

Postural effect on manual laterality during grooming in northern white-cheeked gibbons (*Nomascus leucogenys*)

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ABSTRACT

Investigations on manual laterality in non-human primates can help clarify human evolutionary origins of hand preference and cerebral cognition. Although body posture can influence primate hand preference, investigations on how posture affects hylobatid manual laterality are still in their infancy. This study focused on how spontaneous bipedal behavioral tasks affect hand preference in Hylobatidae. Ten captive northern white-cheeked gibbons (*Nomascus leucogenys*) were chosen as focal subjects. Unimanual grooming during sitting posture and supported bipedal posture were applied as behavioral tasks. The gibbons displayed a modest tendency on left-hand preference during sitting posture and right-hand preference during supported bipedal posture, although no group-level hand preference was detected for either posture. From the sitting to supported bipedal posture, 70% of individuals displayed different degrees of right-side deviation trends. The strength of manual laterality in the supported bipedal posture was higher than that in the sitting posture. We found significant sex differences in manual laterality during supported bipedal posture but not during sitting posture. Thus,

to a certain degree, bipedal posture in *N. leucogenys* facilitates stronger hand preference, elicits a rightward trend in manual laterality, and produces sex-specific hand preference.

Keywords: Grooming; Hand preference; Hylobatidae; Posture

INTRODUCTION

Traditionally, hand preference was viewed as unique to humans (Corballis, 2002; Marchant & McGrew, 1998; Porac & Coren, 1981). However, increasing evidence shows that hand preference is common across vertebrates, including the primate order (Fagot & Vauclair, 1991; Vallortigara & Rogers, 2005; Ward & Hopkins, 1993; Zhao et al., 2016a, 2016b). Considering that behavioral lateralization is an observable measure of hemispheric functional asymmetry (Levy, 1977; Rogers, 2014), intensive studies on hand preference in non-human primates based on phylogenetic relationships can help reveal the evolutionary origins of human hand preference and cerebral cognition (Hopkins, 2007; Rogers et al., 2013; Salva et al., 2012; Wiper, 2017). Many factors (e.g., body posture, task complexity, tool use, emotion, division of labor in hand usage) can influence primate manual laterality, with various evolutionary theories proposed for primate evolution of hand preference (Hopkins, 2007; Leliveld et al., 2013; Mangalam et

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al., 2015; Rogers & Andrew, 2002; Versace & Vallortigara, 2015; Zhao et al., 2015, 2016a, 2016b).

Regarding body posture, the postural origin hypothesis states that (1) arboreal primates prefer using the right hand to support the body in trees and the left hand for manual tasks, whereas (2) more terrestrial primates prefer using the right hand during manual tasks (MacNeilage et al., 1987; MacNeilage, 1991). Increasing primate research lends support to the postural origin hypothesis (MacNeilage, 2007; MacNeilage et al., 2009). For example, with regard to spontaneous bimanual grooming and experimental tube tasks, chimpanzees (*Pan troglodytes*) show group-level right-hand preference (Hopkins, 2007; Hopkins et al., 2007), whereas Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) display group-level left-hand preference (Zhao et al., 2010, 2012). Furthermore, upright or bipedal posture can facilitate greater expression of primate hand preference toward the right or left side (e.g., prosimians: Sanford et al., 1984; Shaw et al., 2004; New World monkeys: Hashimoto et al., 2013; Roney & King, 1993; Old World monkeys: Blois-Heulin et al., 2007; Zhao et al., 2008a; apes: Braccini et al., 2010; Hopkins et al., 1993).

The small apes (family Hylobatidae) consist of the highly arboreal siamangs and gibbons, and are a crucial link connecting monkeys and great apes on the primate evolutionary branch (Guan et al., 2018). Among the increasing number of studies on primate hand preference, the Hylobatidae remain poorly researched (e.g., Heestand, 1987; Olson et al., 1990; Redmond & Lamperez, 2004; Stafford et al., 1990), with fewer than 10 hylobatid laterality studies conducted to date (Table 1). For the small apes, previous findings show that the direction and strength of manual laterality is both species- and task-specific (Table 1), with hylobatids showing stronger hand preference in complex tasks compared with simple tasks (e.g., *Symphalangus syndactylus*: Morino et al., 2017). To date, however, research on how posture affects hylobatid hand preference is still in its infancy, with only one relevant study addressing this topic using experimental bipedal reaching tasks (Olson et al., 1990) (Table 1).

The present study focused on how spontaneous bipedal behavioral tasks influence hand preference in northern white-cheeked gibbons (*Nomascus leucogenys*). We chose unimanual grooming during sitting posture and supported bipedal posture as the measured tasks because these behaviors are common in primates, especially arboreal species, thus facilitating interspecies comparison. As northern white-cheeked gibbons are a highly arboreal species, and based on the posture origin theory, we predicted that these gibbons will show a left-hand bias under any posture. As bipedal posture is reported to induce a right-side shift in hand preference in great apes (Braccini et al., 2010; Hopkins, 1993), we also predicted that the direction of hand preference would generally present a rightward trend from the sitting to supported bipedal posture.

MATERIALS AND METHODS

Study subjects

The focal subjects were 10 captive northern white-cheeked gibbons, which included five males (age range: 4–27; mean age \pm SE: 15.40 \pm 4.20 years) and five females (age range: 4–26; mean age \pm SE: 16.00 \pm 4.39 years). These gibbons lived in different enclosures at Tianjin Zoo and Beijing Zoo in China (Table 2). Zookeepers provided food (e.g., vegetables, fruits) once a day and water *ad libitum*.

We followed all applicable international and Chinese guidelines for the care and use of animals in this study. The academic committee at the College of Life Sciences, Tianjin Normal University of China approved all study procedures.

Behavioral observations

Unimanual grooming in the sitting posture was defined as grooming with one hand, with the other hand placed on the hindlimbs or grasping a branch/rope for support while sitting on the ground or a branch. Unimanual grooming in the supported bipedal posture was defined as grooming with one hand, with the other hand grasping a branch/rope for support while standing bipedally on the ground or a branch.

We collected data from March to June 2016 based on the methods described by Hopkins et al. (2007) and Zhao et al. (2010). The observation time for each study day was from 1000 h to 1500 h. We chose one gibbon subject randomly at a time when it was performing unimanual grooming. Once we identified the focal individual, we recorded data in 5 min observation periods with 10 s sampling intervals. We recorded both hand use (left or right) and mouth use (involved or not involved) in grooming at each sampling point. We excluded unimanual grooming involving the mouth from statistical analyses to avoid the potential effect of mouth use on manual laterality.

If the gibbon stopped unimanual grooming within the 5 min observation period and did not perform unimanual grooming within the following 30 s, observation on that individual was ended and we chose another gibbon based on the method mentioned above. If the gibbon continued unimanual grooming after the 5 min observation period, and no other subjects were observed performing unimanual grooming within visible distance, we continued a new 5 min observation period for the same gibbon. When multiple subjects performed unimanual grooming simultaneously, we chose the closest visible subject. If two subjects were at a similar distance from the observer, we chose the gibbon with less sampling data.

Data analysis

Statistical analyses were conducted on both individual-level and group-level hand preference. We assessed manual laterality at the individual level by the handedness index (HI) and z scores (Hopkins, 1999, 2013). We calculated HI scores based on the following formula: (right-hand use–left-hand use)/(right-hand use+left-hand use) (Hopkins, 1999). The HI scores ranged from –1.0 to 1.0. Positive and negative HI scores represented right- and left-hand preference, respectively. The

Table 1 Previous research on Hylobatidae manual laterality

Species	Condition	Number	Task	Main finding	Reference
<i>Symphalangus syndactylus</i>	Captive	13	Food reaching	(1) No individual was left- or right-handed; (2) No group-level handedness	Heestand, 1987
<i>Hylobates lar</i>	Captive	8	Floor retrieval	(1) Six individuals were left-handed, two individuals were right-handed based on chi-square analyses; (2) No group-level handedness	Olson et al., 1990
<i>H. lar</i>	Captive	6	Mesh retrieval	(1) All individuals were left-handed based on chi-square analyses; (2) Group-level right handedness was found	Olson et al., 1990
<i>H. concolor</i> , <i>H. lar</i> , <i>S. syndactylus</i>	Captive	19	Food reaching	(1) <i>H. concolor</i> , one individual was left-handed, three individuals were right-handed, three individuals were ambipreferent based on z scores; (2) <i>H. lar</i> , one individual was left-handed, three individuals were right-handed based on z scores; (3) <i>S. syndactylus</i> , two individuals were left-handed, three individuals were right-handed, three individuals were ambipreferent based on z scores; (4) No group-level hand preference was conducted for any species, and there was no group-level handedness for the mixed sample; (5) Adults showed stronger hand preference than immature individuals.	Stafford et al., 1990
<i>S. syndactylus</i>	Captive and semi-natural	25	Leading limb during brachiation	(1) For vocal condition, one individual was left-handed, two individuals were right-handed based on z scores; (2) For non-vocal condition, two individuals were left-handed, three individuals were right-handed based on z scores; (3) No group-level handedness was found for vocal and non-vocal conditions.	Redmond & Lamperez, 2004
<i>Nomascus leucogenys</i> , <i>N. gabriellae</i>	Captive	16	Leading limb during brachiation	(1) Two individuals were left-handed, five individuals were right-handed, and nine individuals were ambipreferent based on ABS-HI >0.20 scores; (2) No group-level handedness was found.	Barker, 2008
<i>S. syndactylus</i>	Wild	49	Water collecting	(1) When testing individuals with >6 data points, 22 individuals were left-handed, 10 individuals were right-handed, and four individuals were ambipreferent based on z scores, (2) Group-level left handedness was found.	Morino, 2011
<i>H. agillis</i> , <i>H. albibarbis</i> , <i>H. agillis</i> × <i>H. albibarbis</i> , <i>H. lar</i> , <i>H. muelleri</i> , <i>H. pileatus</i> , <i>N. leucogenys</i> , <i>S. syndactylus</i>	Captive	42	Tube task	(1) When testing individuals with >6 data points, for siamangs, 10 individuals were left-handed, two individuals were right-handed, and eight individuals were ambipreferent based on z scores; for mixed gibbon species, 10 individuals were left-handed, seven individuals were right-handed based on z scores; (2) Group-level left handedness was found in siamangs whereas no group-level handedness was found in mixed gibbon samples.	Morino et al., 2017
<i>N. leucogenys</i>	Captive	9	Ground reaching; Box task; Tube task	(1) For ground-reaching task, three individuals were left-handed, one individual was right-handed, and five individuals were ambipreferent based on chi-square analyses; (2) For box task, three individuals were left-handed, three individuals were right-handed, and three individuals were ambipreferent based on chi-square analyses; (3) For box task, three individuals were left-handed, four individuals were right-handed, and two individuals were ambipreferent based on chi-square analyses; (4) No group-level handedness was found for any task	Fan et al., 2017

absolute value of HI scores (ABS-HI) represented hand preference strength. We calculated z scores using frequency of left- and right-hand use. We considered individuals as left-handed ($z \leq -1.96$), right-handed ($z \geq 1.96$), or ambipreferent ($1.96 > z > -1.96$) based on z scores. Furthermore, we used binomial tests for each subject for both postures and combined the probabilities from separate significance tests (Gibbs et al., 2007; Jones & Fiske, 1953; Zhao et al., 2016b). We assessed manual laterality at the group level by one-sample tests based on individual HI scores (Hopkins, 1999;

Zhao et al., 2012).

We applied Mann-Whitney U tests to examine sex differences in hand preference under different postures. We adopted repeated measures analysis of variance (ANOVA) (independent variable: postural conditions; dependent variable: HI/ABS-HI values) and non-parametric Wilcoxon signed ranks test to explore the postural effect on the direction and strength of manual laterality (Braccini et al., 2010). All statistical analyses were performed using SPSS v21.0, with significance at $P < 0.05$.

RESULTS

In the present study, there were no significant correlations between the number of observations per individual and HI values (sitting: $r=0.185$, $P=0.608$; standing: $r=0.260$, $P=0.467$) and ABS-HI values (sitting: $r=-0.172$, $P=0.635$; standing: $r=-0.473$, $P=0.167$). This suggests that individual differences in the total number of responses did not skew the distribution of handedness values.

Individual-level manual laterality

For the sitting posture, the HI and ABS-HI scores (mean±SE) were -0.009 ± 0.057 and 0.123 ± 0.039 , respectively. From the HI scores, we identified six gibbons as left-handed, three gibbons as right-handed, and one gibbon as ambipreferent (Table 2). From the binomial tests and z scores, we identified one gibbon as left-handed, two gibbons as right-handed, and seven gibbons as ambipreferent (Table 2).

For the supported bipedal posture, the HI and ABS-HI

scores (mean±SE) were 0.035 ± 0.093 and 0.187 ± 0.070 , respectively. From the HI scores, three gibbons were left-handed and seven gibbons were right-handed (Table 2). From the binomial tests and z scores, one gibbon was left-handed, one gibbon was right-handed, and eight gibbons were ambipreferent (Table 2).

For sitting to supported bipedal posture, based on HI scores, 60% of gibbons showed identical manual laterality (right-handed: one male and two females, left-handed: three females) and 40% showed varying degrees of right-side deviation from sitting to standing posture (four males). Based on the direction (i. e., HI values) and strength (i. e., ABS-HI values) of hand preference, 70% of gibbons showed varying degrees of right-side deviation (from negative and zero HI values to positive HI values: four males; increase in positive HI values: one female; decrease in negative HI values: two females) and 30% of gibbons showed varying degrees of left-side deviation (decrease in positive HI values: one male and one female; increase in negative HI scores: one female).

Table 2 Basic information on hand preference for unimanual grooming for each posture

Subject	Source	Gender	Age	Sitting posture					Supported bipedal posture				
				Left	Right	HI	z score	P score	Left	Right	HI	z score	P score
Beib	Beijing Zoo	Male	23	48	72	0.20	2.19	0.035	50	64	0.12	1.31	0.769
Caic	Beijing Zoo	Female	4	49	64	0.13	1.41	0.188	43	60	0.17	1.68	0.114
Hengh	Beijing Zoo	Female	26	50	81	0.24	2.71	0.009	84	88	0.02	0.30	0.819
Jingj	Beijing Zoo	Female	21	54	46	-0.08	-0.80	0.484	52	49	-0.03	-0.30	0.842
Qingq	Tianjin Zoo	Male	12	8	8	0.00	0.00	1.000	44	99	0.38	4.60	<0.001
Xiaoh	Beijing Zoo	Male	27	67	63	-0.03	-0.35	0.793	57	60	0.03	0.28	0.835
Xiaoz	Beijing Zoo	Male	4	99	88	-0.06	-0.80	0.465	66	81	0.10	1.24	0.248
Yuany	Tianjin Zoo	Male	11	106	100	-0.03	-0.42	0.728	11	20	0.29	1.62	0.150
Yuey	Tianjin Zoo	Female	22	51	22	-0.40	-3.39	0.001	54	9	-0.71	-5.67	<0.001
Ziye	Beijing Zoo	Female	7	55	49	-0.06	-0.59	0.624	52	50	-0.02	-0.20	0.921

Left: Frequency of left-hand use; Right: Frequency of right-hand use.

Group-level manual laterality

No group-level hand preference was detected during unimanual grooming for either posture (sitting posture: $t_9=-0.159$, $P=0.877$; supported bipedal posture: $t_9=0.377$, $P=0.715$). For hand use, however, the deviation from random distribution was significant for both postures (sitting posture: summed $\chi^2=38.309$, $df=20$, $P<0.01$; supported bipedal posture: summed $\chi^2=49.562$, $df=20$, $P<0.01$). Considering the mean HI scores for each posture, we found that the gibbons displayed a modest trend towards left-hand use bias during sitting posture and right-hand use bias during supported bipedal posture.

Sex differences

For the sitting posture, we found no significant sex differences in manual laterality (direction: $N_1=5$, $N_2=5$, $U=9.50$, $z=-0.631$, $P=0.528$; strength: $N_1=5$, $N_2=5$, $U=3.50$, $z=-1.892$, $P=0.059$). For the supported bipedal posture, however, significant sex differences were found for direction of hand preference ($N_1=5$,

$N_2=5$, $U=3.00$, $z=-1.984$, $P=0.047$) rather than strength of hand preference ($N_1=5$, $N_2=5$, $U=8.50$, $z=-0.841$, $P=0.401$).

Postural effect

Repeated measures ANOVA indicated no postural effect on manual laterality (direction: $F_{1,9}=0.422$, $P=0.532$; strength: $F_{1,9}=1.120$, $P=0.318$). Non-parametric Wilcoxon signed rank test showed the same result (direction: $z=-0.765$, $P=0.444$; strength: $z=-0.654$, $P=0.513$).

DISCUSSION

We investigated postural influence on manual laterality during spontaneous bipedal tasks in *N. leucogenys*, with the following important results: (1) there was a modest left-hand preference tendency in the sitting posture and a modest right-hand preference tendency in the supported bipedal posture, although group-level hand preference was not found for either posture; (2) from sitting to supported bipedal posture, based

on HI/ABS-HI values, 70% of individuals showed varying degrees of right-side deviation and 30% of individuals showed varying degrees of left-side deviation; (3) strength of hand preference during the supported bipedal posture was higher than that during the sitting posture; (4) significant sex differences in the direction of hand preference were found during supported bipedal posture but not during sitting posture.

Because of our limited sample size, general conclusions based on the present study should be treated with some caution due to potential statistical effects from the obtained data. For both postures, however, no significant correlation was detected between the number of observations per individual and HI/ABS-HI values. This suggests that individual differences in the amount of data collected did not affect the distribution of handedness values, and our findings on *N. leucogenys* can be considered valid.

For the unimanual grooming task, group-level hand preference was not found for either posture. Together with previous findings in the same species, which also showed no group-level hand preference for ground-reaching, tube, and box tasks (Fan et al., 2017), it suggests that neither simple nor complex tasks elicit group-level hand preference, regardless of posture and task spontaneity. This may be the result of selective pressures acting on this arboreal species; however, further research with a larger sample size is required to explore this question.

Hand preference during grooming has been investigated among various primate species (*P. paniscus*: Brand et al., 2017; *P. troglodytes*: Boesch, 1991; Marchant & McGrew, 1996; McGrew & Marchant, 2001; Hopkins et al., 2007; *R. roxellana*: Zhao et al., 2010). Unimanual grooming is a simple behavioral task performed in primates. Consistently, however, no group-level hand preference has been found during unimanual grooming among any tested species (e.g., Zhao et al., 2010). Compared with unimanual grooming, bimanual grooming is considered a complex behavioral task, with previous studies showing both group-level hand preference and stronger hand preference compared with unimanual grooming (Hopkins et al., 2007; Zhao et al., 2010). However, interspecific and intraspecific differences have been reported. For instance, group-level hand preference during bimanual grooming has been found in Sichuan snub-nosed monkeys (Zhao et al., 2010) but not in bonobos (*P. paniscus*) (Brand et al., 2017). For chimpanzees, group-level hand preference during bimanual grooming was found by Hopkins et al. (2007) but not by McGrew & Marchant (2001). For *N. leucogenys*, we found no group-level hand preference during unimanual grooming for either posture, consistent with previous findings in other primate species and, to some extent, supporting the task complexity hypothesis that strong preferences and group-level biases in manual laterality are more likely to appear in complex rather than simple tasks (Fagot & Vauchlai, 1991).

For the sitting posture, we found a modest tendency towards left-hand use for unimanual grooming in *N. leucogenys*. Given that *N. leucogenys* is an arboreal species, this finding agrees, to a certain extent, with the postural origin theory that arboreal species are apt to use the left hand for

manual behaviors when maintaining a quadrupedal or sitting posture in trees (MacNeillage et al., 1987; MacNeillage, 1991, 2007).

With regard to the postural effect on the direction of manual laterality, from sitting to supported bipedal posture, the general laterality tendency for hand preference in *N. leucogenys* shifted from left-hand use to right-hand use, with 70% of individuals displaying varying degrees of right-side deviation based on HI/ABS-HI values. This rightward effect on bipedal posture for *N. leucogenys* agrees with previous findings in great ape species (*Gorilla gorilla*: Olson et al., 1990; *P. paniscus*: Hopkins et al., 1993; except Vleeschouwer et al., 1995; *P. troglodytes*: Braccini et al., 2010; Hopkins, 1993; *Pongo pygmaeus*: Hopkins, 1993) and some monkey species (e.g., *Cebus apella*: Westergaard et al., 1998a; *Lophocebus albigena*: Blois-Heulin et al., 2007; *Macaca mulatta*: Westergaard et al., 1998b), but contrasts to several findings on leftward laterality trends (e.g., *Galago senegalensis*: Sanford et al., 1984; *H. lar*: Olson et al., 1990; *Saimiri sciureus*: King & Landau, 1993). These consistencies and inconsistencies on the postural effect on primate hand preference may be associated with species-specific foraging types (arboreal/terrestrial), bipedal posture habit (frequent/less), and task-specific demands (simple/complex, unimanual/bimanual) (Hanson et al., 2017; Hashimoto et al., 2013; Hopkins, 1993). For instance, the uniformity of the rightward laterality trend in bipedal posture for *N. leucogenys* and all great apes (Braccini et al., 2010; Hopkins, 1993; Hopkins et al., 1993; Olson et al., 1990) suggests that bipedalism may play a crucial role in driving the evolution of primate right handedness (Hopkins, 2007). In addition, while *N. leucogenys* showed a modest tendency towards right-hand use in unimanual grooming during bipedal posture, the lar gibbon (*H. lar*) has been reported to display group-level left handedness in a mesh retrieval task during bipedal posture (Olson et al., 1990). This disparity in manual laterality trends between two gibbon species could be a consequence of task-specific demands, which may require special manual operation of the lateralized brain (Hashimoto et al., 2013; Rogers et al., 2013).

In regard to the postural effect on strength of manual laterality, based on mean ABS-HI scores, *N. leucogenys* displayed a stronger hand preference during supported bipedal posture than during sitting posture, although there was no significant difference between the two postures. This finding to some extent supports current research suggesting that upright or bipedal postures may facilitate greater expression of primate hand preference (Hook-Costigan & Rogers, 1996; Hopkins, 1993; Roney & King, 1993; Westergaard et al., 1998a). For example, hand preference during both unsupported and supported bipedal posture is significantly greater than that during seated posture in chimpanzees (Braccini et al., 2010).

The northern white-cheeked gibbon is a monogamous species, with females bearing more breeding tasks than males (Bleisch et al., 2008; Fan, 2017). This suggests that, compared with males, females should spend more time in trees taking care of the next generation, which would partly

restrict the frequency of bipedal posture during foraging and movement. Sex differences in bipedal posture may drive sex-specific hand preference in response to the postural effect (i. e., from quadrupedal or sitting posture to bipedal posture). The present study preliminarily confirmed this viewpoint: (1) a significant sex difference in hand preference was found in bipedal posture but not in sitting posture; and, (2) in unimanual grooming during bipedal posture, all males showed right-handedness whereas three of the five females showed left-handedness. These results indicate that bipedal posture produces sex-specific manual laterality in this gibbon species.

In the current study, we focused on how posture affects hand preference in spontaneous behavioral tasks in northern white-cheeked gibbons. Results indicated that, to a certain degree, bipedal posture facilitated stronger hand preference, elicited a rightward trend in manual laterality, and exhibited sex-specific hand preference. Further comprehensive study exploring the effect of body posture on different behavioral tasks (e. g., foraging, grooming) under varying postures is required to further test the postural origin hypothesis in this species. In addition, future research should introduce more Hylobatidae species with larger sample size to clarify the postural effect on primate handedness evolution. The postural effect on both hand preference and foot preference in this species as well other non-human primates under natural conditions should also be studied (e.g., Zhao et al., 2008b).

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

D.P.Z. and B.G.L. conceived and designed the study. B.S.L. collected the data. D.P.Z. and B.S.L. analyzed the data. D.P.Z. wrote the manuscript. All authors read and approved the final version of the manuscript.

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