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# A Longitudinal Study of Hand Preference in Chimpanzees (*Pan troglodytes*)

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**ABSTRACT:** A longitudinal study of hand preferences was assessed in a sample of 53 captive chimpanzees. Four measures of laterality assessed during the first 3 months of life were correlated with three measures of hand preferences assessed when the subjects were between 2 and 5 years of age. In addition, the effect of rearing environment on juvenile hand preferences was assessed in a larger sample of 83 chimpanzees. Overall, some early asymmetries were predictive of juvenile hand preferences, notably head orientation and hand-to-hand activities, and a defensive grasping response. No significant effects of rearing on hand preferences were found but males were more right-handed than females for two of the three juvenile measures. The results are discussed within the context of different developmental models of hand preference in humans. © 2000 John Wiley & Sons, Inc. *Dev Psychobiol* 36: 292–300, 2000

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Approximately 90 percent of humans report themselves as being right-handed (Annett, 1985; Corballis, 1992; Porac & Coren, 1981). The historical view holds that nonhuman animals, and particularly nonhuman primates, do not exhibit population-level handedness (see Ettliger, 1988; Warren, 1980). In recent years, behavioral research in a variety of nonhuman primate species using a multitude of tasks have revealed that population-level handedness is evident for certain measures (Bradshaw & Rogers, 1993; Hopkins, 1996; Ward & Hopkins, 1993). In addition to handedness, evidence of perceptual and cognitive asymmetries in a host of animal species have been reported (Bisazza, Rogers, & Vallortigara, 1998; Bradshaw & Rogers, 1993). These cumulative data clearly challenge the

historical view purporting the uniqueness of hemispheric specialization to humans.

With the emergence of evidence for population-level handedness in nonhuman primates, a fundamental question that has arisen is whether similar biological or ontogenetic mechanisms account for the development of handedness in human and nonhuman primates (see Previc, 1991). Unfortunately, there are very few studies that have examined the ontogeny of hand preference in nonhuman primates using longitudinal methods (Hopkins & Bard, 1993a; Marchant & McGrew, 1991). With respect to developmental models of handedness, it has been proposed that early biological asymmetries are predictive of later manifestations of handedness, although the exact mechanism differs between models (see Hopkins & Ronnqvist, 1998; Provins, 1997; Trevarthen, 1996 for reviews). For example, Michel (1981) proposed that handedness, particularly right-hand preferences, de-

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velop from an existing right-sided asymmetry in head orientation observed early in life. In this model, the right-sided head orientation facilitates greater hand–eye coordination that subsequently leads to preferential use of the right hand. Previc (1991) expanded upon the head orientation model by proposing that the initial right-sided asymmetry in head orientation was due to an inherent positional asymmetry of the infant in utero during the last trimester of gestation. According to Previc (1991), the in utero positional asymmetry results in shearing of the otolithic nerves which differentially stimulates the maturation of each cerebral hemisphere. Others have proposed that asymmetries expressed by the fetus determine the development of handedness in humans. For instance, Hepper and colleagues (Hepper, McCartney, & Shannon, 1998; Hepper, Shahidullah, & White, 1991) have reported that fetuses exhibit right-sided asymmetries in thumb-sucking and arm movements within the first trimester. This differential stimulation of the right hand and arm could lead to maturational neural connectivity in the central nervous system that underlies the development of handedness.

One purpose of this study was to assess whether forms of laterality observed in neonatal chimpanzees are predictive of hand preferences assessed during the juvenile period of development. In several published articles, lateral bias for head orientation, hand-to-mouth behavior, hand-to-hand behavior, defensive grasps, and stepping reflexes were reported in infant chimpanzees raised at the Yerkes Regional Primate Research Center (YRPRC) (Bard, Hopkins, & Fort, 1990; Hopkins & Bard, 1993b, 1995). Most of the chimpanzees that served as subjects in the studies of lateral bias in neonatal chimpanzees were tested for hand preference when they reached 2 to 4 years of age. The hand-preference measures included simple reaching, bimanual feeding, and coordinated bimanual actions. Thus, we had a unique opportunity to longitudinally assess the development of lateral bias in chimpanzees. In particular, we wanted to test Michel's (1981) developmental model of hand preference in a sample of chimpanzees. Hopkins and Bard (1995) reported that neonatal chimpanzees exhibit population-level, right-sided biases in head orientation while sleeping in a supine but not prone posture, a result consistent with at least some findings in humans. If the Michel model is correct then individual biases in head orientation should predict hand preference in chimpanzees assessed at a later period in development. We believe that developmental hand-preference data from closely related species, such as the chimpanzee, are valuable from an ontogenetic standpoint because they can provide data that can speak to common biological

mechanisms accounting for similar behaviors between species.

A second purpose of this study was to assess the effect of certain subject variables on the development of hand preference in chimpanzees. Specifically, we were interested in examining the effects of rearing environment and sex on hand preference. With respect to rearing history, in some nonhuman species such as rats, early handling experiences induce functional asymmetries that are not observed in nonhandled rats (see Denenberg, 1988). These results suggest that early environmental experiences induce asymmetry rather than the asymmetries being a consequence of an endogenous asymmetry. Others have suggested that the evidence of population-level asymmetries in captive chimpanzees reflect the fact that they have been raised in human environments and by humans (McGrew & Marchant 1997). Presumably, the exposure to human-rearing practices and human environments biases the subjects toward greater preferential use of the right hand. Because chimpanzees born at the YRPRC are differentially reared by either humans or chimpanzees, it offers a unique paradigm for investigating rearing effects on handedness in a species that is biologically, physiologically, genetically, and psychologically more similar to humans than the rodent.

## METHODS

### Subjects

Eighty-three captive chimpanzees were the subjects in this study, including 43 females and 40 males. There were 30 mother-reared subjects (12 males, 18 females) and 53 nursery-reared subjects (28 males, 25 females), respectively. Any chimpanzee that stayed with its biological mother beyond 30 days or more was considered mother-reared. Chimpanzees that entered the YRPRC nursery were considered nursery-reared. Within the nursery-reared sample, 36 subjects were raised following standard nursery care procedures employed at the YRPRC. The remaining 17 nursery-reared subjects were raised following standard nursery-care procedures but received an additional 3 hr of responsive care interactions with human caretakers during the first year of life (for description see Bard, 1996). The nursery-reared subjects were the subsample of chimpanzees that participated in the longitudinal aspect of this study.

### Measures of Lateral Bias

Because this was a longitudinal study, different measures of lateral bias were taken at different points in

the life span. One set of measures was taken during the first 3 months of life and was collected during administration of the scales of development used to assess neurobehavioral integrity in neonatal chimpanzees. The neonatal measures of lateral bias included head orientation, hand-to-mouth, hand-to-hand, and defensive grasp; the specific details of the testing procedures have been described previously (see Bard, 1994, 1998; Bard et al., 1990; Hopkins & Bard, 1993b, 1995). The second set of measures was obtained when the subjects were between 3 and 5 years of age. Within this period of development, hand preferences were assessed for simple reaching, bimanual feeding, and coordinated bimanual actions following procedures described in detail elsewhere (Hopkins, 1994, 1995a, 1995b; Hopkins, Bennett, Bales, Lee, & Ward, 1993). Listed next is a brief description of each measure and the general procedure used to assess laterality and hand preference.

### Neonatal Measures

**Head Orientation.** Prior to the administration of the NBAS, the experimenter would enter the nursery and make a note of whether the subjects were sleeping or awake. If the subjects were sleeping, the experimenter made a note of their posture and orientation of the head (HEAD; left or right). Only one observation of lateral bias was made per test session.

**Hand-to-Mouth.** This behavior is considered a self-calming behavior. During administration of the NBAS, when infants became fussy or cried, there were allowed 15 s to calm themselves. One manner of self-calming is by exhibiting hand-to-mouth (HTM) behavior. HTM behavior consists of the finger, wrist, fist, or thumb inserted into the mouth and were recorded only after a period of fussiness or crying. The hand/digit inserted was recorded as left or right. All instances of HTM behavior that occurred within a test session were recorded.

**Hand-to-Hand.** This behavior is also considered a self-calming behavior. During administration of the NBAS, when infants became fussy or cried, there were allowed 15 s to calm themselves. Rather than engage in HTM behavior, some infants calmed themselves by exhibiting hand-to-hand (HTH) behavior. HTH behavior consists of grabbing on hand, arm, or wrist with the fingers of the opposite hand as a means of self-calming. The hand performing the grasping was recorded as right or left. All instances of HTH behavior that occurred within a test session were recorded.

**Defensive Grasp.** Defensive grasp (DEF) responses were elicited by placing a blanket over the face of the neonate, which was lying supine on a table. The hand used to swipe at or grasp the cloth is recorded as left or right. Upper quadrant swipes, swipes to the midline, and the actual grasps of the cloth were all recorded for laterality during each test.

### Juvenile Measures

**Simple Reaching.** Peanuts were placed 16 cm from the cage on a cement edge adjacent to the outdoor cage 10 cm above the ground. To retrieve the peanuts, subjects had to reach through the cage mesh, grasp the food item, and pull it back into the cage. The hand used to pick up the peanut was scored each trial (simple reaching [REACH]). A minimum of 30 responses was obtained from each subject.

**Bimanual Feeding.** Each afternoon, the primates housed at the YRPRC receive fruits and vegetables as part of their daily diet. Each subject usually receives two oranges, one banana, some celery stalks, and/or carrots. Hand use was recorded when the subjects were feeding with one hand for a minimum duration of 3 s and the nonfeeding hand was holding the remaining portions of food (bimanual feeding [FEED]). Observations were made over a 60-day period and only one response was recorded each day.

**Coordinated Bimanual Tube Task.** The coordinated bimanual tube task (TUBE) consisted of the following: PVC tubes (24 to 31 cm long, 2.5 cm wide) with peanut butter smeared on the inside were given to the subjects in their home cage. The digit and hand used to remove the peanut butter was recorded each time the subjects inserted their finger, removed peanut butter from the tube, and placed their finger in their mouth. Observations continued until the subjects stopped showing interest in the tube (usually when they have eaten all the peanut butter), dropped it for at least 10 s, or pushed the tube back out of their home cage through the cage mesh. Each subject received two test sessions, separated by at least 1 day.

### Procedure

All chimpanzees that enter the Yerkes Center nursery are administered the Brazelton Neonatal Assessment Scale (NBAS; Brazelton, 1984) during the first 3 months of life (see Bard, 1994; Bard, Platzman, Lester, & Suomi, 1992). The NBAS was administered by two certified raters that were trained to 90% interrater reliability prior to the onset of the study. For the neonatal measures of lateral bias, subjects were

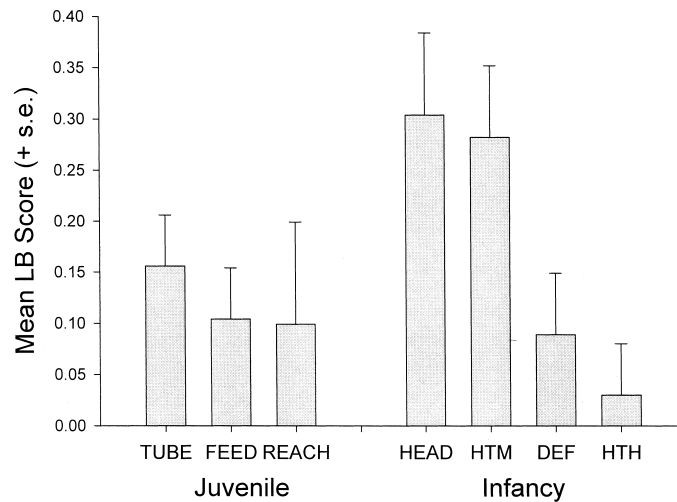


FIGURE 1 Mean LB score and standard error for each measure of laterality.

assessed every other day for the first 6 weeks of life. From 7 to 12 weeks of life, the chimpanzees were assessed once a week. At the end of the 3-month test period, the total number of left- and right-sided responses was calculated for each measure and subject.

With respect to the juvenile measure of handedness, individual data were collected in the subjects' home cage, including the indoor and outdoor portions of the enclosure. The home cages varied in size and shape depending on the housing assignment of each subject but all cages were constructed of 5-cm wire mesh. Additionally, the number of individuals in each home cage varied from 2 to as many as 16 animals. For each measure, focal animal-sampling techniques were used. Thus, individual animals were not separated from their social groups for the purposes of data collection.

Two general procedural controls were followed for all measures. First, the hand used by the experimenter in placing food items or handing test materials to the subjects was always randomized across trials. This randomization was done to assure that the subjects were not imitating the hand use of the experimenters. Second, the presentation of food items, particularly for the simple reaching measure, were displaced temporally and spatially over time. That is, items were not placed in the same location, and subjects were tested over many days rather than collecting all trials during 1 day of testing. For all three measures, test-retest correlations were positive (.65 or higher) and significant over 1 month to 2-year test-retest intervals (see Hopkins, 1994, 1995a, 1995b). During hand-preference testing, the experimenters were blind to the neonatal measures of laterality. Due to changes in the housing conditions and availability for testing, data were not collected in all subjects for each of the measures. The number of chimpanzees tested for the REACH, FEED, and TUBE tasks were 71, 62, and 69, respectively.

## Data Analysis

In order to use one common scale of measurement in laterality, a lateral bias (LB) index was determined for each subject and measure by subtracting the number of left-sided responses from the number of right-sided responses and dividing by the total number of responses. Positive values reflected right-sided biases and negative values reflected left-sided biases. The absolute values of the LB indices (ABS-LB) reflected the strength of lateral bias. Population-level asymmetries were evaluated using one-sample *t* tests. Comparisons between sex and rearing-history variables were performed using parametric statistics (*t* tests and analysis of variance [ANOVA] with alpha at  $p < .05$ ). All post hoc analyses were performed using Tukey's Honestly Significant Difference (HSD) at  $p < .05$ .

## RESULTS

### Population Effects

Depicted in Figure 1 are the mean LB scores for each measure of lateral bias. One-sample *t* tests were used to assess population-level hand preference. Significant right-hand biases were found for the bimanual feeding,  $t(61) = 2.07, p < .05$ , and the coordinated bimanual tube task,  $t(68) = 2.90, p < .02$ . Population-level hand preferences were not found for the simple reaching measure,  $t(70) = 1.03, p > .10$ . Within the infancy period of development, significant right-sided population asymmetries were found for HEAD,  $t(35) = 3.79, p < .001$ , and HTM,  $t(42) = 3.72, p < .001$ . No significant population biases were found for the HTH and DEF measures.

## Sex and Rearing Effects on Juvenile Hand Preferences

Three univariate ANOVAs were performed with the LB and ABS-LB scores for the TUBE, FEED, and REACH task serving as the dependent variables. Sex (male, female) and rearing history (mother, nursery) served as the independent variables. No significant main effects or interactions were found for the TUBE task. For the FEED task, a significant sex difference was found,  $F(1, 58) = 9.77, p < .001$ , with males having significantly higher LB scores ( $M = .286$ ) than females ( $M = -.045$ ). Similarly, for the REACH task, significant sex differences were revealed,  $F(1, 67) = 4.05, p < .05$ , with males having higher HI scores ( $M = .290$ ) than females ( $M = -.131$ ). For the infancy measures,  $t$  tests for independent samples failed to reveal sex differences in laterality for any of the measures. No significant main effects or interactions were found for the ABS-LB scores for each of the three measures of hand preference.

## Regression Analyses: Ontogenetic Determinants

For these analyses, three hierarchical multiple regression analyses were performed with the dependent measures being the LB values for the coordinated bimanual tube, bimanual feeding, and simple reaching measures. For each regression analysis, there were three blocks of independent variables entered into the equation. First, sex was entered as a single predictor variable. Second, two categorical rearing variables were entered. The categorical rearing variables were weighted using polynomial weights, and the two categories included the comparison of individuals that entered the nursery late contrasted with all other individuals. The second rearing contrast was the standard care individuals compared to the responsive care individuals. The final block variable contained the four neonatal measures of lateral bias including HEAD, HTM, HTH, and DEF. The results for the three regression analyses are depicted in Table 1.

For the TUBE, FEED, and REACH tasks, the multiple  $R$  values were .642, .603, and .603, respectively. For the TUBE task, the  $R$  value reached statistical significance,  $F(6, 22) = 2.57, p < .05$ , whereas the  $R$  values were borderline significant for the FEED,  $F(6, 22) = 2.19, p < .10$ , and REACH,  $F(6, 22) = 2.57, p < .10$  tasks. For the TUBE task, rearing history and HEAD orientation accounted for a significant proportion of variance. Chimpanzees receiving responsive care in addition to standard nursery rearing had higher LB scores than chimpanzees reared only in the standard nursery-rearing condition. In addition, chimpan-

**Table 1. Partial Correlation Coefficients for the Three Regression Analyses**

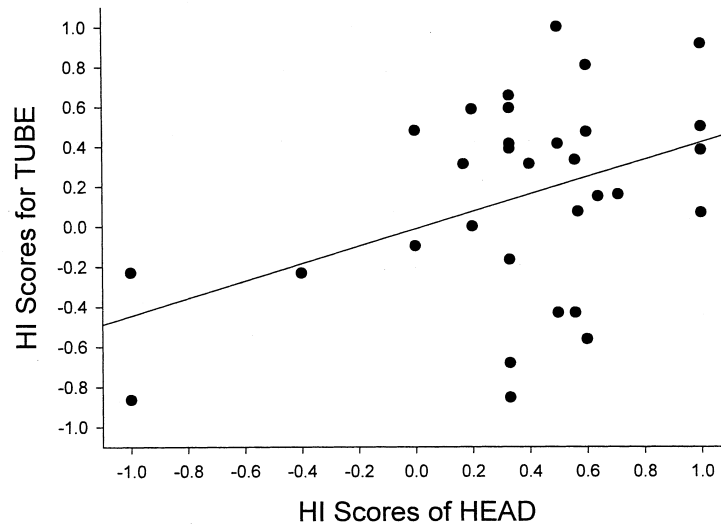
Predictor Variable	Beta	$t$	Significance
<b>TUBE</b>			
Sex	-.225	-1.26	n.s.
LATE	-.067	-0.32	n.s.
STAND	.405	2.11	$p < .05$
Neonatal measures			
HEAD	.453	2.71	$p < .02$
HTM	.094	0.52	n.s.
HTH	-.132	-0.76	n.s.
DEF	.063	0.89	n.s.
<b>FEED</b>			
Sex	-.481	-1.96	$p < .07$ .
LATE	.239	1.19	n.s.
STAND	.025	0.13	n.s.
Neonatal measures			
HEAD	.005	0.04	n.s.
HTM	.037	0.26	n.s.
HTH	-.259	-1.74	$p < .10$
DEF	-.352	-2.39	$p < .03$
<b>REACH</b>			
Sex	-.481	-1.96	$p < .07$ .
LATE	.098	0.48	n.s.
STAND	-.291	-1.49	n.s.
Neonatal measures			
HEAD	.056	0.23	n.s.
HTM	-.375	-1.20	n.s.
HTH	-.683	-2.13	$p < .05$
DEF	-.379	-1.19	n.s.

*Note.* See text for description of measures. LATE = the contrast between subjects who entered the nursery after 2 days of life but before 30 days and those that entered the nursery on Day 1. STAND = the contrast in subjects raised under standard conditions compared to those who received responsive care.

zees with higher LB scores on the HEAD task were more likely to be right-handed on the TUBE task (see Figure 2). For the FEED and REACH measures, none of the blocks accounted for a significant portion of variance although some of the individual predictor variables did reach statistical significance (see Table 1). Notably, for the FEED and REACH tasks, HTH scores were negatively correlated with the LB scores. Thus, subjects with more right-sided biases in HTH were more likely to use their left hands for reaching and feeding. For the REACH task, DEF was also negatively correlated with LB scores with more right-sided biases on the DEF measure predicting higher incidences of left-hand use in reaching.

## DISCUSSION

Several significant findings emerged from this study. First, lateral bias in supine head orientation in neonatal



**FIGURE 2** Scatterplot of LB measures for each subject with data on the HEAD and TUBE measures of laterality.

chimpanzees assessed during the first 3 months of life significantly predicted hand preference for coordinated bimanual actions between 3 to 5 years of age. Second, rearing in a responsive-care environment resulted in higher LB scores for coordinated bimanual actions. Second, sex differences in hand preference were evident for bimanual feeding and reaching, with males being more right-handed than females. Third, for simple reaching, nursery-reared chimpanzees had higher LB scores than mother-reared chimpanzees. Finally, population-level, right-side biases in laterality were evident for head orientation, hand-to-mouth behavior, bimanual feeding, and coordinated bimanual actions.

The evidence of population-level, right-side biases for HEAD, HTM, FEED, and TUBE is consistent with previous findings in our laboratory (Bard et al., 1990; Hopkins, 1994, 1995a, 1995b; Hopkins & Bard, 1993b, 1995). The significance of these findings is mostly relevant to the FEED and TUBE tasks, which have previously been cross-sectional samples of chimpanzees for which population-level right handedness was reported. The results of this study indicate that these asymmetries are present by 5 years of age in chimpanzees and are not restricted to samples of sub-adult or adult populations.

The evidence that lateral bias in head orientation predicted hand preferences for coordinated bimanual actions supports Michel's (1981) model of the development of hand preference in humans. In light of the fact that our observations were made in chimpanzees, it suggests that similar biological and ontogenetic mechanisms may influence the development of laterality in humans and apes. Michel proposed that the

initial head orientation to the right in neonates results in them seeing their right hand at an earlier age. This subsequently leads to differential stimulation of the right-sided hand-eye coordination, which leads to preferential use of the right hand as the infant grows older. We have no data that speak directly to this mechanism and therefore cannot determine whether this accounts for the observed association. Moreover, it is not clear why the HEAD measure correlates with the TUBE task but not the REACH or FEED tasks. Previous cross-sectional studies indicated that hand preferences for the TUBE task do not correlate with the FEED and REACH tasks but do correlate with other measures of hand use for coordinated bimanual actions (Hopkins & Pearson, in press). Hopkins and Pearson interpreted the lack of correlation between the TUBE and other tasks of hand preference as evidence that different neural or motor systems may be involved in the execution of these tasks (e.g., Fagot & Vauclair, 1991; Young, Segalowitz, Corter, & Trehub, 1983). It may be that the neonatal measures of lateral bias tap into different lateralized systems that may or may not predict adult forms of laterality as manifest in hand preferences (See Trevarthen, 1996). For example, Bard (1998) demonstrated in chimpanzees that lateral bias in HTM scores were inversely correlated with measures of affect taken from the Bayley Scales of Infant Development (BSID) in chimpanzees. Similarly, Bard (1998) demonstrated that HTH correlated with BSID scores for motor functions and DEF scores at 3 months of age correlated with affect scores at 9 months of age. Taken together, these data suggest that the HEAD orientation measure of asymmetry may reflect an endogenous asymmetry that is associated with

a specific motor system that is distinct from other measures of lateral biases assessed during the neonatal period of development.

From a comparative perspective, the results in chimpanzees (and humans) differ from those reported in capuchin monkeys (Westergaard, Byrne, & Suomi, 1998). Westergaard et al. (1998) assessed the lateralized location of the head in 16 infant monkeys when riding dorsally on their mothers back during the first two weeks of life. Westergaard and colleagues subsequently tested for hand preference at 24 and 48 weeks of life and found a negative correlation between head orientation and hand preference at 24 weeks. That is, subjects that predominantly had a left-sided head orientation were more right-handed at 24 weeks of age and vice versa. It is difficult to compare these findings due to different methodologies, but the cumulative data clearly support the contention that early mother–infant interactions can have an impact on the development of hand preference in primates (but see Rogers & Kaplan, 1998).

The findings from this study do not address the issue of why there is an initial head-orientation bias to the right in both humans and chimpanzees, at least as it pertains to measures of coordinated bimanual hand use. Previc (1991) proposed that the position of the fetus during the last trimester influences the orientation of the head after birth. Previc theorizes that human and nonhuman primates would differ in the expression of postural asymmetries that lead to the development of right-handedness because of inherent differences in their posture. Accordingly, humans are bipedal whereas nonhuman primates are not, which leads to different gravitational mechanisms of determination in postural asymmetries. Thus, our findings present some problems for Previc's model as it currently stands given the similarity in findings between humans and chimpanzees. We suggest that Previc's model could be modified to account for our findings by simply proposing that positional behavior of primates be considered as a quantitative rather than qualitative trait. Clearly, pregnant female apes and other primates do not spend 100 percent of their time locomoting or standing in a quadrupedal posture. Rather, species likely differ in the amount of time they spend in different positions, which may directly influence the development of head-orientation biases at birth and possibly subsequent postnatal factors that could influence the development of hand preference.

With respect to the effect of rearing on the development of hand preference, there was little support for the premise by McGrew and Marchant (1997) which posited that reports of population-level right-handedness was due to captive rearing. Although the results

indicated that nursery-reared chimpanzees were more right-handed than mother-reared chimpanzees for the REACH task, there was no significant effect of rearing on either the FEED or TUBE tasks. There is no reason to assume that the rearing effects would selectively influence one measure but not others. Additionally, there was no population-level bias for the REACH task, thus the rearing effect, if anything, negated potential population-level asymmetries in the chimpanzees.

One limitation to this study was that our results are limited to chimpanzees reared by humans. Whether the same developmental processes account for the expression of hand preference in mother-reared chimpanzees is not clear. Hopkins, Bard, Jones, and Bales (1993) previously reported an inverse relationship between maternal cradling bias and infant hand preference in mother-raised chimpanzees. Specifically, mothers that cradled and carried their offspring on the left side had offspring that developed right-hand preferences for simple reaching. In contrast, mothers that cradled and carried their offspring on the right side had offspring that developed left-hand preferences. It is not obvious how these findings relate to the associations found between HEAD and the TUBE tasks in this study. However, the rearing effect found for the REACH task may be explained by our previous results on the effect of maternal cradling bias on the development of hand preference. Recall that nursery-reared chimpanzees were more right-handed than mother-reared chimpanzees for the REACH task. If we assume that the humans were more inclined to cradle or carry the neonatal chimpanzees on the left side, as they have been reported to do for human infants (e.g., Salk, 1973), then this biased, differential stimulation of the developing, nursery-reared chimpanzees may explain the higher incidence of right handedness for simple reaching in these subjects (although it did not reach conventional level of statistical significance).

In conclusion, the results of this study indicate that lateral biases during the first 3 months of life are predictive of hand preferences at 3 to 5 years of age in captive-born chimpanzees. These results suggest continuity in the development of laterality in chimpanzees, a finding that challenges historical and some contemporary views of hand preference in nonhuman primates (Ettlinger, 1988; Warren, 1980). To the extent that these findings generalize to other aspects of laterality warrants further investigation in chimpanzees as well as in other nonhuman species. Further longitudinal studies should help to clarify the role of social and biological factors in the expression of brain–behavior relationships in primates, including humans.

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