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3    **Do bimanual coordination, tool use and body posture contribute equally to hand**  
4    **preferences in bonobos?**

5

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16    Key words: bipedalism - complexity - hand preference - lateralization - tool use - tube task

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18    **ABSTRACT**

19    Approximately ninety percent of the human population is right-handed. The emergence of this  
20    hand preference in humans is thought to be linked to the ability to execute complex tasks and  
21    habitual bipedalism. In order to test these hypotheses, the present study explored, for the first  
22    time, hand preference in relation to both body posture (seated and bipedal) and task  
23    complexity (bimanual coordination and two tool use tasks of different complexity) in bonobos  
24    (*Pan paniscus*). Few studies have explored the effects of both posture and task complexity on  
25    handedness and investigations with bonobos are scarce, particularly studies on tool use. Our

study aims to overcome such a gap by addressing two main questions: 1) Does a bipedal posture increase the strength of hand preference and/or create a directional bias to the use of the right hand? 2) Independent of body posture, does task complexity increase the strength of the hand preference and/or create a directional bias to the use of the right hand? Our results show that independent of body posture, the more complex the task, the more lateralization occurred. Moreover, subjects tended to be right-handed for tasks involving tool use. However, posture had no significant effect on hand preference in the tasks tested here. Thus, for a given task, bonobos were not more lateralized in a bipedal posture than in a seated one. Task complexity might thus have contributed more than a bipedal posture to the emergence of human lateralization and the preponderance of right-handedness, even if a larger sample size and more data are needed to be conclusive.

## **Introduction**

Laterality, defined as the functional dominance of one side of the body relative to the other, has been studied primarily in humans (*Homo sapiens*). Broca (1877) studied the relationships between language disorders and brain damage, and was the first to reveal hemispheric functional specialization of the human brain. Moreover, the link between cortical asymmetry and manual asymmetry was established very early in humans (e.g. Broca, 1877; Annett, 1972), and has been confirmed in other vertebrates (Marchant and Steklis, 1986; Bradshaw, 1991; Bisazza et al., 1996; Hopkins and Morris, 1993).

The human population is predominantly right-handed at 90% (Annett, 1985; Perelle and Ehrman, 1994), which would correspond to a left hemisphere specialization for manual control. This phenomenon is thought to have played a prominent role in lateralization of human language (e.g. Warren, 1980; Ettlinger, 1988; Corballis, 1998; Crow, 2004) and other cognitive functions such as tool use (e.g. Kimura, 1979; Gibson and Ingold, 1993; Preston,

1998), manual gestures (Kimura, 1973a; Hopkins and Leavens, 1998; Rizzolatti and Arbib, 1998; Corballis, 2003; Pollick and de Waal, 2007), and throwing (Calvin, 1983; Hopkins et al., 1993, 2005a; Colell et al., 1995). As non-human primates are genetically close to humans, they are often used as models to understand the origins of human brain asymmetry (Cashmore et al., 2008; Fagot and Vauclair, 1991; MacNeilage et al., 1987; McGrew and Marchant, 1997; for a review, see Papademetriou et al., 2005). To date, such a bias of 90% for the right hand has never been observed in any other species of primate (Vallortigara and Rogers, 2005) and the origin of human hand preference remains unclear. However, several hypotheses have been proposed.

MacNeilage and collaborators (2009) suggested that early primates evolved in an ecological context where it was necessary to undertake more difficult and more elaborate tasks than for example simple grasping, in order to find food, which led to a concomitant increase in hand preference. Fagot and Vauclair (1991), according to their “theory of the complexity of the task”, proposed that hand preference would depend on the demands of the task. They defined complexity “in terms of the movement precision, relative to the spatiotemporal dimension of the task” and classified tasks according to two broad categories: “high-level” tasks and “low-level” tasks (Fagot and Vauclair, 1991). High-level tasks are more complex than low-level tasks in terms of postural, perceptual, and cognitive demands. For nonhuman primates, high-level tasks increase the strength of laterality, and induce a preference for the right hand (Fagot and Vauclair, 1991). A large number of studies in nonhuman primates also indicated that individuals were more strongly lateralized during a bimanual task considered as “complex” than during a unimanual task considered as more “simple” (gorilla: Byrne and Byrne, 1991; bonobo: Hopkins and de Waal, 1995; orangutan: Rogers and Kaplan, 1996; chimpanzee: Hopkins et al., 2007a; capuchin: Meunier and Vauclair, 2007). However, if the effect of the task on hand preference has been demonstrated

in many studies, there is a lack of consensus around the definition of the complexity of the task. Indeed, each task has its own constraints and each author identified various criteria depending on the task itself. This may be the reason why many definitions of task complexity are proposed in the literature. In addition, it is difficult to define exactly the various functional and cognitive requirements of a manual task, whereas it could help to define complexity and standardize the procedures and studies. We thus consider, in this study, the previous criteria mentioned in the literature, in addition to those we observed during the tasks in order to define complexity (see methods). Complexity of the task was previously defined according to criteria such as: the use of one hand versus two hands in bimanual coordination (Hopkins, 1995; MacNeilage et al., 1987), the number of stages required to realize the task (Marchant and McGrew, 1991), the level of precision of the required motor acts (Healey et al., 1986; Morris et al., 1993), the use of visual guidance (MacNeilage et al., 1987; Fagot and Vauclair, 1988a, 1988b) or tactile discrimination (Ettlinger, 1961), and finally any combination of these criteria (Fagot and Vauclair, 1991). Regarding the literature, tool use should be considered as a complex task since many of the criteria mentioned above are involved in tool use. Many definitions of tool use exist (reviewed in St. Amant and Horton, 2008) and here we use the widely accepted definition of Beck (1980): “the use of an object to change the shape, position or condition of another object, another body, or the user itself when the user holds or carries the tool during or just before using”. If complex tasks increase laterality (Fagot and Vauclair, 1991), tool use tasks should induce a stronger hand preference than “simpler” tasks, which has been already shown in apes (chimpanzee: Boesch, 1991; Sugiyama et al., 1993; orangutan: O'Malley and McGrew, 2006; gorillas: Pouydebat et al., 2010).

Another factor that might influence hand preference involves body posture. Bipedal or standing postures have been suggested to induce a stronger hand preference than other postures (e.g. chimpanzee and orangutan: Hopkins, 1993; bonobo: Hopkins et al., 1993).

Moreover, a bipedal posture is also thought to influence the direction of laterality with a preference for the right hand (e.g., chimpanzee and orangutan: Hopkins, 1993; bonobo: Hopkins et al., 1993; macaque: Westergaard et al., 1998a; cercopithecus: Chapelain et al., 2006; capuchin: Westergaard et al., 1997). This led Kimura (1979) to suggest both tool use and bipedalism contributed to the emergence of the lateralization of the brain, particularly the strong right hand preference in humans. This suggests the need to evaluate simultaneously the effects of tool use and bipedal posture on hand preference. To date, only two studies have examined hand preference when using tools in bipedal postures: one on chimpanzees (Braccini et al., 2010) and the other one on capuchins (Westergaard et al., 1998b). In both species, authors showed that individuals were more lateralized while manipulating tools in a bipedal posture than in a quadrupedal one, with no significant group-level difference for hand preference. These results tend to validate the hypothesis linking the emergence of lateralization to tool use and bipedalism, but more investigations on other individuals of the same and other species are needed. Specifically, it remains unclear whether task complexity or bipedal posture has the greatest effect on laterality. Moreover, it is unclear if effects of task complexity and bipedalism are independent, additive or interactive. Finally, it remains unknown whether either parameter induces a right or a left hand preference. A combined approach would help us to understand the respective implication of both parameters in the evolution of laterality and the emergence of the right hand bias in humans.

Our main objective was to test the interaction between task complexity and body posture on hand preference simultaneously. To this end, we investigated the interaction of these two parameters in captive bonobos by quantifying, for the first time, hand preference in relation to both body posture (seated and bipedal) and task complexity: (i) bimanual coordination, (ii) food extraction with a tool, and (iii) food recovery in a maze with a tool through a wire netting. The last two tasks required the use of a tool that has never been tested

in bonobos. We conducted this study on bonobos because they are, like chimpanzees (*Pan troglodytes*), close to humans with respect to phylogeny, sharing 98.4% of their coding DNA sequences (Wildman et al., 2003). However, behavioral data are scarce for bonobos, specifically concerning hand preference (around ten studies; e.g. Hopkins et al., 1993; De Vleeschouwer et al. 1995; Christel et al., 1998; Harrison and Nystrom, 2008; Chapelain et al., 2011), hand preference during tool use (Shafer, 1997; Harrison and Nystrom, 2008; Chapelain, 2010), and tool use in general (in wild: Kano, 1982, Ingmanson, 1996; Hohmann and Fruth, 2003; in captivity: Jordan, 1982; Toth et al., 1993; Gold, 2002). Finally, bonobos are often bipedal, similar to chimpanzees, making them an excellent model (Doran, 1993; Videan and McGrew, 2001, 2002; D'Aout et al., 2004).

Based on this existing literature, we thus suggested two main hypotheses (H): H1) bipedal posture increases the strength of hand preference and generates a directional bias to the use of the right hand; H2) the complexity of the task increases the strength of hand preference, and tool use creates a directional bias to the use of the right hand.

## Methods

### *Subjects*

This study was conducted from 19 January to 27 April 2012 at the “Vallée des singes” (France, 86), on a small group of nine captive bonobos (five females and four males), ranging in age from 4 to 43 years (mean age of 15.88 years, SE= 4.12). One young female (4 years old) had not yet included tool use in her behavioral repertoire and she was not included in the analyses. The bonobos were housed in an indoor building consisting of a network of 8 cages from 30 to 98 m<sup>2</sup> with a height of up to 6 m (2 main large cages and 6 smaller cages). Animals had access to a large wooded outdoor island. Water was available *ad libitum* in their pens and the food used for our protocol was part of the daily diet. All subjects were tested within their

social group, in cages not visible to the public. Before our study, this group was already used to receive pipes and pierced logs requiring tools to extract various foods on a weekly basis and was thus already experienced in food extraction.

### *General Procedure*

Hand preference was documented in three tasks differing by their complexity and for each task, in a seated posture and a bipedal posture. We considered individuals to be in a bipedal posture when they were upright, that is to say when the angle between the trunk and the thigh was greater than 90 degrees with the knee extended (thigh-leg angle > 90 degrees). Only one task was imposed each day per session. A session lasted 30 minutes on average and lasted until the food was gone. Two cameras (Sanyo ® Full HD) at 60 frames/second, one fixed and the other one mobile, were used during the tests, thus optimizing the collection of data. The mobile camera was always filming the same cage and the other camera was used to randomly film different cages every day. A focal sampling method of 5 minutes of filming on average for one individual was conducted until the food was eaten. Video analysis was performed with Windows Media Player ® using a focal sampling protocol (Altmann, 1974).

### *Experimental tasks*

Task 1: Coordinated bimanual task The first experiment was the “TUBE” task (Hopkins, 1995). In this task, the individual maintained a tube containing food with one hand, and reached inside the tube with one or more fingers of the other hand (the dominant hand). The tubes presented to the bonobos were made of PVC (30 cm long, 40 mm diameter, 155 g empty, 400 g full). They were filled with sticky food on the inside edge of both extremities. According to the literature, the complexity of this task resides in the fact that the tube requires coordinated bimanual hand movements with different roles for each hand (e.g. Byrne and



Byrne, 1991; Byrne et al., 2001). Two criteria of success were observed for this task: individuals had to grab and hold the tube with one hand and then extract the food with the other hand. We provided fourteen tubes horizontally suspended by the center at a height necessitating a bipedal posture (Fig. 1a) and fourteen tubes on the ground to induce a seated posture. Twenty-eight sessions were conducted with one session per day. On average, each subject was observed on  $12.9 \pm 1.2$  days for the seated posture and  $9.8 \pm 1.4$  days for the bipedal posture. The hand used to extract the food was noted with two different recording techniques: “frequencies” and “bouts”. For the frequencies, we counted each time the subject inserted one or more fingers into the tube and subsequently brought them to its mouth. This variable has been used in most other tube task studies (e.g. Hopkins, 1995; Hopkins et al., 2003; Meunier and Vauclair, 2007) and we used the same technique in order to favor comparisons. However, this method has been criticized as lacking data independence (Marchant and McGrew, 1991; Palmer, 2003). So, to ensure data independence, we also recorded bouts, corresponding to a series of identical actions, by recording only the first pattern of each sequence (e.g. Marchant and McGrew, 1991). A bout was considered completed each time the subject performed an action allowing a change of the dominant hand. Hand preference was analyzed for each individual with a minimum of ten bouts.

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Insert Figure 1 about here

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Task 2: The food extraction task In this task, hand preference was studied during a manipulative task involving tool use for food extraction. The task was comparable to the “termite-fishing” task, well known in wild chimpanzees (Goodall, 1968) but still never observed in wild bonobos (McGrew et al., 2007). To accomplish this task, twelve logs (53.25 cm long; SE =2.90 cm and diameter 9.17 cm; SE=0.88 cm), pierced in their center, were hung

201 vertically at different heights (6 logs hung low and 6 high) so that individuals could perform  
202 this task in seated and bipedal posture (Fig. 1b) within each session. Sticky food was placed  
203 inside the holes. Branches (maximum length of 3 m) were provided to bonobos. The hand  
204 used to hold the branch was recorded each time a subject inserted a branch into a hole of a  
205 log, removed it from the hole, and brought it to its mouth with one hand. We considered this  
206 task more complex than the tube task because more criteria were required to succeed. Indeed,  
207 individuals had to use a tool with one hand to be able to extract the food and visual guidance  
208 was required to insert the tool into the holes. The other hand was placed on the log or on the  
209 mesh. As with the tube task, we used two recording techniques: “frequency” and “bouts”.  
210 Eleven test sessions were conducted with one session per day, and each subject was observed  
211 between five and nine days (mean = 6.875, SE = 0.58).

212 Task 3: The maze task This experimental setup represents a new task, specifically created for  
213 this study. The subject needed to recover walnuts positioned on a wooden maze (Fig. 1c)  
214 outside the cage (grid with a mesh size of 5x5 cm), with a stick. Nine mazes (45 cm wide by  
215 60 cm long) differing in the shape, position, and size of the wooden obstacles (providing a  
216 different potential path of the walnut in each maze), were fixed outside the cages at different  
217 heights. In order to minimize as much as possible the social tensions in the group, the mazes  
218 were moved away from each other and the walnuts were placed in the mazes at the same  
219 moment. Four mazes were placed at 30 cm from the floor in the two main cages and five  
220 mazes at 60 cm height in the smaller cages so that individuals could choose to position  
221 themselves in a seated or bipedal posture. The walnuts were placed at the end of the maze (at  
222 60 cm away from the individual). This task was considered the most complex one in this  
223 study because it required several steps to be performed. As in the food extraction task,  
224 individuals had to use a tool to succeed. However, the maze task requires the use of a tool to  
225 recover the walnut by facing many obstacles: first, obstacles placed inside the maze in order

to complicate the trajectory of the walnut and second, between the maze and the individual (wire netting). These obstacles involved several constraints in terms of forelimb coordination, body posture adjustments, manual skills and vision. The behavior studied was the hand holding the branch. Fifteen sessions (each session comprising between 2 and 8 walnuts by maze per day) were filmed. As for the two other tasks, we first planned to use “frequency” and “bouts” recording techniques, thinking that subjects would have alternated hand use or could leave their tool during the task. However, the individuals never changed hands nor left their tool during all the maze sessions and we have thus recorded frequencies only. The hand holding the branch when recovering the walnut was thus recorded. Each subject was observed between nine and fourteen days (mean = 11.85 and SE = 0.70) and only those who obtained a minimum of six successes for the maze were kept for the analyses. Among our nine subjects, a young male never succeeded to access the mazes and two other individuals (one male and one female) did not perform this task in a bipedal posture.

#### *Data analysis*

The data obtained in this study were analyzed using the methods proposed by Hopkins (1999). For each subject the binomial z-scores were calculated based on frequency (Table 1) and bouts. The z-scores allowed us to categorize the bonobos individually as right-handed ( $z \geq 1.96$ ), left-handed ( $z \leq -1.96$ ), or without hand preference ( $-1.96 < z < 1.96$ ). Next, the individual hand preference index (Handedness Index, denoted by HI) was calculated using the formula:  $HI = (R - L) / (R + L)$ . HI varies from -1 to 1; negative values indicating a left-hand bias, and positive values indicating a right hand bias. Thanks to these individual HI, we evaluated hand preference at group level using a Wilcoxon signed-rank test for one sample. Finally, we calculated for each subject the absolute value of HI (denoted ABS-HI), which indicates the strength of hand preference. The stronger the laterality, the closer the ABS-HI is

to 1. We evaluated if the hand preference based on  $z$ -score changed for each subject between the postures and tasks with a chi-square goodness of fit test (e.g. Bogart et al., 2012). For pairwise comparisons, we considered only the individuals who were represented in both compared tasks. We compared only tasks performed by a minimum of 6 individuals. All statistical tests were performed with the software R (R development Core Team 2013) (exact method) and were two-tailed with a level of significance set at  $p < 0.05$ .

## Results

### *Bouts versus frequency*

Regarding the  $z$ -scores, we found differences between frequency and bout data for the tube task in bipedal posture where two bonobos previously classified as left-handed were classified with no preference (Table 1). To test data independence (Marchant and McGrew, 1991), we compared the HI values found between the two recording techniques (see Methods) for the two postures in the tube task and the food extraction task. For all conditions we found a significant positive correlation between HI measured with frequencies and HI measured using bouts (Spearman correlation,  $N = 8$ : tube task seated  $r = 0.97$ ,  $p < 0.001$ ; tube task bipedal  $r = 0.95$ ,  $p < 0.01$ ; food extraction task seated  $r = 1$ ,  $p < 0.01$ ; food extraction task bipedal  $r = 1$ ,  $p < 0.05$ ) indicating that these two approaches are similarly sensitive to individual hand preferences (Bogart et al., 2012; Hopkins, 2013). Thus, all analyses only used frequency data for determining individual hand preference as has been proposed in other studies (e.g. Bogart et al., 2012).

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Insert Table 1 about here

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### *Quantification of hand preference and influence of posture*

Task 1: The coordinated bimanual task Three bonobos were classified as right-handed, one was classified with no preference, and four were classified as left-handed for both postures. At the group level, we had no differences on the HI values for the seated posture (One-sample Wilcoxon signed-rank test;  $N = 8$ ,  $z = 15$ ,  $p = 0.74$ ) and the bipedal one (One-sample Wilcoxon signed-rank test;  $N = 8$ ,  $z = 20$ ,  $p = 0.84$ ), indicating individualistic hand preferences. A significant difference in the HI values was found between the seated and bipedal postures (Wilcoxon signed-rank test;  $N = 8$ ,  $z = 2$ ,  $p = 0.02$ ) indicating a trend that bonobos were more lateralized in the seated posture over that of the bipedal posture. When we considered hand preferences based on  $z$ -scores for the two postures, a chi-square goodness of fit test revealed that the distribution of hand preference was random [ $\chi^2(2, n = 8) = 0$ ,  $p = 1$ ], indicating that there was no difference in the hand used between the postures. Concerning the ABS-HI values, no difference appeared between seated and bipedal postures, (Wilcoxon signed-rank test;  $N = 8$ ,  $z = 24$ ,  $p = 0.46$ ), indicating that individuals were not more significantly strongly lateralized in seated than bipedal posture.

Task 2: The food extraction task All the individuals were lateralized in the food extraction task for both postures. Seven bonobos were classified as right-handed and one as left-handed. At the group level, a preference for the right hand appeared for seated posture (One-sample Wilcoxon signed-rank test;  $N = 8$ ,  $z = 36$ ,  $p < 0.01$ ) and in bipedal posture individual also seemed to have a preference for the right hand (One-sample Wilcoxon signed-rank test;  $N = 8$ ,  $z = 31$ ,  $p = 0.05$ ). When we considered hand preferences based on  $z$  scores for the two posture, a chi-square goodness of fit test revealed that the distribution of hand preference was not random [ $\chi^2(2, n = 8) = 10.75$ ,  $p < 0.01$ ]. For both posture, there were significantly more right than left handed subject [ $\chi^2(1, n = 8) = 4.5$ ,  $p < 0.05$ ]. No significant difference on HI values (Wilcoxon signed-rank test;  $N = 8$ ,  $z = 2$ ,  $p = 0.59$ ), nor on ABS-HI values (Wilcoxon signed-rank test;  $N = 8$ ,  $z = 0$ ,  $p = 0.11$ ), was observed between bipedal and seated postures.

Task 3: The maze task Individuals were exclusively right- or left-handed and they never changed hand between the nine different mazes suggesting that the manual preference was not affected by the structure of the mazes. Thus, we added the data of each maze to consider hand preference in the seated ( $N = 7$ ) and the bipedal ( $N = 5$ ) postures. Individuals never changed their body posture (from seated to quadrupedal and conversely) during the maze task. Considering hand preference, we showed that in the seated posture six bonobos demonstrated an exclusive use of the right hand and one individual an exclusive use of its left hand. Among the six right-handed individuals in seated posture, only five performed the task in bipedal posture and remained all right-handed in that case. At the group level, a preference for the right hand seemed to appear in seated posture (One-sample Wilcoxon signed-rank test;  $N = 7$ ,  $z = 24$ ,  $p = 0.06$ ) and in bipedal one with only right-handed individuals. For both postures, the strength of lateralization was maximal for all the individuals ( $ABS-HI = 1$ ).

#### *Influence of the complexity of the task and body posture*

In both seated (Fig. 2a) and bipedal postures (Fig. 2b), individuals classified as left handed or no preference during the tube task inverted to the right-hand during the food extraction and the maze task, except one. One individual remained left-handed throughout the study (Table 1).

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Insert Figure 2 about here

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In the seated posture, the HI values were significantly higher for the maze task than during the tube task (Wilcoxon signed-rank test;  $N = 7$ ,  $z = 26$ ,  $p < 0.05$ ) indicating a preference for the right hand during the maze task. Between the HI values of the tube task and the food extraction task we did not find differences in seated posture (Wilcoxon signed-rank test;  $N =$

8,  $z = 8$ ,  $p = 0.19$ ) and in bipedal posture we observed a trend for a preference for the right hand during food extraction than tube task (Wilcoxon signed-rank test;  $N = 8$ ,  $z = 3$ ,  $p = 0.06$ ). When we considered hand preferences categories for the three tasks in seated posture, a chi-square goodness of fit test revealed that the distribution of hand preference was random [ $\chi^2(4, n = 7) = 7.2857$ ,  $p = 0.12$ ], indicating that there was actually no difference in the actual hand used between tasks. When only the right-handed and left-handed categories are examined, we observed a trend for a preference for the right hand than left hand [ $\chi^2(2, n = 7) = 5.4875$ ,  $p = 0.06$ ]. Between the tube and food extraction tasks in bipedal posture, the distribution of hand preference was random [ $\chi^2(2, n = 8) = 4.4$ ,  $p = 0.11$ ], indicating that there was actually no difference in the actual hand used between the two tasks. Considering ABS-HI values, individuals were significantly more strongly lateralized in a seated posture during the maze task compared to the tube task (Wilcoxon signed-rank test;  $N = 7$ ,  $z = 0$ ,  $p < 0.05$ ). Moreover, they were significantly more strongly lateralized in a bipedal posture during the food extraction task compared to the tube task (Wilcoxon signed-rank test;  $N = 8$ ,  $z = 2$ ,  $p < 0.05$ ) (Fig.3).

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Insert Figure 3 about here

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## Discussion

This study is the first to simultaneously analyze both the effect of complexity and body posture on hand preference in bonobos. Our main result indicated that, independent of body posture, task complexity resulted in a greater lateralization for the two tool use tasks, with a tendency to preferentially use the right hand. In addition, one tool task was new and more complex than the other one, and specifically created for this study. Moreover, little research has been conducted on laterality in bonobos (with around ten studies e.g. Hopkins et

al., 1993; De Vleeschouwer et al., 1995; Christel et al., 1998; Harrison and Nystrom, 2008; Chapelain et al., 2011) and very few studies have discussed the effects of both posture and complexity of a tool task on hand preference (e.g. Westergaard et al., 1998b; Braccini et al., 2010). These different arguments make this research useful and compelling in spite of our small sample size. Indeed, even if in our study we analyzed “only” 8 individuals, the large number of independent data points suggests robust results.

#### *Contributions to the theory of task complexity*

We observed a significant increase in the strength of laterality according to task complexity, with a stronger hand preference in both tasks involving tool use. Moreover, four bonobos who were left-handed or with no preference in the tube task were right-handed for both the food extraction task with a tool and the maze task. Our results were in agreement with our hypotheses, based on the task complexity hypothesis (Fagot and Vauclair, 1991) and the tool use hypothesis (Frost, 1980; Kimura, 1979). In the course of evolution, complex behaviors might have increased and demanded greater time and energy costs (Mutha et al., 2013). It has been hypothesized that these costs may have been counterbalanced by the hemispheric specialization that emerged to accommodate increasing motor complexity during hominoid evolution (Mutha et al., 2013). There are probably other correlations with the hemispheric specialization like the evolution of the size of the brain in primates. The evolution of larger brain size in primates would be accompanied by diminished interhemispheric connectivity and augmented intrahemispheric connectivity that might accompany the emergence of cerebral lateralization (Rilling and Insel, 1999). Moreover, the increased motor complexity might lead to larger more gyrified brains, which would then lead to hemispheric specialization (e.g. Aboitiz et al, 1992; Rilling and Insel, 1999). Thus, complex behaviors such as tool use would be strongly lateralized and could be managed in a specific



hemisphere in bonobos such as the left hemisphere, as in humans (reviewed in Johnson-Frey, 2004) and chimpanzees (Hopkins et al., 2007b). The tool use tasks conducted in this study might demand higher and more costly cognitive abilities than the bimanual coordinated task, and as such, might promote the specialization of a cerebral hemisphere, particularly the left hemisphere, which controls the right hand. This could explain why our bonobos tended to preferentially use their right hand during our tool use tasks.

Concerning the tube task in the seated posture, we observed individual preference but no bias at the group level, which contrasts with results obtained for the same task in other species (e.g. chimpanzee: Hopkins, 1995; Hopkins et al., 2003; orangutans: Hopkins et al., 2003; baboon: Vauclair et al., 2005) which showed a bias in hand preference at the group level. One explanation might be our small sample size compared to other studies (e.g. Hopkins, 1995 with 110 Chimpanzees; Vauclair et al., 2005 with 104 Baboons). However, our results converged with a similar study on bonobos (Chapelain et al., 2011), which showed no bias in hand preference at the group level with a sample of 77 bonobos, but rather a pronounced individual hand preference. We have no explanation for this difference between species (Chapelain et al., 2011). Studies on hand preference for bonobos are scarce (e.g. Hopkins et al., 1993; De Vleeschouwer et al., 1995; Christel et al., 1998; Harrison and Nystrom, 2008; Chapelain et al., 2011) and the ecology of bonobos in their natural environment is poorly known (e.g. McGrew et al., 2007). More studies should be conducted to explore if bonobos use bimanual coordination more or less than other species do both in captivity and in the wild. Subsequently one may try to better understand the potential role of bimanual coordination from an evolutionary point of view.

Concerning the tool use tasks tested in this study, our results showed that the hand preference of bonobos was very strong, and even exclusive (i.e. individuals always used the same hand) for the maze task. Even if bonobos did not appear to use tools to obtain food in

401 their natural environment (Ingmanson, 1996), they successfully completed these tool use  
402 tasks. Chapelain (2010) studied tool use with 19 bonobos in a task (“termite fishing”) similar  
403 to our food extraction task and she observed 11 individuals that were lateralized (4 left-  
404 handed and 7 right-handed). Harrison and Nystrom (2008) examined hand preference for tool  
405 use actions that occurred in the daily activities with 12 bonobos. They observed seven  
406 lateralized individuals (3 left-handed, 4 right-handed). These results differ from ours since all  
407 our subjects were lateralized and we found one left-handed and six right-handed individuals  
408 for the food extraction task. This difference could be explained by the fact that during  
409 observations in previous studies, many parameters might have affected hand preference. In  
410 fact, in both studies, they quantified the hand preference without taking into account the  
411 potential influence of the body posture and the potential influence of the variability of the type  
412 of tool used in spite of their potential complexity differences. Regarding the findings in wild  
413 chimpanzees for “termite fishing”, a significant group level left bias was reported by  
414 Lonsdorf and Hopkins (2005) and recently by Bogart and collaborators (2012), who  
415 combined their data with those obtained by McGrew and Marchant (1992 and 1996) and  
416 Lonsdorf and Hopkins (2005) and based on this combined data set showed a left-hand bias  
417 for wild chimpanzees. In captivity, the same left bias was found by Fletcher and Weghorst  
418 (2005) but no bias was detected in the study by Hopkins and Rabinowitz (1997). In wild  
419 chimpanzees, most individuals were lateralized and showed an almost exclusive use of one  
420 hand (Nishida and Hiraiwa, 1982; McGrew and Marchant, 1992, 1999; Marchant and  
421 McGrew, 1996; Lonsdorf and Hopkins, 2005; Bogart et al., 2012), which was more consistent  
422 with our results (all individuals lateralized and 66 % exclusively lateralized). Finally, because  
423 “termite-fishing” behavior has never been observed in wild bonobos (McGrew et al., 2007),  
424 comparison between natural and artificial habitat is still not possible for this task.

The results of the maze task must be considered as preliminary because we had only a limited number of individuals to compare (seated posture  $N = 7$  and bipedal posture  $N = 5$ ). Yet, for both seated and bipedal postures, all individuals showed a strong hand preference with a tendency for the use of the right hand. Moreover, in this novel task we observed an exclusive hand preference, whereas only 66% were exclusively lateralized for the food extraction task with a tool. One explanation might be the task novelty. Indeed, novel tasks are known to elicit higher hand preferences than highly familiar tasks (Fagot and Vauclair, 1991). In fact, bonobos were supplied weekly with pipes and pierced logs requiring tools to extract various foods and thus all of them were already experienced in food extraction before our experiments. However, the maze task was novel for the bonobos we studied, which could explain the greater strength in hand preference compared with the familiar actions of food extraction. Moreover, we considered the maze task more complex (regarding the definitions of literature and the presence of more criteria) than the food extraction task, which could explain why we observed an exclusive hand preference for all individuals in the maze task.

Our results brought additional reflections on hand preference and supplied task complexity data on bonobos, specifically. Indeed, the maze task was interesting in terms of complexity because it required several cognitive processes such as using a tool and moving around obstacles to retrieve walnuts. Bonobos might be exclusively lateralized for this task because it demanded many abilities, which were managed by one hemisphere to optimize manipulation, and specifically by the left one linked to calculation abilities in humans (Popper et al., 1977). However, some authors inferred that there was likely to be right hemisphere specialization for trajectory perception in humans (Boulinguez et al., 2003). In addition, the right hemisphere seems to be used to process geometrical and global spatial cues in many species (humans: Wendt and Risberg, 1994; rats: Cowell et al., 1997; chicks: Tommasi and Vallortigara, 2004). Finally, some authors have suggested that preferred directions of arm

movements are independent of visual perception of spatial directions (Dounskaia et al., 2013) and that hemispheric specialization emerged to accommodate increasing motor complexity during evolution in humans (Mutha et al., 2013). In particular, some studies suggested an enhanced role for the left hemisphere during the learning of new sequences and skills and that this specialization emerged from a left hemisphere specialization for predictive control (the ability to plan and coordinate motor actions) (Mutha et al., 2012). This last idea is in agreement with our results but neurological studies in primates during different manipulation tasks would be needed to better understand the hemispheric specialization for the hand preference.

#### *Effect of posture on hand preference*

Our results did not indicate posture (seated or bipedal) as an influencing factor on the direction of hand preference, nor on the strength of lateralization during the three tasks. Thus, our hypotheses that a bipedal posture should increase the strength of manual preference and generate a directional bias for the right hand were not supported by our data. According to these hypotheses, individuals in a bipedal posture should have been more strongly lateralized and should have had a directional bias in favor of the right hand. Other studies in bonobos showed an increase in the strength of hand preference and a right hand preference for a reaching task, when individuals shifted from a quadrupedal posture to a bipedal one (Hopkins et al., 1993). On the contrary, De Vleeschouwer and colleagues (1995) showed, in a group of five bonobos, a preference for using the left hand while the animals shifted from a seated to a bipedal posture. However, most of these studies considered simple reaching tasks (Fagot and Vauclair, 1991). In our study we examined complex tasks for which individuals were already strongly lateralized in a seated posture, with a tendency to be right-handed. Thus, this could explain the lack of increase in right hand preference in a bipedal posture. However, as

previously discussed, because complexity differences elicited differences in direction and strength of hand preference, our results also suggest that the complexity of the task has a greater effect on hand preference than posture. This idea is supported by a study involving a bimanual coordination similar to the tube task (vertically hung tubes) and taking into account the body posture (crouched and upright), of capuchins (Spinozzi et al., 1998). The results showed that individuals had no significant difference, neither in the direction of hand preference, nor in the strength of lateralization between the two postures. These results are in accordance with ours in that capuchins and bonobos were already lateralized in crouched and seated posture (respectively for the two species) and their hand preference and strength of laterality did not change when they performed the task in an upright posture. This suggests both that a bimanual coordinated task (that requires a precise bimanual coordination while manipulating a tube) is a high level, complex task (Fagot and Vauclair, 1991) and that the bipedal posture might not provide any supplementary bias in laterality. However, the postural effect on bimanual coordination tasks should be studied in many other species of nonhuman primates to confirm this hypothesis.

Our study is the first one involving bipedal tool use in bonobos, and to date, only two studies have been conducted on bipedal tool use in non-human primates: one in chimpanzees (Braccini et al., 2010) and the other one in capuchins (Westergaard et al., 1998b). Our two tasks involving tool use showed no significant difference in direction of hand preference between a seated and a bipedal posture, in agreement with these two previous studies. However, these authors showed that chimpanzees and capuchins were more strongly lateralized when using tools in a bipedal posture, in contrast to our results showing that bonobos were strongly lateralized for both postures. This suggests three possible explanations: (1) our sample size was too small to show a significant effect of the posture, (2) the difference between laterality patterns found in other studies and our results could be due to

an effect of the task (as suggested above), and (3) bonobos may be less sensitive to the effect of bipedalism compared to chimpanzees. Indeed, bonobos seem more adept at maintaining balance in a bipedal posture and might therefore be less susceptible to the effect thereof on hand preference than other species. For instance, Braccini and colleagues (2010) noted that: “the bipedal posture appeared to be difficult for the chimpanzee”. These authors noticed that in a bipedal posture the legs of chimpanzees were shaking and some individuals did not want to perform the task in this posture. We did not observe this phenomenon during our observations in bonobos. However, one can note that two individuals did not use a bipedal posture for the maze task and one, the youngest subordinate male, never had access to mazes for the two postures. We could explain this observation by a problem of access opportunity related to the hierarchy. Indeed, the young subordinate male avoided the small cages that housed the mazes, most likely due to the higher amount of competition and his low ranking status. The second individual was the dominant female who only used the maze of the main cage which necessitated a seated posture. This could be explained by the fact that the dominant female often occupied the large cages in order to keep a close watch on group members. It would be interesting to conduct the maze task with isolated individuals, in the same cage, and/or by proposing only mazes necessitating bipedal posture in order to better understand the influence of comfort and hierarchy.

#### *“Bouts” versus “Frequency”*

Concerning the two different recording techniques (“Bouts” versus “Frequency”), our measurements for HI values were significantly and strongly correlated. Thus, using HI values based on frequency or bouts provided similar results in agreement with other studies (Bogart et al, 2012; Hopkins et al., 2001; Hopkins and Cantalupo, 2003; Hopkins et al., 2004; Hopkins et al., 2005b; Hopkins, 2013; Palmer, 2002; Palmer, 2003; Westergaard and Suomi,

1996). However, regarding the  $z$ -scores, we found differences between frequency and bout data for the tube task in bipedal posture. In this case, the number of data points had an effect on our estimate of laterality. Some authors suggested that the use of frequencies may influence laterality estimates and may thus introduce sampling biases (Hopkins and Cantalupo, 2003; McGrew and Marchant, 1997; Palmer 2002; Palmer 2003). However, in a recent article, Hopkins (2013) suggested that the use of the  $z$ -score with bout data might bias data towards the null hypothesis (no significant hand preference) because the  $z$ -score is sensitive to sample size and with bout data we have typically fewer numbers of right and left hand use for bouts than frequencies. Moreover, Hopkins (2013) suggested that there is no statistical justification for claims that the independence of data points introduces biases in the measurement of hand preference in nonhuman primates. Thus, as suggested by Hopkins (2013), it appears opportune to continue to record and report bouts and frequencies in behavioral asymmetry studies in order to resolve the disagreement about these two recording techniques.

#### *Contributions to human evolution: link between hand preference, tool use, locomotion and language*

Task complexity had a greater effect than posture on hand preference in our subjects. Our results have interesting implications for theories on the emergence of human lateralization in relation with tool use and bipedalism. Even if our data cannot by themselves explain the preponderance of right-handers in the human species, they support the tool use hypothesis (Frost, 1980; Kimura, 1979) which proposed that the preference for the right hand might have emerged in humans as an adaptation for complex tool use and manufacture.

Bonobos do not often use tools in the wild for feeding (Ingmanson, 1996), but in this study they used tools in this context with preferentially the right hand. Moreover, it seemed to

require little effort for them to remain in a bipedal posture. Kimura (1979) suggested that tool use and bipedalism are linked to the emergence of the lateralization of the brain and particularly to the strong right hand preference in humans. In accordance with this hypothesis several studies suggested that hand preference in great apes might be linked to posture and/or tool use (Olson et al., 1990; Hopkins, 1993; Hopkins et al., 2007b; Cantalupo et al., 2008; Braccini et al., 2010). However, the bonobos we studied here often preferentially used the right hand in seated posture and bipedal posture did not have a supplementary effect on hand preference during tool use tasks. Moreover, several studies showed a preference for the right hand when individuals manipulated in bipedal postures but not in other postures such as seated or triped ones (e.g., chimpanzee and orangutan: Hopkins, 1993; bonobo: Hopkins et al., 1993; macaque: Westergaard et al., 1998a; cercopithecus: Chapelain et al., 2006; capuchin: Westergaard et al., 1997). However, only one study directly examined bipedal tool use (Braccini et al., 2010) and did not report a preference for the right hand when chimpanzees used tools in this posture.

It is unlikely that bipedalism had such an important role in the elaboration of tool use and in the preponderance of the right hand preference in humans. Indeed, a recent neurological study conducted by Hashimoto and collaborators (2013) suggested “that adaptations underlying tool use evolved independently of those required for human bipedality”. Hand preference might be older than bipedalism in origin and rather linked to an arboreal lifestyle which requires complex body postures and manipulation. In fact, arboreal locomotion requires fine motor control and the anatomical specializations of the forelimbs of arboreal species are probably associated with a well-developed grasping ability (Fabre et al., 2013). In addition, there might have existed a link between the mode of locomotion and manipulative abilities, with a tendency for an exaptation of manipulation for arboreal species (Sustaita et al., 2013). In this context, the capacity to grasp has been posed as a “critical



adaptive innovation” for arboreal primates (Kivell et al., 2010) and a “key feature” of primate evolution (Ravosa and Dagosto, 2007). An arboreal lifestyle could have led to the elaboration of manual skills and tool use in primates, and hand preference could have emerged from arboreal ancestors coming down on the ground to use tools like some apes today.

Finally, the present work shows that the link between bipedalism and hand preference is far from being established and that the link between bipedalism and the capacity to use and manufacture tools is far from being obvious. It thus remains to be demonstrated and more studies are needed to explore the link between arboreal lifestyle and manual preference. In this framework, species such as gibbons, gorillas, orangutans and bonobos are of particular interest.

Another factor often invoked in the emergence of the strong hand preference for the right hand in humans is language. A predominance of right hand use has been reported in gestures occurring while humans are talking (Kimura, 1973a, 1973b), including communication between deaf people (Grossi et al., 1996). These asymmetrical gestures reflect the dominance of the left hemisphere for the perception and production of speech (Knecht et al., 2000). Moreover, studies in humans showed that brain regions implicated in the perception and production of speech (Broca’s area and Wernicke’s area) were also implicated with tool use behavior (Hopkins et al., 2007a). Some authors suggest that the neuronal substrates of tool use may have served as a preadaptation for the evolution of language and speech in modern humans (e.g. Bradshaw and Rogers, 1993; Greenfield, 1991). Hopkins and collaborators (2007a) reported asymmetries in chimpanzees in the homologues to Broca’s and Wernicke’s areas associated with hand preference for tool use. Consequently, these authors suggested that control of complex motor tool use action may have served as a preadaptation for the emergence of neural capacities required for language in humans (Hopkins et al., 2007a). Our results in bonobos showed a tendency to preferentially use the right hand for tool

use tasks, which reflects the dominance of the left hemisphere for these actions. Moreover, Kanzi, a bonobo, was thought to have rudimentary language comprehension skills of a 2.5 year-old child and also displayed impressive symbolic communicative skills (e.g. Savage-Rumbaugh et al., 1977; Savage-Rumbaugh et al., 1985; Savage-Rumbaugh et al., 1986; Savage-Rumbaugh, 1987). So, it appears interesting to apply in bonobos the same neurological study of Hopkins and collaborators (2007a) to confirm the link between tool use and language. This could bring us more information about the emergence of language regarding hypotheses that propose a relationship between language and hand preference (Corballis, 2003; Hewes, 1973; Vauclair, 2004), in that the emergence of right hand preference would be a pre-adaptation to language. However, more studies are needed to test the hypothesis that lateralization based on tool use preceded that for language (e.g. Steele and Uomini, 2009).

To conclude, although our sample size does not allow us to generalize at the group level, and even less at the population level, our large number of independent data points suggests robust results. It appears therefore essential to replicate our study in more groups of bonobos and to compare the maze task between different species of primates, including humans, in order to provide additional leads on the evolution of hand preference. Comparing this task among different primates would be of particular interest regarding the hypothesis proposing tool use as a selective pressure for hand preference (Frost 1980; Kimura 1979). It would also be essential to quantify hand preference in several primate species during natural activities varying in complexity in their natural habitat, on the ground, but also in trees.

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## References

- Aboitiz, F., Scheibel, A.B., Fisher, R.S., Zaidel, E., 1992. Fiber composition of the human corpus callosum. *Brain Res.* 598(1), 143-153.
- Altmann, J., 1974. Observational study of behavior: Sampling methods. *Behaviour* 49, 227-267.
- Annett, M., 1972. The distribution of manual asymmetry. *Brit. J. Psychol.* 63, 343-358.
- Annett, M., 1985. *Left, Right, Hand and Brain: The Right Shift Theory*. LEA Publishers, London.
- Beck, B.B., 1980. *Animal Tool Behavior: The Use and Manufacture of Tools by Animals*. Garland Press, New York.
- Bisazza, A., Cantalupo, C., Robins, A., Rogers, L., and Vallortigara, G., 1996. Right-pawedness in toads. *Nature* 379, 408.
- Boesch, C., 1991. Handedness in wild chimpanzees. *Int. J. Primatol.* 12, 541-558.
- Bogart, S.L., Pruetz, J.D., Ormiston, L.K., Russell, J.L., Meguerditchian, A., Hopkins, W.D., 2012. Termite fishing laterality in the Fongoli savanna chimpanzees (*Pan troglodytes*

649           *verus*): further evidence of a left hand preference. Am. J. Phys. Anthropol. 149(4),  
 650           591-598.

651   Boulinguez, P., Ferrois, M., Graumer, G., 2003. Hemispheric asymmetry for trajectory  
 652           perception. Cognitive Brain Res. 16(2), 219-225.

653   Braccini, S., Lambeth, S., Schapiro, S., Fitch, W.T., 2010. Bipedal tool use strengthens  
 654           chimpanzee hand preferences. J. Hum. Evol. 58, 234-241.

655   Bradshaw, J.L., 1991. Animal asymmetry and human heredity: Dextrality, tool use and  
 656           language in evolution-10 years after Walker (1980). Brit. J. Psychol. 82(1), 39-59.

657   Bradshaw, J.L., Rogers, L.J., 1993. The evolution of lateral asymmetries, language, tool use,  
 658           and intellect. Academic Press, San Diego, CA.

659   Broca, P., 1877. Perte de la parole. Ramollissement chronique et partiel du lobe antérieur  
 660           gauche du cerveau. Bull. Soc. Anthropol. 2, 235-237.

661   Byrne, R.W., Byrne, J.M., 1991. Hand preferences in the skilled gathering tasks of mountain  
 662           gorillas (*Gorilla gorilla berengei*). Cortex 27, 521-536.

663   Byrne, R.W., Corp, N., Byrne, J.M., 2001. Manual dexterity in the gorilla: bimanual and digit  
 664           role differentiation in a natural task. Anim. Cogn. 4, 347-361.

665   Calvin, W.H., 1983. A stone's throw and its launch window: Timing precision and its  
 666           implication for language and hominids brain. J. Theor. Biol. 104, 121-135.

667   Cantalupo, C., Freeman, H., Rodes, W., Hopkins, W.D., 2008. Handedness for tool use  
 668           correlated with cerebellar asymmetries in chimpanzees (*Pan troglodytes*). Behav.  
 669           Neurosci. 122, 191-198.

670   Cashmore, L., Uomini, N., Chapelain, A., 2008. The evolution of handedness in humans and  
 671           great apes: a review and current issues. J. Anthropol. Sci. 86, 7-35.

672   Chapelain, A., 2010. Hand preferences in bonobos (*Pan paniscus*) for a variety of actions:  
 673           spontaneous daily actions (non-social and social), bimanual coordination ("tube task"),

674 tool-use (“termite fishing”) and induced gestures (begging). Ph.D. Dissertation,  
675 Loughborough University, UK.

676 Chapelain, A., Bec, P., Blois-Heulin, C., 2006. Manual laterality in Campbell's monkeys  
677 (*Cercopithecus c. campbelli*) in spontaneous and experimental actions. Behav. Brain  
678 Res. 173, 237-245.

679 Chapelain, A., Hogervorst, E., Mbonzon, B., Hopkins, W.D., 2011. Hand Preferences for  
680 Bimanual Coordination in 77 Bonobos (*Pan paniscus*): Replication and Extension. Int.  
681 J. Primatol. 32, 491-510.

682 Christel, M.I., Kitzel, S., Niemitz, C., 1998. How precisely do bonobos (*Pan paniscus*) grasp  
683 small objects? Int. J. Primatol. 19, 165-194.

684 Colell, M., Segarra, M.D., Sabater, Pi.J., 1995. Hand preferences in chimpanzees (*Pan*  
685 *troglodytes*), bonobos (*Pan paniscus*), and orangutans (*Pongo pygmaeus*) in food-  
686 reaching and other daily activities. Int. J. Primatol. 16, 413-434.

687 Corballis, M.C., 1998. Cerebral asymmetry: motoring on. Trends Cogn. Sci. 2(4), 152-157.

688 Corballis, M.C., 2003. From mouth to hand: gesture, speech and the evolution of right-  
689 handedness. Behav. Brain Sci. 26, 199-260.

690 Cowell, P.E., Waters, N.S., Denenberg, V.H., 1997. The effects of early environment on the  
691 development of functional laterality in Morris maze performance. Laterality 2, 221-  
692 232.

693 Crow, T.J., 2004. Who forgot Paul Broca? The origin of language as test case for speciation  
694 theory. J. Linguistics 41, 1-24.

695 D’Août, K., Vereecke, E., Schoonaert, K., De Clercq, D., Van Elsacker, L., Aerts, P., 2004.  
696 Locomotion in bonobos (*Pan paniscus*): differences and similarities between bipedal  
697 and quadrupedal terrestrial walking, and a comparison with other locomotor modes. J.  
698 Anat. 204, 353-361.

699 De Vleeschouwer, K., Van Elsacker, L., Verheyen, R.F., 1995. Effect of posture on hand  
700 preferences during experimental food reaching in bonobos. *J. Comp. Psychol.* 109,  
701 203-207.

702 Doran, D., 1993. Comparative locomotor behavior of chimpanzees and bonobos: The  
703 influence of morphology on locomotion. *Am. J. Phys. Anthropol.* 91, 83-98.

704 Dounskaia, N., Wang, W., Sainburg, R.L., Przybyla, A., 2013. Preferred directions of arm  
705 movements are independent of visual perception of spatial directions. *Exp. Brain Res.*,  
706 1-12.

707 Ettlinger, G., 1961. Lateral preferences in monkeys. *Behaviour* 17, 275-287.

708 Ettlinger, G.F., 1988. Hand preference, ability and hemispheric specialization. How far are  
709 these factors related in the monkey? *Cortex* 24, 389-98.

710 Fabre, A.C., Cornette, R., Slater, G., Argot, C., Peigné, S., Goswami, A., Pouydebat, E., 2013.  
711 Getting a grip on the evolution of grasping in musteloid carnivorans: a three-  
712 dimensional analysis of forelimb shape. *J. Evol. Biol.* 26(7), 1521-1535.

713 Fagot, J., Vauclair, J., 1988a. Handedness and bimanual coordination in the lowland  
714 gorilla. *Brain Behav. Evolut.* 32, 89-95.

715 Fagot, J., Vauclair, J., 1988b. Handedness and manual specialization in the baboon.  
716 *Neuropsychologia* 26, 795-804.

717 Fagot, J., Vauclair, J., 1991. Manual laterality in nonhuman primates. A distinction between  
718 handedness and manual specialization. *Psychol. Bull.* 109, 76-89.

719 Fletcher, A.W., Weghorst, J.A., 2005. Laterality of hand function in naturalistically housed  
720 chimpanzees (*Pan troglodytes*). *Laterality* 10, 219-242

721 Frost, G.T., 1980. Tool behavior and the origins of laterality. *J. Hum. Evol.* 9, 447-459.

722 Gibson, K.R., Ingold, T. (Eds.), 1993. *Tools, Language and Cognition in Human Evolution*.  
723 Cambridge University Press, Cambridge.

724 Gold, K.C., 2002. Ladder use and clubbing by a bonobo (*Pan paniscus*) in Apenheul Primate  
725 Park. Zoo Biol. 21, 607-611.

726 Goodall, J., 1968. Behavior of free-living chimpanzees of the Gombe Stream area. Anim.  
727 Behav. Monographs 1, 163-311.

728 Greenfield, P.M., 1991. Language, tools and brain: The ontogeny and phylogeny of  
729 hierarchically organized sequential behavior. Behav. Brain Sci. 14, 531-595.

730 Grossi, G., Semenza, C., Corazza, S., Volterra V., 1996. Hemispheric specialization for sign  
731 language. Neuropsychologia, 34, 737-740.

732 Hashimoto, T., Ueno, K., Ogawa, A., Asamizuya, T., Suzuki, C., Cheng, K., Tanaka, M.,  
733 Taoka, M., Iwamura, Y., Suwa, G., Iriki, A., 2013. Hand before foot? Cortical  
734 somatotopy suggests manual dexterity is primitive and evolved independently of  
735 bipedalism. Phil. Trans. R. Soc. B. 368, 20120417.

736 Harrison, R.M., Nystrom, P., 2008. Handedness in captive bonobos (*Pan paniscus*). Folia  
737 Primatol. 79, 253-268.

738 Healey, J.M., Liederman, J., Geschwind, N., 1986. Handedness is not a unidimensional trait.  
739 Cortex 22, 33-53.

740 Hewes, G.W., 1973. Primate communication and the gestural origin of language. Curr.  
741 Anthropol. 14, 5-24.

742 Hohmann, G., Fruth, B., 2003. Culture in bonobos? Between-species and within species  
743 variation in behavior. Curr. Anthropol. 44, 563-571.

744 Hopkins, W.D., 1993. Posture and reaching in chimpanzees (*Pan troglodytes*) and orangutans  
745 (*Pongo pygmaeus*). J. Comp. Psychol. 107, 162-168.

746 Hopkins, W.D., 1995. Hand preferences for a coordinated bimanual task in 110 chimpanzees  
747 (*Pan troglodytes*): cross-sectional analysis. J. Comp. Psychol. 109, 291-297.

748 Hopkins, W.D., 1999. On the other hand: statistical issues in the assessment and interpretation  
 749 of hand preference data in non-human primates. *Int. J. Primatol.* 25, 1243-1265.  
 750 Hopkins, W.D., 2013. Independence of data points in the measurement of hand preferences in  
 751 primates: Statistical problem or urban myth? *Am. J. Phys. Anthropol.* 151(1), 151-157.  
 752 Hopkins, W.D., Bennett, A., Bales, S., Lee, S., Ward, J., 1993. Behavioral laterality in captive  
 753 bonobos (*Pan paniscus*). *J. Comp. Psychol.* 107, 403-410.  
 754 Hopkins, W.D., Cantalupo, C., 2003. Does variation in sample size explain individual  
 755 differences in hand preferences of chimpanzees (*Pan troglodytes*)? An empirical study  
 756 and reply to Palmer (2002). *Am. J. Phys. Anthropol.* 121, 378-381.  
 757 Hopkins, W.D., Cantalupo, C., Freeman, H., Russell, J., Kachin, M., Nelson, E., 2005b.  
 758 Chimpanzees are right-handed when recording bouts of hand use. *Laterality* 10, 121-  
 759 130.  
 760 Hopkins, W.D., de Waal, F.B., 1995. Behavioral laterality in captive bonobos (*Pan paniscus*):  
 761 Replication and extension. *Int. J. Primatol.* 16(3), 261-276.  
 762 Hopkins, W.D., Fernandez-Carriba, S., Wesley, M.J., Hostetter, A., Pilcher, D., Poss, S.,  
 763 2001. The use of bouts and frequencies in the evaluation of hand preferences for a  
 764 coordinated bimanual task in chimpanzees (*Pan troglodytes*): an empirical study  
 765 comparing two different indices of laterality. *J. Comp. Psychol.* 115, 294-299.  
 766 Hopkins, W.D., Leavens, D.A., 1998. Hand use and gestural communication in chimpanzees  
 767 (*Pan troglodytes*). *J. Comp. Psychol.* 112, 95-99.  
 768 Hopkins, W.D., Morris, R.D., 1993. Handedness in great apes. A review of findings. *Int. J.*  
 769 *Primatol.* 14, 1-25.  
 770 Hopkins, W.D., Rabinowitz, D.M., 1997. Manual specialization and tool use in captive  
 771 chimpanzees (*Pan troglodytes*): the effect of unimanual and bimanual strategies on  
 772 hand preference. *Laterality* 2, 267-277.



773 Hopkins, W.D., Russell, J.L., Cantalupo, C., 2007b. Neuroanatomical Correlates of  
 774 Handedness for Tool Use in Chimpanzees (*Pan troglodytes*): Implication for Theories  
 775 on the Evolution of Language. Psychol. Sci. 18 (11), 971-977.

776 Hopkins, W.D., Russell, J.L., Cantalupo, C., Freeman, H., Schapiro, S.J., 2005a. Factors  
 777 Influencing the Prevalence and Handedness for Throwing in Captive Chimpanzees  
 778 (*Pan troglodytes*). J.Comp. Psychol. 119(4), 363-370.

779 Hopkins, W.D., Russell, J.L., Lambeth, S., Schapiro, S.J., 2007a. Handedness and  
 780 neuroanatomical asymmetries in captive chimpanzees: a summary of 15 years of  
 781 research. Spec. Top. Primatol. 5, 146-181.

782 Hopkins, W.D., Stoinski, T.S., Lukas, K.E., Ross, S.R., Wesley, M.J., 2003. Comparative  
 783 assessment of handedness for a coordinated bimanual task in chimpanzees (*Pan*  
 784 *troglodytes*), gorillas (*Gorilla gorilla*) and orangutans (*Pongo pygmaeus*). J. Comp.  
 785 Psychol. 117, 302-308.

786 Hopkins, W.D., Wesley, M.J., Izard, M.K., Hook, M., Schapiro, S.J., 2004. Chimpanzees  
 787 (*Pan troglodytes*) are predominantly right-handed: replication in three populations of  
 788 apes. Behav. Neurosci. 118, 659-663.

789 Ingmanson, E.J., 1996. Tool-using behavior in wild *Pan paniscus*: social and ecological  
 790 considerations. In: Reaching into thought: the minds of the great apes (Ed. by Russon,  
 791 A.E., Bard, K. A. & Parker, S. T.). Cambridge University Press pp. 190-210.

792 Johnson-Frey, S.H., 2004. The neural bases of complex tool use in humans. Trends  
 793 Cogn. Sci. 8(2), 71-78.

794 Jordan, C., 1982. Object manipulation and tool-use in captive pygmy chimpanzee (*Pan*  
 795 *paniscus*). J. Hum. Evol. 11, 35-59.

796 Kano, T., 1982. The use of leafy twigs for rain cover by the pygmy chimpanzees of Wamba.  
 797 Primates 19, 187-193.

798 Kimura D., 1973a. Manual activity during speaking. I. Right-handers. *Neuropsychologia* 11,  
799 45-50.

800 Kimura D., 1973b. Manual activity during speaking. II. Left-handers. *Neuropsychologia* 11,  
801 45-50.

802 Kimura, D., 1979. Neuromotor mechanisms in the evolution of human communication. In:  
803 Steklis, H.D., Raleigh, M.J. (Eds.), *Neurobiology of social communication in*  
804 *primates: an evolutionary perspective*. Academic press, New York, pp. 197-220.

805 Kivell, T.L., Schmitt, D., Wunderlich, R.E., 2010. Hand and foot pressures in the aye-aye  
806 (*Daubentonia madagascariensis*) reveal novel biomechanical trade-offs required for  
807 walking on gracile digits. *J. Exp. Biol.* 213, 1549-1557.

808 Knecht, S., Deppe, M., Draeger, B., Bobe, L., Lohman, H., Ringelstein, E.B. et al., 2000.  
809 Language lateralization in healthy right-handers. *Brain* 123, 74-81.

810 Lonsdorf, E.V., Hopkins, W.D., 2005. Wild chimpanzees show population-level handedness  
811 for tool use. *Proc. Natl. Acad. Sci.* 102, 12634-12638.

812 MacNeilage, P.F., Rogers, L.J., Vallortigara, G., 2009. Origins of the Left & Right Brain. *Sci.*  
813 *Am.* 301 (1), 60-67.

814 MacNeilage, P.F., Studdert-Kennedy, M.G., Lindblom, B., 1987. Primate handedness  
815 reconsidered. *Behav. Brain Sci.* 10, 247-303.

816 Marchant, L.F., McGrew, W.C., 1991. Laterality of function in apes: a meta-analysis of  
817 methods. *J. Hum. Evol.* 21, 425-438.

818 Marchant, L.F., McGrew, W.C., 1996. Laterality of limb function in wild chimpanzees of  
819 Gombe national park: comprehensive study of spontaneous activities. *J. Hum. Evol.*  
820 30, 427-443.

821 Marchant, L.F., Steklis, H.D., 1986. Hand preference in a captive island group of  
822 chimpanzees (*Pan troglodytes*). *Am. J. Primatol.* 10(4), 301-313.

823 McGrew, W.C., Marchant, L.F., 1992. Chimpanzees, tools and termites: hand preference or  
824 handedness? *Curr. Anthropol.* 33, 114-119.

825 McGrew, W.C., Marchant, L.F., 1996. On which side of the apes? In: McGrew, W.C.,  
826 Marchant, L.F., Nishida, T. (Eds.), *Great Ape societies*. Cambridge: Cambridge  
827 University Press, pp. 255-272.

828 McGrew, W.C., Marchant, L.F., 1997. On the other hand: current issues in and metaanalysis  
829 of the behavioral laterality of hand function in non-human primates. *Yearb. Phys.*  
830 *Anthropol.* 40, 201-32.

831 McGrew, W.C., Marchant, L.F., 1999. Laterality of hand use pays off in foraging success for  
832 wild chimpanzees. *Primates* 40, 509-513.

833 McGrew, W.C., Marchant, L.F., Beuerlein, M.M., Vrancken, D., Fruth, B., Hohmann, G.,  
834 2007. Prospects for bonobo insectivory: Lui Kotal, Democratic Republic of Congo.  
835 *Int. J. Primatol.* 28, 1237-1252.

836 Meunier, H., Vauclair, J., 2007. Hand preferences on unimanual and bimanual tasks in white-  
837 faced capuchins (*Cebus capucinus*). *Am. J. Primatol.* 69, 1-6.

838 Morris, R.D., Hopkins, W.D., Bolser-Gilmore, L., 1993. Assessment of hand preference in  
839 two-language trained chimpanzees (*Pan troglodytes*): a multimethod analysis. *J. Clin.*  
840 *Exp. Neuropsych.* 15, 487-502.

841 Mutha, P.K., Haaland, K.Y., Sainburg, R.L., 2012. The effects of brain lateralization on motor  
842 control and adaptation. *J. Motor Behav.* 44(6), 455-69.

843 Mutha, P.K., Haaland, K.Y., Sainburg, R.L. 2013. Rethinking Motor Lateralization:  
844 Specialized but Complementary Mechanisms for Motor Control of Each Arm. *PloS*  
845 *one*, 8(3), e58582.

846 Nishida, T., Hiraiwa., M., 1982. Natural history of a tool-using behaviour by wild  
847 chimpanzees in feeding upon wood-boring ants. *J. Hum. Evol.* 11, 73-99.

848 Olson, D.A., Ellis, J.E., Nadler, R.D., 1990. Hand preferences in captive gorillas, orangutans,  
849 and gibbons. *Am. J. Primatol.* 20, 83-94.

850 O'Malley, R.C., McGrew, W.C., 2006. Hand preferences in captive orangutans (*Pongo*  
851 *pygmaeus*). *Primates* 47, 279-283.

852 Palmer, A.R., 2002. Chimpanzee right-handedness reconsidered: evaluating the evidence with  
853 funnel plots. *Am. J. Phys. Anthropol.* 118, 191-199.

854 Palmer, A.R., 2003. Reply to Hopkins and Cantalupo: chimpanzee right-handedness  
855 reconsidered- sampling issues and data presentation. *Am. J. Phys. Anthropol.* 121,  
856 382-384.

857 Papademetriou, E., Sheu, C.F., Michel, G.F., 2005. A meta-analysis of primate hand  
858 preferences, particularly for reaching. *J. Comp. Psychol.* 119, 33-48.

859 Perelle, I.B., Ehrman, L., 1994. An international study of human handedness: the data. *Behav.*  
860 *Genet.* 24, 217-227.

861 Pollick, A.S., de Waal, F.B.M., 2007. Ape gestures and language evolution. *P. Natl. Acad.*  
862 *Sci. USA* 104, 8184-8189.

863 Popper, K.R., Eccles, J.C., John, C., Carew, J., 1977. The self and its brain (Vol. 977). Berlin:  
864 Springer International, pp. 1-362.

865 Pouydebat, E., Reghem, E., Gorce, P., Bels, V., 2010. Influence of the task on hand  
866 preference: individual differences among gorillas (*Gorilla gorilla gorilla*). *Folia*  
867 *Primatol.* 81, 273-281.

868 Preston, B., 1998. Cognition and Tool Use. *Mind Lang.* 13(4), 513-547.

869 R Core Team, 2013. R: A language and environment for statistical computing. R Foundation  
870 for Statistical Computing, Vienna, Austria.

871 Ravosa, M.J., Dagosto, M., 2007. Primate origins: adaptations and evolution. In  
872       Developments in Primatology: Progress and Prospects (ed. R.H. Tuttle). Springer,  
873       New York pp. 1829.

874 Rilling, J.K., Insel, T.R., 1999. Differential expansion of neural projection systems in primate  
875       brain evolution. *Neuroreport* 10(7), 1453-1459.

876 Rizzolatti, G., Arbib, M. A., 1998. Language within our grasp. *Trends in Neurosci.* 21, 188-  
877       194.

878 Rogers, L.J., Kaplan, G., 1996. Hand preferences and other lateral biases in rehabilitated  
879       orang-utans (*Pongo pygmaeus*). *Anim. Behav.* 51, 13-25.

880 Savage-Rumbaugh, S., 1987. Communication, symbolic communication, and language: reply  
881       to Seidenberg and Petitto. *J. Exp. Psychol. Gen.* 116, 288-292.

882 Savage-Rumbaugh, S., McDonald, K., Sevcik, R.A., Hopkins, W.D., Rubert, E., 1986.  
883       Spontaneous symbol acquisition and communicative use by pygmy chimpanzees (*Pan*  
884       *paniscus*). *J. Exp. Psychol. Gen.* 115, 211-235.

885 Savage-Rumbaugh, E.S., Sevcik, R.A., Rumbaugh, D.M., Rubert, E., 1985. The capacity of  
886       animals to acquire language: do species differences have anything to say to us? *Philos.*  
887       *Trans. R. Soc. Lond. B. Biol. Sci.* 308, 177-185.

888 Savage-Rumbaugh, E.S., Wilkesron, B.J., Bakeman, R., 1977. Spontaneous gestural  
889       communication among conspecifics in the pygmy chimpanzee (*Pan paniscus*). In:  
890       Bourne (ed): *Progress in ape research*. New York Academic press, pp. 97-116.

891 Shafer, D.D., 1997. Hand preference behaviors shared by two groups of captive bonobos.  
892       *Primates* 38(3), 303-13.

893 Spinozzi, G., Castorina, M.G., Truppa, V., 1998. Hand preferences in unimanual and  
894       coordinated-bimanual tasks by tufted capuchin monkeys (*Cebus apella*). *J. Comp.*  
895       *Psychol.* 112, 183-191.

896 St. Amant, R., Horton, T. E., 2008. Revisiting the definition of animal tool use. *Anim. Behav.*  
897 75 (4), 1199-1208.

898 Steele, J., Uomini, N., 2009. Can the archeology of manual specialization tell us anything  
899 about language evolution? A survey of the state of play. *Camb. Archaeol. J.* 19, 97-  
900 110.

901 Sugiyama, Y., Fushimi, T., Sakura, O., Matsuzawa, T., 1993. Hand preference and tool use in  
902 wild chimpanzees. *Primates* 34, 151-159.

903 Sustaita, D., Pouydebat, E., Manzano, A., Abdala, V., Fritz Hertel, F., Herrel, A., 2013.  
904 Getting a grip on tetrapod grasping: form, function, and evolution. *Biol. Rev.* 88, 380-  
905 405.

906 Tommasi, L., Vallortigara, G., 2004. Hemispheric processing of landmark and geometric  
907 information in male and female domestic chicks (*Gallus gallus*). *Behav. Brain Res.*  
908 155, 85-96.

909 Toth, N., Schick, K.D., Savage-Rumbaugh, E.S., Sevcik, R.A. and Rumbaugh, D.M., 1993.  
910 Pan the tool-maker: investigations into the stone tool-making and toolusing  
911 capabilities of a bonobo (*Pan paniscus*). *J. Archaeol. Sci.* 20, 81-91.

912 Vallortigara, G., Rogers, L.J., 2005. Survival with an asymmetrical brain: Advantages and  
913 disadvantages of cerebral lateralization. *Behav. Brain Sci.* 28, 575-633.

914 Vaucclair, J., 2004. Lateralization of communicative signals in nonhuman primates and the  
915 hypothesis of the gestural origin of language. *Interaction studies* 5, 365-386.

916 Vaucclair, J., Meguerditchian, A., Hopkins, W.D., 2005. Hand preferences for unimanual and  
917 coordinated bimanual tasks in baboons (*Papio anubis*). *Cognitive Brain Res.* 25, 210-  
918 216.

919 Videan, E.N., McGrew, W.C., 2001. Are bonobos (*Pan paniscus*) really more bipedal than  
920 chimpanzees (*Pan troglodytes*)? *Am. J. Primatol.* 54, 233-239.

921 Videan, E.N., McGrew, W.C., 2002. Bipedality in Chimpanzee (*Pan troglodytes*) and Bonobo  
 922 (*Pan paniscus*): Testing Hypotheses on the Evolution of Bipedalism. Am. J. Phys.  
 923 Antropol. 118, 184-190.

924 Warren, J.M., 1980. Handedness and laterality in humans and other animals. Physiol. Psychol.  
 925 8, 351-9.

926 Wendt, P.E., Risberg, J., 1994. Cortical activation during visuospatial processing: relation  
 927 between hemispheric asymmetry of blood flow and performance. Brain Cognition 24,  
 928 87-103.

929 Westergaard, G.C., Kuhn, H.E., Lundquist, T.A.L., Suomi, S.J., 1997. Posture and reaching in  
 930 tufted capuchins (*Cebus apella*). Laterality 2, 65-74.

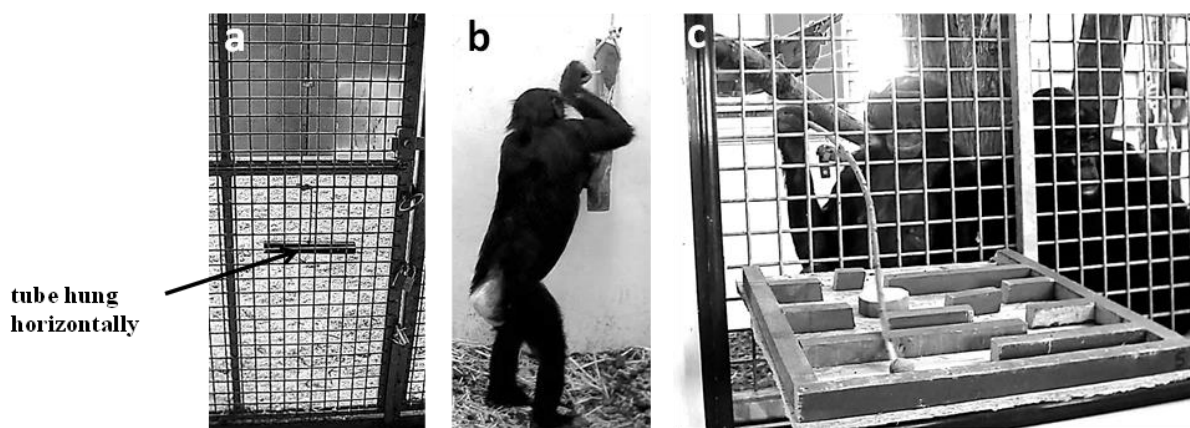
931 Westergaard, G.C., Kuhn, H.E., Suomi, S.J., 1998a. Bipedal posture and hand preference in  
 932 humans and other primates. J. Comp. Psychol. 112, 55-64.

933 Westergaard, G.C., Kuhn, H.E., Suomi, S.J., 1998b. Effects of Upright Posture on Hand  
 934 Preference for Reaching vs. the Use of Probing Tools by Tufted Capuchins (*Cebus*  
 935 *apella*). Am. J. Primatol. 44, 147-153.

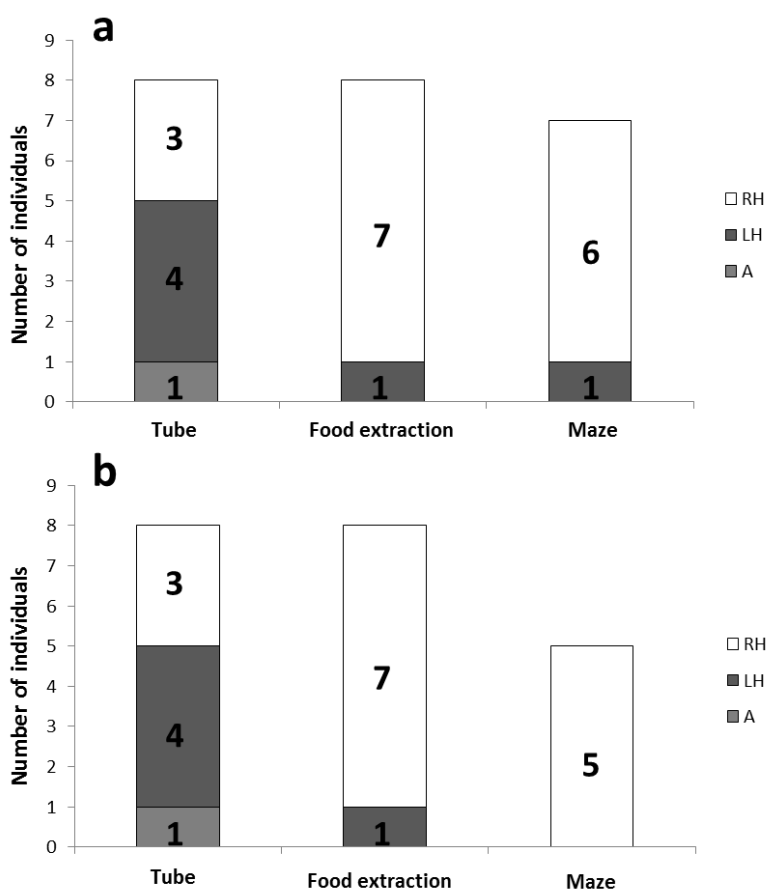
936 Westergaard, G.C., Suomi, S.J., 1996. Hand preference for a bimanual task in tufted  
 937 capuchins (*Cebus apella*) and rhesus macaques (*Macaca mulatta*). J. Comp. Psychol.  
 938 110, 406-411.

939 Wildman, D.E., Uddin, M., Liu, G., Grossman, L.I., Goodman, M., 2003. Implications of  
 940 natural selection in shaping 99.4% nonsynonymous DNA identity between humans  
 941 and chimpanzees: enlarging genus *Homo*. P. Natl. Acad. Sci. U.S.A. 100 (12), 7181-  
 942 7188.

943

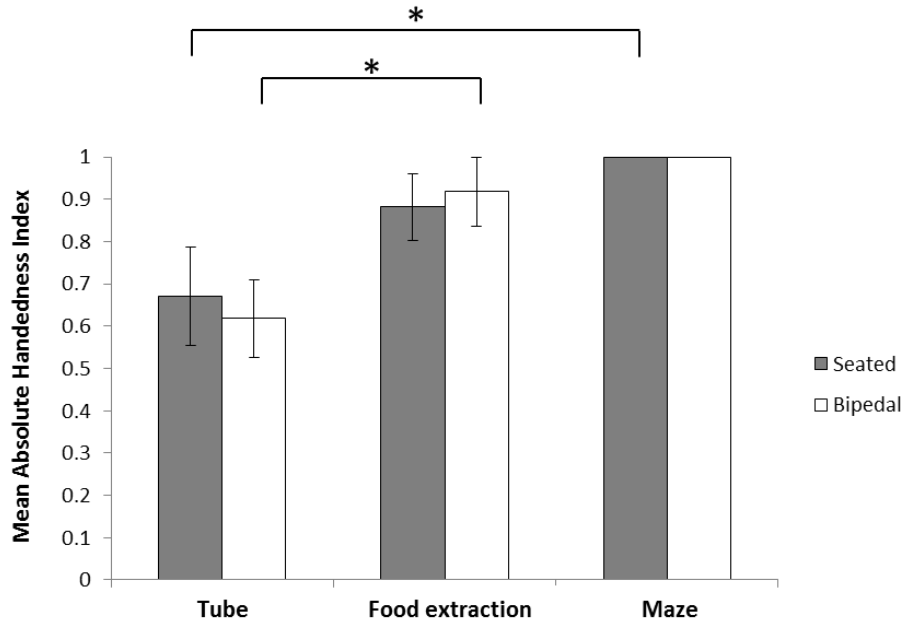


**Fig. 1.** Pictures of the three tasks accomplished by bonobos: the tube task, with a tube hung horizontally (a), the extracting food task with tool, in a bipedal posture (b) and the maze task with a tool, in a seated posture (c).



**Fig. 2.** Number of right-handed (RH); left-handed (LH), and ambiguously-handed (A) subjects by task and by posture: seated (a) and bipedal (b), with frequencies data.





**Fig. 3.** Mean absolute values of individual handedness index (ABS-HI), with frequencies, for the tube task (N = 8), the food extraction task (N = 8) and the maze task (N = 7 for the seated posture and N = 5 for the bipedal posture) depending on the posture. Bars = standard errors. \* =  $p < 0.05$ .

**Table 1.** Raw data and statistical results with frequencies, for the three tasks and the two postural conditions (seated and bipedal).

Individuals		Seated						Bipedal					
		Bout R/L	Freq R/L	HI	ABS-HI	Z	Category	Bout R/L	Freq R/L	HI	ABS-HI	Z	Category
Tube Task	Diwani	1/65	1/161	-0.988	0.988	-12.57	LH	1/26	4/57	-0.869	0.869	-6.786	LH
	Kirembo	51/2	132/4	0.941	0.941	10.976	RH	62/0	110/0	1	1	10.488	RH
	Daniela	46/8	185/24	0.77	0.77	11.137	RH	35/12	93/16	0.70	0.70	7.3753	RH
	Ukela	8/42	15/197	-0.858	0.858	-12.5	LH	3/7	4/22	-0.692	0.692	-3.5301	LH
	Khaya	6/49	12/156	-0.857	0.857	-11.11	LH	6/16	14/35	-0.428	0.428	-3	LH
	Lingala	18/38	35/91	-0.444	0.444	-4.9889	LH	26/29	42/64	-0.207	0.207	-2.1368	LH
	David	28/28	90/86	0.023	0.023	0.03015	A	7/3	12/5	0.412	0.412	1.6977	A
	Kelele	40/14	91/31	0.492	0.492	5.4321	RH	51/16	101/23	0.629	0.629	7.0046	RH
Means		55.5	163.88	-0.115	0.672			37.5	75.25	0.068	0.618		
Standard error		1.647	12.309	0.276	0.116			8.161	14.868	0.249	0.091		
Extracting Food Task	Diwani	70/0	129/0	1	1	11.3578	RH	23/0	25/0	1	1	5	RH
	Kirembo	68/0	86/0	1	1	9.2736	RH	27/0	33/0	1	1	5.7446	RH
	Daniela	54/13	69/28	0.423	0.423	4.1629	RH	37/18	59/22	0.457	0.457	4.1111	RH
	Ukela	0/38	3/67	-0.914	0.914	-7.6495	LH	0/12	0/20	-1	1	-4.4721	LH
	Khaya	57/0	101/0	1	1	10.05	RH	60/0	172/0	1	1	13.115	RH
	Lingala	70/0	163/0	1	1	12.767	RH	60/0	155/0	1	1	12.45	RH
	David	70/0	112/0	1	1	10.583	RH	21/0	26/0	1	1	5.099	RH
	Kelele	44/17	54/23	0.403	0.403	3.5328	RH	22/0	22/0	1	1	4.6904	RH
Means		62.625	104.38	0.614	0.842			35	66.75	0.719	0.932		
Standard error		3.677	10.107	0.238	0.094			6.322	22.449	0.249	0.068		
Maze Task	Diwani		35/0	1	1	5.916	RH		9/0	1	1	3	RH
	Kirembo		30/0	1	1	5.477	RH		33/0	1	1	5.745	RH
	Daniela		33/0	1	1	5.744	RH		26/0	1	1	5.099	RH
	Ukela		0/23	-1	1	-4.796	LH		0				
	Khaya		23/0	1	1	4.796	RH		21/0	1	1	4.582	RH
	Lingala		30/0	1	1	5.477	RH		33/0	1	1	5.744	RH
	David		18/0	1	1	4.242	RH		0				
	Means		27.429	0.714	1				20.333	1	1		
Standard error			2.338	0.285	0				4.467	0	0		

R = Number of right-hand responses. L = Number of left-hand responses. HI = Handedness Index. ABS-HI = Absolute value of HI. z = z-scores. Category (based on the z-scores): LH = left-handed individuals, RH = right-handed individuals, A = ambiguously-handed individuals and in italics the differences based on bout data.