g., hand preference for clinging or nipple preference). In order to address this issue, hand preference for infant cradling was assessed in a group of mother-infant pairs of chimpanzees at the YRPRC when the infants were less than 72 hours of age and therefore incapable of contributing support (Bard n.d.). Infants' hand preferences at two to three years of age were assessed with a simple reaching measure in order to examine the relationship between infant cradling and subsequent infant hand preference.

Observations of throwing were made on 36 chimpanzees (*Pan troglodytes*)—18 males and 18 females (table 1). Observations were made daily between the months of June and August 1992. The number of throwing responses observed per subject ranged from 1 to 45 (M = 10.59). The chimpanzees were observed to throw when unfamiliar humans walked or ran by their outdoor enclosures. They typically threw small objects such as pieces of monkey chow (about 2 cm in diameter). During each observed throwing event, the posture of the chimpanzee (quadrupedal or bipedal), whether the object was thrown underhand or overhand, and which hand was used to throw were recorded.

Using a 50% classification criterion, 24 chimpanzees were categorized as right-handed (>50% right-hand use), 9 as left-handed (<50% right-hand use), and 3 as ambi-

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dextrous (50% right-hand use) (table 1). The distribution differed significantly from chance ($\chi^2[2] = 19.5$, $p < .01$). Comparing only the left- and right-handed subjects revealed a significantly unequal distribution ($\chi^2[1] = 6.82$, $p < .01$). A more conservative estimate was obtained by considering only those chimpanzees with eight or more observations. In this conservative analysis, a significant right-hand population bias was also found (15 right-handed, 4 left-handed: $\chi^2[1] = 6.36$, $p < .01$). No significant gender differences emerged from this analysis.

Posture was an important factor in the expression of right-handed throwing (fig. 1). Percentage right-hand use served as the dependent measure in a two-factor analysis of variance, with gender and posture serving as independent variables. A main effect for posture was found ($F[1, 32] = 6.73$, $p < .05$); chimpanzees that threw while standing bipedally used the right hand significantly more often than the left. When the percentage right-hand use as a function of posture was examined for males and females separately, a significant interaction between right-hand use and bipedal posture was found for males ($F[1, 16] = 8.71$, $p < .01$) but not for females ($F[1, 16] = 0.23$, $p > .10$). Females tended to throw with the right hand in both quadrupedal and bipedal posture; males threw with the right hand when standing bipedally but were less consistent in hand use when throwing from a quadrupedal posture. The modal pattern of throwing can best be described as resembling that of a baseball pitcher. The chimpanzee stood bipedally, stepped forward placing its body weight on the left leg, and hurled the material. In nearly every throwing event, the material hit the target. Moreover, the distribution of bipedal ($N = 13$) and quadrupedal ($N = 5$) throwing was identical for males and females. Finally, the overall frequency of throwing did not differ significantly for males and females ($F[1, 32] = 0.346$, $p > .20$).

Observations of infant cradling were made on 12 captive mother-infant pairs of chimpanzees. Each pair was videotaped for a continuous 60-minute period between 9:30 and 11:00 A.M. within 72 hours of the infant's birth. The beginning and end of each bout of cradling, defined as the mother's actively supporting the infant with her limbs for at least 3 seconds, were recorded, indicating whether the right hand, the left hand, both hands, or the legs/knees were used to support the infant's weight. For each pair, the data were summarized for both frequency and duration (in seconds) of right- and left-hand cradling. A handedness index (l − r/r + l) (see Bard, Hopkins, and Fort 1990) was calculated on the basis of the duration measures of infant cradling for each mother (table 2). Seven mothers exhibited a left-side bias and 5 mothers a right-side bias in cradling their offspring. This distribution did not differ significantly from chance ($\chi^2[1] = 0.67$, $p > .10$). From previous research we determined the hand preferences of 9 of 12 infants on which we had cradling data from their mothers (Hopkins et al. 1993) (table 2). A binomial z-score was determined on the basis of a 50% probability that the infant would have the same preference as the mother. This analysis revealed a significant negative relationship ($p = .004$). In all 9 cases, the infants exhibited hand preferences opposite to their mothers' cradling preferences.

TABLE 1
Sex, Age, and Hand Preference for Throwing

Subject	Age[a]	Left	Right	Sum	Hand[c]
Females					
Alice	31,00[b]	0	16	16	r
Artefee	16,00	0	3	3	r
Augusta	17,11	8	0	8	l
Bertha	15,04	0	1	1	r
Brodie	8,06	0	2	2	r
Buffy	8,06	0	13	13	r
Chrissy	5,06	2	2	4	a
Cissie	16,08	2	2	4	a
Elvira	3,09	0	3	3	r
Jacqueline	15,09	7	17	24	r
Jesse	9,11	1	19	20	r
Lee	8,08	0	4	4	r
Mega	7,08	10	6	16	l
Melissa	11,01	41	1	42	l
Mickie	21,02	2	0	2	l
Suzanna	16,05	4	11	15	r
Valerie	8,01	1	7	8	r
Vivienne	18,00	3	27	30	r
Mean	13,4				
Males					
Artifact	13,01	3	0	3	l
Brian	13,04	0	11	11	r
Carl	6,02	2	1	3	l
Hunter[d]	7,11	6	0	6	l
Jarred	4,11	3	9	12	l
Jorg	24,05	9	0	9	l
Joseph	11,08	0	23	23	r
Justin	5,11	1	0	1	l
Lamar	4,03	0	2	2	r
Lyons[d]	7,11	0	18	18	r
Merv	16,06	0	2	2	r
Mortimer	15,04	0	8	8	r
Ossabaw	15,05	3	3	6	a
Puddin	13,05	0	10	10	r
Sam	10,02	0	13	13	r
Sellers	8,05	0	45	45	r
Tank	6,05	0	3	3	r
Zeb	12,05	0	1	1	r
Mean	11,0				

[a]Years, months.
[b]Estimated.
[c]*r*, right; *l*, left; *a*, ambidextrous.
[d]Twins.

The mothers observed varied in amount of previous maternal experience; 4 were primiparous and 8 multiparous. Under the hypothesis that multiparous females would show more consistent bias in their cradling because of their previous maternal experience, an independent t test was performed with regard to the absolute strength of lateral bias for primiparous contrasted with multiparous females. Although multiparous females had a much stronger lateral bias ($M = 0.65$) than primiparous females ($M = 0.23$), the difference failed to reach statistical significance ($t[10] = 1.72$, $p > .10$).

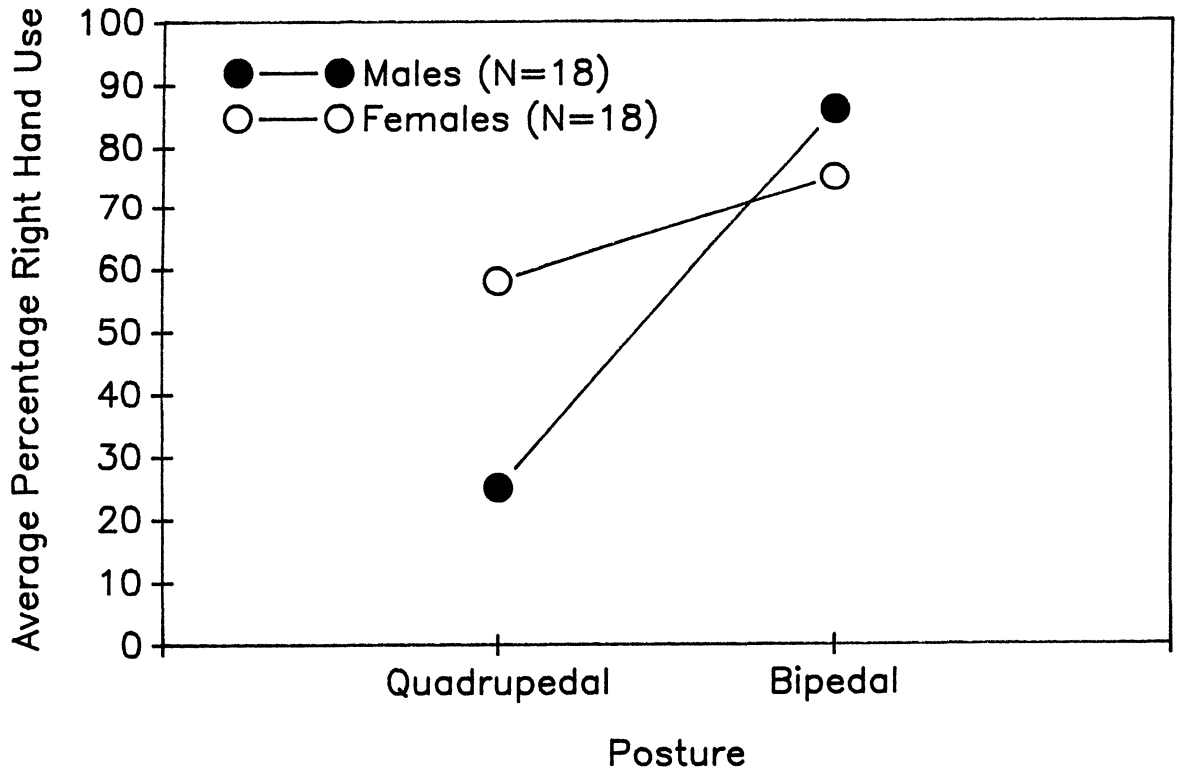

FIG. 1. *Bipedalism and percentage right hand use for throwing.*

TABLE 2
Handedness Index for Infant Cradling

Mother	HI	Hand[a]	Parity[b]	Offspring	HI	Hand[a]
Joice	.53	r	m	Olin	−1.00	l
Leslie	−.98	l	m	Dara	.30	r
Vivienne	−.74	l	m	Wilma	1.00	r
Barbi	−.67	l	p	Elvira	.60	r
Lil'One	.99	r	m	Polyanna	−.81	l
Cynthia	.28	r	p	Alicia	−.88	l
Cissie	.30	r	p	Travis	−.66	l
Tai	−.63	l	m	Daisey	.30	r
Barbara	−.14	l	m	Kevin	1.00	r
Peony	−.89	l	m	Donna	n.a.	n.a.
Suwane	−.02	l	p	Jolson	n.a.	n.a.
Melinda	.24	r	m	Agatha	n.a.	n.a.

[a] *r*, right-side bias; *l*, left-side bias.
[b] *m*, multiparous; *p*, primiparous.

Recent findings have revealed population-level right-handedness for bipedal but not quadrupedal reaching in chimpanzees (Hopkins 1993), orangutans (Hopkins 1993), bonobos (Hopkins et al. n.d.), and gorillas (Olson, Ellis, and Nadler 1990). In contrast, studies of bipedal reaching in monkeys have failed to reveal a significant population-level bias (King 1992), whereas prosimian species have exhibited a population-level left-hand bias (Ward et al. 1990). Thus, the shift toward right-handedness and bipedalism is specific to the pongids. The current finding of a right-hand bias in throwing may simply be an artifact or an extension of a preexisting right-hand bias for reaching, both of which are contingent upon bipedal posture.

With respect to infant cradling, our results are inconsistent with the findings of Manning and Chamberlain (1990) on infant carrying in great apes and the lateralized carrying results reported for bonobos by Hopkins et al. (n.d.), but the data collection procedures of these studies differ from ours in some important ways. Manning and Chamberlain measured the side preference on the infant when clinging to the mother rather than maternal behavior. Furthermore, they included infants up to one and a half years of age (Manning, Hopkins, and Bolser Gilmore 1993), and the infants may have contributed their independent behavior to the creation of side preferences. Hopkins et al. (n.d.) measured carrying bouts that entailed bipedal and quadrupedal locomotion. When both maternal hand use and locomotion were examined in wild chimpanzees, no lateral bias in maternal cradling was found (Nishida 1993). Before concluding that infant cradling or carrying is lateralized in great apes, these discrepancies in findings and methodology will need to be resolved.

We believe that our finding of a relation between side bias in infant cradling by the mother and hand preference for reaching by the infants may explain differences in hand preference in chimpanzees from different rearing environments. Hopkins et al. (1993) found that nurs-

ery-reared chimpanzee infants exhibited higher levels of right-handedness than mother-reared chimpanzees. Nursery-reared chimpanzees receive their primary care from humans, who have been shown to exhibit a population-level left-side bias in infant carrying (Lockard, Daley, and Gunderson, 1979, Manning and Chamberlain 1990). Because we found that left-side cradling by the biological mother is associated with right-hand reaching preference in the infant, it may be that the human caretakers are similarly influencing the hand preferences of nursery-reared chimpanzees. Specifically, we may be finding right-handedness in nursery-reared chimpanzees because of the human tendency to carry infants on the left side. Notwithstanding, nursery-reared chimpanzees exhibit a right-hand bias in hand-to-mouth behaviors as early as three months of age (Bard, Hopkins, and Fort 1990, Hopkins and Bard 1993). We cannot rule out possible effects of these early asymmetries in the care-giving environment on lateral bias in infant behavior.

The negative relationship between infant cradling and hand preference found in this study may explain some conclusions regarding the heritability of hand preference in monkeys (Brinkman 1984, Kubota 1990). We found that if a mother has a left-hand cradling bias, then her infant will reach for objects with the right hand. Presumably the mother will also use her right hand for simple reaching because her left hand is carrying the infant. The infant's right-hand reaching bias is the same as the mother's right-hand reaching, but it is not due to heritability of handedness. Therefore, by extension, an apparent heritability effect can be explained by very different mechanisms.

These first published data on hand preference for throwing in a nonhuman species partially support Calvin's (1983) hypothesis; it appears that the origin of handedness may have been influenced by evolutionary selection for throwing. However, this effect is neither specific to hominid evolution nor especially pronounced in females. The findings from this study suggest that population-level handedness was evident prior to rather than subsequent to the evolution of bipedalism in humans. Most evolutionary theories of hemispheric specialization have assumed that it evolved after the evolution of bipedalism, when the hands were relieved of their principal role in locomotion and consequently developed skills for gestural communication (Hewes 1973) or tool use (Frost 1980)—selective pressure toward bimanual or coordinated hand use eventually resulting in the emergence of asymmetric roles for the two hands. It is suggested here that hemispheric specialization in posture and locomotor systems may instead have served as a selective advantage for the evolution of tool use, throwing, or communication.

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