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

Dapeng ZHAO\textsuperscript{a,b,c,*}, Yuan WANG\textsuperscript{a}, and Xueyan WEI\textsuperscript{a}

\textsuperscript{a}Tianjin Key Laboratory of Animal and Plant Resistance, College of Life Sciences, Tianjin Normal University, Tianjin, 300387, \textsuperscript{b}Wildlife Institute, Beijing Forestry University, and \textsuperscript{c}Eco-Bridge Continental, Beijing 100083, China

*Address correspondence to Dapeng Zhao. E-mail: skyzdp@mail.tjnu.edu.cn.

Received on 10 June 2015; accepted on 29 August 2015

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.
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 troglodytes: 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 gaps 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...
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 ≥ 1.96), left-handed (z ≤ −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. 2001; 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 (Spinozzi 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  | −5.39   | 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 ± SE) (range: 116–694) 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 ± 10.62% (mean ± SE) with the index finger, 18.66% ± 9.89% with the index + the middle fingers, 3.19 ± 0.68% with the index + the middle + the ring fingers, 14.25 ± 6.91% with the index + the middle + the ring + the little fingers, and 2.59 ± 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 (MacNeile et al. 1987; MacNeile 2007). Accordingly, with regard to the TUBE task, Meugerditchian 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 Meugerditchian 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 sylvestris: 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 Vaclaur 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 (Carp and Byrne 2004) rather than in gorillas (Meugerditchian et al. 2010). For the TUBE task, sex effect on hand preference remain unclear based on the existing literature (Meugerditchian 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 capucinus: Meunier and Vauclair 2007; Cercopithecus neglectus: Schweitzer et al. 2007; Maille et al. 2013; Cercocetus torquatus: Maille et al. 2013; Pan paniscus: Chapelain and Hogervorst 2009; Chapelain et al. 2011; Pan tigrinae: Hopkins 1993; Pape 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.

Acknowledgments

We appreciate the staff of Tianjin Zoo for their support. The authors declare that they have no conflict of interest. All applicable international and Chinese guidelines for the care and use of animals were followed.

Funding

This study was funded by Talent Introduction Fund of Tianjin Normal University of China (No. SRL115) and “More Than One Thousand Talents Introduction within Three Years” Fund of Tianjin City of China (No. SKQM110002).

References

Annett M. 2002. Handedness and Brain Asymmetry: The Right Shift Theory. Hove: Psychology Press.

Bennett AJ, Suomi SJ, Hopkins WD, 2008. Effects of early adverse experiences on behavioural lateralisation in rhesus monkeys Macaca mulatta. Laterality 13:282–292.

Blous-Heulin C, Guittion JS, Nedellec-Bienvenue D, Ropars L, Vallet E, 2006. Hand preference in unimanual and bimanual tasks and postural effect on manual laterality in captive red-capped mangabeys Cercococcus torquatus. Am J Primatol 68:429–444.

Bradshaw J, Rogers LJ, 1993. The Evolution of Lateral Asymmetries, Language, Tool Use and Intellect. San Diego: Academic Press.

Brandon-Jones D, Eudey AA, Geissmann T, Groves CP, Melnick DJ et al., 2004. Asian primate classification. Int J Primatol 25:97–164.

Byrne RW, Byrne JM, 1991. Hand preferences in the skilled gathering tasks of mountain gorillas Gorilla gorilla beringei. Cortex 27:521–536.

Canteloup C, Vauclair J, Meunier H, 2013. Hand preference on unimanual and bimanual tasks in Tokean macaques Macaca tonkeana. Am J Phys Anthropol 152:315–321.

Cashmore L, 2009. Can hominin “handedness” be accurately assessed? Ann Hum Biol 36:624–641.
Cashmore L, Uomini N, Chaplain AS, 2008. The evolution of handedness in humans and great apes: a review and current issues. J Anthropol Sci 86:7–35.

Chaplain AS, Bec P, Blois-Heulin C, 2006. Manual laterality in Campbell’s monkeys Cercocebus c. campbelli in spontaneous and experimental actions. Behav Brain Res 173:237–245.

Chaplain AS, Hogervorst E, 2009. Hand preferences for bimanual coordination in 29 bonobos Pan paniscus. Behav Brain Res 196:13–29.

Chaplain AS, Hogervorst E, Mbonzo P, Hopkins WD, 2011. Hand preferences for bimanual coordination in 77 bonobos Pan paniscus: replication and extension. Int J Primatol 32:491–510.

Colell M, Segarra MD, Sabatier-Pi J, 1995. Manual laterality in chimpanzees Pan troglodytes in complex tasks. J Comp Psychol 109:298–307.

Corballis MC, 1983. Human Laterality. New York: Academic Press.

Corballis MC, 2002. From Hand to Mouth: The Origins of Language. Princeton: Princeton University Press.

Corp N, Byrne RW, 2004. Sex difference in chimpanzee handedness. Am J Phys Anthropol 123:62–68.

Fagot J, Vaucclair J, 1988. Handedness and bimanual coordination in the low-land gorilla. Brain Behav Evol 12:89–95.

Fagot J, Vaucclair J, 1991. Manual laterality in nonhuman primates: a distinction between handedness and manual specialization. Psychol Bull 109:76–89.

Groves CP, 2001. Primate Taxonomy. Washington: Smithsonian Institution Press.

Harrison KE, Byrne RW, 2000. Hand preferences in unimanual and bimanual feeding by wild vervet monkeys Cercocebus aethiops. J Comp Psychol 114:13–21.

Hopkins WD, Fernandez-Carriba S, Wesley MJ, Hostetter A, Pilcher D et al., 2011. The evolution of handedness in the small-eared bushbaby Cercocebus torquatus torquatus and extension in a second colony of apes. Int J Primatol 24:677–689.

Hopkins WD, Phillips KA, Bania A, Calcutt SE, Gardner M et al., 2011. Handed preferences for coordinated bimanual actions in 777 great apes: Implications for the evolution of handedness in hominids. J Hum Evol 60:605–611.

Hopkins WD, Phillips KA, Bania A, Calcutt SE, Gardner M et al., 2011. Hand preferences for coordinated bimanual task in 110 chimpanzees Pan troglodytes. Proc Roy Soc B 282:20141223.

Kimura D, 1999. Sex and Cognition. Cambridge: MIT Press.

Knecht S, Drager B, Deppe M, Bobe I, Lohmann H et al., 2000. Handedness and hemispheric language dominance in healthy humans. Brain 123:2512–2518.

Laurence A, Wallez C, Blois-Heulin C, 2011. Task complexity, posture, age, sex: which is the main factor influencing manual laterality in captive Cercopithecus torquatus torquatus? Laterality 16:586–606.

Lilak AL, Phillips KA, 2008. Consistency of hand preference across low-level and high-level tasks in capuchin monkeys Cebus apella. Am J Primatol 70:254–260.

Llorente M, Mosquera M, Fabre M, 2009. Manual laterality for simple reaching and bimanual coordinated task in naturalistic housed Pan troglodytes. International Journal of Primatology 30:183–197.

Llorente M, Ribas D, Palou L, Carrasco L, Mosquera M et al., 2011. Population-level right-handedness for a coordinated bimanual task in naturalistic housed chimpanzees: replication and extension in 114 animals from Zambia and Spain. Am J Primatol 73:281–290.

MacNeile PF, 2007. Present status of the postural origins theory. In: Hopkins WD, editor. The Evolution of Hemispheric Specialization in Primates. San Diego: Academic Press, 59–91.

MacNeile PF, Studdert-Kennedy MG, Lindblom B, 1987. Primate handedness reconsidered. Behav Brain Sci 10:247–303.

Maille A, Belbec’h C, Rossard A, Bec P, Blois-Heulin C, 2013. Which are the features of the tube task that make it so efficient in detecting manual asymmetries? An investigation in two Cercopithecine species (Cercopithecus neglectus and Cercopithecus torquatus). J Comp Psychol 127:366–444.

Marchant LF, McGrew WC, 1998. Human handedness: an ethological perspective. Hum Evol 13:221–228.

Marchant LF, Marchant LF, 1997. On the other hand: current issues in and meta-analysis of behavioral laterality of hand function in primates. Yearb Phys Anthropol 40:201–232.

Meguerditchian A, Calcutt SE, Londorf EV, Ross SR, Hopkins WD, 2010. Brief communication: captive gorillas are right-handed for bimanual feeding. Am J Phys Anthropol 141:638–645.

Meguerditchian A, Donnot J, Molesi S, Francioley R, Vaucclair J, 2012. Sex differences in squirrel monkeys’ handedness for unimanual and bimanual coordinated tasks. Anim Behav 83:635–643.

Meguerditchian A, Vaucclair J, Hopkins WD, 2013. On the origins of human handedness and language: a comparative review of hand preferences for bimanual coordinated actions and gestural communication in nonhuman primates. Dev Psychobiol 55:637–650.

Meunier H, Vaucclair J, 2007. Hand preferences on unimanual and bimanual tasks in white-faced capuchins Cebus capucinus. Am J Primatol 69:1064–1069.

Mülliken GW, Stafford DK, Dodson DL, Pinger CD, Ward JP, 1991. Analyses of feeding lateralization in the small-eared bushbaby Otomona garnettii: a comparison with the ring-tailed lemur Lemur catta. J Comp Psychol 105:274–285.
Nelson EL, Figueroa A, Alberight SN, Gonzalez MF, 2015. Evaluating handedness measures in spider monkeys. Anim Cogn 18:345–353.

Papademetriou E, Shue CF, Michel GF, 2005. A meta-analysis of primate hand preferences for reaching and other hand-use measures. J Comp Psychol 119:33–48.

Phillips KA, Sherwood CC, 2005. Primary motor cortex asymmetry is correlated with handedness in capuchin monkeys Cebus apella. Behav Neurosci 119:1701–1704.

Porac C, Coren S, 1981. Lateral Preferences and Human Behavior. New York: Springer.

Raymond M, Pontier D, 2004. Is there geographical variation in human handedness? Laterality 9:33–52.

Rigamonti MM, Previde EP, Poli MD, Marchant LF, McGrew WC, 1998. Methodology of motor skill and laterality: new test of hand preference in Macaca nemestrina. Cortex 34:693–705.

Rogers LJ, 2014. Asymmetry of brain and behavior in animals: its development, function, and human relevance. Genesis 52:S55–S71.

Rogers LJ, Kaplan G, 1996. Hand preferences and other lateral biases in rehabilitated orangutans Pongo pygmaeus pygmaeus. Anim Behav 51:13–25.

Rogers LJ, Andrew RJ, 2002. Comparative Vertebrate Lateralization. Cambridge: Cambridge University Press.

Rogers L, Vallortigara G, Andrew RJ, 2013. Divided Brains: The Biology and Behaviour of Brain Asymmetries. New York: Cambridge University Press.

Schmitt V, Melchisedech S, Hammerschmidt K, Fischer J, 2008. Hand preferences in barbary macaques Macaca sylvanus. Laterality 13:143–157.

Schweitzer C, Bec P, Blois-Heulin C, 2007. Does the complexity of the task influence manual laterality in De Brazza’s monkey Cercopithecus neglectus? Ethology 113:983–994.

Spinozzi G, Laganà T, Truppa V, 2007. Hand use by tufted capuchins Cebus paella to extract a small food item from a tube: digit movements, hand preference, and performance. Am J Primatol 69:336–352.

Teixeira LA, 2008. Categories of manual asymmetry and their variation with advancing age. Cortex 44:707–716.