



# **Hand preferences on unimanual and bimanual tasks in Tonkean macaques ( *Macaca tonkeana* )**

Charlotte Canteloup, Jacques Vauclair, H  l  ne Meunier

## **► To cite this version:**

Charlotte Canteloup, Jacques Vauclair, H  l  ne Meunier. Hand preferences on unimanual and bimanual tasks in Tonkean macaques ( *Macaca tonkeana* ). American Journal of Physical Anthropology, 2013, 152 (3), pp.315-321. <10.1002/ajpa.22342>. <hal-04756255>

**HAL Id: hal-04756255**

**<https://hal.science/hal-04756255v1>**

Submitted on 28 Oct 2024

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destin  e au d  p  t et    la diffusion de documents scientifiques de niveau recherche, publi  s ou non,   manant des   tablissements d'enseignement et de recherche fran  ais ou   trangers, des laboratoires publics ou priv  s.



HAL Authorization

1 **Hand preferences on unimanual and bimanual tasks in Tonkean macaques (*Macaca***  
2 ***tonkeana*)**

3

4 Charlotte Canteloup<sup>1</sup>, Jacques Vauclair<sup>2</sup> & Hélène Meunier<sup>1,2</sup>

5

6 <sup>1</sup>Primate Center of Strasbourg University, Fort Foch, 67207 Niederhausbergen, France

7 <sup>2</sup> Center for Research on the Psychology of Cognition, Language and Emotion, Aix-Marseille  
8 University, 29 avenue Robert Schuman, 13621 Aix-en-Provence Cedex 1, France

9

10 Number of pages: 23

11 Number of figures: 3

12 Number of tables: 1

13 Word count: 5206

14 Short title: Handedness in Tonkean macaques

15 Key words: bimanual coordination; unimanual grasping; laterality; *Macaca tonkeana*; task  
16 robustness

17

18 Corresponding author:

19 Hélène Meunier, Centre de Primatologie, Université de Strasbourg, Fort Foch, 67207  
20 Niederhausbergen, France

21 email: meunier.h@gmail.com

22 Phone: +33 (0) 3 88 13 78 78

23 Fax: +33 (0) 3 88 13 78 79

24

## 25 ABSTRACT

26 This is the first study to have examined hand preferences in Tonkean macaques on a  
27 bimanual task. One of its objectives was to continue the move toward greater task  
28 standardization, in order to facilitate comparisons between species and studies on handedness.  
29 The main aim was to test and determine task robustness, by varying intratask complexity. To  
30 this end, we administered several different tasks to the subjects: two unimanual tasks  
31 (grasping task featuring items of different sizes) and three coordinated bimanual tasks (tube  
32 task involving different materials, weights and diameters). Although we found no significant  
33 hand preference in either task at the group level, the macaques were more strongly lateralized  
34 for small items than for large ones in the unimanual grasping task. Moreover, the absence of a  
35 correlation between these two versions of the unimanual task confirmed the weakness of this  
36 grasping task for assessing handedness. Regarding the bimanual tube task, no difference was  
37 found between the three versions in either the direction or the strength of hand preference.  
38 Moreover, the highly correlated hand preferences between these three versions suggest that  
39 the tube task provides a more robust means of measuring manual preferences.

40

41

42 *Handedness* refers to the functional dominance of one hand over the other for a given  
43 manual action and has been linked to hemispheric lateralization of the brain. Some  
44 researchers determine handedness on the basis of which hand performs manual tests the  
45 fastest or most accurately, while others define it as the preferred use of a hand, regardless of  
46 performance (Holder, 1992). Humans are predominantly right-handed for object manipulation  
47 and writing (Annett, 1985). Despite numerous studies, the origins and functions of human  
48 brain lateralization and handedness remain unresolved. Several hypotheses identify factors  
49 that may have exerted selective pressure for the emergence of handedness, such as postural

50 demands, bipedalism, tool use, gestural communication and language, precise actions and  
51 bimanual coordination (Cashmore et al., 2008). Contradicting the traditional view that our  
52 species is the only one to exhibit hemispheric and behavioral lateralization, possibly owing to  
53 a link between hemispheric asymmetry and language, several studies have demonstrated  
54 group-level handedness in large groups of nonhuman primates species for specific tasks (for  
55 reviews, see Bradshaw and Rogers, 1993; Fagot and Vauclair, 1991; Hopkins et al., 2003;  
56 MacNeilage et al., 1987; Spinozzi et al., 1998; Ward and Hopkins, 1993; Westergaard &  
57 Suomi, 1996; Zhao et al., 2012). However, some researchers have claimed that reports of  
58 group-level handedness in nonhuman primates could be due to experiential, environmental  
59 and/or situational factors (McGrew and Marchant, 1997; Palmer, 2002; Papademetriou et al.,  
60 2005). A multitude of factors could indeed affect the expression of manual laterality. These  
61 factors could be linked to the environment in which the subject lives and/or to particular  
62 features of the experimental tasks. Hand function laterality certainly seems to be related to  
63 posture. Some authors have reported that individuals are more lateralized in the bipedal  
64 posture than in the quadrupedal one (Blois-Heulin et al., 2006; Larson et al., 1989).  
65 Methodological factors could also have an effect: Meunier et al. (2011) have shown that  
66 baboons predominantly reach for an item located to the right of their body's midline with their  
67 right hand, and vice versa. For their part, Fagot and Vauclair (1991) suggest that the level of  
68 task complexity may influence manual preferences. For these authors, low-level tasks elicit  
69 symmetrical distributions of hand biases within the group. By contrast, high-level tasks lead  
70 to asymmetrical distributions. The communicative or otherwise nature of the task is also  
71 important, as gestural communication has been found to reflect right-hand use preference  
72 (Meguerditchian and Vauclair, 2006). The main difficulty with interpreting findings on  
73 handedness has been the lack of common testing procedures and measures of hand use, both  
74 between and within species.

Owing to discordant results between studies, and in order to facilitate comparisons, researchers have started to administer the same experimental task but with varying degrees of complexity, including a simple reaching (unimanual) task and a coordinated bimanual task (Tube task) (see Hopkins, 1995, for details; e.g., Meunier and Vauclair, 2007; Vauclair et al., 2005; Westergaard and Suomi, 1996). Fagot and Vauclair (1991) proposed a theory whereby handedness depends on task complexity. These authors divided tasks into two categories, according to their degree of complexity: low-level and high-level. Low-level tasks involve grossly regulated, familiar, practiced and simple activities requiring undemanding cognitive processes. They are assumed not to induce biases at the group level and thus do not reflect hemispheric specialization. This would be the case, for example, of reaching for food items scattered on the ground. High-level tasks involve novel, fine-tuned motor actions that are demanding both spatio-temporally and in terms of complex cognition. These tasks produce a manual bias at the group level, thus providing evidence of hemispheric specialization. This would be the case of a coordinated bimanual manipulative action in which one hand manipulates an object held by the other hand. Many studies have supported this theory for unimanual tasks (Cordeiro de Sousa et al., 2001; Leca et al., 2010; Meunier and Vauclair, 2007; Vauclair et al., 2005; Zhao et al., 2010) and for coordinated bimanual tasks (Leca et al., 2010; Vauclair et al., 2005; Zhao et al., 2010; Zhao et al., 2012).

Continuing these moves toward greater task standardization, we carried out the first ever quantitative investigation of the manual preferences displayed by an Old World monkey species, the Tonkean macaque (*Macaca tonkeana*), in different versions of unimanual and bimanual tasks. Tonkean macaques live in lowland and hill forests on Sulawesi Island in Indonesia. These macaques are predominantly frugivorous, with a diet consisting of fruit, young leaves and a small proportion of flowers, stems, birds' eggs and insects. Tonkean macaques appear to have particular manipulative skills and reportedly use tools to obtain food

(Anderson, 1985; Ducoing & Thierry, 2005). The only study to allude to hand preferences in Tonkean macaques concerned only one subject during spontaneous tool use. This subject exhibited a left-hand preference when reaching for a stick on the left. (Ueno and Fujita, 1998; but see also Meunier et al., submitted). The two main purposes of our study were thus to gauge the robustness (i.e., the hand preference consistency) of two tasks of varying complexity and to assess handedness in Tonkean macaques. Two versions of a simple grasping task (small items in the shape of chocolate puffed rice and large food items in the shape of apple pieces) and three versions of a coordinated bimanual tube task (tubes varying in material, diameter and weight) were used to test task robustness and intratask complexity. Based on the model proposed by Fagot and Vauclair (1991), we predicted that the macaques would be lateralized at the group level for the coordinated bimanual task (high-level task) but not for the unimanual task (low-level task). For the unimanual grasping task, we expected the macaques to be more strongly lateralized for the small-item version than for the large-item one, given that the small brown grains would be harder to make out in the grass than the apple pieces. For the bimanual task, we expected the macaques to be more strongly lateralized for the lighter, narrower tube, which would be more difficult to handle and require more stability and precision than the heavier and/or wider tubes.

## **METHODS**

### **Subjects**

The subjects were 19 Tonkean macaques (*Macaca tonkeana*), all housed and raised at the Primate Center of Strasbourg University, France. The group comprised 10 adults (five males and five females aged 6-15 years), four subadults (three males and one female aged 4-5 years) and five juveniles (three males and two females, aged two years). The macaques lived

in a 5000 m<sup>2</sup> wooded enclosure. All the subjects were tested in their social group, inside their enclosure. Animals were fed with commercial pellets and water *ad libitum*. Fruit and vegetables were distributed twice a week, outside the observation sessions. Observations were performed in real time by CC from February 2011 to April 2011. All the experiments adhered to the American Association of Physical Anthropologists Code of Ethics.

### Unimanual Task

Two versions of a simple grasping task were administered to the subjects in order to test the effect of item size on hand preferences: a grain (chocolate-coated puffed rice grains measuring approx. 3 x 6 mm) grasping task, conducted in February 2011, and an apple (pieces measuring approx. 3 x 3 cm) grasping task, conducted in March 2011. Several handfuls of items were scattered in the macaques' enclosure to minimize competition between subjects. Each daily session lasted approximately one hour. Hand preferences in this unimanual task were assessed by following one individual at the time (focal sampling method; Altmann, 1974). We recorded which hand was used when it reached for food. A response was recorded each time the subject was in a quadrupedal or seated posture, grasped food in front of it in a sagittal median plane (to control for the influence of item position; see Meunier et al., 2011) and moved between reaches. We collected no more than 10 bouts per individual per day. In all, a minimum of 100 bout-responses was required per subject for the grain-grasping task, while a minimum of 20 bout-responses per subject was collected for the apple-grasping task. This difference in the number of minimum responses between these two tasks can be explained by the fact that when we administered the grain-grasping task, we found that there was no difference between a handedness index (number of right-hand responses minus number of left-hand responses / total responses; HI) calculated with 100 responses and a HI calculated with the first 20 responses (Pearson product-moment correlation coefficient:  $r =$

0.76;  $p = 0.0001$ ;  $N = 19$ ). We therefore decided to retain only 20 responses for this task and to collect only 20 responses for the subsequent apple-grasping task. Nineteen individuals performed the grain-grasping task and 17 individuals the apple-grasping task.

#### Bimanual Coordinated Task

Three versions of a bimanual task featuring a tube containing chocolate paste were administered to the subjects to assess the effects of tube weight and diameter on hand preferences. In the first block of trials, between six and eight stainless-steel tubes measuring 2.8 cm in diameter and 10 cm long, attached to a metal chain and with a total weight of about 300 g (Fig. 1a) were simultaneously given to the animals, in order to avoid competition among individuals. In the second block of trials, between six and eight PVC tubes measuring 2.8 cm in diameter and 10 cm long, attached to a metal cable and with a total weight of about 80 g (Fig. 1b) were given to the macaques. In the third block of trials, between six and eight PVC tubes measuring 1.8 cm in diameter and 10 cm long, attached to a metal cable and with a total weight about of 80 g (Fig. 1c) were given to the animals. The macaques removed the chocolate paste by holding the tube in one hand and inserting one or several fingers of the other hand into one of the two open ends of the tube. We noted which hand was used to remove the chocolate paste and carry it to the mouth, and recorded both frequency (i.e., all the occurrences of this behavior) and the number of bouts (i.e., one sequence of identical actions). We considered that a new bout began whenever the subject dropped the tube, changed the hand holding the tube, brought it to its mouth or manipulated the tube with both hands. Bouts were thus regarded as independent. For the metal tube task, 14 individuals were tested and a minimum of 100 responses were obtained from each one across approximately 10 sessions. For the two PVC tube tasks, 13 individuals were tested and a minimum of 20 responses were obtained from each one across three or four sessions. The numbers of minimum responses for



the three versions of the tube task differed for the same reasons as for the two versions of the unimanual task, in that there was a significant positive correlation between the HIs calculated with 100 responses and the HIs calculated with the first 20 responses for the metal tube task (Pearson's product-moment correlation coefficient:  $r = 0.91$ ;  $p < 0.00001$ ;  $N = 14$ ).

---

INSERT FIGURE 1 ABOUT HERE

---

### Data analysis

As in many earlier studies of primate handedness (Hopkins, 1999), we calculated two types of index to assess individual hand preferences in each task. First, we used  $z$  scores as a qualitative indicator ( $z = [R - (R+L)/2] / \sqrt{[(R+L)/4]}$ , where  $R$  = number of right-hand responses, and  $L$  = number of left-hand responses) to classify the macaques as left-handed ( $z \leq -1.96$ ), right-handed ( $z \geq 1.96$ ), or ambiguously handed ( $-1.96 < z < 1.96$ ). Second, a HI, varying from -1.0 to 1.0, was calculated to quantify the degree of individual lateral bias. Negative values indicated a left-hand bias, positive values a right-hand one. Absolute values (ABS-HI) reflected the strength of hand preference. Because of the relatively small size of the sample, we ran nonparametric permutation tests for paired replicates (Siegel & Castellan, 1988) to test for the effect of task complexity on handedness (exact method or Monte Carlo method software StatXact 3.1). When running multiple comparisons (between tasks), we corrected our  $p$  values using the sequential Bonferroni-Holm procedure (Rice, 1989). All the permutation tests and correlations were performed on the individual HI values. Pearson's correlation tests were run in order to test the tasks' robustness and data consistency (20-100 trials; see Methods section). We tested the effects of age, sex and relatedness on individual

HIs using nonparametric permutation tests for two independent samples (Siegel & Castellan, 1988).

## RESULTS

### Comparison between the two versions of the unimanual task

Seventeen macaques were tested in the two versions of the unimanual task. On the basis of individual  $z$  scores, six macaques were classified as right-handed, five as left-handed and six as ambiguously handed for the grain-grasping task (Table 1). The mean HI score for this first task was 0.11 (standard error of the mean,  $SEM = 0.03$ ), representing a slight right-hand preference. On the basis of individual  $z$  scores, three macaques were classified as right-handed, one as left-handed and 13 as ambiguously handed for the apple-grasping task (Table 1). The mean HI score for this second task was 0.10 ( $SEM = 0.02$ ), illustrating a weak right-hand preference. A nonparametric permutation test failed to revealed a hand preference at the group level, either for the grain-grasping task ( $p = 0.34$ ) or for the apple-grasping task ( $p = 0.27$ ). No difference was found in the direction of hand preference between these two versions of the unimanual task ( $p = 0.76$ ) (Fig. 2a), and there was no correlation between them ( $r = 0.48$ ,  $p = 0.056$ ,  $N = 17$ ). Nevertheless, the macaques were more strongly lateralized for the small-item grasping task than for the large-item one ( $p = 0.0096$ ) (Fig. 2b).

---

INSERT FIGURE 2 ABOUT HERE

---

### Comparison between the three versions of the bimanual task

Thirteen macaques were tested in each of the three versions. On the basis of individual  $z$  scores, two macaques were classified as right-handed, five as left-handed and six as

ambiguously handed for the metal tube task (Table 1). The mean HI score for this task was -0.09 ( $SEM = 0.04$ ), representing a very slight left-hand preference. For the wide PVC tube task, four macaques were classified as right-handed, five as left-handed and four as ambiguously handed (Table 1). The mean HI score for this task was -0.05 ( $SEM = 0.06$ ). For the narrow PVC tube task, four macaques were classified as right-handed, four as left-handed and five as ambiguously handed (Table 1). The mean HI score for this task was -0.10 ( $SEM = 0.05$ ). A nonparametric permutation test failed to reveal hand preferences at the group level for the metal tube task ( $p = 0.60$ ), the wide PVC tube task ( $p = 0.83$ ), or the narrow PVC tube task ( $p = 0.58$ ). No difference was found between these three versions of the bimanual task in either direction or strength of hand preference ( $p > 0.05$ ), and there were strong positive correlations between the wide and narrow PVC tube tasks ( $r = 0.91$ ,  $p_1 = 0.0001$ ,  $N = 13$ ), the metal tube and wide PVC tube tasks ( $r = 0.71$ ,  $p_2 = 0.0082$ ,  $N = 13$ ), and the metal tube and narrow PVC tube tasks ( $r = 0.59$ ,  $p_3 = 0.037$ ,  $N = 13$ ). These results remained significant even after a sequential Bonferroni-Holm procedure had been applied ( $p'_1 = 0.0003$ ,  $p'_2 = 0.0164$ ,  $p'_3 = 0.037$ ) (Fig. 3). Spearman's rank correlation coefficient was calculated to test the effect of dependence of data points. This revealed strong positive correlations between the HI values calculated on the basis of frequency and the HI values calculated on the basis of bouts for the metal tube task ( $r = 0.96$ ,  $p < 0.00001$ ,  $N = 14$ ), the wide PVC tube task ( $r = 0.98$ ,  $p < 0.00001$ ,  $N = 13$ ) and the narrow PVC tube task ( $r = 0.95$ ;  $p < 0.00001$ ;  $N = 13$ ).

---

INSERT FIGURE 3 ABOUT HERE

---

#### Comparison between unimanual and bimanual tasks

The HIs of the two versions of the unimanual task were compared with those of the three versions of the bimanual task, taking them in pairs in order to test inter-task complexity.

The Tonkean macaques appeared to be more strongly lateralized for the wide PVC tube task than for the large-item grasping task ( $p = 0.02$ ), but this result lost its significance after the sequential Bonferroni-Holm procedure was applied ( $p' = 0.12$ ). The pairwise comparisons failed to reveal any differences between the other versions of the unimanual and bimanual tasks, in either the direction or strength of hand preferences, and there were no significant correlations between them ( $p > 0.05$ ).

## Effect of sociodemographic factors on hand preferences

We found no significant effect of age (adults vs. juveniles), sex, or relatedness (kin vs. nonkin) on individual HIs, whatever the task.

---

INSERT TABLE I ABOUT HERE

---

## DISCUSSION

This study, the first to investigate the hand preferences of Tonkean macaques in a bimanual task, sought to assess task robustness and measure the impact of intratask complexity on handedness. Our results confirmed many previous findings (e.g., Fagot and Vauclair, 1991; Vauclair et al., 2005; Zhao et al., 2012), by highlighting the weakness of the unimanual grasping task and the greater reliability of the tube task for measuring manual preferences in nonhuman primates.

In line with our hypothesis, the unimanual task results showed that the macaques were more strongly lateralized for the grain-grasping task than for the apple-grasping task. This difference can be attributed to the greater complexity of the former in which the puffed rice grains to be picked up were very small and spread out in the grass, thus requiring visual

discrimination and precision grasping. The level of precision in motor actions and visual guidance are two determinants of task complexity (Fagot and Vauclair, 1991). Our result suggests that task complexity influences the strength of manual preferences more than their direction. Furthermore, the hand preferences assessed with the unimanual task seemed to be affected by methodological factors such as substrate and item size. These factors had not been considered in previous studies (e.g., Forsythe and Ward, 1988). Furthermore, the absence of a correlation between these two versions of the same unimanual task suggests individual inconsistency between them and underscores the weakness of simple reaching tasks for measuring handedness. The manual preferences observed with these unimanual measures seemed to be a poor indicator of hemispheric specialization. Moreover, many studies have reported the absence of a significant group bias for one particular hand in simple reaching within groups of different primate species and for different sample sizes (e.g., 46 marmosets: Cordeiro de Sousa et al., 2001; eight capuchins: Meunier and Vauclair, 2007; 52 Barbary macaques: Schmitt et al., 2008; 94 baboons: Vauclair et al., 2005), as well as in small-bodied rooting quadrupedal mammals such as the tree shrew (Joly et al., 2012). The absence of a significant group bias for one hand in the two versions of our grasping task seems to be consistent with these findings and with the task-complexity model, given their low level of complexity. However, we cannot completely endorse this model, given our relatively small sample.

Concerning the results of the three versions of the tube task, the absence of a significant group bias for one hand contradicted the task-complexity model, which predicts manual specialization for tasks with a high level of complexity (Fagot & Vauclair, 1991). Other studies have also failed to demonstrate a hand bias at the group level for the tube task: neither a group of 30 Barbary macaques (Schmitt et al., 2008) nor a large group of 124 rhesus monkeys exhibited hand preferences (Bennett et al., 2008). Therefore, our results contradict

299 those of several other studies with apes and baboons (e.g., Hopkins, 1995; Hopkins et al.,  
300 2011; Vauclair et al., 2005). Most notably, this coordinated bimanual task was administered to  
301 a group of 55 rhesus macaques, in which a significant right-hand group bias emerged  
302 (Westergaard and Suomi, 1996) and to a small sample of 19 nursery-reared infant rhesus  
303 monkeys in which a significant left-hand bias emerged (Westergaard et al., 1997). In the first  
304 study (Westergaard and Suomi, 1996), the tubes used (plastic tubes 10 cm long and 2.5 cm in  
305 diameter) were similar to our wide PVC tube (2.8 cm), except perhaps for the weight, which  
306 was not indicated by the authors. This study had a larger sample than ours, which could  
307 explain the discrepancy between the results. It would be useful to increase the size of our  
308 sample for the tube task, in order to compare our results at the group level with the findings  
309 yielded by previous studies. In order to verify one of our hypotheses, we set out to test intra-  
310 task complexity by varying the weight and diameter of the tubes in the tube task. However,  
311 we can now hypothesize that the variations in weight and diameter were too small to elicit  
312 behavioral differences. It would be interesting to replicate the tube task with greater  
313 differences in tube weight and diameter, in order to test the degree of manual precision  
314 required more accurately. Nonetheless, individual hand preferences for the three versions of  
315 the tube task were highly correlated, suggesting a similar strength of these three tasks and,  
316 more generally, attesting to the robustness of the tube task. Even if no group bias for the left  
317 or right hand was highlighted in the tube task, individuals were mainly consistent in their  
318 hand preferences across the three versions, unlike the two versions of the unimanual grasping  
319 task. The absence of a difference in manual preference direction between these three versions  
320 can be explained by the fact that they were all very similar, and all of them required the same  
321 precision and distal movements. These results underscore the robustness of the tube task and  
322 its reliability for assessing handedness in nonhuman primates due to the stable data it yields.

In conclusion, we observed hand preferences in Tonkean macaques at an individual level in coordinated bimanual actions and in simple reaching, but not at the group level. Given the fact that our sample size was relatively small, it is difficult to reach any conclusions at the group level. Even so, our study underlines the weakness of the unimanual grasping task, and the robustness of the tube task for assessing handedness in nonhuman primates.

## ACKNOWLEDGMENTS

The authors are sincerely grateful to Nicolas Herrenchmidt and all his team for allowing them to conduct the study at the Primate Center of Strasbourg University in France. The authors are thankful to Jonas Fizet for collecting some of the data and also to Jean-Luc Durand for his advice on the statistical analyses. We also thank Jean-Marc Woock, Adrien Panter and Steve Lapp for their logistical aid, all the caretakers for their helpful assistance throughout the study, and Christine Libéras and Elizabeth Portier for correcting the English. The study was partly supported by a French National Research Agency (ANR) grant ref. ANR-08-BLAN-0011 01.

## REFERENCES

- Altmann J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227-267.
- Anderson JR. 1985. Development of tool use to obtain food in a captive group of *Macaca tonkeana*. *Journal of Human Evolution* 14(7):637-645.
- Annett M. 1985. Left, right, hand and brain: the right shift theory. Hillsdale: Erlbaum.
- Bennett AJ, Suomi SJ, Hopkins WD. 2008. Effects of early adverse experiences on behavioral lateralization in rhesus monkeys (*Macaca mulatta*). *Laterality* 13(3):282-292.

- 348 Blois-Heulin C, Guitton JS, Nedellec-Bienvenue D, Ropars L, Vallet E. 2006. Hand  
349 preference in unimanual and bimanual tasks and postural effect on manual laterality in  
350 captive red-capped mangabeys (*Cercocebus torquatus torquatus*). American Journal of  
351 Primatology 68:429-444.
- 352 Bradshaw JL, Rogers LJ. 1993. The evolution of lateral asymmetries, language, tool use and  
353 intellect. San Diego, CA: Academic Press.
- 354 Cashmore L, Uomini N, Chapelain A. 2008. The evolution of handedness in humans and great  
355 apes: a review and current issues. Journal of Anthropological Sciences 86:7-35.
- 356 Cordeiro de Sousa MB, Xavier NS, Alves da Silva HP, Souza de Oliveira M. 2001. Hand  
357 preference study in marmosets (*Callithrix jacchus*) using food reaching tests. Primates  
358 42(1):57-66.
- 359 Ducoing AM, Thierry B. 2005. Tool-use learning in Tonkean macaques (*Macaca tonkeana*).  
360 Animal Cognition 8:103-113.
- 361 Fagot J, Vauclair J. 1991. Manual laterality in nonhuman primates: a distinction between  
362 handedness and manual specialization. Psychological Bulletin 109(1):76-89.
- 363 Forsythe C, Ward JP. 1988. Black lemur (*Lemur macaco*) hand preference in food reaching.  
364 Primates 29(3):369-374.
- 365 Holder MK. 1992. Hand preference questionnaires: one gets what one asks for. M. Phil.  
366 thesis, Department of Anthropology, Rutgers University, New Brunswick, NJ.
- 367 Hopkins WD. 1995. Hand preferences for a coordinated bimanual task in 110 chimpanzees  
368 (*Pan troglodytes*): cross-sectional analysis. Journal of Comparative Psychology  
369 109(3):291-297.
- 370 Hopkins WD. 1999. On the other hand: statistical issues in the assessment and interpretation  
371 of hand preference data in nonhuman primates. International Journal of Primatology  
372 20(6):851-866.



- 373 Hopkins WD, Hook M, Braccini S, Schapiro SJ. 2003. Population-level handedness for a  
 374 coordinated bimanual task in chimpanzees: replication and extension in a second colony  
 375 of apes. *International Journal of Primatology* 24(3):677-689.
- 376 Hopkins WD, Phillips KA, Bania A, Calcutt SE, Gardner M, Russell J, Schaeffer J, Lonsdorf  
 377 EV, Ross SR, Schapiro SJ. 2011. Hand preferences for coordinated bimanual actions in  
 378 777 great apes: implications for the evolution of handedness in hominins. *Journal of*  
 379 *Human Evolution* 60(5):605-611.
- 380 Joly M, Scheumann M, Zimmermann E. 2012. Posture does not matter! Paw usage and  
 381 grasping paw preference in a small-bodied rooting quadrupedal mammal. *PLoS ONE*  
 382 7(5):e38228.
- 383 Larson CF, Dodson DL, Ward JP. 1989. Hand preferences and whole body turning biases of  
 384 lesser bushbabies (*Galago senegalensis*). *Brain, Behavior and Evolution* 33:261-267.
- 385 Leca J-B, Gunst N, Huffman MA. 2010. Principles and levels of laterality in unimanual and  
 386 bimanual stone handling patterns by Japanese macaques. *Journal of Human Evolution*  
 387 58:155-165.
- 388 MacNeilage PF, Studdert-Kennedy MG, Lindblom B. 1987. Primate handedness  
 389 reconsidered. *Behavioral and Brain Sciences* 10:247-263.
- 390 McGrew WC, Marchant LF. 1997. On the other hand: current issues in and meta-analysis of  
 391 the behavioral laterality of hand function in nonhuman primates. *Yearbook of Physical*  
 392 *Anthropology* 40:201-232.
- 393 Meguerditchian A, Vauclair J. 2006. Baboons communicate with their right hand. *Behavioural*  
 394 *Brain Research* 171:170-174.
- 395 Meunier H, Vauclair J. 2007. Hand preferences on unimanual and bimanual tasks in white-  
 396 faced capuchins (*Cebus capucinus*). *American Journal of Primatology* 69:1064-1069.

- 397 Meunier H, Blois-Heulin C, Vauclair J. 2011. A new tool for measuring hand preference in  
 398 non-human primates: adaptation of Bishop's quantifying hand preference task for olive  
 399 baboons. *Behavioural Brain Research* 218:1-7.
- 400 Meunier H, Fizet J, Vauclair J. Tonkean macaques communicate with their right hand.  
 401 Submitted.
- 402 Palmer A. 2002. Chimpanzee right-handedness reconsidered: evaluating the evidence with  
 403 funnel plots. *American Journal of Physical Anthropology* 118(2):191-199.
- 404 Papademetriou E, Sheu C-F, Michel GF. 2005. A meta-analysis of primate hand preferences,  
 405 particularly for reaching and other hand use preferences. *Journal of Comparative*  
 406 *Psychology* 119(1):33-48.
- 407 Rice RW. 1989. Analysing tables of statistical tests. *Evolution* 43(1):223-225.
- 408 Schmitt V, Melchisedech S, Hammerschmidt K, Fischer J. 2008. Hand preferences in Barbary  
 409 macaques (*Macaca sylvanus*). *Laterality* 13(2):143-157.
- 410 Siegel S, Castellan NJ Jr. 1988. Nonparametric statistics for the behavioral sciences (2<sup>nd</sup> Ed.).  
 411 New York: Mc Graw-Hill.
- 412 Spinozzi G, Castorina MG, Truppa V. 1998. Hand preferences in unimanual and coordinated-  
 413 bimanual tasks by tufted capuchin monkeys (*Cebus apella*). *Journal of Comparative*  
 414 *Psychology* 110:406-411.
- 415 Ueno Y, Fujita K. 1998. Spontaneous tool use by a Tonkean macaque (*Macaca tonkeana*).  
 416 *Folia Primatologica* 69:318-324.
- 417 Vauclair J, Meguerditchian A, Hopkins WD. 2005. Hand preferences for unimanual and  
 418 coordinated bimanual tasks in baboons (*Papio anubis*). *Cognitive Brain Research*  
 419 25:210-216.
- 420 Ward JP, Hopkins WD (Eds). 1993. Primate laterality: current behavioral evidence of primate  
 421 asymmetries. New York: Springer-Verlag.

- 422 Warren JM. 1980. Handedness and laterality in humans and other animals. *Physiological*  
423 *Psychology* 8(3):351-359.
- 424 Westergaard GC, Suomi SJ. 1996. Hand preference for a bimanual task in tufted capuchins  
425 (*Cebus apella*) and rhesus macaques (*Macaca mulatta*). *Journal of Comparative*  
426 *Psychology* 110(4):406-411.
- 427 Westergaard GC, Champoux M, Suomi SJ. 1997. Hand preference in infant rhesus macaques  
428 (*Macaca mulatta*). *Child Development* 68:387-393.
- 429 Zhao D, Gao X, Li B. 2010. Hand preference for spontaneously unimanual and bimanual  
430 coordinated tasks in wild Sichuan snub-nosed monkeys: implications for hemispheric  
431 specialization. *Behavioural Brain Research* 208:85-89.
- 432 Zhao D, Hopkins WD, Li B. 2012. Handedness in nature: first evidence on manual laterality  
433 on bimanual coordinated tube task in wild primate. *American Journal of Physical*  
434 *Anthropology* 148:36-44.
- 435

## Figure legends

### Figure 1

The three different types of tubes used to assess manual preferences in the tube task: a) metal tube (length 10 cm; diameter 2.8 cm; weight approx. 300 g) attached to a metal chain; b) PVC tube (length 10 cm; diameter 2.8 cm; weight approx. 80 g) attached to a metal cable; c) PVC tube (length 10 cm; diameter 1.8 cm; weight approx. 80 g) attached to a metal cable.

### Figure 2

Comparisons of a) mean individual handedness indices (HIs) and b) mean absolute values of individual HIs (ABS-HIs) between the two versions of the unimanual simple grasping task: grains (small items) and apple pieces (large items) (20 responses),  $N = 17$ . The error bars represent the standard error of the mean (*SEM*) for the mean HIs and ABS-HIs. Asterisks indicate the mean ABS-HIs that differed significantly from zero.  $** = p < 0.01$ .

### Figure 3

Comparison of the handedness indices (HIs) for the three versions of the tube task and for each individual.

### Table 1

Table setting out the  $z$  score, handedness index (HI) and preferred hand (PH) for each individual for each version of the grasping task and the tube task, calculated on the basis of 20 bouts per individual.

Figure 1

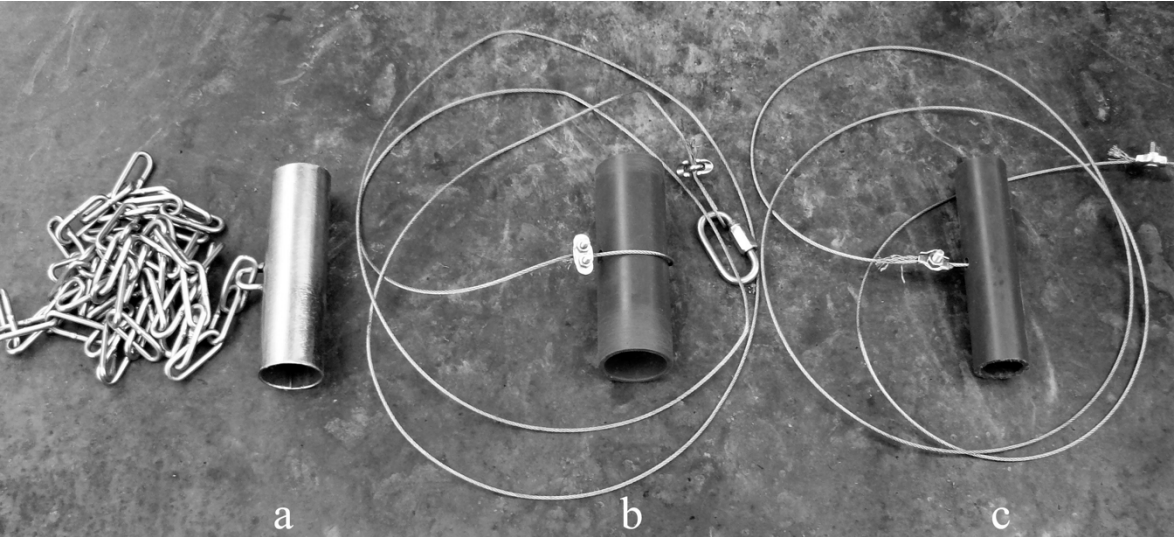


Fig. 1. The three different types of tubes used to assess manual preferences in the tube task:  
(a) metal tube (length 10 cm; diameter 2.8 cm; weight approx. 300 g) attached to a metal  
chain; (b) PVC tube (length 10 cm; diameter 2.8 cm; weight approx. 80 g) attached to a  
metal cable; (c) PVC tube (length 10 cm; diameter 1.8 cm; weight approx. 80 g) attached  
to a metal cable.

Figure 2

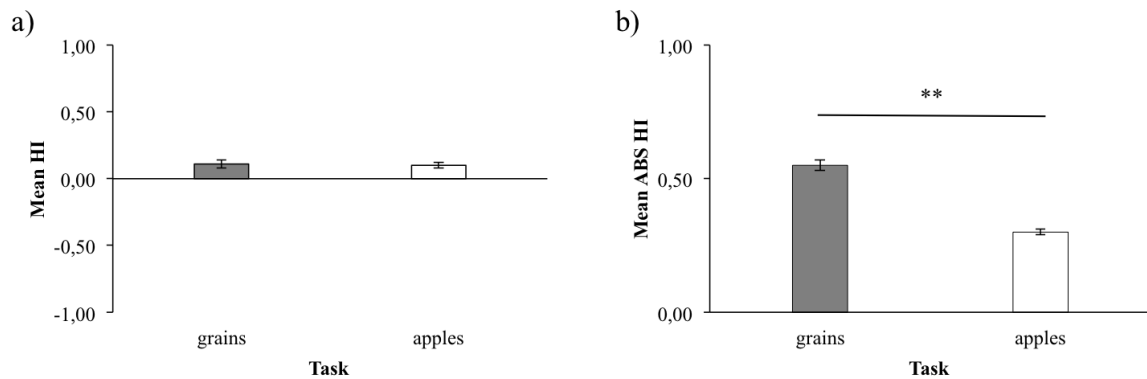
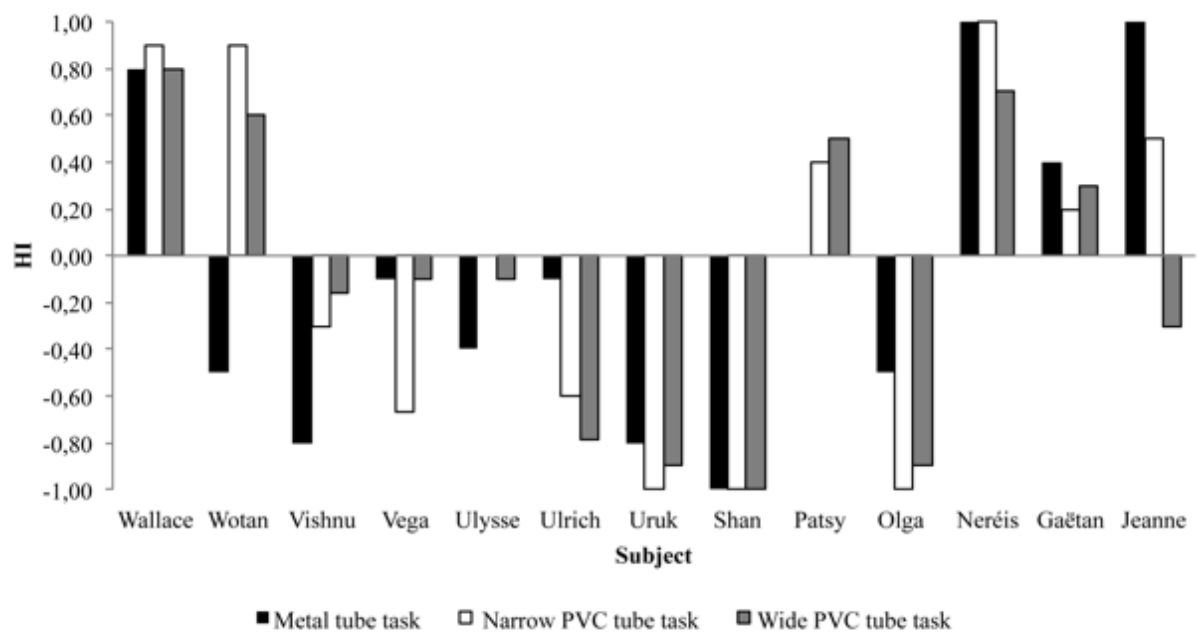


Fig. 2. Comparisons of (a) mean individual handedness indices (HIs) and (b) mean absolute values of individual HIs (ABS-HIs) between the two versions of the unimanual simple grasping task: grains (small items) and apple pieces (large items) (20 responses), N = 17. The error bars represent the standard error of the mean (SEM) for the mean HIs and ABS-HIs. Asterisks indicate the mean ABS-HIs that differed significantly from zero. \*\* = P < 0.01.

482 Figure 3

483



484

485 Fig. 3. Comparison of the handedness indices (HIs) for the three versions of the tube task  
486 and for each individual.

Subject	Grain grasping task			Apple grasping task			Metal tube task			Wide PVC tube task			Narrow PVC tube task		
	HI	z score	Preferred Hand	HI	z score	Preferred Hand	HI	z score	Preferred Hand	HI	z score	Preferred Hand	HI	z score	Preferred Hand
Yin	-0.13	-0.73	NP												
Yoh	0.04	0.19	NP												
Walt	0.38	1.50	NP	0.70											
Yang	0.67	2.31	R	-0.20											
Yannick	0.77	3.92	R	0.00	0.00	NP									
Lady	-0.45	-2.41	L	0.40	1.79	NP	0.20	0.89	NP						
Wallace	-0.30	-1.46	NP	-0.10	-0.45	NP	0.80	3.58	R	0.90	4.02	R	0.80	3.58	R
Wotan	-0.09	-0.30	NP	0.30	1.34	NP	-0.50	-2.24	L	0.90	4.02	R	0.60	2.68	R
Vishnu	-0.33	-1.15	NP	-0.10	-0.45	NP	-0.80	-3.58	L	-0.30	-2.83	L	-0.16	-0.45	NP
Vega	-0.65	-2.67	L	-0.50	-2.24	L	-0.10	-0.45	NP	-0.67	-1.34	NP	-0.10	-0.69	NP
Ulysse	-0.68	-2.98	L	-0.26	-1.15	NP	-0.40	-1.79	NP	0.00	0.00	NP	-0.10	0.45	NP
Ulrich	0.64	3.40	R	0.10	0.45	NP	-0.10	-0.45	NP	-0.60	-2.68	L	-0.79	-3.44	L
Uruk	0.63	2.50	R	0.20	0.89	NP	-0.80	-3.58	L	-1.00	-4.47	L	-0.90	-4.02	L
Shan	-0.04	-0.20	NP	0.50	2.24	R	-1.00	-4.47	L	-1.00	-4.47	L	-1.00	-4.47	L
Patsy	0.74	3.54	R	0.30	1.34	NP	0.00	0.00	NP	0.40	1.79	NP	0.50	2.24	R
Olga	-0.62	-2.84	L	0.10	0.45	NP	-0.50	-2.24	L	-1.00	-4.47	L	-0.90	-4.02	L
Neréis	-1.00	-4.58	L	-0.30	-1.34	NP	1.00	4.47	R	1.00	4.47	R	0.70	3.13	R
Gaëtan	1.00	4.47	R	0.80	3.58	R	0.40	1.79	NP	0.20	0.89	NP	0.30	1.34	NP
Jeanne	0.37	1.61	NP	-0.20	-0.89	NP	1.00	4.47	R	0.50	2.24	R	-0.30	-1.34	NP



489 Table setting out the  $z$  score, handedness index (HI) and preferred hand (PH) for each  
490 individual for each version of the grasping task and the tube task, calculated on the basis of  
491 20 bouts per individual.

492