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Maternal Cradling and Infant Nipple Preferences in Rhesus Monkeys (*Macaca mulatta*)

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ABSTRACT: *This study investigated lateral biases in nipple preferences, maternal cradling, carrying, and retrieval in 41 rhesus macaque (*Macaca mulatta*) mother–infant dyads living in two captive social groups. Observations were made during the first 6 weeks of infant life using*

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a combination of scan sampling and ad-libitum sampling techniques. Infants exhibited a significant left-nipple preference in the first weeks of life but the bias decreased with infant age. Mothers showed a left-arm bias in carrying their infants but no significant lateral bias in cradling or retrieval. Our results suggest that the left-side cradling bias reported in studies of humans and some other primates reflects a bias in the infant's nipple preference rather than in maternal behavior. The infants' preference for the left nipple is consistent with both Salk's (1960) heartbeat hypothesis and with more recent hypotheses linking this lateral bias with brain asymmetry and hemispheric specialization for mother–infant communication. © 1998 John Wiley & Sons, Inc. Dev Psychobiol 32: 305–312, 1998

Keywords: laterality; maternal cradling; nipple preference; brain asymmetry

A number of observational studies and analyses of photographs and works of art from both different cultures and historical periods have shown that most people have a preference for holding infants on the left side of their body. The left-side cradling bias is present in both right-handed and left-handed people (Bogren, 1984; De Chateau, Holmberg, & Winberg, 1978; Saling & Bonert, 1983; Salk, 1973; Weiland, 1964) and is stronger in women than in men (Bolton, 1978; Brusser, 1981; De Chateau & Andersson, 1976; De Chateau et al., 1978; Finger, 1975; Lockard, Daley, & Gunderson, 1979; Manning, 1991; Manning & Denman, 1994; Rheingold & Keene, 1965; Richards & Finger, 1975; but see Bogren, 1984; Bundy, 1979; De Chateau, 1983; Harris & Fitzgerald, 1985; Nakamichi, 1996). Among women, the left-side bias appears early in life (De Chateau, 1987; De Chateau & Andersson, 1976; Saling & Bonert, 1983; Saling & Tyson, 1981), is quite specific to holding infants or dolls (De Chateau & Andersson, 1976; Rheingold & Keene, 1965; Salk, 1973; Weiland, 1964; Weiland & Sperber, 1970; but see Hanaway & Burghardt, 1976), and decreases with infant age (Dagenbach, Harris, & Fitzgerald, 1988; Lockard et al., 1979). There is no relationship between lateral cradling preferences in married couples (Bogren, 1984) but such preferences appear to be correlated between related females, within and across generations (Manning & Denman, 1994).

Several hypotheses have been proposed to explain the left-side cradling bias. Although some cultural influences on this phenomenon cannot be ruled out (see Alvarez, 1990; Finger, 1975; Grusser, 1983), most explanations involve biological mechanisms. Salk (1960, 1973) first hypothesized that the fetus becomes imprinted to the heartbeat of its mother, and that left-side cradling has a soothing effect on the infant because it allows the infant to be close to the heart (see also Weiland, 1964; Weiland & Sperber, 1970). According to another hypothesis, the cradling bias may be determined by the head-turning preferences of the infant (Ginsburg, Fling, Hope, Musgrove, & Andrews,

1979), which in turn may result from neural asymmetries related to handedness (Michel, 1981), or the different tactile sensitivity of the right and left female breast (Kaplan-Solms & Saling, 1988; Saling & Cooke, 1984; but see Thompson & Smart, 1993). Finally, other hypotheses link the left-side cradling bias to brain hemispheric specializations for information processing. Manning and Chamberlain (1990, 1991) argued that left-side cradling enables the mother to monitor her infant with her left eye and ear and process the information with her right hemisphere, the hemisphere specialized for emotional processing. Moreover, left-side cradling would also enable the infant to monitor the mother's emotional condition through her most expressive left side of the face (but see Lucas, Turnbull, & Kaplan-Solms, 1993). More recently, Sieratzki and Woll (1996) argued that in the left-side position, the maternal prosodic sounds known as motherese would be mostly perceived by the infant's left ear and processed by the right hemisphere, the hemisphere specialized for the reception and processing of prosody.

The study of cradling biases in humans was first stimulated by an observation of rhesus macaques (Salk, 1960, 1973), and, in turn, human studies have further stimulated the investigation of this phenomenon in primates. Evidence that nonhuman primates show a left-side cradling bias similar to that of humans would confirm the prominence of biological versus cultural factors in the causation of this phenomenon and could also elucidate both its functional significance and evolutionary origin. Unequivocal evidence that primates exhibit a left-side cradling bias, however, is still lacking. Data on infant nipple preferences in macaques suggest that such preferences develop soon after birth (2–8 weeks in *Macaca fuscata*: Hiraiwa, 1981; Nakamichi, 1983; Ota, Makino, & Kimura, 1991; Tanaka, 1989; 2–6 weeks in *Macaca mulatta*: Deets & Harlow, 1970; Hinde, Rowell, & Spencer-Booth, 1964; Lindburg, 1971; Spencer-Booth, 1968). Studies with larger sample sizes, however, revealed

either no population bias in nipple preferences (Hiraiwa, 1981; Tanaka, 1989) or a right-nipple bias (Lindburg, 1971). Tanaka (1989) showed that nipple preferences changed between siblings, with infants preferring the nipple not used by their older sibling. Infant nipple preferences, however, seem unrelated to the yield or composition of milk produced by the preferred and nonpreferred nipple (Ota et al., 1991). In chimpanzees, Nishida (1993) reported that infants have a preference for the left nipple (see also van Lawick-Goodall, 1967) whereas Dienske, Hopkins, and Reid (1995) found that infants tended to use only one nipple (left or right) from 0 to 6 months of age, and then they alternated.

With regard to infant holding, Tanaka (1989) found no population bias in Japanese macaques, although mothers were consistent in their cradling preferences with successive infants. Another study of macaques, however, using individuals from three different species (3 *Macaca fuscata*, 4 *Macaca cyclopis*, and 1 *Macaca radiata*) reported that mothers used their left hand to retrieve their infants in response to fearful stimuli (Hatta & Koike, 1991). In chimpanzees, different studies reported a significant left-side cradling bias (Manning & Chamberlain, 1990; Manning, Heaton, & Chamberlain, 1994), a slight left-side bias (Nishida, 1993), a slight right-side bias (Dienske et al., 1995), or no bias at all (Hopkins, Bard, Jones, & Bales, 1993).

The variability in the nonhuman primate data is difficult to interpret due to methodological differences among studies, including the age range of infants and the criteria for measurement of cradling. Some studies focused on newborns (Hopkins et al., 1993) whereas in others infant age ranged from 0 to almost 2 years (Dienske et al., 1995; Manning et al., 1994). Moreover, some authors assessed chimpanzee cradling preferences by recording whether the infant's head was on the mother's left side, right side, or the midline (Manning et al., 1994), whereas others recorded which arm was used by mothers to hold the infant while sitting or walking (Hopkins et al., 1993). Because of the methodology used, when a left-side preference was reported it was not clear whether it reflected a bias in infant behavior, in maternal behavior, or a combination of both. Thus, in order to unequivocally assess the occurrence of a left-side cradling bias and elucidate its determinants, it is important that the age range of infants be restricted and that clear and distinct operational definitions of the different maternal and infant behaviors be used.

In the present study we investigated infant nipple preferences, maternal cradling, carrying, and retrieval

over the first 6 weeks of infant life in a large sample of group-living mother–infant dyads. Our aims were to assess whether rhesus macaques show evidence of a left-side cradling bias, to assess the relative contribution of mother and infant to lateral cradling, and to investigate the effect of several maternal and infant characteristics on lateral cradling.

METHODS

Subjects and Housing

Subjects were 41 rhesus macaque mother–infant pairs living in two multimale–multifemale social groups. The groups were housed in 38 × 38 m outdoor compounds with attached indoor quarters at the Field Station of the Yerkes Regional Primate Research Center in Lawrenceville, GA (U.S.A.). The groups were composed of 2–3 adult males and 40–50 adult females with their subadult, juvenile, and infant offspring. Of the 41 infants observed in this study, 25 were females and 16 were males. Group composition remained relatively stable throughout the study period. Five infant subjects (3 females, 2 males) died during the course of the study, and 1 female infant was removed from the group to receive medical treatment. Most subjects of this study were part of a project investigating the effects of prenatal androgens and androgen antagonists on somatic and behavioral development. Preliminary analyses (ANOVAs) comparing the lateral bias index (see below) for the measures of nipple preference, cradling, carrying, and retrieval did not reveal any significant differences among infants receiving prenatal treatments.

Procedure

The study was conducted from April to August 1996. Behavioral observations of mother–infant pairs began on either the 1st or 2nd day of the infant's life, and continued until the infant was 6 weeks old. Throughout the first 6 weeks, all mother–infant pairs were observed three times weekly in 1-hr observation sessions. During observation sessions, the doors connecting the indoor and outdoor housing areas were locked so that all animals could be observed in the outdoor compound. Three observers watched each subject simultaneously and collected the data using a check sheet.

A scan-sampling technique with 60-s intervals (Martin & Bateson, 1986) was utilized to collect data on infant nipple preference and laterality in maternal cradling. A total of 60 scan samples were completed

for each observation session. At each sampling point, the observers scanned the compound for each mother–infant pair, noting whether each infant was nursing from the mother’s left nipple, right nipple, or not nursing. It was also noted whether the mother was cradling her infant with the left arm, the right arm, both arms, or not cradling. Nipple use and cradling were independent of each other. For example, left-nipple nursing could have been associated with left- or right-arm cradling or no cradling at all. If the infant nursed or was cradled for several successive 60-s intervals, each scan was considered a separate instance. If the nipple or cradling position was not clearly visible (e.g., the mother was in a huddle with other monkeys) or if the three observers did not agree on the score to be assigned, the sampling point was skipped. The nipple and cradling preference data were analyzed in terms of mean percentage of sample points (per individual per hour) in which the right or left nipple, or the right or left arm, were used. Maternal carrying and retrieval were recorded ad libitum throughout the observation sessions. Whenever a mother supported her infant with her arm while walking, the observer recorded whether the right or left arm, or both, was used. Similarly, the observer recorded which arm was used to retrieve the infant when the infant was out of contact with the mother. The carrying and retrieval data were analyzed in terms of mean rates of events per individual per hour.

Data Analysis

To assess the presence of a population bias in nipple preference, cradling, carrying, and retrieval, the scores for each subject were totaled for the 6 weeks of observation. Based on these totals, a lateral bias (LB) score was calculated by subtracting the number of left-sided observations from the number of right-sided observations and dividing by the total number of observations ($R - L/R + L$). The resulting values ranged from -1.0 to 1.0 reflecting extreme left- to right-sided biases. Population biases were assessed using one-sample t tests for each measure and the LB scores were compared to a normal distribution with a mean of zero. Correlations between LB scores of nipple preference, cradling, carrying, and retrieval scores were assessed with the Pearson Product-Moment correlation coefficient. The same test was also used to assess correlations between LB scores for each measure and several characteristics of the subjects. Repeated measures ANOVA was used to assess the effects of infant age on nipple preference, cradling, carrying, and retrieval.

The developmental data were incomplete for 6 subjects, thus the sample was reduced to 35 individuals for these analyses. The effects of infant sex on direction of lateral bias was assessed with a t test for independent samples. All results were evaluated with alpha at $p < 0.05$ and all post-hoc analyses were performed using Tukey’s Honestly Significant Difference (HSD) with $p < 0.05$.

RESULTS

Descriptive Data

Depicted in Table 1 are the descriptive summaries of nipple preference and infant cradling, carrying, and retrieval bouts. Over the first 6 weeks of life, the infants spent, on average, 62% of their time on their mother’s nipple. The percentage of time spent on the nipple decreased from 79% during Week 1 to 51% by Week 6. Infant cradling and carrying followed similar trends with decreased amounts from Weeks 1 to 6. Infant retrieval was observed less often with only 19 mothers exhibiting any instances of this behavior during the 6-week observation period. However, infant retrieval increased from Week 1 to 6.

Lateral Biases in Infant and Maternal Behavior

When data were combined over the 6 weeks of infant life, a significant left-side population bias was found for nipple preference, $t(38) = 2.66, p < 0.01$, and carrying, $t(38) = 2.38, p < 0.01$. No population bias was found for cradling or retrieval. The mean LB score for each measure can be seen in Figure 1. The lateral bias (LB) scores for nipple preference, cradling, and carrying were positively correlated with each other with

Table 1. Mean Percentage of Sampling Points Spent on Nipple and Cradling and Mean Hourly Rate of Carrying and Retrieval Per Individual Per Week During the First 6 Weeks of Life

Measure	Infant Age (in weeks)					
	1	2	3	4	5	6
Nipple	79	70	63	55	52	51
Cradling	37	28	23	18	15	15
Carrying	.53	.56	.45	.29	.31	.22
Retrieval	.01	.02	.08	.06	.10	.07

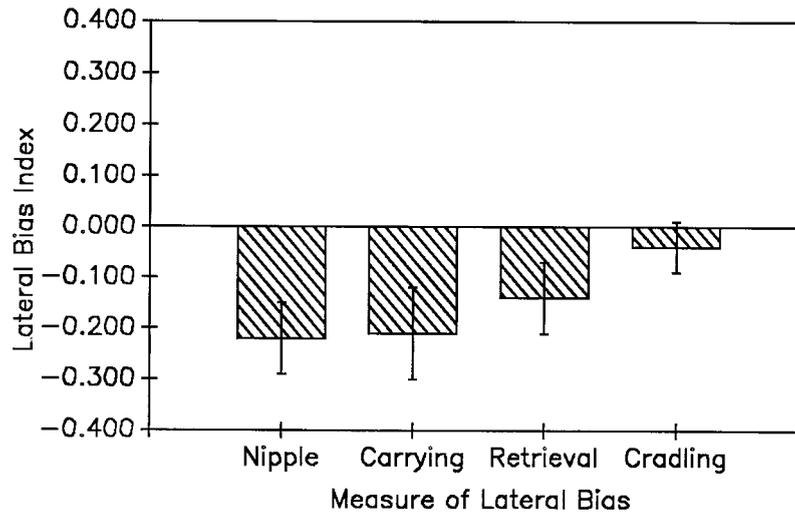


FIGURE 1 Mean (+SEM) LB scores per individual for nipple preference, carrying, cradling, and retrieval. Nipple and carrying scores were significantly higher than cradling and retrieval scores. Moreover, nipple and carrying scores differed significantly from chance (see Results). Data from the first 6 weeks of infant life were pooled.

the highest association between the cradling and carrying (see Table 2). Infant retrieval did not significantly correlate with any of the other three measures.

Effects of Infant Age

For nipple preference, there was a significant interaction between infant age and lateral bias, $F(5, 170) = 5.83$, $p < 0.001$. These data can be seen in Figure 2. Post-hoc analyses indicated significant left-nipple preferences during Weeks 1, 2, and 3 but no significant preferences for Weeks 4, 5, and 6. For cradling, carrying, and retrieval, no significant interactions were found between infant age and lateral bias; however, for all three measures, significant main effects for infant age were found, carrying: $F(5, 160) = 3.20$, $p < 0.001$; cradling: $F(5, 160) = 11.88$, $p < 0.001$; retrieval: $F(5, 95) = 2.93$, $p < 0.03$. These results are consistent with the means reported in Table 1.

Table 2. Intercorrelations in Lateral Bias Between Measures

	Nipple	Cradling	Carrying
Cradling	.484*		
Carrying	.364*	.632*	
Retrieval	.175	-.104	-.271

*indicates $p < .05$.

Effects of Maternal Age, Experience, Dominance Rank, Infant Sex, and Birth Weight on Lateral Bias

Depicted in Table 3 are the correlations between the measures of lateral bias and several characteristics of the subjects including maternal age, experience (measured as the number of previous offspring), dominance rank (high, middle, or low), and infant birth weight. The only significant correlation was between cradling and maternal experience showing that cradling became more left-sided with increasing maternal experience. No significant effects of infant sex on lateral bias were found for any of the measures considered (nipple preference: $t(38) = -0.39$; cradling: $t(38) = 0.16$; carrying: $t(38) = -0.57$; retrieval: $t(38) = -0.62$).

DISCUSSION

The results of this study show that rhesus infants have a significant preference for their mother's left nipple. The left-nipple bias is apparent from the 1st week of life and decreases steadily over the next 5 weeks, becoming nonsignificant after the 3rd week. Rhesus mothers exhibited a significant left lateral bias for infant carrying; namely, they preferentially used their left arm to support their infants while walking. No significant lateral bias was found for maternal cradling or retrieval at the population level, although lateral bias scores for cradling, carrying, and nipple use were

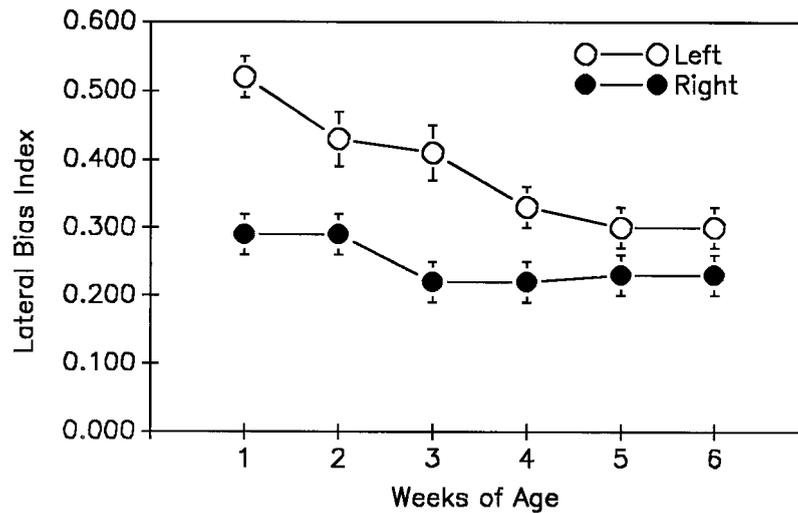


FIGURE 2 Developmental changes in LB scores for infant nipple preferences over the first 6 weeks of life (mean values + SEM). The values were averaged across the entire sample of subjects. Open circles represent left-nipple preference and the closed circles represent right-nipple preference.

positively correlated with each other. Infant retrieval was a relatively infrequent behavior and its lateral bias scores did not correlate with any of the other measures. Nipple preferences, carrying, cradling, and retrieval were not significantly correlated with infant sex and birth weight or maternal age and dominance rank. However, there was a positive correlation between the cradling bias and maternal experience, as measured by the number of previous offspring.

Our finding of a left-nipple preference is consistent with Nishida's (1993) study in young chimpanzees, but inconsistent with other studies of macaques, which reported either no population bias in nipple preferences (Hiraiwa, 1981; Tanaka, 1989), or a right-nipple bias (Lindburg, 1971). This discrepancy could be due to the small sample sizes of other studies or the age

differences of the animals studied. The Japanese macaques studied by Tanaka (1989), for example, ranged in age from 0 to 3 years, whereas our study focused only on the first 6 weeks of infant life. Our results are also inconsistent with studies of macaques indicating that nipple preference strengthens with infant age (see Introduction for references). Data on humans, however, suggest that the left-cradling bias decreases with infant age (Manning, 1991; Salk, 1960).

Most studies of great apes and humans reporting a left-side bias did not differentiate between the infant's nipple preference and the mother's lateral bias for cradling and carrying the infant. Because we did not find a lateral bias in maternal cradling, our results suggest that the cradling bias found in great apes and humans may reflect a bias in the infant's nipple preference rather than a bias in the mother's behavior. In this view, the correlation between maternal cradling and experience may reflect the fact that experience enables mothers to recognize their infant's nipple preference and adjust their cradling behavior to facilitate the expression of such preferences. The correlation between cradling and experience, however, was weak and may have arisen by chance. Rhesus mothers exhibited a left-carrying bias while walking, but this may be unrelated to cradling or infant nipple preferences. In fact, human and nonhuman primates appear to have a left-sided postural asymmetry in carrying, which is unrelated to infant cradling biases (Hopkins & de Waal, 1995; Porac & Coren, 1981).

The presence of a left-nipple preference in the infant is consistent with Salk's (1960, 1973) heartbeat

Table 3. Intercorrelations Between Measures of Lateral Bias and Subject Variables

Variable	Measure of Lateral Bias			
	Carrying	Cradling	Nipple	Retrieval
Maternal Age	.154	.276	-.025	-.076
Maternal Experience	.179	.312*	.032	-.012
Infant Birth Weight	-.229	-.202	-.128	-.267
Maternal Rank	-.216	-.281*	-.085	-.103

*indicates $p < .05$.

hypothesis. The fact that the left-nipple bias decreases with infant age is also consistent with Salk's hypothesis because proximity to the heart may be especially important early in life to facilitate the transition between the infant's prenatal and postnatal environment. Our findings are also consistent with the hypotheses linking left-side cradling to brain lateralization and hemispheric specialization for sensory communication between mother and infant (e.g., Manning & Chamberlain, 1990; Sieratzki & Woll, 1996). The fact that the left-side bias is present in rhesus macaques, however, suggests that the processing of verbal information (e.g., motherese) may not have had an important role in the evolution of this phenomenon in humans. Moreover, if the communication hypothesis is correct, our data suggest that infants play a larger role in regulating this process than previously thought.

Overall, our data lend support to biological explanations of left-side cradling in humans and, possibly, also to theories linking this lateral bias to the evolution of cerebral asymmetries in the Primate order (Corballis, 1991). Given the discrepancy between different studies with great apes (see Introduction), however, further investigations using large sample sizes, similar methodological criteria, and focusing on the same developmental period are needed. Future research should also attempt to test some of the functional implications of the various hypotheses concerning nipple preferences and/or lateral-cradling biases. For example, Salk's hypothesis needs to be tested to assess whether different nipple preferences early in life result in subsequent temperamental and/or behavioral differences among infants. Similarly, whether different nipple preferences and/or cradling biases have short- or long-term consequences for communication between mother and infant, and more generally, the quality of their relationship need further investigation.

NOTES

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