Asymmetries in mother-infant behaviour in Barbary macaques (*Macaca sylvanus*)

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Asymmetries in the maternal behaviour and anatomy might play an important role in the development of primate manual lateralization. In particular, early life asymmetries in mothers and infants behaviour have been suggested to be associated with the development of the hand preference of the offspring. The aim of this study was to investigate the presence of behavioural asymmetries in different behavioural categories of mother-infant dyads of zoo-living Barbary macaques (*Macaca sylvanus*). The study subjects were 14 Barbary macaques involved in seven mother-infant dyads housed in Parco Natura Viva, Italy. For the mothers, frequencies of hand preference for maternal cradling and infant retrieval were collected. For the infants, we focused on nipple preference and hand reference for clinging on mother ventrum. Moreover, we collected frequencies of hand preference for food reaching in both groups. No significant group-level bias was found for any of the behavioural categories in both mothers and infants behaviour. However, at the individual level, all infants showed a significant nipple preference, six toward the mother’s right nipple, one toward the left nipple. Further, a significant correlation was found between the infant nipple preference and their hand preference for food reaching, suggesting that maternal environment rather than behaviour might affect the development of hand preference in Old World monkeys. Given the incongruences between our study and previous research in great apes and humans, our results seem to suggest possible phylogenetic differences in the lateralization of mothers and infants within the *Primates* order.

RUNNING HEAD: Lateral biases in Barbary macaques

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Abstract

Asymmetries in the maternal behaviour and anatomy might play an important role in the development of primate manual lateralization. In particular, early life asymmetries in mothers and infants behaviour have been suggested to be associated with the development of the hand preference of the offspring. The aim of this study was to investigate the presence of behavioural asymmetries in different behavioural categories of mother-infant dyads of zoo-living Barbary macaques (*Macaca sylvanus*). The study subjects were 14 Barbary macaques involved in seven mother-infant dyads housed in Parco Natura Viva, Italy. For the mothers, frequencies of hand preference for maternal cradling and infant retrieval were collected. For the infants, we focused on nipple preference and hand reference for clinging on mother ventrum. Moreover, we collected frequencies of hand preference for food reaching in both groups. No significant group-level bias was found for any of the behavioural categories in both mothers and infants behaviour. However, at the individual level, all infants showed a significant nipple preference, six toward the mother's right nipple, one toward the left nipple. Further, a significant correlation was found between the infant nipple preference and their hand preference for food reaching, suggesting that maternal environment rather than behaviour might affect the development of hand preference in Old World monkeys. Given the incongruences between our study and previous research in great apes and humans, our results seem to suggest possible phylogenetic differences in the lateralization of mothers and infants within the *Primates* order.

Keywords: *Macaca sylvanus*, laterality, maternal cradling, nipple preference, hand preference

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Introduction

Among mammals the right hemisphere has been found to be more involved in social processing, such as monitoring conspecifics and attending social responses (Rogers, Vallortigara & Andrew, 2013; Gilijov, Karenina & Malashichev, 2018). In particular, the left-cradling bias found in humans has been hypothesized to be related to: the infant imprinting to the mother heartbeat, with left-cradling allowing the infant to be close to the mother hearth (Salk, 1973); the head-turning preferences of the infants, resulting from brain asymmetries possibly related to handedness (Ginsburg et al., 1979). According to recent research, the right hemisphere involvement in social stimuli control has also been hypothesized to be a reason for the left-cradling bias reported in the maternal behaviour of humans and some great apes (Hopkins, 2004; Rosa-Salva, Regolin, Mascalzoni & Vallortigara, 2012; Giljov et al., 2018). Indeed, research on humans revealed that mothers prefer to cradle their infant on the left side (Salk, 1960; Damerose & Vauclair, 2002) and similar findings have been reported in chimpanzees (*Pan troglodytes*) (Manning & Chamberlain, 1990; Hopkins, Bard, Jones & Bales, 1993; Manning et al., 1994; Toback, 1999) and gorillas (*Gorilla gorilla*) (Manning et al., 1994). On the other hand, asymmetries in maternal cradling seem to be less clear in Old World monkeys. Indeed, no group-level bias was found for this behaviour in Japanese macaques (*Macaca fuscata*) (Tanaka, 1989), rhesus macaques (*Macaca mulatta*) (Tomaszycki et al., 1998), olive baboons (*Papio anubis*) (Damerose & Hopkins, 2002) and Sichuan snub-nose monkeys (*Rhinopithecus roxellana*) (Zhao, Gao, Li & Watanabe, 2008), suggesting phylogenetic differences between taxonomic primate groups. In Old World monkeys, the lack of lateral biases has been found also in other kind of mother-infant interactions, particularly infant retrieval. Indeed, research on rhesus macaques and olive baboons did not report any group-level side preferences in the hand used to retrieve the infant by the mother (Tomaszycki et al., 1998; Damerose & Hopkins, 2002).

Infant nipple preference has been investigated in different non-human primate species, revealing a bias toward the left nipple in wild chimpanzees (Nishida, 1993), captive chimpanzees and bonobos (*Pan paniscus*) (Hopkins & De Lathouwers, 2006). As reported for maternal cradling, in general no group-level bias in nipple preference has been reported in past research on Old World monkeys, particularly Japanese macaques (Hiraiwa, 1981; Tanaka, 1989), pig-tailed macaques (*Macaca nemestrina*) (Erwin et al., 1975), olive baboons (Damerose & Hopkins, 2002) and Sichuan snub-nose monkeys (Zhao et al., 2008). On the other hand, wild rhesus macaques have been found to show a right nipple preference (Lindburg, 1971) whereas an opposite bias has been reported in a captive group of this species, showing a slight group-level left nipple preference (Tomaszycki et al., 1998). In contrast, more recent research on a large troop of wild rhesus macaques found no group-level nipple preference in this species (Jaffe et al., 2006).

Research on hand preference on different tasks in monkeys and, to a lesser extent, great apes has given rise to a heterogeneous picture of their manual lateralization (for review Papademetriou, Sheu & Michel, 2005; Fitch & Braccini, 2013). The inconsistency between different studies might be due to methodological differences as well as to the potential influence of factors such as posture (Forsythe et al., 1988; MacNeilage, 2007), task (Fagot & Vauclair, 1991), and individual experience and learning (Westergaard & Suomi, 1993; Hopkins, 1995; Meunier et al., 2011). One of the main hypotheses aiming to explain patterns of hand preference in primates is the Postural Origin Theory (POT) by MacNeilage (2007). According to the POT, the adoption of terrestrial habits during primate evolution allowed the right hand to become free from postural support duties, getting gradually more involved in tasks requiring specific skill. This process resulted in the pronounced right handedness characterizing humans with their bipedal posture (MacNeilage, 2007; Meguerditchian et al., 2013; Blois-Heulin et al., 2006). In addition, also the asymmetries in the intrauterine environment as well as in the maternal behaviour and anatomy might play an important role in the development of primate manual lateralization (Previc, 1991; Hepper et al., 1997; Hopkins, 2004). In fact basing on previous research, early life asymmetries in mothers and infants have been suggested to be associated with the development of the hand preference of the offspring (Hopkins, 1994; 1995; Westergaard, Byrne & Suomi, 1998; Hopkins, 2004). Moreover, mothers and infant might reciprocally impact their manual lateralization (Scola & Vauclair, 2010). Investigating behavioural asymmetries in mothers and infants might therefore be useful to better understand the development of motor lateralization, particularly handedness in non-human primates, gaining new insight into factors driving the evolution of manual laterality in these species (Hopkins, 2004). However, although literature on humans and chimpanzees is relatively well-represented, more studies are needed involving monkey and prosimian mother-infant dyads (Hopkins, 2004).

The aim of the current study was to verify the presence of behavioural asymmetries in mother-infant dyads in a sample of zoo Barbary macaques (*Macaca sylvanus)*, investigating whether mother lateralization correlates with that of the infant. In particular, for mother macaques we assessed lateralization in maternal cradling and infant retrieval, whereas for the infants we focused on nipple preference and hand use to cling on the mother belly. In addition, we tested and investigated the relationship between mother and infant hand preference for food reaching. Basing on previous literature on Old World monkeys, specifically macaques, we expect no bias in maternal cradling and infant retrieval by the mothers (Tomaszycki et al., 1998, Damerose & Hopkins, 2002). More studies on nipple preference and infant hand preference for clinging on mother belly are needed to better understand the presence of biases in non-human primates.

Methods

Study subjects and area

The study was carried out with 14 Barbary macaque involved in seven mother-infant dyads. The study dyads lived in a multimale-multifemale social group composed of 24 macaques: a dominant male, four sub-adult males, five one-year old juveniles and the seven adult females with their offspring (seven infants in total) involved in the study. All infants were born in June and at the time of data collection they were between 20 to 30 days of age. All subjects were hosted at Parco Natura Viva, a zoological garden in Verona (Italy). The macaques were housed in a 870 m^2 naturalistic enclosure made of grassy areas, plants and trees, rocks, high ropes, artificial shelters and a water pool. Barbary macaques were fed twice a day and water was available to the animals ad libitum. The diet was made of fruits and vegetables, seeds, cereals and mealworms. On a daily basis, macaques were involve in an environmental enrichment program and could receive manipulative devices to be opened to reach for food as well as foraging enrichment. In this latter case, small pieces of food were scattered around in the enclosure or hidden in hay or straw mounds.

All subjects of the study were born in captivity and were not used to interact with humans. The study was carried out through the live observation of spontaneous behaviours of macaques in their social context. No invasive or stressful techniques were used and the study procedure was in accordance with the EU Directive 2010/63/EU for animal research and the Italian legislative decree 26/2014 for Animal Research.

Procedure and data collection

The study was carried when the infants were between 20 to 30 days of age. For each mother and for each infant, fourteen 15-minute sessions were carried out. In particular, two sessions per day were done, one in the morning, one in the afternoon. A continuous focal animal sampling method was used to collect the frequencies of right and left hand use for different behavioural categories in both mothers and infants and to collect the frequencies of infant nipple preference. Regarding the mother, data on the hand preference for maternal cradling and infant retrieval were collected. Maternal cradling was defined as the mother holding the offspring ventrally (Damerose & Hopkins, 2002). Retrieval was defined as the mother reaching to retrieve for any reason for the infant, which was apart from her. In particular, we collected only unbiased events of cradling and infant retrieval with the right and left hand, whereas events carried out with both hands were not considered. Regarding the infant, data on the nipple preference and the hand preference for clinging on the mothers ventrum were collected. For nipple preference, we recorded the frequencies of suckling on the mother right and left nipple. All contacts with the nipple by the infant were considered in the study, with no distinction between different suckling phases (Damerose & Hopkins, 2002). For clinging on the mothers ventrum, we recorded the hand used by the infant to hold to the mother ventrum, while the other hand was doing a different actions or was not involved in any activity. In addition, for both mothers and infants, data on the hand used to reach for food (this behavioural category will be defined "food reaching" throughout the manuscript) in the feeding points of the enclosure were collected. In particular, only unbiased events that were performed by the macaques were considered, whereas bimanual reaching, ambiguous events and reaching events from asymmetrical postures (e.g.: laying on the side) were discarded. For the infants, we considered only those reaching events that took place when the subject was on the ground and no hand was in contact with the mother.

Data analysis

Given that Kolmogorov-Smirnov Goodness-of-Fit tests revealed that not all data were normally distributed, non-parametric statistic tests were used. Individual-level lateralization was evaluated using binomial z-scores, to classify the subjects as left-handed ($z < -1.96$), right-handed ($z > 1.96$) and ambi-preferent ($-1.96 < z < 1.96$) (Michel, Sheu & Brumley, 2002). For each behavioural category considered in the study, only subjects that reached a minimum of ten events were included in the individual-level analysis (Meguerditchian, Vauclair & Hopkins, 2010). Moreover, for each subject a Laterality Index score (LI) was calculated. The LI was given by the formula $LI = (R – L)/(R + L)$; R stands for the frequencies of the right side/hand use and L stands for the frequencies of the left side/hand use. The LI varies between –1.0 and 1.0 with negative values indicating a left side bias, whereas positive values indicate a right side bias (Westergaard, Byrne & Suomi, 1997; Tomaszycki et al., 1998; Hopkins & De Lathouwers, 2006; Zhao et al., 2008; Gilijov et al., 2018). Moreover, to compare the strength of the hand preference for food reaching between mother and infants, the absolute values of the LI (ABS-LI) were considered. Group-level side or hand preferences were evaluated using a one-sample sign-test with the Laterality Index serving as dependent measure and chance level was set at 0. For the mothers, correlations between LI scores of cradling, nipple chosen by the infant, infant retrieval and food reaching were assessed using the Spearman correlation coefficient. The same analysis was used for the infants to assess correlation between the LI scores of nipple preference, clinging on mother ventrum and food reaching. Finally, to compare handedness between mother and infants, we compared the LI and the ABS-LI score for food reaching between the two groups using a Mann-Whitney test. All tests were two-tailed. The significance level was set at $p < 0.05$.

Results

Maternal cradling and infant retrieval

The mean LI (±SD) for maternal cradling was -0.01 ± 0.57. At the individual-level, six out of seven subjects showed a significant cradling bias, three toward the left hand and three toward the right hand (Table 1). The Binomial test revealed no significant difference between the number of lateralized and that of ambi-preferent individuals ($p = 0.063$). According to a one-sample sign-test, no bias in the distribution of the LI was found ($p = 1$, N = 7) (Fig. 1). The mean LI (±SD) for infant retrieval was 0.04 ± 0.14. At the individual-level, no macaque showed a significant lateralization (Table 1) and, according to a one-sample sign-test, no bias in the distribution of the LI was found ($p = 0.453$, N = 7) (Fig. 1).

Nipple preference and clinging on the mothers ventrum

Regarding infant nipple preference, the mean LI (±SD) was 0.51 ± 0.54. At the individual-level, all subjects showed a significant nipple preference, one toward the mother's left nipple and six toward the right nipple (Table 1). The Binomial test revealed a significant difference between the number of lateralized and that of ambi-preferent individuals ($p = 0.016$). According to a one-sample sign-test, no bias in the distribution of the LI was found ($p = 0.125$, N = 7) (Fig. 1). In the case of the hand preference for clinging on the mothers ventrum, the mean LI (±SD) was -0.01 ± 0.06. At the individual-level, no macaque showed a significant lateralization (Table 1). One-sample sign-test revealed no bias in the distribution of the LI ($P = 0.453$, N = 7) (Fig. 1).

Hand preference for food reaching

The mean LI (±SD) for food reaching was 0.06 ± 0.30 for the mothers and -0.14 ± 0.40 for the infants. Four out of seven mother macaques showed a significant hand preference, with one left- and three were right-handed individuals. The Binomial test revealed no significant difference between the number of lateralized and that of ambi-preferent individuals (*p* = 1) and the one-sample sign-tests revealed no significant biases for both mothers (*p* = 0.453, N = 7) and infants (*p* = 0.453, N = 7). In the case of the infants, six out of seven subjects were involved in the analysis due to the low number of reaching events collected for Vanda's infant, that was excluded from the analysis. None of the infants showed a significant hand preference. When comparing the hand preference for food reaching between the two groups, the Mann-Whitney test revealed no significant differences between both the LI (*U* = 15.5; *P* = 0.276) and the ABS-LI (*U* = 18; *p*= 0.441).

Lateral biases in mother and infant behaviour

To investigate the relationship between the lateral bias in the parental behaviours and the manual lateralization of the mothers, Spearman correlations between the LI for cradling, nipple of the mother chosen by the infant, infant retrieval and food reaching were run. No significant correlations were found between any of the behavioural categories of the mothers (see Table 2 for *rho* and *p* values). For infant lateral biases, Spearman correlations between the LI for nipple preference, clinging on mother belly and food reaching were run. A significant positive correlation between the LI scores for nipple preference and food reaching was found (*rho* = 0.786; *P* = 0.036) (see Table 3 for all *rho* and *p* values).

Discussion

Findings from this study highlighted no group-level biases in cradling and infant retrieval by the mothers and the same results emerged for nipple preference and clinging on mothers ventrum in infants Barbary macaques. Regarding maternal cradling, this study is in agreement with previous literature on macaques, particularly on rhesus macaques (Tomaszycki et al., 1998) and Japanese macaques (Tanaka, 1989) as well as on other Old World primates, particularly Sichuan snub-nose monkeys (Zhao et al., 2008). On the other hand, our results are in disagreement with previous studies reporting a left bias in maternal cradling in great apes, chimpanzees and gorillas (Manning et al., 1994; Toback, 1999) and in humans (Salk, 1960; Damerose & Vauclair, 2002), suggesting that consistent behavioural lateralization in mother-infant interactions might have first appeared in hominids. However, further studies involving a greater sample of subjects and species are needed to understand the phylogeny of cradling biases in primates. Regarding the hand preference for infant retrieval by the mother, no group-level bias was reported. This finding is in agreement with previous studies in rhesus macaques (Tomaszycki et al., 1998) and olive baboons (*Papio anubis*) (Damerose & Hopkins, 2002).

In the case of infant nipple preference, the finding of a lack of group-level bias is in agreement with previous research on Japanese macaques (Hiraiwa, 1981), pig-tailed macaques (Erwin et al., 1975) and wild rhesus macaques (Jaffe et al., 2006). Similar findings were found in other Old World primates, specifically wild Sichuan snub-nose monkeys (Zhao et al., 2008). However, at the individual-level six out of seven infant macaques showed a significant right-nipple preference. Given the small sample size, this high percentage of right biased infants seems to highlight a tendency toward the right nipple. This finding adds consistency to previous research on wild rhesus macaques (Lindburg, 1971) in which a bias toward the right nipple was found. However, the reported right nipple preference is not in agreement with the study on rhesus macaques by Tomaszycki et al. (1998), in which a slight group-level left nipple preference was found. Incongruences between studies might be due to differences in sample size, as the current study has a limited sample, and age of the study subjects. Indeed, the age range of the subjects is smaller in the current study than in previous one on rhesus macaques, as our Barbary macaque infants were less than one month old whereas rhesus macaques were observed from birth until they were six weeks old. Further studies on larger samples of animals are needed, considering the potential impact of factors such as age and species on the development of lateral biases in infant primates. Moreover, there might be other possible explanations to the inconsistencies between studies on lateral biases in mothers and infants. For example, it is possible that not all Old World monkey species share similar mechanism for nipple preference and different housing conditions between studies might also affect the results (Jaffe et al., 2006), as described for other lateralized behaviour (e.g., handedness) (MacNeilage et al., 1987). As reported for maternal cradling, our findings are in contrast with previous studies on chimpanzees and bonobos (Nishida, 1993; Hopkins & De Lathouwers, 2006), highlighting a left-nipple preference in these species, suggesting differences in lateralization of mother-infant interactions between Old World monkeys and great apes. These findings seem to support the hypothesis relating taxonomic differences in maternal cradling bias and nipple preference to differences in hand preference. In particular, Hopkins (2004) suggested that great apes such as chimpanzees and bonobos showing a left-side bias for cradling and nipple preference tend to have a more pronounced right hand preference, whereas species with right or no bias in mother-infant interactions tend to be left-handed or ambi-preferent.

In addition, we investigated the hand preference for food reaching in both mother and infant macaques. At the group-level, no bias in hand preference was found, neither for the mothers nor for the infants. Moreover, no significant differences were found between mothers and infants in both the LI and the ABS-LI scores, suggesting that mother and infant hand preference is similar in terms of both direction and strength. However, at the individual-level, four out of seven mother macaques showed a significant hand preference, whereas no infant was significantly lateralized. This finding seems partially to support the hypothesis that manual lateralization in non-human primates might be affected by the age of the subjects, with older individuals showing a more pronounced hand preference than juveniles (Warren, 1977; Lilak & Phillips, 2008; Meguerditchian, Molesti & Vauclair, 2011). Given the small sample size and the lack of significant differences at the group level, this conclusion is rather speculative and more studies are needed to test the effect of age on the hand preference and to compare manual lateralization between mothers and their infants.

We further investigated the relationship between the lateral biases in both mothers and infants, by comparing the LI score of all behavioural categories within each group. Among the mothers, nipple preference, maternal cradling and infant retrieval were not significantly correlated with each other and with hand preference for food reaching. Among the infants, nipple preference and clinging on mother belly were not significantly correlated and the same finding was reported for clinging and food reaching. On the other hand, a positive correlation between nipple preference and food reaching was reported. Therefore, the position of the nipple chosen to nurse seems to affect the hand preference to reach for food of the infant. A possible explanation could be that the position of the nipple might affect the hand used to hold on the mother body side. For example, if the infants are suckling on the mother right nipple, which is on the left side with respect to the nursing infants, they could be more comfortable to cling on the mother fur on their left, using the ipsilateral hand. Having a nipple preference might therefore lead to the specific and routine use of one hand for support that may persist also outside the nursing and maternal context. This result seems partially to support the Postural Origin Theory, suggesting a left hand involvement for posture related activities and the right hand availability for other tasks (MacNeilage, 2007). Similar influence of infant early bias on hand preference has been reported in capuchin monkeys (*Cebus apella*). In this species, early bias in head orientation seemed to be related to a body weight displacement of the infant, leading to a manual lateralization for grasping to the mother and to the hand preferences later in development (Westergaard et al., 1998). Taken together, our findings seem to underline that the maternal environment and anatomy rather than the mother behaviour and side biases would affect the development of handedness in the infants.

Conclusion

The results of this study showed that at the individual level, infant Barbary macaques showed a distinct nipple preference and similar findings have been found for maternal cradling in mother macaques. However, at the group-level, no significant biases were found for any of the behavioural categories considered. This lack of group-level side biases in both the mothers and the infants, specifically for maternal cradling and nipple preference, is not in agreement with previous research on great apes. This discrepancy between studies might be due to taxonomic differences in the infant development and interaction with the mother that might affect the handedness. In other words, the influence of maternal behaviour on the infant lateralization reported in great apes and humans might have appeared late in the phylogeny of primates. However, as suggested by our finding in Barbary macaques, the maternal environment and early choice characterizing the life of the infants might affect their hand preference later in development. The differences in lateral biases in maternal and infant behaviour between monkeys and great apes might also explain incongruences between studies on handedness between the two groups. Indeed, some evidence of population-level right handedness has been frequently reported in great apes (Hopkins, 2007; Meguerditchian et al., 2015; Regaiolli, Spiezio & Hopkins, 2016) but rarely in monkeys, especially during spontaneous unimanual tasks (*e.g.*, Fitch & Braccini, 2013; Regaiolli et al., 2016). Overall, our study seems to support the hypothesis that maternal environment and anatomy in early life might affect the development of hand preference in non-human primates (Hopkins, 1994: 1995; Westergaard et al., 1998; Hopkins, 2004). However, due to the small sample size of the current work and the age differences between different studies, further research on a larger number of mother-infant dyads is needed, in Barbary macaques as well as in other species.

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Table 1(on next page)

Measures of lateral biases in mother and infants Barbary macaques.

For each subject and for each behavioural category the table reports the frequencies of right (R) and left (L) hand (or mother nipple in the case of nipple preference), the Laterality Index score (LI = [R-L]/[R+L]), the *z*-score and *P*-value from the Binomial test. Only subject that reached a minimum of ten events were included in the binomial test. Asterisks indicate a significant lateral bias (toward the left: *z*-score < -1.96 and toward the right: *z*-score > 1.96). The upper part of the table report the behavioural categories collected for the mothers (Maternal cradling and infant retrieval), whereas the lower part present data collected for the infants (nipple preference and clinging on mother belly).

	Maternal cradling					**Infant retrieval**				
Subject	**R**	**L**	**LI**	***z*-score**	***P*-value**	**R**	**L**	**LI**	***z*-score**	***p*-value**
Budda	101	34	0.50	5.68*	< 0.0001	13	11	0.08	0.2	0.839
Funny	51	77	-0.20	-2.21*	0.0267	11	11	0.00	0	0.168
Katrina	5	27	-0.69	-3.71*	0.0001	3	4	-0.14	#	#
Last	11	51	-0.65	-4.95*	< 0.0001	11	7	0.22	0.71	0.481
Mirror	49	71	-0.18	-1.92	0.0548	18	12	0.20	0.91	0.362
Vanda	98	16	0.72	7.59*	< 0.0001	14	14	0.00	0	1.000
Violetta	74	27	0.47	4.58*	< 0.0001	24	28	-0.08	-0.42	0.678
	Infant nipple preference					**Hanging on belly**				
	R	**L**	**LI**	**Z-score**	***p*-value**	**R**	**L**	**LI**	**Z-score**	***p*-value**
Budda's Infant	66	1	0.97	7.82*	< 0.0001	121	143	-0.08	-1.29	0.196
Funny's Infant	63	8	0.77	6.41*	0.0001	122	128	-0.02	-0.32	0.752
Katrina's Infant	26	6	0.63	3.36*	0.0005	96	86	0.05	0.67	0.505
Last's Infant	69	6	0.84	7.16*	< 0.0001	122	102	0.09	1.27	0.204
Mirror's Infant	32	7	0.64	3.84*	< 0.0001	143	149	-0.02	-0.29	0.770
Vanda's Infant	51	26	0.32	2.74*	0.0059	107	115	-0.04	-0.47	0.639
Violetta's Infant	11	46	-0.61	-4.5*	< 0.0001	159	169	-0.03	-0.5	0.619

Excluded from the Binomial test due to data deficiency.

Table 2(on next page)

Inter-correlations between measures of lateral biases within mother Barbary macaques.

For every pair-wise comparison the table reports the *Rho* and *P* values from Spearman correlations. Asterisks indicate significant correlations ($P < 0.05$).

	Cradling	Retrieval	Food reaching
Cradling	#		
Retrieval	*Rho* = 0.072 *P* = 0.878	#	
Food reachng	*Rho* = 0.607 *P* = 0.148	*Rho* = 0.216 *P* = 0.641	#

Table 3(on next page)

Inter-correlations between measures of lateral biases within infant Barbary macaques.

For every pair-wise comparison the table reports the *Rho* and *P* values from Spearman correlations. Asterisks indicate significant correlations ($P < 0.05$).

	Nipple Pref.	Hanging belly	Food reaching
Nipple Pref.	#		
Hanging belly	*Rho* = 0.090 *P* = 0.848	#	
Food reaching	*Rho* = 0.786 *P* = 0.036*	*Rho* = -0.162 *P* = 0.728	#

Figure 1

Lateral biases in the behaviour of mother and infant Barbary macaques.

For each behavioural category the bar plot reports the mean LI score. Error bars represent standard deviation.