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Hand preference during bimanual coordinated task in northern pig-tailed macaques *Macaca leonina*

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Abstract

In humans, handedness is one defining characteristic regardless of cultures and ethnicity. Population-level right handedness is considered to be related with the evolution of left hemisphere for manual control and language. In order to further understand evolutionary origins of human cerebral lateralization and its behavioral adaptation, standardized measures on hand preference are required to make reliable comparison in nonhuman primate species. In this study, we present the first evidence on hand preference during bimanual coordinated tasks in northern pig-tailed macaques *Macaca leonina*. The classical TUBE task was applied to examine hand preference among nine individuals from Tianjin Zoo of China. We recorded and made analysis on both frequency and bout data on manual laterality. The results consistently show that subjects displayed strong individual hand preferences, whereas no significant group-level handedness was found. There were no sex and age significant differences on both direction and strength of hand preference. The *M. leonina* preferred to use the index finger to extract the baited food inside the tube. Our findings fill the knowledge gap on primate handedness, and efficiently affirm the robustness of the TUBE task as one efficient measure of hand preference in primates.

Key words: bimanual coordination, hand preference, *Macaca leonina*, primate evolution.

Handedness is one defining characteristic of humans across a variety of cultures and ethnicity, and almost 90% of adults are right-handed (Porac and Coren 1981; Annett 2002; Corballis 2002; Cashmore 2009). Population-level right handedness is considered to be related with the evolution of left hemisphere for manual control and language (Corballis 1983; Marchant and McGrew 1998; Knecht et al. 2000; Raymond and Pontier 2004). Based on current research findings, the evolutionary characteristic of human right-handedness remains unsolved. Interests in manual laterality in non-human primates could improve our understanding on evolutionary origins of human cerebral lateralization and its behavioral adaptation (Fagot and Vauclair 1988 1991; Bradshaw and Rogers 1993; Ward and Hopkins 1993; Rogers and Andrew 2002; Vallortigara and Bisazza 2002; MacNeilage et al. 2009; Rogers 2014; Hopkins et al. 2015).

Nowadays a variety of naturalistic and experimental behavioral tasks have been applied to assess hand preference in nonhuman primates (Hopkins 2007; Rogers et al. 2013). Fagot and Vauclair (1991) proposes the task complexity theory that high-level tasks requiring accurate motor coordination and complex cognitive process (e.g. bimanual grooming: Zhao et al. 2010) is more likely to elicit stronger hand preference than simple low-level tasks (e.g., unimanual reaching: Papademetriou et al. 2005), and this view has been gaining support from increasing research evidences (*Cebus apella*: Westergaard and Suomi 1996; Spinozzi et al. 1998; Lilak and Phillips 2008; *Cercopithecus torquatus*: Blois-Heulin et al. 2006; Laurence et al. 2011; *Cercopithecus c. campbelli*: Chapelain et al. 2006; *Cercopithecus neglectus*: Trouillard and Blois-Heulin 2005; Schweitzer et al. 2007; *Chlorocebus aethiops*: Harrison and Byrne 2000; *Gorilla gorilla*: Byrne and Byrne 1991;

Macaca tonkeana: Canteloup et al. 2013; *Pan troglodytes*: Colell et al. 1995; *Rhinopithecus roxellana*: Zhao et al. 2010). Moreover, it is considered that experimental tasks demanding precise manipulation induce greater strength of manual laterality than spontaneous reaching or grasping tasks (e.g., *Cercopithecus neglectus*: Schweitzer et al. 2007). Therefore, given that tasks diversity could generate potential inconsistency across findings, standardized methods are beneficial to make reliable comparison on hand preference among nonhuman primate species and contribute to continuities of handedness between human and nonhuman primates.

The TUBE task, firstly designed by Hopkins (1995), is a complex experimental task requiring bimanual role differentiation (Hopkins 1995). In this measure, the primate subject should hold the tube with one hand and extract the baited food inside the tube with the other hand (Hopkins 1995). The TUBE task removes the potential situational influence that might influence hand use (Hopkins 1995; Spinozzi et al. 1998; Hopkins and Cantalupo 2005), and has been found to be related to neuroanatomical asymmetries within the primary motor cortex in nonhuman primates (Hopkins and Cantalupo 2004; Phillips and Sherwood 2005). For example, hand preference for the TUBE task significantly correlates with the motor hand area of brains in chimpanzees (Hopkins and Cantalupo 2004). Canteloup et al. (2013) examined three TUBE tasks involving different materials, weights, and diameters, and found there was no significant difference between them on both direction and strength of hand preference. The TUBE task is recognized as one standard and robust action to measure primate hand preference, and has been tested in captive or wild primate species, including New World monkeys (*Ateles fusciceps rufiventris*: Nelson et al. 2015; *Cebus apella*: Westergaard and Suomi 1996; Phillips and Sherwood 2005; Lilak and Phillips 2008; Spinozzi et al. 2007; *Cebus capucinus*: Meunier and Vauclair 2007; *Saimiri sciureus*: Meguerditchian et al. 2012), Old World monkeys (*C. neglectus*: Schweitzer et al. 2007; Maille et al. 2013; *Cercopithecus troquatus*: Maille et al. 2013; *Macaca mulatta*: Westergaard and Suomi 1996; Westergaard et al. 1997; *M. tonkeana*: Canteloup et al. 2013; *Papio anubis*: Vauclair et al. 2005; *Rhinopithecus roxellana*: Zhao et al. 2012) as well as apes (*Gorilla*:

gorilla: Hopkins et al. 2003a, 2011; *Pan paniscus*: Chapelain and Hogervorst 2009; Chapelain et al. 2011; *Pan troglodytes*: Hopkins 1995, 1999a; Hopkins et al. 2001, 2003a, 2003b, 2004, 2005; Hopkins and Cantalupo 2003; Llorente et al. 2009, 2011; *Pongo pygmaeus*: Hopkins et al. 2003a). However, there are still knowledge gap on primate hand preference in the TUBE task which could help for further understanding the evolution of primate handedness.

The pig-tailed macaque belongs to Old World monkeys, and in the 21st century has been reclassified into two separated species, northern pig-tailed macaque *Macaca leonina* and Sundaland pig-tailed macaques *M. nemestrina* based on genetic information and characteristic of sex skin swelling (Groves 2001; Brandon-Jones et al. 2004). With regard to *M. nemestrina*, its manual laterality has been tested for two tasks in three studies. For the quadrupedal reaching task, juvenile and adult *M. nemestrina* showed individual hand preference while the left group-level handedness was only found in adults (Westergaard et al., 2001a, 2001b). For the experimental task requiring individuals to remove small food rewards embedded in a vertical array, only female *M. nemestrina* was chosen as subjects. They showed individual hand preference, and there was no group-level handedness. Adult subjects performed quicker with the left hand than with the right hand (Rigamonti et al. 1998). With regard to *M. leonina* (Figure 1), it is a rarely studied species and there is only one report on hand preference (Zhao et al. 2015a). It was found that northern pig-tailed macaques generally showed a bias towards left-hand use although there was no group-level handedness in the unimanual task (Zhao et al. 2015a). The main purposes of the present study were to: 1) for the first time investigate hand preference during the TUBE task in northern pig-tailed macaques, 2) compare the results with previous findings in the closely related species, Sundaland pig-tailed macaques, as well as other species in order to make comprehensive assessment of primate manual laterality and discuss primate evolution on cerebral lateralization. Based on the current finding in pig-tailed macaques, it is hypothesized that *M. leonina* shows a bias towards left-hand use overall in the TUBE task. In addition, on account of task complexity theory, it is hypothesized that



Figure 1. The northern pig-tailed macaque *Macaca leonina*.

M. leonina shows stronger hand preference in the bimanual TUBE task than in the unimanual task.

Materials and Methods

Study population

Nine northern pig-tailed macaques (mean age ± standard error (SE): 5.83 ± 1.67 years) were together housed in one outdoor room and one indoor room at Tianjin Zoo, China (Table 1). All individuals were born in captivity and mother-reared (Zhao et al. 2015b). Monkeys could freely shuttle back and forth via the hatch between two rooms. Food was presented two times per day and water was provided ad libitum. Our study adhered to animal care regulations and national laws in China.

Data collection

Data were collected from September to November 2014. We followed the method described by Hopkins (1995) and Hopkins (2013). The opaque polyvinyl-chloride tube (3 cm in diameter, 10 cm in length) was applied in the assessment of manual laterality. Peanut butter mixed with corn kernels were smeared inside, approximately 2 cm from both ends of the tube. Six PVC tubes were placed on the room ground simultaneously during each test so as to reduce competition among individuals. If multiple individuals performed the TUBE task at the same time, we selected the individual with the nearest visible distance from the observer. If more than one individual were the same visible distance from the observer, we selected the monkey who had the fewest number of responses. Every effort was made to balance sampling responses among subjects. All data were only taken into account when individuals had both hands free before starting the activity on the ground.

Both the frequency and bout were recorded in hand use as described by Hopkins et al. (2001) and Zhao et al. (2012). With regard to the frequency, we recorded the finger and hand use each time, and the hand used to extract the food was considered as the dominant hand (Hopkins 1995). Data were collected until the subject either dropped the tube or stopped extracting corn kernels for at least 10 s. With regard to the bout, we defined one bout as each sequence of identical actions and recorded only the first occurrence of such sequences. The identification of dominant hand was done as for frequencies. The new bout in hand use was noted when the subject either dropped the tube, changed the hand catching the tube, held the tube with both hands or moved to another area to continue feeding (Chapelain and Hogervorst 2009; Zhao et al. 2012). In addition, the digit used to extract the food from the tube each time was

also recorded. Feeding attempts while using the feet to hold the tube were not considered based on the method described by Zhao et al. (2012). In order to assess consistency of hand preference on this experimental task, we divided individual observation period into two halves. Totally, a minimum of 100 responses (frequency) was obtained from each subject.

Data analysis

Hand preferences on the individual level were characterized using two methods (Hopkins 1999b, 2013). First, to identify the degree of individual lateral bias, the handedness index (HI) was calculated based on frequency and bout data for each subject following the formula: (right-hand use – left-hand use)/(right-hand use + left-hand use) (Hopkins 1999b). The HI varied between –1.0 and 1.0. Based on the guideline suggested by Hopkins (2013), HI scores higher than 0.20 were considered as right-handed, HI scores lower than –0.20 were considered as left-handed, and other HI scores from –0.20 to 0.20 were considered as ambipreferent. The absolute value (ABS-HI) reflects the strength of hand preference. Second, the z-score is one common statistical use in nonhuman primate handedness, and z-score values of ± 1.96 are the critical values when using the normal distribution to represent the sample distribution. Based on z-scores, the subjects were categorized as right-handed ($z \geq 1.96$), left-handed ($z \leq -1.96$), or ambipreferent ($1.96 > z > -1.96$) (Hopkins et al. 2013). Group-level hand preference was analyzed via one-sample t-tests with individual HI scores (Hopkins 1999b; Hopkins et al. 2011; Zhao et al. 2012).

We adopted the Pearson correlation coefficient test to evaluate whether individual hand preferences were consistent across observation periods. The Spearman correlation test was applied to evaluate the relationship between the number of data points per subject and HI/ABS-HI scores as well as the relationship between HI/ABS-HI scores of bouts and that of frequencies. We used paired-samples t-tests to make comparison on the direction and strength of hand preference between the bimanual tube task in this study and unimanual reaching task in the previous report (Zhao et al. 2015a) among the same subjects in northern pig-tailed macaques. The Mann–Whitney U-test was used to evaluate sex and age differences on manual laterality. Finally, we used analysis of variance (ANOVA) to evaluate the difference of digit use within subjects (Spinuzzi et al. 2007; Zhao et al. 2012). We used the SPSS 21.0 to conduct all the analyses, with an alpha level of 0.05.

Table 1. Individual data on hand preference in pig-tailed macaques

Subject	Gender	Age	Age group	Frequency data						Bout data					
				Left	Right	HI	ABS-HI	z-score	Preference	Left	Right	HI	ABS-HI	z-score	Preference
TWF001	Female	14.5	Adult	264	234	–0.06	0.06	–1.34	no	115	104	–0.05	0.05	–0.74	no
TWM002	Male	13.5	Adult	222	25	–0.80	0.80	–12.57	left	117	23	–0.67	0.67	–7.93	left
TWM003	Male	6.5	Adult	135	154	0.07	0.07	1.19	no	49	58	0.08	0.08	0.83	no
TWM004	Male	5.5	Adult	181	89	–0.34	0.34	–5.59	left	113	57	–0.33	0.33	–4.30	left
TWM005	Male	4.5	Adult	98	506	0.68	0.68	16.71	right	48	203	0.62	0.62	9.82	right
TWF004	Female	3.5	Juvenile	249	57	–0.63	0.63	–11.02	left	117	28	–0.61	0.61	–7.35	left
TWM006	Male	2.5	Juvenile	223	41	–0.69	0.69	–11.21	left	97	27	–0.56	0.56	–6.24	left
TWF005	Female	1.5	Juvenile	272	55	–0.66	0.66	–11.93	left	140	26	–0.69	0.69	–8.89	left
TWF006	Female	0.5	Juvenile	29	87	0.50	0.50	5.39	right	27	81	0.50	0.50	5.20	right

Results

We recorded totally 2921 frequency data and 1430 bout data on hand use (Table 1). With regard to frequency data, the mean number per subject was 324.56 ± 48.01 (mean \pm SE) (range: 116–604) and the mean HI and ABS-HI scores were -0.21 ± 0.18 (range: $-0.80 - 0.68$) and 0.49 ± 0.09 (range: $0.06 - 0.80$), respectively. With regard to bout data, the mean number per subject was 158.89 ± 16.38 (range: 107–251) and the mean HI and ABS-HI scores were -0.19 ± 0.17 (range: $-0.69 - 0.62$) and 0.46 ± 0.08 (range: $0.05 - 0.69$), respectively.

The number of observations per individual was not significantly correlated with the HI values (frequency: $r = 0.333$, $P = 0.381$; bout: $r = 0.050$, $P = 0.898$) and ABS-HI values (frequency: $r = -0.233$, $P = 0.546$; bout: $r = 0.133$, $P = 0.732$). Therefore, individual differences in the total number of responses did not skew the distribution of handedness values.

Data consistency

A significant positive correlation was found between HI scores in two observation halves (frequency: $r = 0.825$, $P = 0.006$; bout: $r = 0.813$, $P = 0.008$), which suggests that individual hand preferences were stable over the observational period. There was a significant positive correlation between the HI score of bouts and that of frequencies ($r = 0.917$, $P = 0.001$), as well as between the ABS-HI score of bouts and that of frequencies ($r = 0.833$, $P = 0.005$).

Individual and group-level hand preference

On the individual level, five individuals were classified as left-handed (55.56%), two right-handed (22.22%), and two ambiguous-handed (22.22%) based on HI and z -scores when calculated on the basis of frequency and bout data (Table 1). There was no significant group-level handedness in the TUBE task (frequency: $t = -1.182$, $P = 0.271$; bout: $t = -1.129$, $P = 0.291$).

Sex and age effects

No significant sex difference was found either in direction of hand preference (frequency: $U = 9.00$, $P = 0.806$; bout: $U = 8.00$, $P = 0.624$) or in the strength of hand preference (frequency: $U = 6.00$, $P = 0.327$; bout: $U = 10.00$, $P = 1.000$) (Figure 2). Similarly, we found no significant difference between adults and juveniles in the direction of hand preference (frequency: $U = 7.00$, $P = 0.462$; bout: $U = 6.00$, $P = 0.327$) as well as the strength of

hand preference (frequency: $U = 7.00$, $P = 0.462$; bout: $U = 6.00$, $P = 0.327$).

Digit use

Generally, there are five extractive-act categories involved in the TUBE task. We performed ANOVA on the percentages of responses of each category for each individual, and found a significant difference across categories ($F = 10.951$, $P < 0.001$). The mean percentage for each extractive act were $61.31 \pm 10.62\%$ (mean \pm SE) with the index finger, $18.66\% \pm 9.89\%$ with the index + the middle fingers, $3.19 \pm 0.68\%$ with the index + the middle + the ring fingers, $14.25 \pm 6.91\%$ with the index + the middle + the ring + the little fingers, and $2.59 \pm 2.58\%$ with others. A post hoc analysis using the least significant difference test revealed a significantly higher percentage of responses made with the index finger compared to all other extractive-act categories (all $P < 0.005$).

Discussion

This study presents the first evidence on manual laterality during bimanual tasks in northern pig-tailed macaques. As expected, *M. leonina* displayed a bias towards left-hand use overall. More than half individuals were left-handed based on HI scores in the TUBE task. This finding in *M. leonina* with the left predominance was generally consistent with previous findings in the closed related species *M. nemestrina*, and further comparison on hand preference with the same task is needed. We also found that, for both frequency and bout data, mean HI and ABS-HI scores in the TUBE task were higher than that in the unimanual reaching task shown by the same subjects of *M. leonina* (mean HI score: -0.03 ; mean ABS-HI score: 0.17 ; Zhao et al. 2015a). The strength rather than the direction of hand preference was significantly higher in bimanual tasks than that in unimanual tasks among northern pig-tailed macaques (strength: frequency: $t = -3.296$, $P = 0.011$; bout: $t = -3.041$, $P = 0.016$; direction: frequency: $t = 1.042$, $P = 0.328$; bout: $t = 0.950$, $P = 0.370$). These results in *M. leonina* support to some extent task complexity theory (Fagot and Vauclair 1991).

In the present study, we made analyses on both frequency and bout data simultaneously and found a significant correlation between HI/ABS-HI measures based on frequencies and bouts of hand use, respectively. Furthermore, the identification of left-handed, right-handed, and ambiguous-handed individuals when considering bout data was as same as that when considering frequency data.

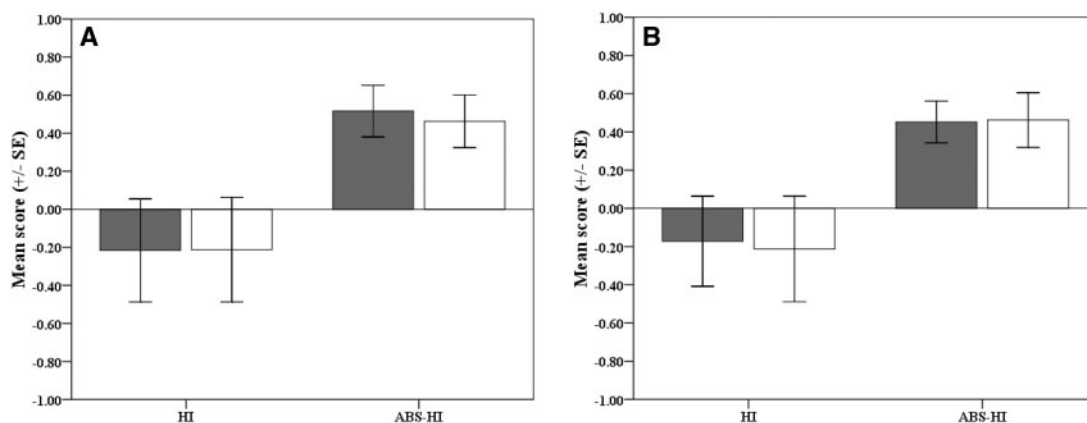


Figure 2. Sex differences on hand preference in the tube task (black color: males; white color: females). (A) Frequency data. (B) Bout data.

These findings deny the notion that frequency data in hand use does cause skewed distributions of hand preference (McGrew and Marchant 1997; Cashmore et al. 2008), and adequately support the statement that frequency and bout measures could quantify the same hand preference (Hopkins et al. 2013).

Posture plays an important role in the evolution of cerebral and behavioral lateralization in primates (Hopkins 2007). The postural origin hypothesis proposes that arboreal primates prefer to use the left hand for manual tasks and the right hand is used to support the body in the trees, whereas more terrestrial primates show right hand preference for manual tasks (MacNeilage et al. 1987; MacNeilage 2007). Accordingly, with regard to the TUBE task, Meguerditchian et al. (2013) summarizes the general pattern for left hand preference in arboreal primate species (e.g., Sichuan snub-nosed monkeys: Zhao et al. 2012) and right hand preference in terrestrial primate species (e.g., chimpanzees: Hopkins et al. 2011). Of course, some studies found no group-level handedness, which do not accord with this pattern (see review by Meguerditchian et al. 2013). Regarding the *Macaca* genus that is more terrestrial species, current findings on hand preference in the TUBE task are inconsistent. The group-level handedness with opposite dominance was only found in rhesus macaques (right handedness: Westergaard and Suomi 1996; left handedness: Westergaard et al. 1997; exception: Bennett et al. 2008). The mean HI score varied and consistently showed toward the left side among other macaques (*Macaca leonina*: the present study, Zhao et al. 2015a; *Macaca sylvanus*: Schmitt et al. 2008; *Macaca tonkeana*: Canteloup et al. 2013). There were three potential causes explaining divergent findings on the TUBE task among macaques. The first is that there was significant interspecific variation during the development of hand preference within the *Macaca* genus (Westergaard et al. 2001a). Both juveniles and adults were chosen in these studies, which influence the results of hand preference. The second is the effect of individual rearing history. Nursery-reared macaques showed significantly greater left-hand bias than mother-reared individuals (Bennett et al. 2008). The last is the variance of sample size which may influence statistic power. For instance, in the present study, the failure to find a group-level handedness is likely due to the limitation of statistical power caused by small sample size. The limited sample size may also to some extent influence the corresponding analysis on sex and age differences. Further research is required to make comparative investigation on hand preference among various macaque species with larger sample size.

How sex impacts primate hand preference is mixed, and studies reporting sex difference on the bimanual coordinated task is inconsistent (Fagot and Vauclair 1993; Rogers and Kaplan 1996; Kimura 1999; Hopkins 2007). For example, in the bimanual coordinated feeding task, males showed more obvious and stronger left-hand preference than females in wild chimpanzees (Corp and Byrne 2004) rather than in gorillas (Meguerditchian et al. 2010). For the TUBE task, sex effect on hand preference remain unclear based on the existing literature (Meguerditchian et al. 2013), and the significant sex difference has been found in one New World monkey species (*Cebus apella*: Spinozzi et al. 1998, but Spinozzi et al. 2007; Lilak and Phillips 2008) and one great ape species (*Pan paniscus*: Chapelain et al. 2011, but Chapelain and Hogervorst 2009). The *M. leonina* on the TUBE task did not present significant sex difference, which is congruent with the absence of population-level handedness on the TUBE task generally reported in primate order, especially in other Old World monkeys (McGrew and Marchant 1997).

Some evidences show that adults show stronger hand preferences than the immature (Vauclair and Fagot 1987; Milliken et al. 1991;

Hopkins 1994, 1995; McGrew and Marchant 1997; Hook and Rogers 2000; Teixeira 2008). As the first study examining age differences of hand preference in *M. leonina*, we found no significant effect of age on both the strength and the direction of hand preference.

The *M. leonina* preferred to use the index finger in the TUBE task, which is consistent with other primate species when performing the same task (e.g., *Cebus apella*: Spinozzi et al. 2007; *Cebus capucinus*: Meunier and Vauclair 2007; *Cercopithecus neglectus*: Schweitzer et al. 2007; Maille et al. 2013; *Cercocebus torquatus*: Maille et al. 2013; *Pan paniscus*: Chapelain and Hogervorst 2009; Chapelain et al. 2011; *Pan troglodytes*: Hopkins 1995; *Papio anubis*: Vauclair et al. 2005; *Rhinopithecus roxellana*: Zhao et al. 2012). These joint findings support the viewpoint of Hopkins (1995) and Maille et al. (2013) that the TUBE task requires bimanual role differentiation and precise digit use; therefore, it is a highly efficient measure of cerebral specialization and manual laterality in primates.

On the whole, we demonstrate the first evidence on hand preference during bimanual tasks in northern pig-tailed macaques. Our results in *M. leonina* showed hand preference during bimanual coordinated TUBE task on the individual level rather than on the group level. There was no significant sex and age difference on the direction and strength of hand preference. The consistent findings from frequency and bout measures affirm the robustness of the TUBE task as a standard measure of primate handedness.

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