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1 **ACCEPTED VERSION BEFORE THE PROOF CORRECTIONS**

2

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

5

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20

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

22

23 Abbreviated title: Tool use abilities among some hominids

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

25

26 **ABSTRACT**

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

32

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

37

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

44

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

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

52

53

INTRODUCTION

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

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

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

121 of social rank in species studied in their social group; Bardo et al., 2016), and that quantifying
122 manual performance with other motor skill parameters could allow us a better comparison
123 between species. We chose to compare the manual abilities and performance of these species
124 using the maze task because it required complex tool manipulation for bonobos (Bardo et al.,
125 2016) navigating obstructions (i.e. obstacles placed inside the maze, and also the wire netting
126 placed between the maze and the subject) to collect a walnut. This task involved several
127 constraints (i.e. forelimb coordination, body posture adjustments, manual abilities, and vision)
128 and allowed us to quantify other parameters of performance (e.g. number of wooden obstacles
129 touched, tool repositioning in the grid). We expected that the variability these of constraints
130 could influence the manual techniques and the manual performance among species. Moreover,
131 this experimental task was easy to implement using identical conditions for all the species. Such
132 an approach provides a comparative functional analysis of the manual abilities and performance
133 in great apes and humans, allowing us to test if humans are unique in an experimental context.

134

135

METHODS

136

Subjects and housing

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

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

151

152

Insert Table 1 about here

153

154

Apparatus and procedure

155 The maze task was an experimental task which consisted of using a tool to collect
156 walnuts positioned on a wooden maze (45 cm wide by 60 cm long). The mazes were the same
157 for all the species and were composed of 10 wooden obstacles of different shapes and sizes
158 (Figure 1ab). For great apes, the mazes were attached outside the cage on the wire mesh (size
159 = 5x5 cm) and were positioned between 40 and 60 cm from the ground. To avoid competition
160 and social tension for great apes, we simultaneously placed around the cages the same number
161 of mazes as the number of tested subjects. Moreover, we offered the task after feeding to avoid
162 social tension and to avoid subjects' appetites having an effect on the results. For humans, the
163 maze was placed on a table 70 cm from the ground, with a piece of wire mesh (100x100 cm)
164 placed in front of the maze (Figure 1b). The position of the maze was related to the size of each
165 species and placed at an average height, allowing subjects to perform the task using any body
166 postures they wished. For humans, a chair (45 cm height) was positioned just in front of the
167 maze. The walnuts were placed at the end of the maze (60cm away from the subject). We

168 provided standardized tools made of bamboo branches for all species (length between 45cm
169 and 1m depending on subject hand size); the tools for humans had smaller diameters (between
170 0.5 and 1cm) than the tools for gorillas and orangutans (between 1 and 1.5 cm) to account for
171 different hand sizes among species. The tools were provided directly in the cages for great apes
172 and placed beside the maze for humans. The only instruction for humans was to collect the
173 walnut placed at the end of the maze through the wire netting, to extract a naïve behavior
174 comparable to great apes.

175 We recorded six sessions per individual, one session corresponding to one walnut
176 collected. The aim was to capture the variation among species and individuals, in three sessions
177 per day and per individual over two days. A sequence began when a subject started to put the
178 tool through the wire mesh and ended when he/she could collect the walnut. One fixed camera
179 (CANON 600D©) was used during experiments with humans. For great apes, one camera
180 (SONY Handycam HDR-CX240) was placed in front of each maze. Videos were recorded at
181 50 frames/second.

182 For all sessions, humans used exclusively a bipedal posture and gorillas used exclusively
183 a seated posture. For orangutans, we observed that during one session they changed their body
184 posture 2.98 times (± 0.93). They spent more time to perform the task in seated posture (45.6
185 % of the time) and hanging on the wire netting (40.9 % of the time) than in bipedal posture
186 (13.5 % of the time), but without significant differences (Friedman rank sum tests, $Q = 2$, $df =$
187 6 , $p > .05$). These differences suggested a possible effect of the body postures on the manual
188 function, but in the present study the number of sessions for each individual was insufficient to
189 test this effect. Thus, we decided not to take into account the different body postures used by
190 the species in the analyses, but we discuss the potential effects in later sections.

191 Insert Figure 1 about here

193 **Data scoring and classification system**

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

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

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

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

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

223

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

233

234 Insert Table 2 about here

235

236

Video Coding and Reliability Assessment

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

246 Twenty percent of sessions were also coded by a second observer to assess inter-
247 observer reliability, which was excellent for all the parameters quantified (Pearson's correlation
248 coefficient = 0.98, $N = 660$) and good for the combinations of contact areas (Cohen's kappa κ
249 = 0.63, $N = 216$). Therefore, only the data from the first observer were used for analysis.

250

251

Data analysis

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

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

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

274

275

RESULTS

276

Grip techniques

277 Unimanual grip was the preferred technique, but more used at 100 % of the time by
278 gorillas and 90.6 % by orangutans, than 46.9 % by humans ($Z = 3.962$, $N = 26$, $p' < .001$; $Z =$
279 2.738 , $N = 27$, $p' < .05$, respectively). Humans also used symmetrical bimanual grip at 46.2 %
280 and asymmetrical bimanual grip at 6.9 %. No particular grip was preferred in the human group
281 ($Q = 5.0586$, $df = 19$, $p > .05$), indicating inter-individual differences and also intra-individual

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

285

286

Grasping postures

287 Unimanual grip technique results are presented in Figure 2 as the mean percentage of
288 different grasping posture categories used by each species. “Precision grips” were not used by
289 gorillas and were used more by humans than orangutans ($U = 109, N = 27, p < .01$). “Thumb
290 lateral” was not used by gorillas, and we did not observe differences in usage of this grip
291 between humans and orangutans ($U = 69, N = 27, p > .05$). “Without thumb” was not used by
292 humans, and we did not observe differences between gorillas and orangutans ($U = 18, N = 13,$
293 $p > .05$). “Palm grips” showed differences among species ($H = 11.793, df = 2, p < .01$) - gorillas
294 and orangutans used more palm grips than humans (respectively, $Z = 2.431, N = 26, p' < .05$; Z
295 $= 3.002, N = 27, p' < .01$). “Other grips” also showed differences among species ($H = 8.127, df$
296 $= 2, p < .05$) - gorillas used more grasping postures classified in this category than did humans
297 ($Z = 2.72, N = 23, p' < .05$).

298 The detail of all the grasping postures observed for each species is presented in Table 2.

299 We recorded ten grasping postures used by humans (mean by individual = $2.65 \pm \text{SD } 0.4$)
300 without preference within the group ($Q = 13.299, df = 16, p > .05$). Humans seemed to use more
301 “Lateral tripod grasp” (34.7 %), “Four-finger grasp” (30.5 %) and “Dynamic tripod grip” (13.8
302 %) as primary grasping postures. We recorded eight grasping postures used by gorillas (mean
303 by individual = 3.16 ± 0.9) without preference ($Q = 6.8041, df = 5, p > .05$). Gorillas seemed to
304 use mainly interdigital finger brace grasping postures, such as “Interdigital 2/3 brace” (33.6 %),

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

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

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

315

316 Insert Figure 2 about here

317

318 **Tool repositioning**

319 Tool repositioning frequency differed by species ($H = 14.884$, $df = 2$, $p < .001$), with
320 orangutans’ mean incidence of tool repositioning being higher than humans’ ($Z = 3.603$, $N =$
321 27 , $p' < .001$). We recorded four distinct techniques used to move and reposition the tool in the
322 hand, with some differences among species (Figure 3). The hand that did not hold the tool was
323 used in a similar manner by all the species ($H = 0.1811$, $df = 2$, $p > .05$). The mouth was used
324 by gorillas and orangutans, while the foot was used only by orangutans. Orangutans used their
325 mouths more than gorillas did ($U = 37$, $N = 13$, $p < .05$). In-hand movements were mainly
326 recorded in humans and gorillas, without species differences ($W = 76.5$, $N = 26$, $p > .05$) (Figure
327 3 and Table 3). Only one Sumatran orangutan (Kawan) was observed to use in-hand

328 movements. We recorded 11 types of in-hand movements by humans, three types by gorillas
329 and two by orangutans. Also, these types of movements were not used by every individual
330 (Table 3) or during every session. Humans used simple and complex movements involving
331 fingertips whereas gorillas and orangutans used simple movements involving the palm (Table
332 3).

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

338

339 Insert Figure 3 about here

340

341 Insert Table 3 about here

342

343 **Performance**

344 We found significant differences between humans and great apes according to our
345 measured performance parameters (reported as mean values; Supplementary Material 2). On
346 average, gorillas and orangutans needed more time to collect the walnut than humans ($p' <$
347 $.001$), they used more wrist movements than humans ($p' < .001$), they touched more obstacles
348 than humans (respectively, $p' < .001$ and $p' < .01$), and they changed the position of the tool in
349 the grid more often than humans (respectively, $p' < .01$ and $p' < .001$).

350 The PCA in figure 4 shows three axes that explain 87 % of the total variance on six
351 variables (see Methods) quantified during the best session for each individual. The first axis (40
352 %) was determined by the time needed to collect the walnut (loading = 0.59), the number of
353 touched obstacles (loading = 0.53), the number of tool repositionings in the grid (loading =
354 0.41), and the number of wrist movements used to collect the walnut (loading = 0.34). The
355 second axis (26 %) was determined by the number of tool repositionings in the hand (loading
356 = -0.84) and the number of tool repositionings in the grid (loading = 0.49). The third axis (21%)
357 was determined by the number of touched obstacles (loading = 0.72), the number of tool
358 repositionings in the grid (loading = -0.43), the number of tool repositionings in the hand
359 (loading = -0.41), and the total number of combinations of contact areas used (loading = -0.32).
360 The PCA distinguished the performance and techniques used by humans from some great apes
361 (PC1, Fig. 4a) and also distinguished individuals within each species (PC2 and PC3, Fig. 4b-
362 5c). Humans were almost all situated along the negative side of PC1; orangutans and gorillas
363 were almost all situated along the positive side of PC1; in the center there was overlap among
364 some individuals of all three species. The majority of the great apes and the few humans along
365 the positive side of PC1 needed more time to collect the walnut, touched more wooden
366 obstacles, changed the place of the tool in the grid more often, and used more wrist movements
367 to collect the walnut in comparison to the other humans and the two great apes (one gorilla and
368 one orangutan) situated along the negative side of this axis. PC1 indicates better performance
369 in humans according to these four parameters, but also displayed inter-species variation by
370 placing one gorilla and one orangutan within the humans' range of variability. PC2 illustrates
371 inter-species performance in respect to two different techniques. Individuals situated along the
372 negative side of PC2 repositioned the tool in their hand more often compared to individuals
373 situated along the positive side of PC2, who instead more often repositioned the tool in the grid.

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

381

382

Insert Figure 4 about here

383

384

DISCUSSION

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

394

395

Specific grip techniques according to species

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

408 We observed the use of symmetrical bimanual coordination only once in each of two
409 different orangutans. This result could be explained by the fact that one hand was employed in
410 hanging from the wiring most of the time. It has been shown that wild orangutans use unimanual
411 feeding more than feeding involving two limbs (hand-hand or hand-foot) (Peters and Rogers,
412 2008). Orangutans likely used specific grip techniques including the mouth and the foot due to
413 their high arboreal lifestyle. Orangutans showed a strong preference for oral tool use over
414 manual tool use in a previous study (O'Malley and McGrew, 2000), yet in the present study
415 oral tool use occurred less than 10 % of the time. This could be due to the cage wiring used in
416 the current study, which is not similar to the arboreal substrate where orangutans use tools in
417 the wild. As orangutans are able to adopt many body postures (Thorpe and Crompton, 2006),
418 the prevalence of non-oral manipulation could be linked to the task itself requiring both force
419 and precision that the mouth might not provide. Gorillas exclusively used a unimanual grip

420 technique, which is consistent with recent reports on tool use in wild gorillas (Breuer et al.,
421 2005; Kinani and Zimmerman, 2014).

422

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

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

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

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

466

467

Specifics techniques according to individuals

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

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

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

494 Gorillas showed less inter-individual variability in their techniques, using the same
495 techniques repeatedly to perform the task. Even if our sample did not allow us to test the effect
496 of body posture on manual abilities, we can suggest that compared to orangutans, gorillas are
497 more terrestrial and are less constrained by high body posture variability compared to arboreal
498 behaviors. They may be free to develop specific manipulative abilities including tool use and
499 complex bimanual coordination (e.g. Meulman et al., 2012). Strong inter-individual variability
500 was also demonstrated in the techniques used by bonobos (Bardo et al., 2016) which seems to
501 be intermediate between gorillas and orangutans. Thus, gorillas, with their more terrestrial
502 lifestyle, could have developed different manual techniques and more specific ones than
503 arboreal species such as orangutans. Moreover, these specific techniques could be shared
504 among individuals. The cognitive and manual abilities of gorillas are poorly understood, and
505 should be explored because gorillas display high manipulative ability in the wild (Byrne et al.,
506 2001) including recently-observed tool use (Breuer et al., 2005; Kinani and Zimmerman, 2014).

507

508

Performance

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

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

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

533

534

CONCLUSION

535 Our results indicated that all the species in this study were able to perform the task using
536 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.

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579

AUTHOR CONTRIBUTION

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

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807

808 **Figure legends**



809

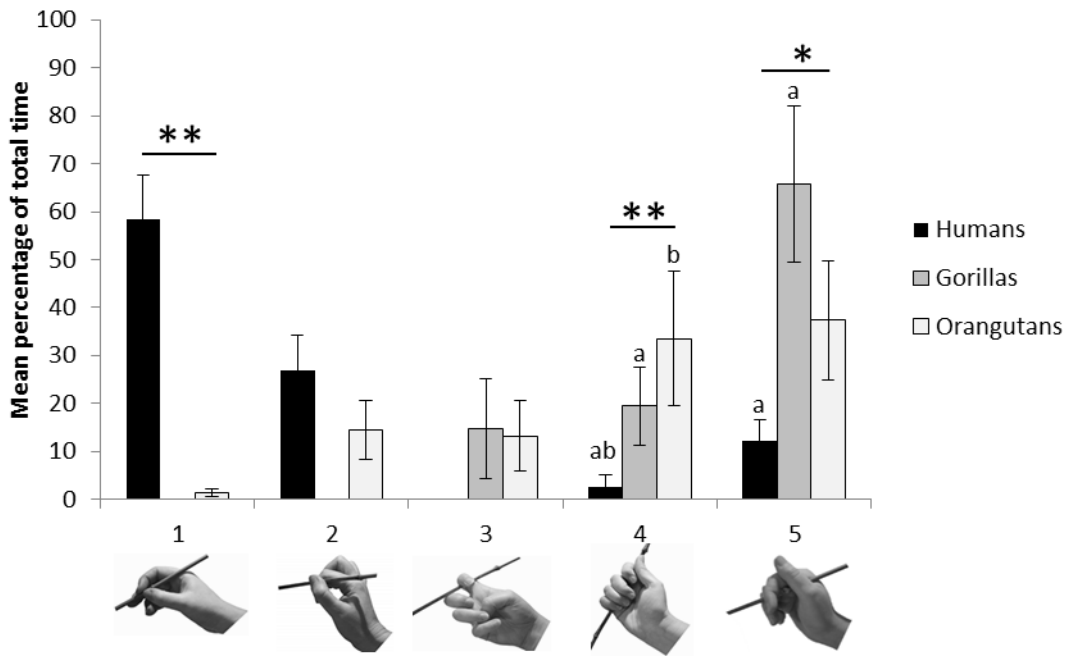
810 **Figure 1.** Testing setup of the maze task. In (a) gorilla seated and (b) human in bipedal posture.

811 The maze was assembled with obstacles inside and was the same for all species. In (a) the

812 gorilla used a unimanual grip technique with an interdigital 2/3 brace grasp, and in (b) the

813 human used an asymmetric bimanual grip technique with two tools held by a dynamic tripod

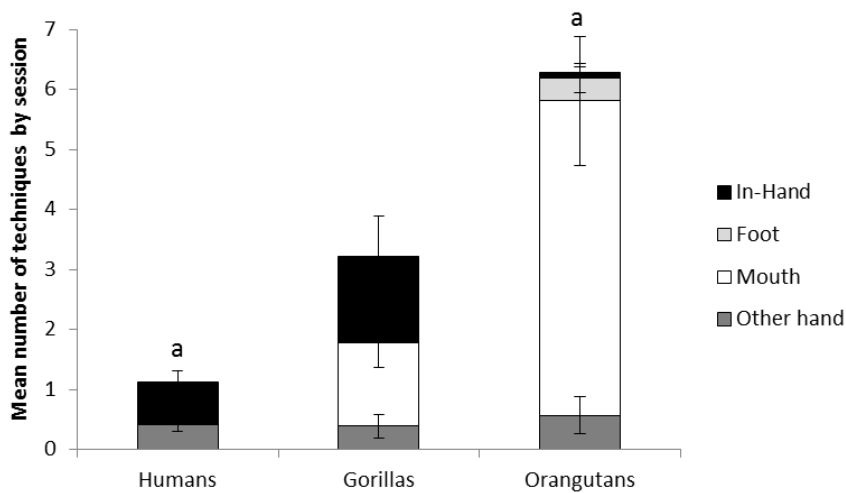
814 grasp with both hands (See Methods and Table 2).



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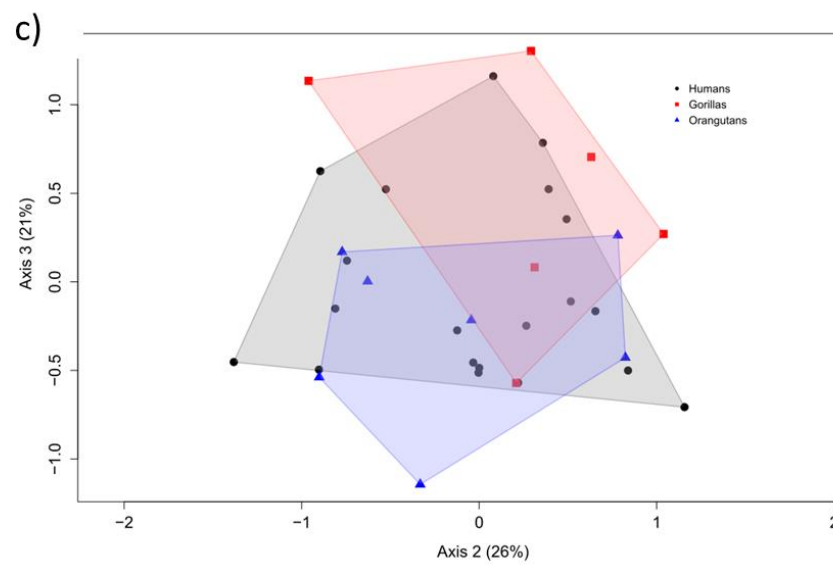
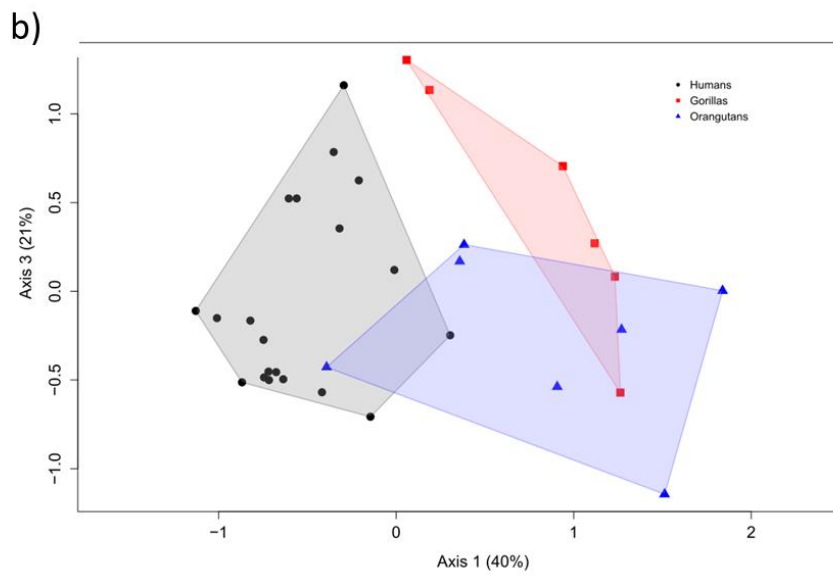
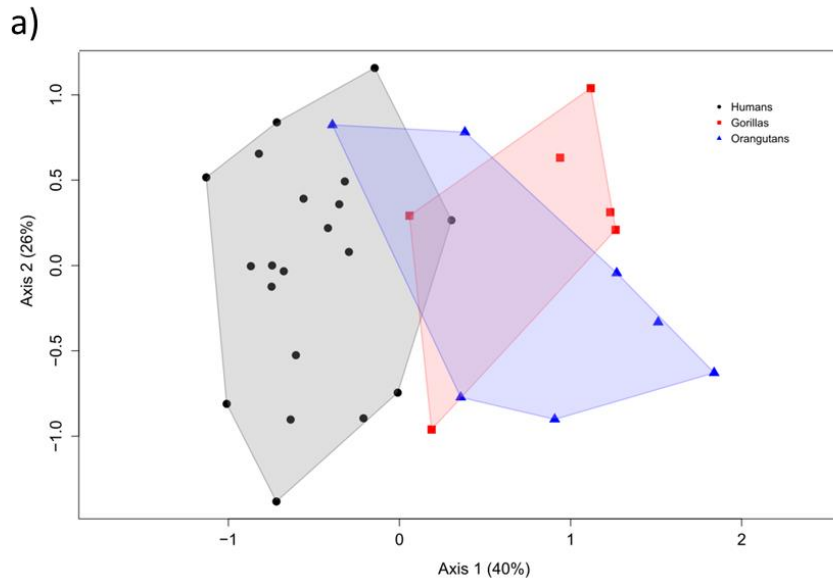
816 **Figure 2.** Mean percentage of total time of the use of the five different grip categories by each
 817 species to grasp and use tools during unimanual grips. 1. Precision grips; 2. Thumb lateral; 3.
 818 Without thumb; 4. Palm grips; 5; Other grips. Kruskal-Wallis rank sum test $* = p < .05$;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

820



821

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



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











831













832 **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

833

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”.

Category of grasping postures	Name	Description	Humans					Gorillas	Orangutans	Illustrations
			Unimanual	Bimanual symmetric		Bimanual asymmetric				
				M1	M2	M1	M2			
<i>Precision grips</i>	Two-jaw chuck tip-to-tip ^a	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 ^b	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 ^c	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 ^c	Tool held between the pad of the thumb and the pad of other fingers.	0.1	3.3	15.2	1	1.4	-	-	
<i>Thumb lateral</i>	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 ^a	Tool held between pad of the thumb and side of the pad of the index finger.	-	-	-	-	-	-	11.1	
	Lateral tripod grasp ^d	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 ^e	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 ^f	Tool held between two fingers, excluding thumb.	-	-	-	-	-	1.2	2	
	Fingers hook ^a	Tool is enclosed by 1, 2 or 3 flexed fingers.	-	-	-	-	-	-	0.1	
	Transverse hook ^a	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 ^a	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 ^g	The thumb and the index cross over the tool.	0.6	1	-	1.4	-	-	-	
	V pocket ^f	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 ^h	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 ^h	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 ^f	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 ^a	Thumb moved toward midline of the hand and moved the tool that it already touched.	N = 3	N = 1	-	-
	Thumb abduction ^a	Thumb moved away from midline of the hand and moved the tool that it already touched.	N = 2	N = 1	-	-
<i>Simple synergies^b</i>	Index and thumb extension and flexion ^b	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^b</i>	Roll ^a	Fingers move opposite to one another to twist or roll the tool along one axis.	N = 4	-	-	-
	Thumb push ^a	Fingers grasp the tool and thumb extended and abducted to push out the tool from the palm.	N = 1	N = 1	-	-
COMPLEX MOVEMENTS	Rock ^b	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 ^b	The fingers "walking" linearly on the tool with adduction and abduction of the thumb.	N = 9	N = 4	-	-
	Interdigital step ^b	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 ^c	"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: ^{a-c} In-hand movements describe in: ^a Crast et al., 2009; ^b Elliot and Connolly, 1984; ^c 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).

Subject	Sex	Age	Sessions													
			1		2		3		4		5		6			
			D	G	D	G	D	G	D	G	D	G	D	G		
Homo sapiens																
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	
Gorilla gorilla														
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
Pongo pygmaeus														
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
Pongo abelii														
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
All species	<i>H = 22.958, df = 2, p < .001</i>	<i>H = 23.006, df = 2, p < .001</i>	<i>H = 22.837, df = 2, p < .001</i>	<i>H = 20.306, df = 2, p < .001</i>
Humans/Gorillas	<i>Z = 3.592, N = 26, p' < .001</i>	<i>Z = 3.557, N = 26, p' < .001</i>	<i>Z = 4.214, N = 26, p' < .001</i>	<i>Z = 3.131, N = 26, p' < .01</i>
Humans/Orangutans	<i>Z = 3.953, N = 27, p' < .001</i>	<i>Z = 3.989, N = 27, p' < .001</i>	<i>Z = 3.215, N = 27, p' < .01</i>	<i>Z = 3.908, N = 27, p' < .001</i>
Gorillas/Orangutans	<i>Z = 0.115, N = 13, p' > .05</i>	<i>Z = 0.173, N = 13, p' > .05</i>	<i>Z = 0.988, N = 13, p' > .05</i>	<i>Z = 0.465, N = 13, p' > .05</i>