



Hand Preference in *Rhinopithecus roxellana* Infants: Is It Influenced by Familial Inheritance?

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Abstract: The Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) is a typical arboreal group-living Old-World primate and has been studied broadly in hand preference. However, infants have not been tested independently from other immature individuals to date. The purpose of the present study was to investigate hand preference in a spontaneously unimanual feeding task in nine infants at 12 months and the relationship of hand preference with their parents in *R. roxellanae*. Most infants (89%) showed individual-level hand preference. No correlation was found in the direction of hand preference between infant and its parents, and a significant negative correlation in the strength of hand preference was found between infants and their mothers (r = -0.715, p = 0.03). Moreover, there was no sex difference in the direction and strength of hand preference both in infants and adults (i.e., parents). Meanwhile, the strength of hand preference in adults was stronger than that in infants. This study is a first and preliminary exploration for the expression of hand preference in *R. roxellanae* infants and whether their hand preference was influenced by familial inheritance.

Keywords: Rhinopithecus roxellana; infants; hand preference; familial inheritance

1. Introduction

Handedness was considered as the most obvious index and an exclusive characteristic in human brain asymmetry and has been greatly studied [1,2]. Almost 90% of humans showed right-hand preference at a population level [3]. However, the evolution and origin of human right-handedness remain unsolved [4,5]. Previous studies showed that hand preference was present at birth and appears gradually during development in humans. For example, no more than 6-month-old infants begin to present strong hand preference, become stronger at 6 months of life and are tending towards stability over these ages [6–9]. More recently one review summarized that no one study can completely excluded genetic or environmental influence on the formation of hand preference [10]. One previous review, meanwhile, also emphasized the genetic influence (i.e., familial inheritance) on the development of handedness and indicated that the influence was supported by compelling evidence [1]. The handedness of a child showed a positive correlation with that of its biological parents, but not with that of adoptive parents [11–13]. In addition, a child was more likely to be right-handed when its parents were right-handed compared with its parents that were left-handed or different direction of handedness [13–15]. Although these research studies showed the impact of familial inheritance, at least to some extent, on the development of handedness, the question about the inheritance of handedness is not so straightforward [1,10].



Research on the development of limb preferences had been reported in many other nonhuman mammalian species (e.g., carnivorous [16], marsupials [17] and nonhuman primates [18]). In these species, only nonhuman primates were considered as an excessive model for exploring the origin and evolution of human hemispheric specialization because of the similar brain asymmetry and the relatively close biological systems with humans [19]. However, it is less clear when infant handedness appears. One early study in marmosets (Callithrix jacchus) reported that significant hand preference was developed by 5–8 months in an unimaual holding task and was maintained from 10 to 70 months [18]. Although there were some studies related to infants, these studies were not completely removed in infants from other ages [20–22], nor neglected a difference on handedness among species [23]. In addition, the influence of familial inheritance on handedness is rarely focused on nonhuman primates, and existing data were contradictory. Some research results showed a significant correlation between the handedness of offspring and that of its parents (mainly of its mother), including New World monkeys (common marmosets (Callithrix jacchus jacchus) [24]; capuchins (Cebus paella) [22]) and Old World monkeys (rhesus macaques (Macaca mulatta) and pit-tailed macaques (M. leonine) [25]). On the contrary, no significant correlation was founded in other studies, including Old World monkeys (bonnett macaques (M. radiate) [26]) and apes (gorillas (Gorilla gorilla berengei) [27]; chimpanzees (Pan troglodyte) [28]). The current research findings are not enough to reveal the complex relationships of familial inheritance and handedness, and more investigation is needed in other species for further understanding the development mechanism of handedness in non-human primates.

The Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) is a typical arboreal group-living Old-World primate and has been studied broadly in hand preference in different behavioral tasks [29–33]. Although some studies focus on adults and immatures [29,30], infants have not been tested independently in hand preference to date. The close relationship with their mothers in their first years makes us recognize the infants from other individuals of the same age. The main purpose of the present study was to investigate hand use of 12-month-old infants during unimanual feeding in the wild. Meanwhile, the relationship with their parents will also be investigated for exploring the development level of handedness in the first year of life and the potential factor influencing the expression of handedness in *R. roxellana*.

2. Materials and Methods

2.1. Study Site and Species

Our study site was in Guanyinshan National Nature Reserve (1150–2574 m above sea level) on the southern slopes of Qinling Mountains in China. For *R. roxellanae* lived in the Qinling Mountains, deciduous broadleaf forests at 1400–2200 m above sea level are their most favorite, the mixed coniferous broadleaf forests at 2200–2600 m above sea level are the second favorite, and finally the coniferous forests at 2600–2900 m above sea level are the third favorite. Two wild populations were observed at the study site and the focus population was the one that was found in 2008, which consists of multi-one-male units and one-multi-male unit. During the observation period, the field assistants began to search for the focus population at about 5:00 a.m. every day. Once the monkeys in the focus population were found, field assistants attracted them to the provisioning site [34]. Approximately 200 g of corn grain, sliced apple and radish were provided per monkey per day at three-time points (9:00 a.m., 12:00 a.m. and 3: 00 p.m.) [34,35]. All adult individuals were identified mainly via their physical characteristics by a close distance observation (5–50 m). The mother-offspring dyads were determined based on suckling of infants and 9 infants and their parents (9 females and 5 males) were involved in this study. Our study conformed to the national laws and regulations on animal care in China.

2.2. Data Collection

Data were collected between 9:00 a.m. and 7:00 p.m. over 56 days from December 2019 to May 2020. Unimanual feeding was used for the assessment of hand preference in *R. roxellanae*. Hand use during feeding on the ground was developed in *R. roxellanae* at the third month of life. We only recorded the behavior when a subject began to feed on the ground and kept a bipedal posture. In this posture, two hind limbs were mainly used to suspending its body weight and one of forelimbs was sometimes used as a supplementary role to maintain stability (Figure 1). The individual, sex, age and the dominant hand were recorded as a data point. The dominant hand was the one that firstly grasped the food on the ground and brought it into its mouth, and then the other hand considered as subordinate tended to be unused or placed on its hind limb. Data of individual dominant hand were recorded as the word "L" if the individual showed left-side dominant and right-side subordinate, or as "R" if the one showed right-side dominant and left-side subordinate in unimanual feeding.



Figure 1. Unimanual feeding behavior in *R. roxellanae*. One 12-month-old infant (the intermediate individual), its father (the right individual) and its mother (the left individual) were all feeding on the ground under a bipedal posture.

Focus animal sampling and behavioral sampling [36] were used for the data collection of hand preference in *R. roxellanae*. Behavioral sampling was used at the beginning of the observation, while focus animal sampling was only used to obtain reasonable data points per subject at the final stage of the observation. If the focal subject was continuing feeding under the same place and time, the data were recorded only once. A minimum of 30 data points per subject was collected in our study.

2.3. Data Analyses

There have been three indexes for the analysis of hand preference. The handedness index (HI) and the absolute value of HI (ABS-HI) were used to assess the degree and strength of individual hand preference, respectively. The HI score was obtained from the formula: (R - L)/(R + L), and the scores varied between -1.0 and 1.0, indicating left and right hand preference, respectively. The last index was the binomial *z*-score, which was used to determine whether the frequency of right- or left-hand use was higher than that was expected by chance (50% right-hand use). The subjects were classified as left-hand preference ($z \le -1.96$), right hand preference ($z \ge 1.96$) and ambidextrous (-1.96 < z < 1.96) according to the *z*-scores [28].

To exclude the influence of the number of observations, we used the Spearman correlation test to test the relationship between the number of data points per subject and the HI scores and ABS-HI

scores. We performed one-sample tests to evaluate the population-level hand preference based on individual HI scores. Finally, we used the Mann–Whitney *U*-test to evaluate sex and age influences on hand preference. SPSS 23.0 and a two-tailed test with a level of significance of $p \le 0.05$ were used in all analyses.

3. Results

3.1. Hand Preference in Infants

In total, 329 data points were recorded in 9 *R. roxellana* infants. The number of observations per individual was 36.56 ± 1.67 (range: 31-47) and was no significant correlation with HI scores (r = -0.49, p = 0.181) and ABS-LI scores (r = -0.029, p = 0.941), respectively, indicating that handedness was not affected by the number of observations. Moreover, the mean HI and ABS-HI scores were -0.21 ± 0.13 (range: -0.56-0.35) and 0.41 ± 0.04 (range: 0.14-0.56), respectively (Table 1). Based on the *z*-scores, there were six left side (67%), two right bias (22%) and one ambidextrous (11%) hand preferences at an individual level (Figure 2); no significant hand preference was showed at a population level in infant *R. roxellana* ($t_8 = -1.59$; p = 0.150). Then we evaluated the sex effect on hand preference of infants and showed no significant differences between females and males in both HI scores ($N_a = 5$, $N_b = 4$; U = 10.00, p = 0.142) (Figure 3A).

Number	Sex	L/R	HI	z-Score	Handedness	
1	Female	34/13	-0.45	-3.06	Left	
2	Female	24/10	-0.41	-2.40	Left	
3	Male	7/24	0.55	3.05	Right	
4	Female	24/12	-0.33	-2.00	Left	
5	Male	25/7	-0.56	-3.18	Left	
6	Female	20/15	-0.14	-0.85	Ambidextrous	
7	Male	11/23	0.35	2.06	Right	
8	Male	28/12	-0.40	-2.53	Left	
9	Male	30/10	-0.50	-3.16	Left	

Table 1. Hand preference in 12-month-old R. roxellana infants.

L, left-side dominant/right-side subordinate; R, right-side dominant/left-side subordinate; HI, the handedness index.

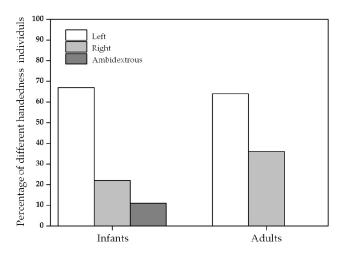


Figure 2. The percentage of individuals exhibiting left-side, right-side and ambidextrous hand preference in *R. roxellana* infants and adults based on the *z*-scores. There is no one showing ambidextrous in adult individuals.

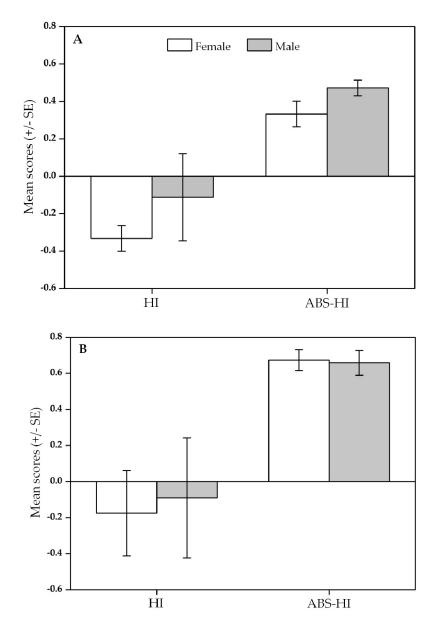


Figure 3. Sex differences on the direction and strength of hand preference in *R. roxellana* based on HI scores and ABS-HI scores, respectively. (**A**) Sex differences in adult individuals. (**B**) Sex differences in infant individuals. There were no significant sex differences both in adult and infant *R. roxellan.* ABS-HI, the absolute value of HI.

3.2. Hand Preference in Adults

We recorded the parents of *R. roxellana* infants as for adults and 732 data points were recorded in all 14 adults. The number of observations per individual was 52.29 ± 4.51 (range: 34–88) and was no significant correlation with HI scores (r = 0.261, p = 0.367) and ABS-LI scores (r = -0.197, p = 0.499), respectively, indicating that handedness was not affected by the number of observations. The mean HI and ABS-HI scores were -0.14 ± 0.18 (range: -0.80-0.90) and 0.67 ± 0.04 (range: 0.36-0.90), respectively (Table 2). Based on the *z*-scores, nine individuals were left-handed (64%) and five right-handed (36%) were found in individual level, and there was no one showed ambidextrous handedness (Figure 1); there was no significant hand preference was showed at a population level in adults ($t_{13} = -0.780$; p = 0.449). As with as the sex effect on handedness in infants, there was also no significant differences between females and males in both HI scores ($N_a = 9$, $N_b = 5$; U = 21.00, p = 0.841) and ABS-HI scores ($N_a = 9$, $N_b = 5$; U = 20.00, p = 0.739) in adults (Figure 3B).

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Number	Mother				Father					
	Name	L/R	HI	z-Score	Handedness	Name	L/R	HI	z-Score	Handedness
1	QB	28/6	-0.65	-3.77	Left					
2	MB	36/8	-0.64	-4.22	Left	HD	46/5	-0.80	-5.74	Left
3	FB	36/17	-0.36	-2.61	Left					
4	XF	32/4	-0.78	-4.67	Left	DX	7/81	0.84	7.89	Right
5	PP	41/7	-0.71	-4.91	Left					
6	KD	2/38	0.90	5.69	Right	YQ	6/22	0.57	3.02	Right
7	CY	32/6	-0.68	-4.22	Left					
8	YK	3/42	0.87	5.81	Right	BD	44/15	-0.49	-3.78	Left
9	LS	19/53	0.47	4.01	Right	XL	64/17	-0.58	-5.22	Left

Table 2. Hand preference of adult R. roxellana.

3.3. Relationship between Infants and Their Parents

We firstly compared the effect of familial inheritance on handedness in *R. roxellana*. Based on HI scores, the handedness of infants was no significant correlation with their mothers (r = -0.119, p = 0.761) and their fathers (r = -0.013, p = 0.974). Based on ABS-HI scores, there was also no significant correlation between infants and their fathers (r = -0.420, p = 0.260), but a significant negative correlation was found between infants and their mothers (r = -0.715, p = 0.03). Moreover, we considered the effects of age on hand preference in *R. roxellana*. No significant difference was found between infants and adults in HI scores ($N_a = 14$, $N_b = 9$; U = 51.00, p = 0.450), while the hand preference of adults was stronger than that in infants in strength of hand preference ($N_a = 14$, $N_b = 9$; U = 12.00, p = 0.001) in *R. roxellana* (Figure 4).

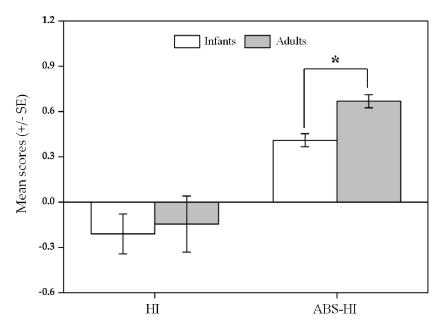


Figure 4. Comparison between adults and infants in the direction and strength of hand preference in *R. roxellana* based on HI scores and ABS-HI scores, respectively. * represented a significant difference between adults and infants in the strength of hand preference ($p \le 0.05$).

4. Discussion

This is the first study on hand preference in 12-month-old *R. roxellana* infants in wild settings. Studying handedness in infants has been motivated by accumulated evidence suggesting that hand preference can be identified during early infancy. A majority of infants (89%) show a significant hand preference at the individual level at 12 months. The result reveals obvious brain function asymmetry at

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12 months of age in *R. roxellana*. Previous research showed that when an individual reached a particular age (e.g., proximately 14 months in bonnett macaques [26]; 3-year-old in gorillas [27]), the degree of laterality was no longer increasing with age. Concerning *R. roxellana*, it is not enough to assess the particular age and the developmental trajectories of infant handedness need to be investigated in the next. Additionally, no sex effect was found in hand preference in infants, revealing brain development between sexes reached the same extent at 12 months. The finding was consistent with that in other nonhuman primates (such as 12-month-old capuchins and bonnett macaques) [26,37].

No significant correlations were obtained in the direction of hand preference between infants and their parents in this study. The result was consistent with that in bonnet macaques [26], rather than rhesus macaques and pig-tailed macaques [25], although they all belong to Old World monkeys. Previous studies also used the unimanual reaching to investigate the hand preference. As with as our finding in *R. roxellana*, bonnet macaques did not show a significant population-level handedness [26]. On the contrary, rhesus macaques and pit-tailed macaques showed hand preference at a population level because they reached food in a quadrupedal posture [25]. Although there was no evidence that supported that the direction of handedness was influenced by either parent in reaching task in capuchin monkeys, a correction was found in the direction of looking bias between offspring and parents [22]. Based on these findings [22,25,26], we should select the lateralized behavior that can elicit a stronger preference than simple reaching task (such as bimanual coordinated task [29,32]) or other lateralized behaviors (such as turning [22]) to further exclude the influence of manual tasks on handedness.

Surprisingly, the present research showed a negative correlation in the strength of hand preference between the infant and its mother. The finding is inconsistent with results from other nonhuman primates in showing no correlation between parents and offspring in the strength of hand preference (such as capuchins [22] and chimpanzees [38]). Although the strength of lateralization increased as monkeys matured and finally reached the same lateralization degrees as adults, it is unknown how long the negative correlation was maintained before the monkey matured.

No population-level hand preference was found in adult *R. roxellana*, which is not consistent with one previous study on a unimanual task of the same species [29]. The low sample size in our study may be one of the reasons for the difference found in the same task and species. The difference between the provisioned foods also may lead to the different results. The focal population in the previous study was provisioned by more corn than that provisioned to our focus population. Corn was so small and light that the monkeys required precision grasping and therefore, were more likely to elicit greater hand preference at a population level [29,39]. Besides, our focus population was provisioned for about six years, while the one in the previous study had been provisioned for more than ten years during the collection of data [29,40]. Thus, the focus population in the previous study may have more obvious and steady manual skills in feeding artifact provisioned food than our focus population.

Compared with infants, adults showed stronger handedness in the present study. Hopkins and Bard in their early study mentioned a positive correlation between the strength of hand preference and age [4] and the view was supported by other studies in nonhuman primates. For example, adult capuchins (mean age per subject: 12.1) also expressed a stronger hand preference than did immature individuals (mean age per subject: 1.4) [21]. Likewise, the degree of laterality increased with age in bonnett macaques before 14 months [26]. The result is also quite similar to these obtained in humans [41].

As with infants, adults also showed no sex effect in hand preference. The result agreed with previous studies in the same task and species [29–31] as well as other nonhuman primates [42,43]. It is important to note that some studies reported sex difference, especially on the bimanual coordinated task, including apes (e.g., gorillas [43]; chimpanzee [44]; orangutans (*Pongo pygmaeus pygmaeus*) [45]), Old-World monkeys (e.g., de Brazza's monkeys (*Cercopithecus neglectus*) [46]) and New-World monkeys (e.g., capuchins [47]; white-face capuchins (*C. capucinus*) [39]). However, for the unimanual reaching task, a sex effect on hand preference was reported in very few research studies. For example, Meguerditchian and colleges found that a significant right-handedness was mostly found only in

female squirrel monkeys (*Saimiri sciureus*), while a higher degree of population-level left-handedness was found in males than that in females [20]. About the previous studies on *R. roxellana*, no sex effect was found either in the unimanual task [29–31] or in the bimanual coordinated task [33], which was also supported by the current study.

5. Conclusions

This is the first investigation on the expression of hand preference in 12-month-old *R. roxellana* infants and the relationship with their parents. Our results showed hand preference at the individual level during unimanual feeding at 12 months of age. The important result of this study was no correlation in the direction of hand preference between infants and their parents, and a negative correlation in the strength of hand preference was only found in the mother–offspring relationship. Moreover, we also found no sex difference in the direction and strength of hand preference in infants and adults (i.e., their parents). Meanwhile, the strength of hand preference in adults was stronger than that in infants in our study. These findings were consistent with previous studies on the same species [29–33] and provided some new evidence for the research on sex and age influences on hand preference in *R. roxellana*.

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