International Journal of Primatology, Vol. 27, No. 6, December 2006 (© 2006)
DOI: 10.1007/s10764-006-9086-4

Left Nipple Preferences in Infant *Pan paniscus* and *P. troglodytes*

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Received July 20, 2005; accepted October 25, 2005;
Published Online November 29, 2006

We investigated laterality in nipple preference in 16 mother-infant dyads, 8 bonobos, and 8 chimpanzees via an event sampling procedure in infants 5–55 mo of age. Both bonobo and chimpanzee infants preferred the left nipple, and the results were stable over time. Maternal age, experience, and rearing history did not influence laterality in offspring nipple preferences. We discuss the results in the context of the role of early mother-infant interactions on the development of laterality in primates.

KEY WORDS: laterality; mother-infant behavior; cradling; nipple preference.

Damerose and Vauclair (2002) and Hopkins (2004) recently suggested that early asymmetries in mother-infant behaviors may be the basis for the development of handedness. In particular, Hopkins (2004) argued that infant primates are not born into symmetrical environments but instead are exposed to imposed asymmetries by the caretaker, in the form of cradling biases, or the infants show explicit asymmetries in reflexive behaviors such as head orientation or limb strength (Fagot and Bard, 1995; Hopkins and

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Bard, 1995; Hopkins *et al.*, 1997). Presumably, the early asymmetries result in differential stimulation of the limbs, which leads to preferential use of one or the other during infant development.

There is a growing body of evidence for asymmetries in early mother-infant interactions and the results are not restricted to nonhuman primates. For example, humans, particularly women, show universal left-sided biases in cradling infants (Damerose and Vauclair, 2002). Researchers have reported a similar left-sided maternal cradling bias in great apes, notably in chimpanzees and gorillas, but not in other primates (Cunningham *et al.*, 1989; Damerose and Vauclair, 2002; Dienske *et al.*, 1995; Fischer *et al.*, 1982; Hopkins, 2004; Hopkins *et al.*, 1993; Lockard, 1984; Manning and Chamberlain, 1990; Manning *et al.*, 1994; Rogers and Kaplan, 1995; Toback, 1999). Evidence of asymmetries in other early mother-infant behaviors of primates, such as nipple preferences, is less clear. In humans and in 1 study in wild chimpanzees, there is some evidence of left nipple preferences by infants but very few studies (Nishida, 1993; Stables and Hewitt, 1995; Vieira *et al.*, 1996). Old World monkey infants clearly show nipple preferences but the evidence of population-level asymmetries is inconsistent among species and studies (Damerose and Hopkins, 2002; Erwin *et al.*, 1975; Hinde *et al.*, 1964; Hiraiwa, 1981; Jaffe *et al.*, 2006; Lindburg, 1971; Tanaka, 1989, 1997; Tomaszycki *et al.*, 1998). Interestingly, among New World monkeys that twin, such as the common marmoset, infants adopt opposite nipple preferences (Dienske *et al.*, 1995; Rogers and Kaplan, 1998, *cf.* Deets and Harlow, 1970; Nakamichi, 1983; Winkler and Prestel, 1989).

We assessed laterality in nipple preferences in 2 species of great apes: bonobos and chimpanzees. Some apes show a left-side cradling bias but it is unclear whether the left-sided bias is imposed by the female or potentially influenced by the positional or nipple preferences of the infant. Instead of focusing on maternal cradling bias, we examined nipple preferences in 8 bonobos and 8 chimpanzee infants. There is no prior study on nipple preferences in bonobos and only 2 studies in chimpanzees, which contain inconsistent results. Nishida (1993) reported left nipple preferences in 33 wild chimpanzees whereas Dienske *et al.* (1995) reported no consistent nipple preference in 9 captive chimpanzees. If infant chimpanzees and bonobos show laterality early in development then we hypothesized that the infants would show population-level nipple preferences.

METHODS

Subjects

We studied 16 infants: 8 bonobos (*Pan paniscus*) and 8 chimpanzees (*P. troglodytes*). The subjects comprised 8 mother-infants pairs for each species

Table I. Subject information and ages of offspring at each observation period

Institution	Female	Offspring	Sex	Date of birth	Age at observation
Bonobos					
Apenheul	Jill	Tarisha	M	9/17/1998	16, 28, 32, 36
Apenheul	Molaso	Kumbaka	F	9/7/1999	6, 18, 22, 26
Apenheul	Zuani	Liboso	F	1/17/1998	24, 36, 40, 44, 56
Frankfurt	Salonga	Ferry	F	9/25/1999	5, 17, 21, 26
Frankfurt	Natalie	Heri	M	3/23/2001	5, 10
Planckendael	Hermien	Zomi	F	1/28/1998	23, 27, 32, 25, 39, 43, 55
Planckendael	Hortense	Zamba	M	4/16/1998	21, 25, 29, 33, 36, 41, 52
Wuppetal	Lisala	Opala	F	8/4/1998	23, 35, 39, 43, 54
Chimpanzees					
Amersfoort	Sjors	Glafula	F	4/27/1999	9, 21, 25, 30, 41
Amersfoort	Nicole	Dwangko	M	4/22/1999	9, 21, 25, 29, 41
Amersfoort	Silvia	Karibuna	M	10/24/2000	7, 11, 23
Burgers Zoo	Amber	Allity	F	12/27/1998	14, 26, 30, 34, 47
Burgers Zoo	Gaby	Galatea	F	2/24/1999	12, 24, 28, 32, 45
Burgers Zoo	Zaira	Zwala	F	4/16/1999	10, 22, 26, 30, 43
Burgers Zoo	Roosje	Raimee	F	5/15/1999	21, 25, 29, 42
Edinburgh	Lucy	Liberius	M	1/20/1999	14, 26, 30, 34, 47

Note. For age at observation, values represent age in months. F = female, M = male.

in 7 zoos (Table I). The sample includes 5 female and 3 male infants of each species. Infant age ranged from 5 to 56 mo in the bonobo sample, and 7–47 mo in the chimpanzee sample. The age of the bonobo mothers ranged from 10 to 39 yr and from 12 to 37 yr for the chimpanzee mothers.

Data Collection

We conducted focal individual sampling on mother-infant dyads between January 2000 and December 2002. We scored nipple contact with the left or right nipple via instantaneous scan sampling with an interval of 15 s. Observation periods consisted of 5–6 d and the number of observational periods per mother-infant pair varied between 2 and 7. In some cases observation during consecutive days was not possible owing to husbandry management. Interruptions never lasted >1 d. Each day, we randomly carried out 5 sessions of 30 min, rendering 2.5 h of observation/d and 15 h per observation period. In total, we collected 1090 h of data.

All mother-infant pairs lived in multimale multifemale social groups including individuals of different age classes, except for the mother-infant pairs kept at Frankfurt Zoo, where group composition changed owing to fission-fusion management. The bonobo group sizes ranged from 8 to 12 individuals; the chimpanzee group sizes ranged from 12 to 34 individuals. Because the study lasted 3 yr, group compositions inevitably changed as a result of natural dynamics.

Data Analysis

We determined laterality in nipple preference in 3 ways. First, we calculated the total number of observed left and right nipple contacts across all observations periods and subjects. From the data, we computed a laterality index (SUM-LI) following the formula [LI = (no. L − no. R)/(no. R + no. L)]. LI values ranged from −1 to 1, with negative values reflecting left-sided biases and positive values reflecting right-sided biases. The frequency of left- and right-sided nipple contacts varied between observation periods and it could be argued that more observations from one session to the next may have skewed the laterality data. Therefore, we calculated a second laterality index (MEAN-LI). We derived the MEAN-LI by calculating separate laterality index values for each observation period and averaging the laterality index values across all periods. Lastly, based on the total frequencies of left and right nipple contacts, we calculated a z-score for each subject. We classified subjects with z-scores >1.95 or ≤ 1.95 as having a left preference or a right preference, respectively. We classified all others as having no preference.

RESULTS

Population-Level Asymmetries

Summed across all observation sessions, the average number of nipple contacts per subject is 524.23 (SD = 84.44). The range of responses between subjects is 88–1230. There is no significant difference in the number of nipple contacts between the chimpanzees and bonobos or between males and females.

We conducted one-sample t-tests on the SUM-LI and MEAN-LI scores to evaluate whether the distributions in nipple preferences deviated from a mean of 0, which would be the predicted values if preferences were normally or bimodally distributed. For both the SUM-LI $t(15) = -3.71$, $p < .001$ and MEAN-LI $t(15) = 4.23, p < .01$ scores, significant population leftward biases occur in nipple preferences (Fig. 1). Based on the z-scores, 10 subjects have a left nipple preference, 1 has a right nipple preference, and 5 subjects have no preference. The number of subjects with a left nipple preference differs significantly from the number with a right preference ($z = 2.71, p < .01$) but not from the number with no preference ($z = 1.28$, n.s.). Mann-Whitney U-tests reveal significant no specific or sexual differences in the SUM-LI or MEAN-LI scores. Separate one-sample t-tests for each species reveal significant leftward biases for both bonobos $t(7) = 3.18$,

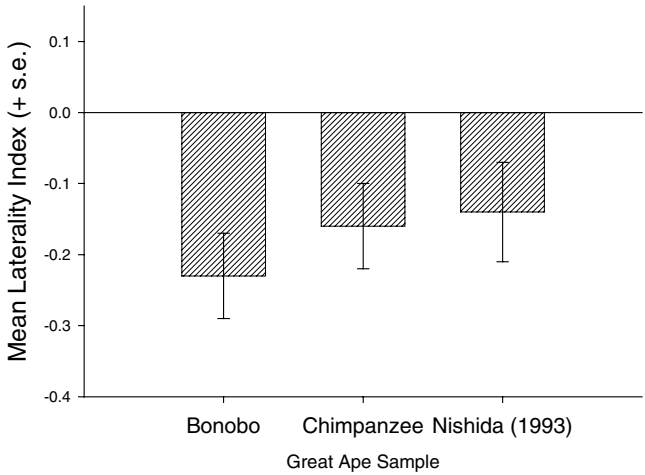

Fig. 1. Mean SUM-LI and MEAN-LI scores for infant bonobos and chimpanzees. Data from wild chimpanzees are also shown for comparison (Nishida, 1993).

$p < .02$ and chimpanzees $t(7) = 4.23, p < .01$. For comparison, we plotted the mean asymmetry coefficient from the 33 chimpanzees Nishida (1993) studied.

Longitudinal Analysis

The number of observational sessions varied between 2 and 7. We observed 15 of the 16 apes at 4 different time intervals. The average ages of the infants at the 4 intervals were 14, 23, 29, and 34 mo, respectively. To evaluate possible longitudinal changes in nipple preferences, we compared the LI scores at the first 4 observational periods via a repeated measure ANOVA. Observational period is the repeated measure while species is the intra group variable. There is no significant main effect or interaction. The mean LI scores for observational periods 1, 2, 3, and 4 are $-.19$, $-.13$, $-.19$, and $-.15$, respectively. Thus, the apes show a significant left nipple preference at each observational period.

Consistency in Nipple Preferences

To evaluate consistency, we correlated the LI values during the first observation session with the 3 subsequent observational sessions to evaluate

consistency in nipple preferences over time. Observation period 1 does not significantly correlate with observational period 2 ($r = -.28$, df $= 15$, n.s.) but significantly positively correlates with observational periods 3 ($r = .776$, df $= 14$, $p < .01$) and 4 ($r = .769$, df $= 14$, $p < .01$).

Potential Influence of Maternal Factors on Nipple Preference

Lastly, we correlated the age of the mothers and the parity of the offspring with the MEAN-LI scores to assess whether the maternal age or previous experience with offspring influenced nipple preferences of the offspring. Neither maternal age ($r = .131$, df $= 14$, n.s.) nor parity of the offspring ($r = -.352$, df $= 14$, n.s.) correlates significantly with nipple preferences. Eight of the females were wild-caught while the remaining 8 were born in captivity. To evaluate whether the rearing history of the females influenced nipple preferences, we compared the MEAN-LI scores for offspring born to the 2 rearing groups via a Mann-Whitney *U*-test. There is no significant difference, though the bias is more pronounced for the offspring born to captive-born (mean $= .30$) than to wild-caught apes (mean $= .10$).

DISCUSSION

The results are straightforward. Infant bonobos and chimpanzees showed significant left nipple preferences, which were consistent over time and did not differ between sexes. Our study is the first evidence of nipple preferences in bonobos and, for the chimpanzees, the results are consistent with previous reports in wild chimpanzees (Nishida, 1993) but differ from 1 previous study in captive chimpanzees (Dienske *et al.*, 1995). The findings on left nipple preferences are also consistent with other studies in some macaques (*Macaca mulatta*) and baboons (Lindburg, 1971; Tomaszynski *et al.*, 1998) but not other macaque species (Erwin *et al.*, 1975; Tanaka, 1989) including other rhesus monkeys (Jaffe *et al.*, 2006).

The origin of the left nipple preference is not clear. Females may exhibit left cradling biases, which influences the nipple preferred by the offspring, as expected given the previous reports of left-sided cradling biases in great apes (Manning and Chamberlain, 1990; Manning *et al.*, 1994). We recorded no maternal cradling bias, and hence cannot address the issue. In addition, early orienting or positional asymmetries may influence the nipple preference. Human-reared neonatal chimpanzees exhibit a right head orientation bias (Hopkins and Bard, 1995), a right thumb-sucking

bias (Hopkins and Bard, 1993), and have stronger right hands and feet (Fagot and Bard, 1995). The early orienting or strength asymmetries may result in the infant being in greater proximity to the left nipple of the female, which may promote the preference. Lastly, Salk (1973) initially proposed that infants cradle on the left side owing to its closer proximity to the heart. According to Salk (1973), the heart is a familiar stimulus to the infant and thus serves as a soothing stimulus. Though Salk (1973) proposed the theory to explain cradling biases, it can similarly be applied to the observed pattern of left nipple preference. Infants may prefer to suckle on the left nipple because it places them in closer proximity to the heart of the female. No matter what the potential mechanisms might be for the nipple preference, the results indicate that the early postnatal experience of the infant is not symmetrical, which may have a significant influence on the development of other behavioral asymmetries, including handedness.

The evidence of left nipple preferences in infant bonobos and chimpanzees adds to a growing body of data demonstrating population-level laterality in nonhuman primates (Ward and Hopkins, 1993). It is important to recognize that the observed pattern of laterality in nipple preferences cannot be attributed to measurement issues, such as whether the data points are independent of each other, as argued in the case of studies on hand use in monkeys and apes (McGrew and Marchant, 1997). Like previous studies in monkeys (Damerose and Hopkins, 2002), nipple preferences in the bonobos and chimpanzees were consistent and stable over time. If asymmetries in nipple preference were unpredictable and an artifact of the sampling procedure, there is no reason for significant biases throughout development. The LI scores, in this case, should have been much more randomly distributed over time. Moreover, the left nipple preferences were evident when we averaged the LI scores across observation periods and when we considered the overall frequency of left and right nipple contacts. Thus, one cannot attribute the results to a greater representation of lateralized data points during one observation period compared to another. Lastly, some researchers have attributed evidence of population-level asymmetries in hand use to human-rearing (McGrew and Marchant, 1997; Palmer, 2003; *cf.* Hopkins and Cantalupo, 2005). Because all apes were raised by their conspecific mothers and were present, on average, by 14 mo of age, human rearing as a potential explanation for the observed nipple preferences is ruled out. The most parsimonious explanations appears to be that the nipple preferences are imposed by the mothers' cradling preferences or are endogenous to the infants.

In conclusion, infant bonobos and chimpanzees show left nipple preferences and the results are relatively stable over time. The findings are consistent with a growing body of evidence on asymmetries in early mother-infant

relationships in human and nonhuman primates (Damerose and Vauclair, 2002). The cause of the left nipple preference and its possible consequences for the behavioral, emotional, and neurological development of the infant are unclear. Additional longitudinal studies on the interrelationship between early mother-infant asymmetries and development of the offspring should provide important data on the issue.

ACKNOWLEDGMENTS

NIH grants NS-36605 and NS-42867 supported W. D. Hopkins. M. De Lathouwers received a BOF-Dehousse grant (October 2000–September 2001) from the University of Antwerp and a Dehousse grant (February 2002–January 2004) from the Royal Zoological Society of Antwerp in association with the University of Antwerp, Belgium. We thank the Flemish Government for the structural support to the Centre for Research and Conservation (CRC) of the Royal Zoological Society of Antwerp (RZSA).

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