



# Manual function and performance in humans, gorillas, and orangutans during the same tool use task

Ameline Bardo, Raphaël Cornette, Antony Borel, Emmanuelle Pouydebat

## ► To cite this version:

Ameline Bardo, Raphaël Cornette, Antony Borel, Emmanuelle Pouydebat. Manual function and performance in humans, gorillas, and orangutans during the same tool use task. *American Journal of Physical Anthropology*, 2017, 164 (4), pp.821-836. 10.1002/ajpa.23323 . hal-02138002

**HAL Id: hal-02138002**

**<https://hal.science/hal-02138002>**

Submitted on 2 Jan 2023

**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 destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

2  
3 **Manual function and performance in humans, gorillas and orangutans during the same**  
4 **tool use task**

5  
6 Ameline Bardo <sup>a,b,\*</sup>, Raphaël Cornette <sup>c</sup>, Antony Borel <sup>d</sup>, Emmanuelle Pouydebat <sup>b</sup>

7  
8 <sup>a</sup> Paris Descartes University, Sorbonne Paris Cité, Paris, 75006, France.

9 <sup>b</sup> Department of Ecology and Management of Biodiversity, UMR 7179–CNRS/MNHN,  
10 MECADEV, Paris, 75321, France.

11 <sup>c</sup> Institute of Systematic, Evolution, Biodiversity (ISYEB), UMR 7205–  
12 CNRS/MNHN/UPMC/EPHE, National Museum of Natural History, 45 rue Buffon, Paris,  
13 75005, France.

14 <sup>d</sup> Department of Prehistory, UMR 7194–CNRS–MNHN, Musée de l'Homme, Paris, 75116,  
15 France.

16  
17 \* Corresponding author: Ameline Bardo, Department of Ecology and Management of  
18 Biodiversity, UMR 7179–CNRS – National Museum of Natural History, 55 rue Buffon, 75321  
19 Paris Cedex 5, France. E-mail: [abardo@mnhn.fr](mailto:abardo@mnhn.fr)

20  
21 **KEY WORDS:** grasping; hominids; manipulation; maze task; performance

22  
23 **Abbreviated title:** Tool use abilities among some hominids

Number of text pages: 37; 4 figures, 3 tables, and 2 supplementary materials.

## ABSTRACT

**Objectives:** Humans are known to possess more complex manual abilities than other primates. However, the manual abilities of primates have not been fully explored, and we still do not know if the manipulative abilities we attribute to humans are unique. The aim of this study was to compare the manual function and performance developed by humans, gorillas and orangutans while performing the same experimental tool use task.

**Materials and Methods:** The study was conducted on 20 humans, six gorillas, and seven orangutans. Each individual had to use a tool to collect food from a maze during six experimental sessions while maintaining the same unconstrained body posture condition. We quantified the different manual techniques used and the manual performance.

**Results:** Each species used different techniques. Humans used bimanual grip techniques, pad-to-pad precision grasping postures, and in-hand movements involving fingertips. Gorillas used unimanual grip techniques and simple in-hand movements while orangutans used a variety of strategies (e.g. hand or mouth). With these techniques, humans performed the task better than both gorillas and orangutans (e.g. by being quicker to collect the food).

**Discussion:** This study highlights other ways in which humans' manual dexterity differs from that of other species and emphasizes the distinct manipulative function of orangutans. The differences between the species could be due to the differing muscular anatomy and morphology of the hands, with hand proportion possibly placing particular biomechanical

constraints on each species. The differences between gorillas and orangutans could result from their different locomotor behaviors, and we hypothesize terrestriality facilitates the development of complex manipulation.

## INTRODUCTION

For decades, the evolution of human manipulative abilities has been of great interest and researchers have developed hypotheses that these abilities coevolved with bipedalism, tool-making and -use, brain enlargement and laterality, and/or language in humans (Wilson, 1998). Humans are known for their enhanced dexterity compared to other primates. It has been largely assumed that this dexterity of the human hand is linked to specific morphological features, such as a long, mobile, and powerful thumb, which are considered to be associated with stone tool-making (Napier, 1960; Marzke, 1997, Susman, 1998; Tocheri, 2008; Kivell, 2015). These morphological features are considered beneficial to our ability to use more forceful precision grips (i.e. between the pads of the thumb and fingers) than the other primates (Marzke, 1997; Marzke et al., 1992). However, other primates, such as great apes (Christel, 1993; Jones-Engels and Bard, 1996; Marzke and Wullstein, 1996; Christel et al., 1998; Byrne et al., 2001; Pouydebat et al., 2009, 2011), capuchin monkeys (Costello and Fragaszy, 1988; Christel and Fragaszy, 2000; Spinozzi et al., 2004; Pouydebat et al., 2009), and macaques (Christel, 1993; Tanaka, 1998; Macfarlane and Graziano, 2009; Pouydebat et al., 2009) use a diversity of grasping postures that are comparable to those used by humans, including precision grips. In addition, an orangutan and a bonobo were trained to strike stones to produce flakes during experiment in captivity (Wright, 1972; Schick and Toth, 1993; Schick et al., 1999), and even though this was not a natural behavior for them. Regardless, these subjects showed the morpho-functional capability required to perform the task. The manipulative abilities of some primates

(primarily great apes, capuchin monkeys and macaques) have been studied for decades (e.g. Parker and Gibson, 1977; Torigoe, 1985, 1987; Byrne et al., 2001; Corp and Byrne, 2002; Macfarlane and Graziano, 2009) and compared directly with humans performing both simple tasks like reaching (Christel, 1993; Lacreuse and Fragaszy, 1997; Pouydebat et al., 2009, 2011) and more complex routine tasks (Heldstab et al., 2016). However, as far as we know, no experiment in captivity has compared manual abilities during the same complex tool use task. Thus, the questions about humans' enhanced dexterity and how manipulation abilities evolved in hominids are still unresolved.

One recent study suggests that humans, having the most complex foraging niche, have developed complex manual abilities as a result, and that manipulation complexity would have coevolved with brain size and terrestriality in primates (Heldstab et al., 2016). However, in-hand manipulation was not taken into account when classifying manipulation complexity, despite a recent paper showing that a complex tool use task or complex object manipulation can require in-hand movements depending on the number of steps needed to perform the task (Crast et al., 2009; Bardo et al., 2016). In-hand movements were characterized by finger movements that involved object movement on the surface of the palm and the fingers. Thus, it appears necessary to take in-hand movements into detailed account to classify manipulation complexity and to draw conclusions about humans' specialization. Dynamic aspects of manual function have been described in humans (Exner, 1992; Santello et al., 1998; Braido and Zhang, 2004; Bullock and Dollars, 2011) and a detailed taxonomy of the various forms of in-hand movements is available (Elliot and Connolly, 1984). In contrast, in-hand manipulation studies among non-human primates are scarce and have been investigated mainly in chimpanzees (Boesch and Boesch, 1993; Marzke and Wullstein, 1996; Corp and Byrne, 2002; Crast et al., 2009; Marzke et al., 2015). Other primates such as gorillas (*Gorilla* sp.; Byrne et al., 2001), bonobos (*Pan*

97 *paniscus*; Bardo et al., 2016), and capuchin monkeys (Crast, 2006) have been the focus of even  
98 fewer studies, and orangutans' (*Pongo* sp.) in-hand movements have been almost entirely  
99 ignored. Although chimpanzees are our closest relatives (such as bonobos), and show the most  
100 complex tool use behavior among great apes in the wild, it is important to observe, measure,  
101 and analyze the other great apes in the effort to recount the evolution of complex manipulation  
102 in hominids. Studying the manual abilities of gorillas and orangutans is very important because  
103 they show strong manipulative abilities when processing food in the wild (e.g. orangutans: van  
104 Schaik et al., 1996; Russon, 1998; gorillas: Byrne and Byrne, 1991; Byrne et al., 2001), have  
105 different lifestyles (arboreal for orangutans and terrestrial for gorillas), and differ in hand  
106 morphology (Schultz, 1930). Finally, it is valuable to compare manual abilities between humans  
107 and great apes to better understand the conditions and restrictions underlying the occurrence of  
108 complex manipulative abilities, and the potential factors that may have bolstered humans into  
109 our position as the most eminently tool-using primates.

110 The objective of this study is to experimentally compare three different species of hominids  
111 in the same tool use task to determine the manual function and manual performance of each  
112 species. We use a novel quantification for the manual function (grip techniques, grasping  
113 postures, tool repositioning) and manual performance of humans compared to the most  
114 terrestrial (gorillas, *Gorilla gorillas*) and the most arboreal (orangutans, *Pongo* sp.) of the great  
115 apes during the same tool use tasks (i.e. the maze task used in Bardo et al., 2015, 2016). Some  
116 previous studies quantified performance according to the time humans needed to accomplish  
117 one bout of actions (Sollerman and Ejekkar, 1995; Turgeon et al., 1999; Aaron and Jansen,  
118 2003; Schoneveld et al., 2009), and the time non-human primates also needed to perform bouts  
119 of actions (Fragaszy and Mitchell, 1990; Albiach-Serrano et al., 2012). However, we suggest  
120 that time needed to perform an action could be influenced by a diversity of factors (e.g. effect

of social rank in species studied in their social group; Bardo et al., 2016), and that quantifying manual performance with other motor skill parameters could allow us a better comparison between species. We chose to compare the manual abilities and performance of these species using the maze task because it required complex tool manipulation for bonobos (Bardo et al., 2016) navigating obstructions (i.e. obstacles placed inside the maze, and also the wire netting placed between the maze and the subject) to collect a walnut. This task involved several constraints (i.e. forelimb coordination, body posture adjustments, manual abilities, and vision) and allowed us to quantify other parameters of performance (e.g. number of wooden obstacles touched, tool repositioning in the grid). We expected that the variability these of constraints could influence the manual techniques and the manual performance among species. Moreover, this experimental task was easy to implement using identical conditions for all the species. Such an approach provides a comparative functional analysis of the manual abilities and performance in great apes and humans, allowing us to test if humans are unique in an experimental context.

## METHODS

### Subjects and housing

Thirty-three subjects participated in the present study between 2014 and 2015: 20 *Homo sapiens*, 6 gorillas (*Gorilla gorilla*) and 7 orangutans (4 *Pongo Pygmaeus* and 3 *Pongo abelii*) (Table 1). The gorilla group consisted of 5 males (mean age = 18.6 years old, age range: 10-31 years) and 1 female (31 years old); the orangutan group consisted of 3 males (mean age = 16.3 years old, age range: 12-20 years) and 4 females (mean age = 20.5 years old, age range: 9-38 years). Non-human subjects were housed in different zoos (Table 1) and were naïve to the maze task when we presented it, as were the humans. The human sample was constituted of students and researchers from the National Museum of Natural History of Paris (NMNH; France), and

were not selected according to their handedness or personal habits or activities (we selected the first people who agreed to participate in the study). The groups of great apes were housed in indoor and outdoor enclosures with regular feedings, daily enrichment (e.g. food extraction) and water *ad lib*. The great ape portion of the study was conducted in the main cage in the indoor enclosure and subjects spontaneously participated. Humans were tested with the presence of one observer in a closed room at the NMNH of Paris.

---

Insert Table 1 about here

---

### **Apparatus and procedure**

The maze task was an experimental task which consisted of using a tool to collect walnuts positioned on a wooden maze (45 cm wide by 60 cm long). The mazes were the same for all the species and were composed of 10 wooden obstacles of different shapes and sizes (Figure 1ab). For great apes, the mazes were attached outside the cage on the wire mesh (size = 5x5 cm) and were positioned between 40 and 60 cm from the ground. To avoid competition and social tension for great apes, we simultaneously placed around the cages the same number of mazes as the number of tested subjects. Moreover, we offered the task after feeding to avoid social tension and to avoid subjects' appetites having an effect on the results. For humans, the maze was placed on a table 70 cm from the ground, with a piece of wire mesh (100x100 cm) placed in front of the maze (Figure 1b). The position of the maze was related to the size of each species and placed at an average height, allowing subjects to perform the task using any body postures they wished. For humans, a chair (45 cm height) was positioned just in front of the maze. The walnuts were placed at the end of the maze (60cm away from the subject). We



provided standardized tools made of bamboo branches for all species (length between 45cm and 1m depending on subject hand size); the tools for humans had smaller diameters (between 0.5 and 1cm) than the tools for gorillas and orangutans (between 1 and 1.5 cm) to account for different hand sizes among species. The tools were provided directly in the cages for great apes and placed beside the maze for humans. The only instruction for humans was to collect the walnut placed at the end of the maze through the wire netting, to extract a naïve behavior comparable to great apes.

We recorded six sessions per individual, one session corresponding to one walnut collected. The aim was to capture the variation among species and individuals, in three sessions per day and per individual over two days. A sequence began when a subject started to put the tool through the wire mesh and ended when he/she could collect the walnut. One fixed camera (CANON 600D©) was used during experiments with humans. For great apes, one camera (SONY Handycam HDR-CX240) was placed in front of each maze. Videos were recorded at 50 frames/second.

For all sessions, humans used exclusively a bipedal posture and gorillas used exclusively a seated posture. For orangutans, we observed that during one session they changed their body posture 2.98 times ( $\pm 0.93$ ). They spent more time to perform the task in seated posture (45.6 % of the time) and hanging on the wire netting (40.9 % of the time) than in bipedal posture (13.5 % of the time), but without significant differences (Friedman rank sum tests,  $Q = 2$ ,  $df = 6$ ,  $p > .05$ ). These differences suggested a possible effect of the body postures on the manual function, but in the present study the number of sessions for each individual was insufficient to test this effect. Thus, we decided not to take into account the different body postures used by the species in the analyses, but we discuss the potential effects in later sections.

---

Insert Figure 1 about here

---

### **Data scoring and classification system**

**Manual techniques.** We classified six categories of different grip techniques used to hold and use the tool: unimanual grip involved one hand; symmetrical bimanual grip involved both hands simultaneously on one tool; asymmetrical bimanual grip involved both hands simultaneously on two tools (see for example Figure 1b); mouth grip; foot grip; and other grip with combinations of two grips (e.g. one foot and one hand).

The grasping postures were recorded, including quantification of hand contact areas with the tool, following the same method and anatomical terminology of Borel et al. (2016) and Bardo et al. (2016). This method allowed also us to quantify the number of different combinations of contact areas used for each individual (for more details see Borel et al. 2016 and Bardo et al. 2016). To name the grasping postures we used existing typology for humans and great apes (see Table 2 footnote) and we classified them into five main categories as done previously (Bardo et al., 2016).

We recorded the different techniques used to reposition the tool in the hand, such as the use of in-hand movements, the hand that was not holding the tool, the mouth, and/or the feet. In-hand movements were classified in two categories: simple movements and complex movements. This classification was created by observing the subject's movements and by adapting the classification system of Elliot and Connolly (1984) and Crast et al. (2009). In this study, we included movement of individual digits as in Bardo et al. (2015) unlike the two previous studies. Simple movements are movements of one finger (e.g. flexion/extension of the thumb), and movements of two fingers with simple and reciprocal synergies (Elliot and

Connolly, 1984). Simple synergies are defined as convergent flexor synergies between the digits (e.g. flexion/extension of the thumb and the index finger), and reciprocal synergies are defined as dissimilar or reciprocating movements of the digits (e.g. flexion of the fingers with adduction of the thumb). Complex movements are defined as independent and uncoordinated movements of the fingers which grasp and regrasp the object using a characteristic sequence of grasps and simple movements (Crast et al., 2009).

Finally, our sample size and the number of sessions are too small to address population bias in manual preference, but for potential future use in meta-analysis, individual hand biases are presented in Supplementary Material 1.

**Manual performance.** We investigated the manual performance for each session and individual by quantifying the time needed (in seconds) to collect the walnut, adding other motor skill parameters such as the number of wrist movements used to finally collect the walnut (defined by the sum of wrist flexion/extension and abduction/adduction movements), the number of touched wooden obstacles (placed inside the maze), and the number of times the tool was repositioned in the grid. We considered that an obstacle was touched when the obstacle stopped the advancement of the walnut in the maze. We considered touching an obstacle to be due to a lack of control of the walnut's movement, and thus this parameter allowed us to quantify the control of the movement.

---

Insert Table 2 about here

---

## Video Coding and Reliability Assessment

Videos were played with VLC media player and analyzed frame by frame using a focal sampling protocol (Altmann, 1974). We recorded events each time a subject moved his/her fingers (e.g. displacements), stopped moving the tool for more than 20s, and when a subject changed the position of the tool in the grid and recorded the time for each event. We started to collect data when the tool was within the wire mesh. Including all subjects and all sessions, we recorded 1158 events: 502 events for humans, 268 events for gorillas, and 388 events for orangutans. The duration (in seconds) was used as a measure to quantify grip techniques and grasping postures, and number of events was used as a measure to quantify the techniques to reposition the tool and the performance parameters.

Twenty percent of sessions were also coded by a second observer to assess inter-observer reliability, which was excellent for all the parameters quantified (Pearson's correlation coefficient = 0.98,  $N = 660$ ) and good for the combinations of contact areas (Cohen's kappa  $\kappa = 0.63$ ,  $N = 216$ ). Therefore, only the data from the first observer were used for analysis.

## Data analysis

The mean percentage of total time of the use of each grip technique and grasping posture were calculated relative to the time needed to perform the task for each individual. For the other parameters, we used mean values for each individual. Because some of our data did not meet the normality and homogeneity assumptions for parametric tests, we used nonparametric statistics. The comparisons between species were performed by using Mann-Whitney tests ( $U$ ) for two species, and the three-species comparison by using Kruskal-Wallis rank sum tests ( $H$ ). If the latter tests were significant, we used Dunn's tests for multiple comparisons of independent

samples ( $Z$ ). The comparisons among individuals of each species were performed by using Friedman rank sum tests ( $Q$ ) and, if the tests were significant, we performed pairwise comparisons using the Wilcoxon signed rank test ( $W$ ) with continuity correction. Tests were two-tailed with a significance level set at 0.05. Bonferroni correction was applied in the case of multiple comparisons (corrected  $p$  values are marked as  $p'$ ). All the tests were performed using R (R Core Team 2016).

In order to characterize the performance among all the individuals ( $N = 33$ ) according to their techniques used, a Principal Component Analysis (PCA) was performed on six variables during the best session of each individual. The six variables were the four performance parameters (time needed to perform the task, number of wrist movements, number of touched obstacles, number of tool repositionings in the grid), the number of tool repositionings in the hand, and the number of changes of combinations of contact areas. The best session was defined as the session with the least time needed to collect the walnut. If several sessions had the same time needed, we used the one with the least wrist movement involved. The PCA was performed using R (R Core Team 2016), with the data normed for all the variables of all individuals.

## RESULTS

### Grip techniques

Unimanual grip was the preferred technique, but more used at 100 % of the time by gorillas and 90.6 % by orangutans, than 46.9 % by humans ( $Z = 3.962$ ,  $N = 26$ ,  $p' < .001$ ;  $Z = 2.738$ ,  $N = 27$ ,  $p' < .05$ , respectively). Humans also used symmetrical bimanual grip at 46.2 % and asymmetrical bimanual grip at 6.9 %. No particular grip was preferred in the human group ( $Q = 5.0586$ ,  $df = 19$ ,  $p > .05$ ), indicating inter-individual differences and also intra-individual

variations for sixteen individuals. Orangutans additionally used mouth grip (7.7 %) and other grip techniques, such as mouth with one foot (0.1 %; used by one individual), symmetrical bimanual grip (0.3 %; used by 2 individuals), and foot grip (1.3 %, used by 2 individuals).

### Grasping postures

Unimanual grip technique results are presented in Figure 2 as the mean percentage of different grasping posture categories used by each species. “Precision grips” were not used by gorillas and were used more by humans than orangutans ( $U = 109$ ,  $N = 27$ ,  $p < .01$ ). “Thumb lateral” was not used by gorillas, and we did not observe differences in usage of this grip between humans and orangutans ( $U = 69$ ,  $N = 27$ ,  $p > .05$ ). “Without thumb” was not used by humans, and we did not observe differences between gorillas and orangutans ( $U = 18$ ,  $N = 13$ ,  $p > .05$ ). “Palm grips” showed differences among species ( $H = 11.793$ ,  $df = 2$ ,  $p < .01$ ) - gorillas and orangutans used more palm grips than humans (respectively,  $Z = 2.431$ ,  $N = 26$ ,  $p' < .05$ ;  $Z = 3.002$ ,  $N = 27$ ,  $p' < .01$ ). “Other grips” also showed differences among species ( $H = 8.127$ ,  $df = 2$ ,  $p < .05$ ) - gorillas used more grasping postures classified in this category than did humans ( $Z = 2.72$ ,  $N = 23$ ,  $p' < .05$ ).

The detail of all the grasping postures observed for each species is presented in Table 2. We recorded ten grasping postures used by humans (mean by individual =  $2.65 \pm \text{SD } 0.4$ ) without preference within the group ( $Q = 13.299$ ,  $df = 16$ ,  $p > .05$ ). Humans seemed to use more “Lateral tripod grasp” (34.7 %), “Four-finger grasp” (30.5 %) and “Dynamic tripod grip” (13.8 %) as primary grasping postures. We recorded eight grasping postures used by gorillas (mean by individual =  $3.16 \pm 0.9$ ) without preference ( $Q = 6.8041$ ,  $df = 5$ ,  $p > .05$ ). Gorillas seemed to use mainly interdigital finger brace grasping postures, such as “Interdigital 2/3 brace” (33.6 %),

“Interdigital 3/4 brace” (28.2 %) and “Power grip” (19.6 %). We recorded 16 grasping postures for orangutans ( $6.14 \pm 1.3$ ), who used mainly “Power grip” (33.4 %) and “V pocket” (33.8 %).

In the two bimanual grip techniques for humans, we observed no categorical differences in grasping posture between the dominant hand and the support hand ( $p > .05$ ). We only observed the use of “Without thumb” grasping postures in the support hand during symmetrical bimanual grip technique (M2 in the Table 2).

Concerning changes in contact area combinations, orangutans altered their contact area on average 3.8 times ( $\pm 0.7$ ) per session, while gorillas changed 2.9 times ( $\pm 0.6$ ) per session, and humans 2.3 times ( $\pm 0.1$ ) per session. We observed no significant differences in mean number of contact area combinations used among species ( $H = 3.0842$ ,  $df = 2$ ,  $p > .05$ ).

---

Insert Figure 2 about here

---

### **Tool repositioning**

Tool repositioning frequency differed by species ( $H = 14.884$ ,  $df = 2$ ,  $p < .001$ ), with orangutans’ mean incidence of tool repositioning being higher than humans’ ( $Z = 3.603$ ,  $N = 27$ ,  $p' < .001$ ). We recorded four distinct techniques used to move and reposition the tool in the hand, with some differences among species (Figure 3). The hand that did not hold the tool was used in a similar manner by all the species ( $H = 0.1811$ ,  $df = 2$ ,  $p > .05$ ). The mouth was used by gorillas and orangutans, while the foot was used only by orangutans. Orangutans used their mouths more than gorillas did ( $U = 37$ ,  $N = 13$ ,  $p < .05$ ). In-hand movements were mainly recorded in humans and gorillas, without species differences ( $W = 76.5$ ,  $N = 26$ ,  $p > .05$ ) (Figure 3 and Table 3). Only one Sumatran orangutan (Kawan) was observed to use in-hand

movements. We recorded 11 types of in-hand movements by humans, three types by gorillas and two by orangutans. Also, these types of movements were not used by every individual (Table 3) or during every session. Humans used simple and complex movements involving fingertips whereas gorillas and orangutans used simple movements involving the palm (Table 3).

Gorillas and orangutans did not significantly prefer any one strategy for repositioning the tool in their hand ( $p > .05$ ), but orangutans appeared to use their mouths for repositioning the tool more often (83 %). Humans showed no difference in the number of in-hand movements used in the dominant hand, regardless of each grip technique used (unimanual, symmetrical bimanual or asymmetrical bimanual;  $Q = 26.708$ ,  $df = 19$ ,  $p > .05$ ).

---

Insert Figure 3 about here

---

---

Insert Table 3 about here

---

## Performance

We found significant differences between humans and great apes according to our measured performance parameters (reported as mean values; Supplementary Material 2). On average, gorillas and orangutans needed more time to collect the walnut than humans ( $p' < .001$ ), they used more wrist movements than humans ( $p' < .001$ ), they touched more obstacles than humans (respectively,  $p' < .001$  and  $p' < .01$ ), and they changed the position of the tool in the grid more often than humans (respectively,  $p' < .01$  and  $p' < .001$ ).



The PCA in figure 4 shows three axes that explain 87 % of the total variance on six variables (see Methods) quantified during the best session for each individual. The first axis (40 %) was determined by the time needed to collect the walnut (loading = 0.59), the number of touched obstacles (loading = 0.53), the number of tool repositionings in the grid (loading = 0.41), and the number of wrist movements used to collect the walnut (loading = 0.34). The second axis (26 %) was determined by the number of tool repositionings in the hand (loading = -0.84) and the number of tool repositionings in the grid (loading = 0.49). The third axis (21%) was determined by the number of touched obstacles (loading = 0.72), the number of tool repositionings in the grid (loading = -0.43), the number of tool repositionings in the hand (loading = -0.41), and the total number of combinations of contact areas used (loading = -0.32). The PCA distinguished the performance and techniques used by humans from some great apes (PC1, Fig. 4a) and also distinguished individuals within each species (PC2 and PC3, Fig. 4b-5c). Humans were almost all situated along the negative side of PC1; orangutans and gorillas were almost all situated along the positive side of PC1; in the center there was overlap among some individuals of all three species. The majority of the great apes and the few humans along the positive side of PC1 needed more time to collect the walnut, touched more wooden obstacles, changed the place of the tool in the grid more often, and used more wrist movements to collect the walnut in comparison to the other humans and the two great apes (one gorilla and one orangutan) situated along the negative side of this axis. PC1 indicates better performance in humans according to these four parameters, but also displayed inter-species variation by placing one gorilla and one orangutan within the humans' range of variability. PC2 illustrates inter-species performance in respect to two different techniques. Individuals situated along the negative side of PC2 repositioned the tool in their hand more often compared to individuals situated along the positive side of PC2, who instead more often repositioned the tool in the grid.

Humans who used bimanual coordination grip are found principally along the positive side of PC2, and thus more often repositioned the tool in the grid than in their hands. PC3 also shows inter-species performance and describes two different techniques. The individuals situated along the negative side of PC3 repositioned the tool more often in the grid and in their hand and used greater combinations of contact areas, but also touched fewer obstacles than individuals situated along the positive side of PC3. We suggest that each individual performed the task differently due to their different grip techniques and grasping postures.

---

Insert Figure 4 about here

---

## DISCUSSION

In the present study, the same complex tool use task was tested on three species of hominids to compare their manual function and manual performance. The results clearly showed that each species used different techniques. Humans used bimanual grip techniques, pad-to-pad precision grasping postures, and in-hand movements involving fingertips. Gorillas used a unimanual grip technique and simple in-hand movements, while orangutans used a variety of strategies (e.g. hand, mouth or feet). Humans performed the task better than gorillas and orangutans (e.g. by being quicker and using less wrist movements to collect the food), but these inter-species differences seemed less apparent during their best performance sessions. More detailed results are discussed below.

### Specific grip techniques according to species

In the present study, bimanual coordination grips were employed half of the time and nearly exclusively by humans, while the ability to perform many two-handed tasks has been well documented in both humans (Corbetta and Thelen, 1996) and great apes (e.g. chimpanzees: Marzke et al, 2015; gorillas: Byrne et al., 2001; orangutans: Peters and Rogers, 2008). In our study, humans displayed both symmetrical bimanual coordination (both hands grasp the same tool) and asymmetrical bimanual coordination (each hand grasps separate tools). These bimanual coordination grips increase the complexity of manipulation (MacNeilage et al., 1987; Hopkins, 1995; Heldstab et al., 2016). Indeed, asymmetrical bimanual coordination appears to be a more difficult task and requires eye coordination with both distant hands. The complexity of the maze task, which involves several constraints such as forelimb coordination, manual abilities and vision, could lead to expression of different grip techniques among species according to their muscular control and their morphology (Wainwright et al., 2008).

We observed the use of symmetrical bimanual coordination only once in each of two different orangutans. This result could be explained by the fact that one hand was employed in hanging from the wiring most of the time. It has been shown that wild orangutans use unimanual feeding more than feeding involving two limbs (hand-hand or hand-foot) (Peters and Rogers, 2008). Orangutans likely used specific grip techniques including the mouth and the foot due to their high arboreal lifestyle. Orangutans showed a strong preference for oral tool use over manual tool use in a previous study (O'Malley and McGrew, 2000), yet in the present study oral tool use occurred less than 10 % of the time. This could be due to the cage wiring used in the current study, which is not similar to the arboreal substrate where orangutans use tools in the wild. As orangutans are able to adopt many body postures (Thorpe and Crompton, 2006), the prevalence of non-oral manipulation could be linked to the task itself requiring both force and precision that the mouth might not provide. Gorillas exclusively used a unimanual grip

technique, which is consistent with recent reports on tool use in wild gorillas (Breuer et al., 2005; Kinani and Zimmerman, 2014).

### **Specific grasping postures and in-hand movements to species**

We already know that great apes can use precision grips (Christel, 1993; Jones-Engels and Bard, 1996; Marzke and Wullstein, 1996; Christel et al., 1998; Byrne et al., 2001; Pouydebat et al., 2009, 2011) and in-hand movements (Craet et al., 2009; Bardo et al., 2016) like humans. The human subjects in this study used pad-to-pad precision grip and in-hand movements with fingertips, while gorillas and orangutans used more grasping postures in which the tool is blocked into the hand (e.g. power grip) and in-hand movements which engage the palm. First, the fact that humans used “pencil grip” (called also dynamic tripod grip) as their preferred grasping posture as well as variants of this grasping posture like the four finger grasp (Schneck and Henderson, 1990) is certainly influenced by the way human children are taught to grasp a pen or pencil for writing. Gorillas better preferred “interdigital finger brace”, which was similarly observed in chimpanzees and bonobos during tool use (Lesnik et al., 2015; Bardo et al., 2016). Orangutans, however, used their palms more than the other species, favoring the “power grip,” and were the only ones to use the grasping posture called “V pocket”, also observed in chimpanzees and bonobos during tool use (Marzke et al., 2015; Bardo et al., 2016).

The differences between humans and great apes could be also explained by the different muscular anatomy and morphology of their hands. Indeed, gorillas (and gibbons) have the highest thumb-forefinger index among apes, while orangutans have the lowest (Schultz, 1930). Thus, the gorillas could more handily have involved their thumbs than orangutans could during in-hand movements, which is consistent with our results. The differences between humans and

great apes could be due to the absence of several anatomical features in the latter. It appears that some human hand muscles, such as *flexor pollicis longus* (FPL) and *extensor pollicis brevis* (EPB) which are related to the movement of the thumb, are not present or not independent in the hands of great apes, except hylobatids (Diogo and Wood, 2011; Diogo et al., 2012; Myatt et al., 2012). Nevertheless, gorillas and orangutans have a tendon of the *flexor digitorum profundus* running to the thumb, so it is questionable if the lack of the FPL and EPB could be linked to differences in manipulation. Moreover, in contrast to humans (Vigouroux et al., 2011; Goislard de Monsabert et al., 2012), the muscle activities and muscular coordination required to grasp an object for great apes are not known. Liu and collaborators (2016) recently used a virtual kinematic model to demonstrate that the different hand proportion in anthropoid hands results in a large disparity of manipulative potential among their hands. Consequently, the rare use of fingertips for both great apes could be the result of a choice based on biomechanical loadings, which cannot be balanced by their musculature when grasping with the thumb. For example, a shorter thumb would generate a different finger joint angle, corresponding to different moment arms, and probably would engage different joint and muscle loadings. However, since the model of Liu and collaborators did not take muscles into account, questions remain about how the loading of the hand, and thus the biomechanical constraints, affect inter-digital mobility in object manipulation. To better understand this point, it would be very useful to develop a musculoskeletal model based on ape morphological (e.g. size of the hand segments) and biomechanical data (e.g. force, kinematics, muscle activities) as has been done for humans (see Fernandez et al., 2016). Another interesting perspective would be to investigate the influence of grip strength on hand bone micro-architecture in great apes to access these biomechanical constraints, as is studied in humans (Reina et al., 2017).

### **Specifics techniques according to individuals**

Inter-individual variability was present in humans, high for orangutans and low for gorillas. Because the tasks in this study were not habitual, individuals adapted their techniques according to their individual experiences. For example, human children learn to write using the pencil grip between four and six years old, and there is variation in the development of this grasping posture (Schneck and Henderson, 1990). Moreover, some individuals may be athletes and/or musicians, and previous studies show that these activities have an effect on fine motor abilities (e.g. for music Costa-Giomi, 2005) and on prehensile capabilities (e.g. for sports Cutts & Bollen, 1993; Shea et al., 1992). In other words, learning and practising certain activities could influence manipulative abilities in human adults, which could explain the different techniques used by humans. We cannot draw conclusions on the influence of experience in gorillas' and orangutans' manipulative abilities since we do not know when they began to manipulate tools, and in what context (e.g. social, non-social). We know only that all individuals had previous access to various enrichments, such as food extraction with a tool. A longitudinal study could make it possible to deal with this unknown factor.

We found orangutans showed more inter-variability in their techniques than humans and gorillas. The fact that orangutans frequently changed their body posture could have generated changes in their grasping postures and also could have necessitated more frequent repositioning of the tool, especially with the mouth. Interestingly, despite our small sample size and even though it was not a focus of the study, we observed differences between Bornean orangutans and their Sumatran relatives. We know that Sumatran forests tend to be more productive and less seasonal than Bornean forests, and these differences could potentially have generated different behavioral responses such as foraging strategies and sociality (Wich, 2009; van Schaik, 2013). There is also a difference in general morphology between the two orangutan

species (Courtenay et al., 1988; Groves et al., 1992) and we do not know if their hand morphology differs. These differences between species could explain different manipulative abilities and should be explored in future studies.

Gorillas showed less inter-individual variability in their techniques, using the same techniques repeatedly to perform the task. Even if our sample did not allow us to test the effect of body posture on manual abilities, we can suggest that compared to orangutans, gorillas are more terrestrial and are less constrained by high body posture variability compared to arboreal behaviors. They may be free to develop specific manipulative abilities including tool use and complex bimanual coordination (e.g. Meulman et al., 2012). Strong inter-individual variability was also demonstrated in the techniques used by bonobos (Bardo et al., 2016) which seems to be intermediate between gorillas and orangutans. Thus, gorillas, with their more terrestrial lifestyle, could have developed different manual techniques and more specific ones than arboreal species such as orangutans. Moreover, these specific techniques could be shared among individuals. The cognitive and manual abilities of gorillas are poorly understood, and should be explored because gorillas display high manipulative ability in the wild (Byrne et al., 2001) including recently-observed tool use (Breuer et al., 2005; Kinani and Zimmerman, 2014).

## **Performance**

Our results showed that performance for the six sessions differed according to species, with better overall performance in humans. However, an interesting result was that when we compared performance during the best session across all individuals, we observed a less marked difference in manual performance among species. Humans collected the walnut faster than gorillas and orangutans during the six sessions. Time needed to perform the task has been

previously considered as an important measure of performance (Sollerman and Ejekkar, 1995; Schoneveld et al., 2009; Albiach-Serrano et al., 2012), however, during their best session, some gorillas and orangutans succeeded in collecting the walnut in a similar period to the humans'. For gorillas and orangutans, social pressure may have influenced task duration and their performance, as was observed in bonobos performing the same task (Bardo et al., 2016). Subordinate individuals tested in groups would act more quickly than high ranking individuals.

During the six sessions humans, used fewer wrist movements to collect the walnut, touched fewer obstacles, and used less tool repositioning in their hand and in the grid. These results could demonstrate a lack of efficiency and precision of wrist movements for both great apes. Moreover, the precision grasping postures used by humans could represent a good compromise between the mobility allowed by these grips for the object grasp and the relative stability produced by the pulp surfaces of the fingers (Marzke, 1997). Interestingly, the two gorillas who had better performances used on average more in-hand movements and used exclusively a preferential grasping posture that was the "interdigital 2/3 brace" grasping posture. This grasping posture was also observed in chimpanzees and bonobos, who also used in-hand movements (Crast et al., 2009; Bardo et al., 2016), and was defined as an inefficient variant of pencil grasp in humans (Selin, 2003). This grasping posture could allow more in-hand movement compared to the other grasping postures and so would favour in-hand manipulation.

## CONCLUSION

Our results indicated that all the species in this study were able to perform the task using different manual specificities and showing different performance. Historically, attention has



537 focused on the movements of the thumb (e.g. Napier, 1956; Lewis, 1989; Rafferty, 1990;  
538 Marzke et al., 1992; Rose, 1992). This study provides novel information on the manual function  
539 of hominids, highlights other ways in which humans' manual dexterity differs from other  
540 species' dexterity (i.e. bimanual grip technique, pad-to-pad precision grasping postures and in  
541 hand-movements involving fingertips) and emphasizes the distinct manipulative function in  
542 orangutans. Our results supported the theory of Heldstab et al. (2016) that primates may have  
543 developed complex manual abilities in respect to their foraging niche, and that manipulation  
544 complexity would have coevolved with brain size and terrestriality. Moreover, our results  
545 support the hypothesis that a terrestrial lifestyle plays a role in facilitating the development of  
546 complex tool use (Meulman et al., 2012). Extensive, but time-consuming, studies in the wild  
547 could help improve our knowledge about interactions between environment, body posture,  
548 natural manual tasks and manipulative techniques. Moreover, we can investigate if the different  
549 manual abilities of great apes might also be due to different brain networks and access to  
550 cognitive skills that are needed to complete tool use tasks. Indeed, we know little about  
551 sensorimotor control in the hand of great apes. An interesting recent study by Putt et al. (2017)  
552 investigated the brain activity during Oldowan and Acheulian stone tools learning in modern  
553 human participants. These authors suggested that a homologous cognitive network can be found  
554 in other species who use stone tools such as chimpanzees (e.g. Matsuzawa, 1994; Inoue-  
555 Nakamura and Matsuzawa, 1997) or capuchin monkeys (Proffitt et al., 2016). Investigations  
556 about the brain network during tool use in great apes, macaques (Malaivijitnond et al., 2007)  
557 and capuchin monkeys could be very useful to better understand humans' enhanced dexterity  
558 and how complex manipulative abilities evolved in primates.

## ACKNOWLEDGMENTS

We thank the general directors of the Palmyre Zoo (P. Caillé), Ménagerie of Paris (M. Saint-Jalme), Amnéville (M. Louis) and La Vallée des Singes (E. Le Grelle) for their hospitality and for allowing us to conduct our experiments in their parks. We also thank all of the zoos' staff, the zoological director, the great apes headkeeper and the animal keepers of these zoos - without them we could not work with animals in these ideal conditions. Thanks to H. Clamouze for manufacturing the mazes. We also thank the Action Transversale of National Museum of Natural History (Paris, France, E.P.). We thank K.S. Boyle, B.A. Wehrle and N.J. Gold for the correction of the English language and their very useful comments. We also thank T. Kivell, D.M. Fragaszy for their very useful comments. A. Bardo thanks the doctoral school FdV, the Fondation Bettencourt-Schueller and Paris Descartes University for PhD funding. Finally, thanks to the Société Francophone De Primatologie (SFDP) for their financial help with the Bourse Tremplin 2014. Finally, we thank the two anonymous reviewers for their comments which greatly improved this article. This research adhered to the legal requirements of France and all the experiments were carried out following the principles of laboratory animal care in accordance with the CNRS guidelines and comply with the American Association of Physical Anthropologists Code of Ethics as it pertains to living human and nonhuman subjects.

## AUTHOR CONTRIBUTION

Conceived and designed the experiments: AmB EP. Performed the experiments: AmB. Analyzed the data: AmB RC AnB. Contributed reagents/materials/analysis tools: AmB RC AnB EP. Wrote the manuscript: AmB RC AnB EP.

- 585 Aaron, D.H., Jansen, C.W. (2003). Development of the Functional Dexterity Test (FDT):  
586 construction, validity, reliability, and normative data. *Journal of Hand Therapy*, 16, 12-2.
- 587 Albiach-Serrano, A., Bugnyar, T., Call, J. (2012). Apes (*Gorilla gorilla*, *Pan paniscus*, *P.*  
588 *troglodytes*, *Pongo abelii*) versus corvids (*Corvus corax*, *C. corone*) in a support task: The  
589 effect of pattern and functionality. *Journal of Comparative Psychology*, 126(4), 355.
- 590 Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour* 49:227-  
591 267.
- 592 Bardo, A., Borel, A., Meunier, H., Guéry, J.P., Pouydebat, E. (2016). Behavioral and functional  
593 strategies during tool use in bonobos (*Pan paniscus*). *American Journal of Physical*  
594 *Anthropology*, 161 (1), 125-140.
- 595 Bardo, A., Pouydebat E., Meunier H. (2015). Do bimanual coordination, tool use, and body  
596 posture contribute equally to hand preferences in bonobos? *Journal of Human Evolution*, 82,  
597 159-169.
- 598 Benbow, M. (1997). Neurokinesthetic approach to hand function and handwriting. Workshop  
599 handout. Rocky Mount: Advanced Seminars Inc.
- 600 Boesch, C., Boesch, H. (1993). Different hand postures for pounding nuts with natural hammers  
601 by wild chimpanzees. In: Preuschoft, H., Chivers, D.J., (Eds), *Hands of primates* (pp. 91-108).  
602 New York: Springer-Verla.
- 603 Borel, A., Chèze, L., Pouydebat, E. (2016). Sequence analysis of grip and manipulation during  
604 tool using tasks: a new method to analyze hand use strategies and examine human specificities.  
605 *Journal of Archaeological Method and Theory*, 23, 1-25.
- 606 Braidó, P., Zhang, X. (2004). Quantitative analysis of finger motion coordination in hand  
607 manipulative and gestic acts. *Human Movement Science*, 22, 661-678.
- 608 Breuer, T., Ndoundou-Hockemba, M., Fishlock, V. (2005). First observation of tool use in wild  
609 gorillas. *PLoS Biology*, 3, e380.
- 610 Bullock, I.M., Dollar, A.M. (2011). *Classifying human manipulation behavior* (pp. 532-537).

611 Paper presented at IEEE International Conference on Rehabilitation Robotics, Zurich.

612 Byrne, R.W., Byrne, J.M.E. (1991). Hand preferences in the skilled gathering tasks of mountain  
613 gorillas (*Gorilla g. beringei*). *Cortex*, 27, 521-546.

614 Byrne, R.W., Corp, N., Byrne, J.M. (2001). Manual dexterity in the gorilla: bimanual and digit  
615 role differentiation in a natural task. *Animal Cognition*, 4, 347-361.

616 Christel, M. (1993). Grasping techniques and hand preferences in hominoidea. In: Preuschoft  
617 H, Chivers DJ., (Eds), *Hands of primates* (pp. 91-108). Springer, Wien New York.

618 Christel, M.I., Frigaszy, D. (2000). Manual function in *Cebus apella*. Digital mobility,  
619 preshaping, and endurance in repetitive grasping. *International Journal of Primatology*, 21(4),  
620 697-719.

621 Christel, M.I., Kitzel, S., Niemitz C. (1998). How precisely do bonobos (*Pan paniscus*) grasp  
622 small objects? *International Journal of Primatology*, 19, 165-194.

623 Corbetta, D., Thelen, E. (1996). The developmental origins of bimanual coordination: A  
624 dynamic perspective. *Journal of Experimental Psychology-Human Perception and*  
625 *Performance*, 22(2), 502-522.

626 Corp, N., Byrne, R.W. (2002). Leaf processing of wild chimpanzees: physically defended  
627 leaves reveal complex manual skills. *Ethology*, 108, 673-696.

628 Costa-Giomi, E. (2005). Does Music Instruction Improve Fine Motor Abilities? *Annals of the*  
629 *New York Academy of Sciences*, 1060, 262-264

630 Costello, M. B., Fragaszy, D. M. (1988). Prehension in *Cebus* and *Saimiri*: I. Grip type and  
631 hand preference. *American Journal of Primatology*, 15(3), 235-245.

632 Courtenay, J., Groves, C.P., Andrews, P. (1988). Inter- or intra-island variation? An assessment  
633 of the differences between Bornean and Sumatran Orang-utans. In: Schwartz (Ed) *Orang-utan*  
634 *Biology* (pp 19–29). Oxford University Press, Oxford.

635 Crast, J. (2006). A comparison of dynamic hand movements in chimpanzees (*Pan troglodytes*)  
636 and capuchin monkeys (*Cebus apella*). Master's thesis, University of Georgia.

637 Crast, J., Fragaszy, D., Hayashi, M., Matsuzawa, T. (2009). Dynamic in-hand movements in

638 adult and young juvenile chimpanzees (*Pan troglodytes*). *American Journal of Physical*  
639 *Anthropology*, 138(3), 274-285.

640 Cutts, A. and Bollen, S.R. (1993). Grip strength and endurance in rock climbers. *Proceedings*  
641 *of the Institution of Mechanical Engineers*, 207, 87-92.

642 Diogo, R., Richmond, B.G., Wood, B. (2012). Evolution and homologies of primate and  
643 modern human hand and forearm muscles, with notes on thumb movements and tool use.  
644 *Journal of Human Evolution*, 63(1), 64-78.

645 Diogo, R., Wood, B. (2011). Soft-tissue anatomy of the primates: phylogenetic analyses based  
646 on the muscles of the head, neck, pectoral region and upper limb, with notes on the evolution  
647 of these muscles. *Journal of Anatomy*, 219(3), 273-359.

648 Elliott, J.M., Connolly, K.J. (1984). A classification of manipulative hand movements.  
649 *Developmental Medicine & Child Neurology*, 26, 283-296.

650 Exner, C.E. (1992). In-hand manipulation skills. In: Case-Smith, J., Pehoski, C., (Eds),  
651 *Development of hand skills in the child* (pp. 1-11). Bethesda, MD: American Occupational  
652 Therapy Association.

653 Fernandez, J., Zhang, J., Heidlauf, T., Sartori, M., Besier, T., Röhrle, O., Lloyd, D. (2016).  
654 Multiscale musculoskeletal modelling, data-model fusion and electromyography-informed  
655 modelling. *Interface focus*, 6(2), 20150084.

656 Frigaszy, D.M., Mitchell, S.R. (1990). Hand preference and performance on unimanual and  
657 bimanual tasks in capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*,  
658 104(3), 275.

659 Gesell, A. (1940). *The first five years of life*. New York Harper & Row.

660 Goisard de Monsabert, B., Rossi, J., Berton, E., Vigouroux, L. (2012). Quantification of hand  
661 and forearm muscle forces during a maximal power grip task. *Medicine & Science in Sports &*  
662 *Exercise*, 44(10), 1906-1916.

663 Groves, C. P., Westwood, C., Shea, B.T. (1992). Unfinished business: Mahalanobis and a  
664 clockwork orang. *Journal of Human Evolution*, 22(4-5), 327-340.

665 Heldstab, S.A., Kosonen, Z.K., Koski, S.E., Burkart, J.M., van Schaik, C.P., Isler, K. (2016).  
666 Manipulation complexity in primates coevolved with brain size and terrestriality. *Scientific*  
667 *Reports*, 6, 24528.

668 Hopkins, W.D. (1995). Hand preferences for a coordinated bimanual task in 110 chimpanzees  
669 (*Pan troglodytes*): cross-sectional analysis. *Journal of Comparative Psychology*, 109, 291-297.

670 Inoue-Nakamura, N., Matsuzawa, T. (1997). Development of stone tool use by wild  
671 chimpanzees (*Pan troglodytes*). *Journal of comparative psychology*, 111(2), 159.

672 Jones-Engels, L., Bard, K.A. (1996). Precision grips in young chimpanzees. *American Journal*  
673 *of Primatology*, 39(2), 1-15.

674 Kivell, T.L. (2015). Evidence in hand: recent discoveries and the early evolution of human  
675 manual manipulation. *Philosophical Transactions of the Royal Society B*, 370(1682),  
676 20150105.

677 Kinani, J.F., Zimmerman, D. (2014). Tool use for food acquisition in a wild mountain gorilla  
678 (*Gorilla beringei beringei*). *American Journal of Primatology*, 77(3), 353-357.

679 Lacreuse, A., Frigaszy, D.M. (1997). Manual exploratory procedures and asymmetries for a  
680 haptic searching task: a comparison between capuchins (*Cebus apella*) and humans. *Laterality*,  
681 2, 247-266.

682 Lesnik, J.J., Sanz, C.M., Morgan, D.B. (2015). The interdigital brace and other grips for termite  
683 nest perforation by chimpanzees of the Goulougo Triangle, Republic of Congo. *American*  
684 *Journal of Physical Anthropology*, 157, 252-259.

685 Lewis, O.J. (1989). *Functional Morphology of the Evolving Hand and Foot*. Clarendon Press,  
686 Oxford.

687 Liu, M. J., Xiong, C. H., Hu, D. (2016). Assessing the manipulative potentials of monkeys, apes  
688 and humans from hand proportions: implications for hand evolution. *Proceedings of the Royal*  
689 *Society B*, Vol. 283, No. 1843, p. 20161923.

690 Macfarlane, N.B., Graziano, M. S. (2009). Diversity of grip in *Macaca mulatta*. *Experimental*  
691 *brain research*, 197(3), 255-268.

692 MacNeilage, P.F., Studdert-Kennedy, M.G., Lindblom, B. (1987). Primate handedness  
693 reconsidered. *Behavioral and Brain Sciences*, 10, 247-303.

694 Malaivijitnond, S., Lekprayoon, C., Tandavanittj, N., Panha, S., Cheewatham, C., Hamada, Y.  
695 (2007). Stone-tool usage by Thai long-tailed macaques (*Macaca fascicularis*). *American*  
696 *Journal of Primatology*, 69(2), 227-233.

697 Marzke, M.W. (1997). Precision grips, hand morphology, and tools. *American Journal of*  
698 *Physical Anthropology*, 102(1), 91-110.

699 Marzke, M.W., Marchant, L.F., McGrew, W.C., Reece, S.P. (2015). Grips and hand movements  
700 of chimpanzees during feeding in Mahale Mountains National Park, Tanzania. *American*  
701 *Journal of Physical Anthropology*, 156(3), 317-326.

702 Marzke, M.W., Wullstein, K.L. (1996). Chimpanzee and human grips: a new classification with  
703 a focus on evolutionary morphology. *International Journal of Primatology*, 17(1), 117-139.

704 Marzke, M.W., Wullstein, K.L., Viegas, S.F. (1992). Evolution of the power (“squeeze”) grip  
705 and its morphological correlates in hominids. *American Journal of Physical Anthropology*, 89,  
706 283-298.

707 Matsuzawa, T. (1994). Field experiments on use of stone tools by chimpanzees in the wild.  
708 *Chimpanzee cultures*, 351-370.

709 Meulman, E.J., Sanz, C.M., Visalberghi, E., van Schaik, C.P. (2012). The role of terrestriality  
710 in promoting primate technology. *Evolutionary Anthropology: Issues, News, and Reviews*,  
711 21(2), 58-68.

712 Myatt, J.P., Crompton, R.H., Payne-Davis, R.C., Vereecke, E.E., Isler, K., Savage, R., D’Aout,  
713 K., Gunther, M.M., Thorpe, S.K.S. (2012). Functional adaptations in the forelimb muscles of  
714 non-human great apes. *Journal of Anatomy*, 220, 13-28.

715 Napier, J.R. (1960). Studies of the hands of living primates. In *Proceedings of the Zoological*  
716 *Society of London*. Blackwell Publishing Ltd. Vol. 134, No. 4, pp. 647-657.

717 Napier, J.R. (1956). The prehensile movements of the human hand. *The Journal of Bone and*  
718 *Joint Surgery*, 38(4), 902-913.

719 O'Malley, R.C., McGrew, W.C. (2000). Oral tool use by captive orangutans (*Pongo pygmaeus*).  
720 *Folia Primatology*, 71(5), 334-341.

721 Parker, S.T., Gibson, K.R. (1977). Object manipulation, tool use and sensorimotor intelligence  
722 as feeding adaptations in *cebus* monkeys and great apes. *Journal of Human Evolution*, 6(7),  
723 623-641.

724 Peters, H.H., Rogers, L.J., 2008. Limb use and preferences in wild orang-utans during feeding  
725 and locomotor behavior. *American Journal of Primatology*, 70, 261-270.

726 Pont, K., Wallen, M., & Bundy, A. (2009). Conceptualising a modified system for classification  
727 of in-hand manipulation. *Australian occupational therapy journal*, 56(1), 2-15.

728 Pouydebat, E., Gorce, P., Bels, V. (2009). Biomechanical study of grasping according to the  
729 volume of the object: human versus non-human primates. *Journal of Biomechanics*, 42(3-9),  
730 266-272.

731 Pouydebat, E., Reghem, E., Borel, A., Gorce, P. (2011). Diversity of grip in adults and young  
732 humans and chimpanzees (*Pan troglodytes*). *Behavioural Brain Research*, 218(1), 21-28.

733 Proffitt, T., Luncz, L. V., Falótico, T., Ottoni, E. B., de la Torre, I., Haslam, M. (2016). Wild  
734 monkeys flake stone tools. *Nature*, 539, 85-88.

735 Putt, S.S., Wijekumar, S., Franciscus, R.G., Spencer, J.P. (2017). The functional brain  
736 networks that underlie Early Stone Age tool manufacture. *Nature Human Behaviour*,  
737 10.1038/s41562-017-0102.

738 R Core Team (2016). R: A language and environment for statistical computing. R Foundation  
739 for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

740 Rafferty, K.L. (1990). *The functional and phylogenetic significance of the carpometacarpal*  
741 *joint of the thumb in anthropoid primates*. M.A. dissertation, New York University.

742 Reina, N., Cavaignac, E., Trousdale, W. H., Laffosse, J. M., Braga, J. (2017). Laterality and  
743 grip strength influence hand bone micro-architecture in modern humans, an HRpQCT study.  
744 *Journal of Anatomy*, 10.1111/joa.12608.

745 Rose, M.D. (1992). Kinematics of the trapezium-1st metacarpal joint in extant anthropoids and



746 Miocene hominoids. *Journal of Human Evolution*, 22, 255–266.

747 Russon, A.E. (1998). The nature and evolution of orangutan intelligence. *Primates* 39, 85-503.

748 Santello, M., Flanders, M., Soechting, J.F. (1998). Postural hand synergies for tool use. *Journal*  
749 *of Neuroscience*, 18, 10105-10115.

750 Schick, K.D., Toth, N. (1993). *Making Silent Stones Speak. Human Evolution and the Dawn of*  
751 *Technology*. New York: Simon and Schuster.

752 Schick, K.D., Toth, N., Garufi, G., Savage-Rumbaugh, E.S., Rumbaugh, D., Sevcik, R. (1999).  
753 Continuing investigations into the stone tool-making and tool-using capabilities of a bonobo  
754 (*Pan paniscus*). *Journal of Archaeological Science*, 26(7), 821-832.

755 Schneck, C.M. (1987). Developmental change in the use of writing tools in normal 3.6 to 6 a  
756 year old children. Unpublished manuscript.

757 Schneck, C. M., Henderson, A. (1990). Descriptive analysis of the developmental progression  
758 of grip position for pencil and crayon control in nondysfunctional children. *The American*  
759 *Journal of Occupational Therapy*, 44(10), 893-900.

760 Schoneveld, K., Wittink, H., Takken, T. (2009). Clinimetric evaluation of measurement tools  
761 used in hand therapy to assess activity and participation. *Journal of Hand Therapy*, 22(3), 221-  
762 236.

763 Schultz, A.H. (1930). The skeleton of the trunk and limbs of higher primates. *Human Biology*,  
764 2(3), 303-438.

765 Selin, A. (2003). *Pencil grip. A descriptive model and four empirical studies*. Abo: Abo  
766 Akademi University.

767 Shea, K.G., Shea, O.F. and Meals, R.A. (1992). Manual demands and consequences of rock  
768 climbing. *Journal of Hand Surgery*, 17, 200-205.

769 Sollerman, C., Ejekkar, A. (1995). Sollerman hand function test. A standardized method and its  
770 use in tetraplegic patients. *Scandinavian Journal of Plastic and Reconstructive Surgery and*  
771 *Hand Surgery*, 29, 167-76.

772 Spinozzi, G., Truppa, V., Lagana, T. (2004). Grasping behavior in tufted capuchin monkeys

773 (*Cebus apella*): grip types and manual laterality for picking up a small food item. *American*  
774 *Journal of Physical Anthropology*, 125(1), 30-41.

775 Susman, R.L. (1998). Hand function and tool behavior in early hominids. *Journal of Human*  
776 *Evolution*, 35(1), 23-46.

777 Tanaka, I. (1998). Social diffusion of modified louse egg-handling techniques during grooming  
778 in free-ranging Japanese macaques. *Animal Behaviour*, 56, 1229-1236.

779 Thorpe, S.K., Crompton, R.H. (2006). Orangutan positional behavior and the nature of arboreal  
780 locomotion in Hominoidea. *American Journal of Physical Anthropology*, 131(3), 384-401.

781 Tocheri, M.W., Orr, C.M., Jacofsky, M.C., Marzke, M.W. (2008). The evolutionary history of  
782 the hominin hand since the last common ancestor of Pan and Homo. *Journal of Anatomy*,  
783 212(4), 544-562.

784 Torigoe, T. (1985). Comparison of object manipulation among 74 species of non-human  
785 primates. *Primates*, 26(2), 182-194.

786 Torigoe, T. (1987). Further report on object manipulation in non-human primates: A  
787 comparison within 13 species of the genus *Macaca*. *Primates*, 28(4), 533-538.

788 Turgeon, TR, MacDermid, JC, Roth, JH. (1999). Reliability of the NK dexterity test. *Journal*  
789 *of Hand Therapy*, 12, 7-15.

790 van Schaik, C.P. (2013). "The costs and benefits of flexibility as an expression of behavioural  
791 plasticity: a primate perspective." *Philosophical Transactions of the Royal Society B*,  
792 368(1618).

793 van Schaik, C.P., Fox, E.A., Sitompul A.F. (1996). Manufacture and use of tools in wild  
794 Sumatran orangutans. *Naturwissenschaften*, 83(4), 186-188.

795 Vigouroux, L., Domalain, M., Berton, E. (2011). Effect of object width on muscle and joint  
796 forces during thumb/index fingers grasping. *Journal of Applied Biomechanics*, 27, 173-180.

797 Wainwright, P.C., Mehta, R.S., Higham, T.E. (2008). Stereotypy, flexibility and coordination:  
798 key concepts in behavioral functional morphology. *Journal of Experimental Biology*, 211(22),  
799 3523-3528.

Wich, S. A. (2009). *Orangutans: geographic variation in behavioral ecology and conservation*.  
Oxford biology. Oxford University Press.

Wilson, F.R. (1998). *The hand: how its use shapes the brain, language, and human culture*.  
New York: Pantheon Books

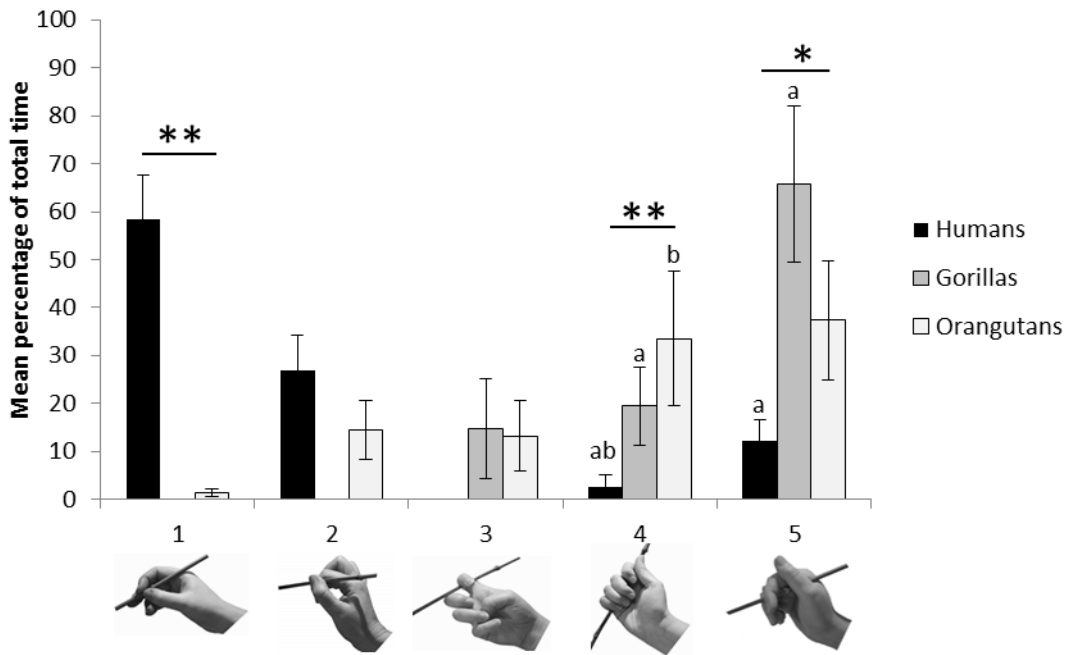
Wright, R.V. (1972). Imitative learning of a flaked stone technology—the case of an orangutan.  
*Mankind*, 8(4), 296-306.

Wynn-Parry, C.B. (1966). *Rehabilitation of the Hand* (2nd edn.). London: Butterworth.

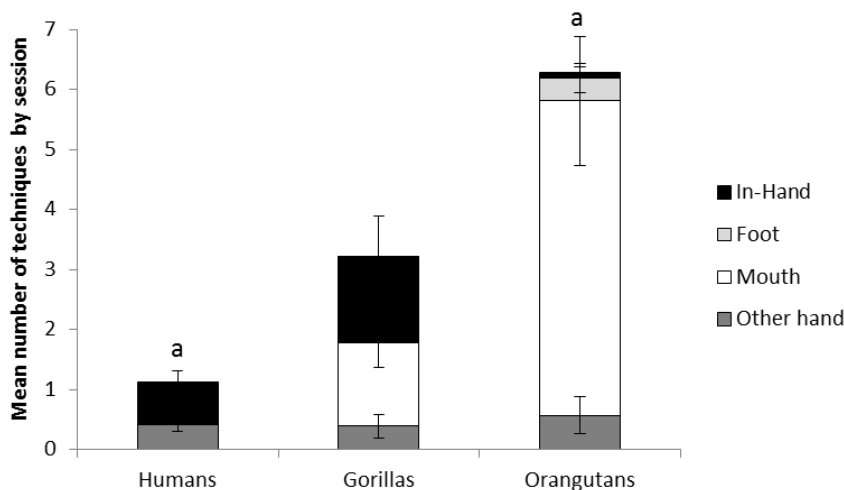
## Figure legends



**Figure 1.** Testing setup of the maze task. In (a) gorilla seated and (b) human in bipedal posture. The maze was assembled with obstacles inside and was the same for all species. In (a) the gorilla used a unimanual grip technique with an interdigital 2/3 brace grasp, and in (b) the human used an asymmetric bimanual grip technique with two tools held by a dynamic tripod grasp with both hands (See Methods and Table 2).

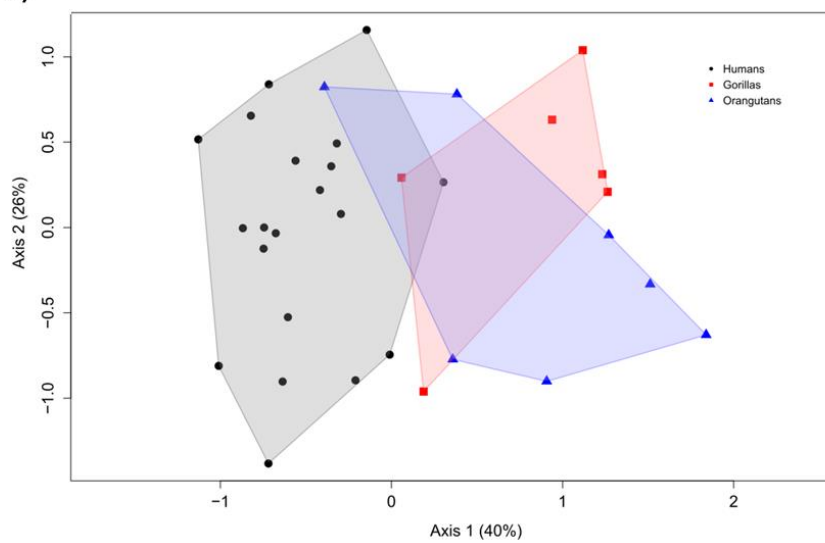


**Figure 2.** Mean percentage of total time of the use of the five different grip categories by each species to grasp and use tools during unimanual grips. 1. Precision grips; 2. Thumb lateral; 3. Without thumb; 4. Palm grips; 5; Other grips. Kruskal-Wallis rank sum test  $* = p < .05$ ; Dunn's-test for multiple comparisons of independent samples  $a, b = p' < .05$ .

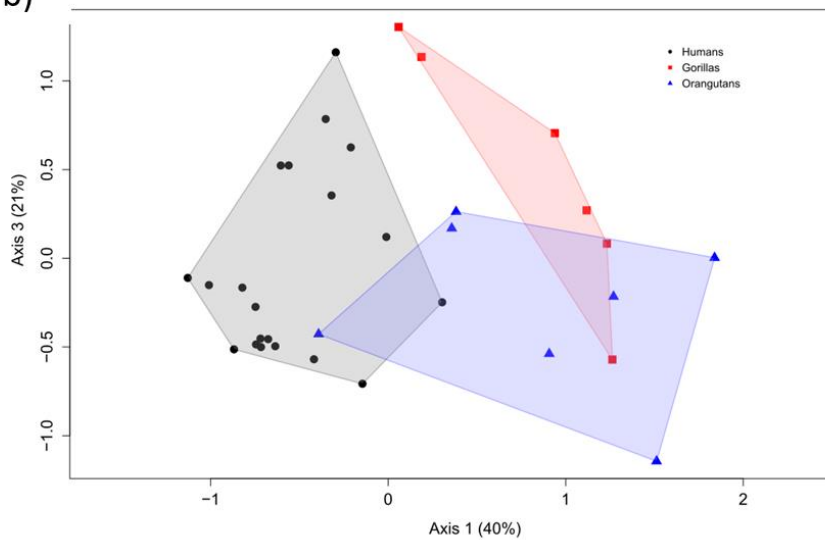


**Figure 3.** Mean number of techniques used by session for tool repositioning in the hand by each species. Dunn's-test for multiple comparisons of independent samples  $a = p' < .001$ .

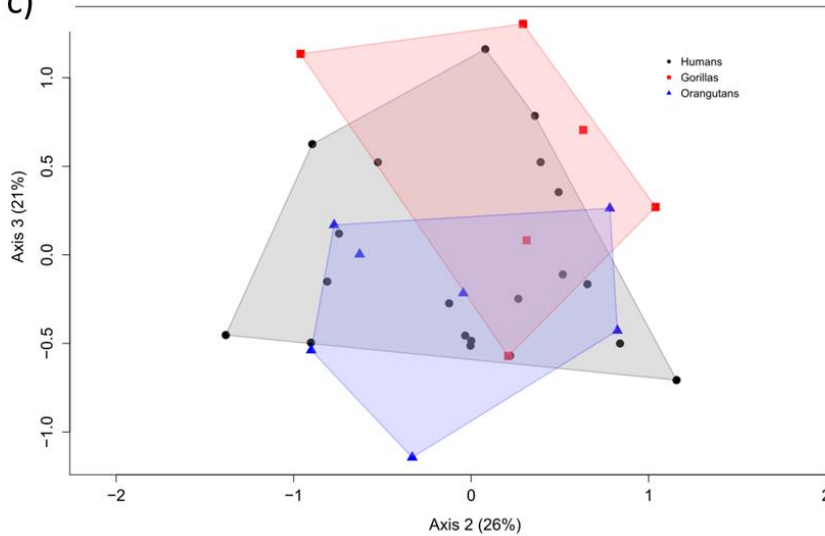
a)



b)



c)

























**Figure 4.** Principal Component Analysis performed on six manual function and performance variables (see Methods) for the best session of each individual. Polygons represent species and points individuals. Axis 1 (PC1) distinguished the performance and techniques used by humans and some great apes, showing inter-species variation. Axis 2 (PC2) and axis 3 (PC3) distinguished the performance and techniques used by the individuals in each species, showing intra-species variation.

**Table 1.** Details individuals tested.











Species	Subject	Sex	Age (years)	Observation locations (France)
<i>Homo sapiens</i>	10 individuals	M	Age range 22-41 (mean =28)	National Museum of Natural History in Paris
<i>Homo sapiens</i>	10 individuals	F	Age range 22-30 (mean=26)	National Museum of Natural History in Paris
<i>Gorilla gorilla</i>	Ya Kwenza	M	30	Zoo of Amnéville
<i>Gorilla gorilla</i>	Meru	M	11	Zoo of Amnéville
<i>Gorilla gorilla</i>	Lengai	M	11	Zoo of Amnéville
<i>Gorilla gorilla</i>	Yaounde	M	31	Zoo of La Vallée des Singes
<i>Gorilla gorilla</i>	Sango	M	10	Zoo of La Vallée des Singes
<i>Gorilla gorilla</i>	Moseka	F	31	Zoo of La Vallée des Singes
<i>Pongo pygmaeus</i>	Sandai	M	20	Zoo of La Palmyre
<i>Pongo pygmaeus</i>	Tiba	F	38	Zoo of La Palmyre
<i>Pongo pygmaeus</i>	Theodora	F	26	Zoo of La Ménagerie du jardin des plantes à Paris
<i>Pongo pygmaeus</i>	Tamou	F	9	Zoo of La Ménagerie du jardin des plantes à Paris
<i>Pongo abelii</i>	Ludi	M	17	Zoo of Amnéville
<i>Pongo abelii</i>	Kawan	M	12	Zoo of Amnéville
<i>Pongo abelii</i>	Putri	F	9	Zoo of Amnéville

**Table 2.** Variability of the grasping postures used to hold a tool and the percentage of uses by species. For humans, M1 corresponds to the dominant hand during unimanual grip technique and during asymmetrical bimanual grip technique (defined as the hand that directed movements of the tool and walnut), and M2 corresponds to the support hand during asymmetrical bimanual grip technique. Illustration examples of the grasping postures were realized with a human hand and so the position of the fingers could be changed according to the morphometric of the hand of the species. Humans used more “precision grips”, gorillas used more “other grips”, and orangutans used as much “other grips” as “palm grips”.

			Humans					Gorillas	Orangutans	Illustrations
			Unimanual	Bimanual symmetric		Bimanual asymmetric				
				M1	M2	M1	M2			
Category of grasping postures	Name	Description								
Precision grips	Two-jaw chuck tip-to-tip <sup>a</sup>	Tool held between the tip of the thumb and the tip of index finger.	-	0.1	1.3	-	-	-	-	
	Two-jaw chuck pad-to-pad	Tool held between the pad of the thumb and the pad of index finger.	-	-	0.4	-	-	-	-	
	Two-jaw chuck pad-to-pad side	Tool held between the pad of the thumb and the side of the pad of index finger.	-	-	-	-	-	-	1.4	
	Dynamic tripod grip <sup>b</sup>	Tool stabilizes against radial side of third finger by thumb pulp with index pulp on top of the tool.	13.8	7.6	23.4	32	24	-	-	
	Four-fingers grasp <sup>c</sup>	Tool held between the pad of the thumb and the pad of other fingers except fifth finger.	30.5	33.5	14.8	44.9	31.8	-	-	
	Five-fingers grasp <sup>c</sup>	Tool held between the pad of the thumb and the pad of other fingers.	0.1	3.3	15.2	1	1.4	-	-	
Thumb lateral	Two-jaw chuck tip-to-side	Tool held between tip of the thumb and side of the pad of the index finger.	-	-	1	-	-	-	3.2	
	Two-jaw chuck pad-to-side <sup>a</sup>	Tool held between pad of the thumb and side of the pad of the index finger.	-	-	-	-	-	-	11.1	
	Lateral tripod grasp <sup>d</sup>	Tool stabilize against radial side of third finger with index pulp on top of the tool, and thumb adducted and braced over or under anywhere along lateral side of index finger.	34.7	30.4	4.4	11.9	14.8			
	Lateral four fingers grasp	Tool stabilize against radial side of index finger with index pulp on top of the tool and between tip or pad of third and fourth fingers with thumb adducted and braced over or under anywhere along lateral side of index finger.	-	-	1.1	-	-	-	-	

	Lateral five fingers grasp	Tool stabilize against radial side of index finger with index pulp on top of the tool and between tip or pad of the other fingers with thumb adducted and braced over or under anywhere along lateral side of index finger.	-	-	5.7	-	11	-	-	
	Cross thumb grasp <sup>e</sup>	Tool held against index finger with thumb crossed over object toward index finger, fingers fisted loosely into palm.	-	-	1.3	-	-	-	-	
<i>Without thumb</i>	Scissor hold <sup>f</sup>	Tool held between two fingers, excluding thumb.	-	-	-	-	-	1.2	2	
	Fingers hook <sup>a</sup>	Tool is enclosed by 1, 2 or 3 flexed fingers.	-	-	-	-	-	-	0.1	
	Transverse hook <sup>a</sup>	Tool held by all fingers flexed at interphalangeal joints, the thumb may be adducted or opposed, and the distal part of the palm was not involved.	-	-	-	-	-	1.7	0.4	
	Diagonal hook <sup>a</sup>	Tool held by decreasingly flexed distal fingers 5-1; the distal part of the palm was not involved.	-	-	-	-	-	-	0.1	
	Interdigital 2/3 finger hook	Tool held by flexed index and exits the hand between the proximal or middle phalanges of the index and third fingers.	-	-	-	-	-	0.5	2	
	Interdigital 3/4 finger hook	Tool held by flexed third finger and exits the hand between the proximal or middle phalanges of the third and fourth fingers.	-	-	-	-	-	-	0.4	
	Interdigital 3/4 fingers hook	Tool held by flexed third and fourth fingers and exits the hand between the proximal or middle phalanges of the third and fourth fingers.	-	-	-	-	-	10.7	8.2	
	Interdigital 4/5 finger hook	Tool held by flexed fourth finger and exits the hand between the proximal or middle phalanges of the fourth and fifth fingers.	-	-	-	-	-	-	0.1	
	Interdigital 4/5 fingers hook	Tool held by flexed third and fourth fingers and exits the hand between the proximal or middle phalanges of the fourth and fifth fingers.	-	-	-	-	-	4.3	-	
	Medial phalanges fingers support	Areas of the fingers, without thumb, just posed on the tool but do not hold it.	-	-	4	-	-	-	-	
	Fingers tips support		-	-	11.7	-	-	-	-	



<i>Palm grips</i>	Thumb lateral with passive palm	Tool held between thumb and index finger with passive contact of the palm with the tool.	-	-	-	-	-	-	0.2	
	Power grip	Tool held in opposition between the palm and flexed fingers with a possible pressure applied by the thumb.	4.8	5.7	10.8	8.9	12	19.8	33.4	
	Brush grasp	All the fingers are gathered along the tool with the object end against the palm.	-	2.8	-	-	-	-	-	
<i>Other grips</i>	Thumb wrap <sup>g</sup>	The thumb and the index cross over the tool.	0.6	1	-	1.4	-	-	-	
	V pocket <sup>f</sup>	Tool held in web between full thumb and index finger, other fingers were flexed but not in contact with the tool.	-	-	-	-	-	-	33.8	
	Interdigital 2/3 brace <sup>h</sup>	Tool is bracing in the webbing of the thumb, weaving under the index finger and exist the hand between fingers 2 and 3.	3.8	3.6	2.6	-	-	33.6	2.3	
	Interdigital 3/4 brace <sup>h</sup>	Tool is bracing in the webbing of the thumb, weaving under the second and third fingers and exist the hand between fingers 3 and 4.	-	0.8	2	-	-	28.2	1.3	
	Index grip <sup>f</sup>	Tool hooked by the index fingers and held by the thumb and the third fingers against the fourth and fifth fingers pad.	0.5	5.1	0.3	-	-	-	-	
	Index tripod grip	Tool stabilize against radial side of third finger by thumb pulp and hooked by index finger.	7.3	6.1	-	-	5	-	-	
	Transversal tripod grasp	Tool held between flexed index and third finger and pad of adducted thumb.	3.9	-	-	-	-	-	-	

**Table footnote:** a-h Named and described in a Marzke and Wullstein, 1996; b Wynn-Parry, 1966; c Schneck and Henderson, 1990; d Schneck, 1987, as cited in Schneck and Henderson, 1990; e Gesell, 1940, as cited in Schneck and Henderson, 1990; f Marzke et al., 2015; g Benbow, 1997; h Lesnik et al., 2015.

**Table 3.** Description of the in-hand movements observed and number of individuals who used each kind of movement (N). For humans, M1 corresponds to the dominant hand during unimanual grip technique and during asymmetrical bimanual grip technique, and M2 corresponds to the support hand during asymmetrical bimanual grip technique. Humans used simple and complex movements whereas gorillas and one orangutan, used only simple movements.

Category	Type	Definition	Humans (N =14/20)		Gorillas (N =5/6)	Orangutans (N = 1/7)
			M1	M2		
SIMPLE MOVEMENTS	Thumb extension and flexion	Extension of the thumb that already touched the tool which slides on/in finger or palm and flexion of the thumb to stop the tool sliding.	N = 1	N = 1	N = 2	N = 1
	Index extension and flexion	Extension and flexion of the index finger to hook and to stabilize the tool (mostly used during interdigital 2/3 brace). The thumb could move but did not touch and move the tool.	N = 1	-	N = 5	-
	Thumb adduction <sup>a</sup>	Thumb moved toward midline of the hand and moved the tool that it already touched.	N = 3	N = 1	-	-
	Thumb abduction <sup>a</sup>	Thumb moved away from midline of the hand and moved the tool that it already touched.	N = 2	N = 1	-	-
<i>Simple synergies</i> <sup>b</sup>	Index and thumb extension and flexion <sup>b</sup>	Simultaneous extension and flexion of the thumb and the index, the tool moved in a linear direction while the palm and fingers grasped it again.	-	N = 1	N = 3	N = 1
<i>Reciprocal synergies</i> <sup>b</sup>	Roll <sup>a</sup>	Fingers move opposite to one another to twist or roll the tool along one axis.	N = 4	-	-	-
	Thumb push <sup>a</sup>	Fingers grasp the tool and thumb extended and abducted to push out the tool from the palm.	N = 1	N = 1	-	-
COMPLEX MOVEMENTS	Rock <sup>b</sup>	Tool held transversally in the fingers and rocked. Thumb and third fingers tend to be stationary and flexion of the fourth and fifth fingers is accompanied by extension of the index (passive movement caused mechanically).	N = 1	-	-	-
	Linear step <sup>b</sup>	The fingers "walking" linearly on the tool with adduction and abduction of the thumb.	N = 9	N = 4	-	-
	Interdigital step <sup>b</sup>	The tool held with dynamic tripod grasp and was turned between index and third fingers to again grasp transversally with the extension of the index.	N = 2	-	-	-
	Complex shift <sup>c</sup>	“Walking” movement of the fingers on the tool used to reposition it. The tool moved in a linear direction. The thumb and the index finger moved simultaneously by extension and flexion.	N = 3	-	-	-

**Table footnotes:** <sup>a-c</sup> In-hand movements describe in: <sup>a</sup> Crast et al., 2009; <sup>b</sup> Elliot and Connolly, 1984; <sup>c</sup> Pont et al., 2009. See these references for more functional details and illustrations of these in-hand movements.

**Supplementary Material 1** Hand preferences were presented as a percentage of the duration the dominant hand was used relative to the total time needed to perform the task for each individual. The dominant hand was defined as the hand that directed movements of the tool and walnut during symmetrical bimanual grip or the hand that directed movements of the walnut during asymmetrical bimanual grip. Twelve humans used exclusively the right hand and two used exclusively the left hand (out of 20 individuals). No hand preference was observed for the group of gorillas ( $W = 7$ ,  $N = 6$ ,  $p > .05$ ): four used exclusively the left hand and two used exclusively the right hand. For orangutans we did not observe a preferred hand ( $W = 7$ ,  $N = 7$ ,  $p > .05$ ). Five individuals were ambidextrous and two individuals (Putri and Kawan) used exclusively the left hand.

The table shows the individual hand bias for each session. For humans, the percentages are presented according to the grip techniques used: U = unimanual grip; BiS = symmetrical bimanual grip involved both hands simultaneously on one tool; BiA = asymmetrical bimanual grip involved both hands simultaneously on two tools. Percentages in bold are for the best session of each individual. All orangutans have <100 % hand preference percentages because they used other grip techniques (mouth, foot, and mouth with one foot).

			Sessions											
			1		2		3		4		5		6	
Subject	Sex	Age	D	G	D	G	D	G	D	G	D	G	D	G
<i>Homo sapiens</i>														
1	M	22	100 U		100 U		100 U		100 U		100 U		44.7 BiA, 27.7 U	27.6 BiA
2	M	25	100 U		100 U		100 U		95.7 BiS, 4.3 U		71.4 BiS, 28.6 U		100 U	
3	M	23	100 U		100 U		100 U		100 U		100 U		100 U	
4	M	26		100 BiS		100 BiS		100 BiS	48.1 BiS	51.9 BiS		100 BiS		93.8 BiS, 6.2 U
5	M	40		93.8 U, 6.2 BiS		100 U		100 U		100 U		100 U		100 U
6	M	31	95.2 U, 4.8 BiS		100 U		67.7 U, 32.3 BiS		100 U		100 U		100 U	
7	M	22	100 U		81.5 BiA, 18.5 U		91.5 BiA, 8.5 BiS		100 U		100 U		100 U	
8	M	33	100 U		100 U		100 U		100 U		100 U		100 U	

9	M	26		60 BiA, 40 U		74.1 U, 25.9 BiA	4.2 U	95.8 U	3.6 U	71.4 BiA, 25 U		92.3 BiA, 7.7 U		61.3 BiA, 38.7 U
10	M	29	100 BiS		81.5 U, 18.5 BiS		73.9 U, 26.1 BiS		82.1 U, 17.9 BiS		81.5 U, 18.5 BiS		76.2 U, 23.8 BiS	
1	F	24	53.8 U	46.2 BiA	79.5 U, 20.5 BiS		64.4 BiS, 35.6 U		100 U		70 U, 30 BiS		89.7 U, 10.3 BiS	
2	F	30		79.5 BiS, 20.5 U		100 BiS		100 BiS		100 BiS		100 BiS		100 BiS
3	F	25	100 U		100 U		76 U, 24 BiS		51.2 U, 48.8 BiS		81.8 BiS, 18.2 U		55 BiS, 45 U	
4	F	25	51.5 U, 38.8 BiS, 9.7 BiA		73 BiS, 27 U		84.8 BiS, 15.2 U		100 U		96.9 U, 3.1 BiS		89.3 U, 10.7 BiS	
5	F	28	100 BiS		100 BiS		100 BiS		76.9 BiS, 23.1 U		80 BiS, 20 U		53.7 BiS, 46.3 BiA	
6	F	24	89 BiS, 11 U		78.9 U, 21.1 BiS		72.2 U, 27.8 BiS		82.8 U, 17.2 BiS		96.9 U, 3.1 BiS		60 U, 40BiS	
7	F	23	100 BiS		100 BiS		100 BiS		11.1 BiS	88.9 BiS	10 BiS	90 BiS	11.1 BiS	88.9 BiS
8	F	30	37.5 BiS	50 U, 12.5 BiS	77.8 U	14.8 BiS, 7.4 BiA		100 BiS		100 BiS	21.4 BiS	78.6 BiS		100 BiS
9	F	22	89.5 U, 10.5 BiS		52.4 U, 47.6 BiS		56.5 BiS, 43.5 U		78.3 U, 21.7 BiS		81 BiS, 19 U		100 BiS	
10	F	27	100 BiS		100 BiS		100 BiS		100 BiS		100 BiS		100 BiS	
<b>Gorilla gorilla</b>														
Ya Kwenza	M	30	100		100		100		100		100		100	
Meru	M	11	100		100		100		100		100		100	
Lengai	M	11		100		100		100		100		100		100
Yaounde	M	31		100		100		100		100		100		100
Sango	M	10		100		100		100		100		100		100
Moseka	F	31		100		100		100		100		100		100
<b>Pongo pygmaeus</b>														
Sandai	M	20	71.6	28.4	71.3	28.8	79.4	20.6	65.2	34.8	61.8	38.2	83.3	16.7
Tiba	F	38	3.3	83.4	0.8	75.1	4.6	56.9	7.0	93.0	97.7	0.0	27.8	60.9
Theodora	F	26	68.7		31.6	65.4	42.1	50.9	27.0	73.0	27.8	70.1	74.6	25.4
Tamou	F	9	100		100		65.7	34.3	69.6	28.1	38.9	61.1	86.1	13.9
<b>Pongo abelii</b>														
Ludi	M	17	7.6	86.6	18.8	43.8	57.0		91.5		3.3	96.7		100
Kawan	M	12		100		100		100		100		100		90.2
Putri	F	9		100		100		100		100		100		100

**Supplementary Material 2** Statistical results from the comparison of performance parameters among species. Significant results are in red. We found differences between humans and the great ape species, but no differences between gorillas and orangutans.

	Duration to perform the task	Number of wrist movements	Number of touched obstacles	Number of tool repositioning in the grid
<b>All species</b>	$H = 22.958, df = 2,$ $p < .001$	$H = 23.006, df = 2,$ $p < .001$	$H = 22.837, df = 2,$ $p < .001$	$H = 20.306, df = 2,$ $p < .001$
<b>Humans/Gorillas</b>	$Z = 3.592, N = 26,$ $p' < .001$	$Z = 3.557, N = 26,$ $p' < .001$	$Z = 4.214, N = 26,$ $p' < .001$	$Z = 3.131, N = 26, p' <$ .01
<b>Humans/Orangutans</b>	$Z = 3.953, N = 27,$ $p' < .001$	$Z = 3.989, N = 27,$ $p' < .001$	$Z = 3.215, N = 27,$ $p' < .01$	$Z = 3.908, N = 27, p' <$ .001
<b>Gorillas/Orangutans</b>	$Z = 0.115, N = 13,$ $p' > .05$	$Z = 0.173, N = 13,$ $p' > .05$	$Z = 0.988, N = 13,$ $p' > .05$	$Z = 0.465, N = 13, p' >$ .05