Population-level right handedness for a coordinated bimanual task in naturalistic housed chimpanzees: replication and extension in 114 animals from Zambia and Spain

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ABSTRACT

Recently many studies have been conducted on manual laterality in chimpanzees. Nevertheless, whether nonhuman primates exhibit population-level handedness remains a topic of considerable debate. One of the behaviors studied has been bimanual coordinated actions. Although recent studies have highlighted that captive chimpanzees show handedness at population level for these tasks, some authors have questioned the validity and consistency of these results. The first reason has been the humanization of the samples. The second one has been that the results refer to animals in American biomedical centers and the studies were conducted by the same team (WD Hopkins and colleagues). This paper aims to assess the laterality in bimanual coordination (tube task) activities in animals housed in an intermediate environment (Chimfunshi Sanctuary, Zambia). This has been conducted by replicating previous studies on similar samples (Mona Foundation, Spain), and then by extending the results to chimpanzees housed in intermediate settings. Individuals were evaluated through four experimental sessions (tests). Results indicated that 86% of the Chimfunshi sample was lateralized (48% RH, 38% LH). Furthermore, the sample showed population-level right handedness in the mean handedness index, in test 1, test 2 and the first half of the study (test 1+2). Rearing experience did not have an influence on hand preference. Taken together, the two sample (intermediate settings: Chimfunshi and Mona) results indicate a clear right handedness. In conclusion, this replication and extension shows that: (1) chimpanzees in intermediate environments (naturalistic housed) are right-handed at population-level, (2) the results are consistent with those obtained by Hopkins in captive settings and, (3) the humanization of the samples does not affect manual laterality, (4) the direction of hand preference differs between sexes: most males are left-handed whereas most females are

right-handed, and (5) these results reinforce the fact that the complexity of the task plays a dominant role in the expression of hand laterality among chimpanzees.

Keywords: chimpanzee handedness; bimanual coordination; hand preferences; replication; intermediate environments.

INTRODUCTION

The study of hand laterality in non-human primates offers a major background to understand human evolution for brain hemispheric specialization, asymmetries of the motor cortex, language and hand dominance at population level [Bradshaw and Rogers 1993].

Unlike humans, non-human primates have evidenced to be a very heterogeneous biological order regarding manual asymmetries, as studies during the last 25 years have shown. Globally, these studies yield wide variability concerning the methodology used, the tasks observed, and the environments in which the work was carried out. This has caused strong limitations for making reliable comparisons both at inter and intra-specific level [McGrew and Marchant 1997]: at the individual level, hand preferences seem to be consistent in all taxa from prosimians to great apes. At population level, evidence focuses in complex tasks; that is, those requiring coordinated bimanual and sequential actions, and also some other behaviours that need for bipedal posture and postural readjustment, among others [Blois-Heulin et al. 2006; Braccini et al. 2010; Colell et al. 1995a; Colell et al. 1995b; Hopkins 1993; Hopkins et al. 1993; Hopkins et al. 2003b; Hopkins and Pearson 2000; Hopkins and Rabinowitz 1997; Vauclair et al. 2005; Wesley et al. 2002; Westergaard and Suomi 1996; Zhao et al. 2010]. This heterogeneous pattern is even more stressed on comparing wild and captive chimpanzees. Explanations of this heterogeneity are still in debate, and they represent one of the major keys around which the subject on manual laterality in these species turns.

Several researchers have suggested major factors such as the human environment. In

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this sense, some authors [McGrew and Marchant 1997; Palmer 2003; Warren 1980] claim that evidences of right-handedness at population level may be related to the humanized or enculturated environments where subjects grew up. However, other researchers as Hopkins and Cantalupo [2005] support that the use of different methodologies (experimental *versus* observational), and protocols of recording and analyzing among the studies may also cause this disparity of results . Finally, other authors [Fagot and Vauclair 1991; Hopkins and Cantalupo 2005; Schweitzer et al. 2007a] support the importance of variables inherent to the task, such as the morphology of gripping, the posture, bimanual coordination *versus* unimanual tasks, etc.

~~prensión, la postura, la coordinación bimanual versus tareas unimanuales), como otras explicaciones.~~

The tube task is one of the tasks more used in experimental studies with non-wild animals. It was proposed by Hopkins [1995], and it consists of extracting the food from a tube through bimanual coordinated actions, where one hand acquires the dominant role and the other subordinates. For this task, most of the studies done over the years have shown clear evidence of right asymmetries at the population level [Hopkins and Bard 2000; Hopkins and Cantalupo 2003; Hopkins and Pearson 2000; Hopkins et al. 2004; Wesley et al. 2002]. However, some authors question the validity and consistency of these results [Annett 2006; Crow 2005; McGrew and Marchant 1997; Palmer 2002; Palmer 2003], particularly because of the possible humanization of the samples and

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their origin, since all the evidence was obtained from animals belonging to American research centres, and also it was also obtained by the same research team (Hopkins and colleagues).

Therefore, in our view, it is important to replicate the same experiments with other types of chimpanzees, those sheltered in naturalistic settings, in order to check the validity and consistency of the right-handedness in captive samples. Despite the fact that naturalistically housed chimpanzees are also held in captivity, they are sheltered in environments that try to emulate the conditions of chimpanzees in the wild, and allow the animals to develop specific behaviours. Therefore, studies with naturalistically housed chimpanzees increase the ecological validity of previous results.

This study aims to assess the laterality in bimanual coordination (tube task) in animals housed in an intermediate environment (Chimfunshi Sanctuary, Zambia), by replicating previous studies done on similar samples (Mona Foundation, Spain), in order to extend the results to chimpanzees housed in these settings.

METHODS

Project structure

This study replicates the first experimental test of the tube task carried out at Mona Foundation (MF) in 2007 [Llorente et al. 2009]. This replica has later been performed at Chimfunshi Wildlife Orphanage (CWO), following the same methodology.

Subjects and housing

Chimfunshi Wildlife Orphanage

120 Chimpanzees (*Pan troglodytes*) distributed in seven captive groups were studied at the Chimfunshi Wildlife Orphanage. Their ages ranged between 0 and more than 33 years old. Table 1 shows additional information about age classes, sex and the rearing history of each group. Most of the chimpanzees were used for trading (smuggling, circuses and shows) before being sheltered in this Centre.

The groups were living in different enclosures, which were distributed between two main areas: the Project Area and the Orphanage, which were physically separated from one another. In the Project Area, groups 1, 2, 3 and 4 were housed in large outdoors compounds (enclosures 1, 2, 3 and 4, respectively) and they had attached indoor quarters in which the animals were placed daily during feeding time (from 11:30 am to 13:30 pm). These indoors handling facilities consisted of different rooms of similar sizes and layouts. Specifically, the average size of the rooms was 6x4 meters. Outdoor enclosures were carved out of the forest and floodplains along the Upper Kafue River, with enough thick jungle and fruit groves and open grasslands to allow the chimpanzees to roam as if in the wild. Enclosure 1, 2 and 3 measured 150 ha, while enclosure 4

141 measured 80 ha. In all the studied groups, access to the outside enclosure was blocked
142 during data collection.

143 The Orphanage was home to the other 3 groups of chimpanzees (groups 5, 6, 7), which
144 could not be relocated. In those cases, each group lived in different conditions. Some of
145 the individuals in group 5 remained all day long inside the indoor enclosures for
146 security reasons, and the same happened with the enclosed chimpanzees in group 6. In
147 contrast, group 7 spent the night and feeding time in the indoor facilities, but during the
148 rest of the day, they enjoyed a 5 ha enclosure.

149 Mona Foundation (MF) Sanctuary

150 Three captive groups of chimpanzees (*Pan troglodytes*) were studied at Mona
151 Foundation Primate Rescue Center (Girona, Spain) [Llorente et al. 2009; Mosquera et
152 al. 2007]. They were between 4 and 51 years old. Animals were in their social groups
153 during the tests sessions. The first group (A) was composed of 4 males; the second
154 group (B) was composed of 4 males and 3 females, and third group (C) was composed
155 of 3 males. Table 2 shows individual information, characteristics and their background
156 before arriving at Mona. The subjects were housed in a naturalistic outdoor enclosure of
157 5,640m^2, with wooden structures and natural ground with Mediterranean and riverside
158 vegetation. Furthermore, the Center has two socialization enclosures of each measuring
159 25 m^2, connected to a 140m^2 primate pavilion.

160

161 **Procedure**

162 We used the same procedure to evaluate hand laterality in complex bimanual tasks
163 as that applied in the previous study in MF [Llorente et al. 2009]. Evaluation was based

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on the tube task proposed by Hopkins [1995] as a bimanual coordinated task sensitive to determine hand motor bias. For the tube task we used cylindrical rubber hoses with 25 to 25.5 cm in length and with a diameter 2,5 cm instead of rigid tubes**.** Therefore, we call this experiment "hose task". In MF, the first author (MLl) carried out all the observations and the experiments. This study was conducted from January 2007 to April 2007. In CWO, LP and LC carried out all the observations and experiments. That study was conducted between October and November 2008.

The usefulness of the tube task as a manual laterality indicator has been proven by Hopkins in several studies with captive chimpanzees [Hopkins 2006; Hopkins et al. 2004], and it has also been used with other primate species as *Cebus apella* [Lilak and Phillips 2008], *Cebus capucinus* [Meunier and Vauclair 2007] *Cercopithecus neglectus* [Schweitzer et al. 2007b], *Papio anubis* [Vauclair et al. 2005], *Pan paniscus* [Chapelain and Hogervorst 2009] and other ape species [Hopkins et al. 2003a]. Hoses were filled with food, thus preventing its extraction with the tongue or by hitting it. In MF the food was honey, peanuts, muesli and seeds. In CWO the food was peanut butter, honey, peanuts, banana, apple, chow and nshima. Animals had to remove the food with their fingers or by using tools such as sticks, branches or canes to facilitate extraction. We used a focal animal sampling [Altmann 1974]; the session continued until the individual lost interest or left the hose for one minute. Each individual was tested four times and test sessions were separated by a minimum of two days between sessions. Each animal needed to obtain a minimum of 50 responses. Each test was valid if the animal obtained a minimum of six responses. The hand used to extract the food was recorded each time the subject inserted its finger/tool, removed the food, and placed its finger/tool in its mouth. We also recorded the finger used to remove the food (thumb, index, middle,

ring, little).

Procedural considerations

Some authors have criticized recording behaviors as events, since it may cause problems in the data independence [McGrew and Marchant 1997]. According to this criticism, recording repetitive motor actions of the subjects could increase the sample size and would thus increase the probability of detecting significant asymmetries in the hand use at individual level. To date, some authors have found effects of the methodology used [Chapelain and Hogervorst 2009]. However, other authors have failed to detect significant differences in recording manual behaviors as events or bouts, both being sensitive to detect lateral biases [Hopkins 2006; Hopkins et al. 2004; Meguerditchian et al. 2010]. We have chosen to record the data as events; that is, considering the total frequency of manual use. In this way, we can replicate and compare our present results and our previous results [Llorente et al. 2009] with most other experimental studies, since they follow this same procedure.

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Data analysis

We used a similar methodology to that carried out by other authors for similar experiments [Hopkins et al. 2004]. Data analyses were performed at the individual and at the group level. At the individual level, we first calculated binomial tests on data for each individual to evaluate if they were significantly lateralized. Secondly, a handedness index (HI) suggested by Hopkins [1995] was calculated for each subject to quantify individual laterality bias. This measure was estimated using the formula

R-L/R+L (R=number of times right hand was used; L=number of times left hand was used). Positive values show right hand bias, and negative values show left hand bias.

For the hose task, we calculated an individual HI adding the total frequencies obtained throughout 4 tests sessions mixed in HOSE (SUM-HI), following the same formula for HI. We used absolute values of HI (ABS-HI) as a reflection of the strength of hand preference, independent of the direction. We calculated a mean HI averaging the HI values (MHI) of 4 hose task tests. To evaluate population level handedness we used a one sample t-test based on individuals HI values and Z-scores. We used non parametric tests (Chi square) to estimate the proportion of right, left or non preferent individuals. We used the Spearman correlation test to evaluate the consistency of hand preference throughout test sessions in the hose task. Wilcoxon tests assessed differences in direction and strength of hand preferences among tasks. We used U-Mann Whitney and Kuskal Wallis to test sample variables (sex, place of birth, group or age class).

All the field protocols, data collection procedures and data analyses were conducted in accordance with all the principles of ethical treatment established by ASAB, the Spanish and Catalonian governments, the Zambian government and the internal rules and guidelines of the Mona Foundation and Chimfunshi Wildlife Orphanage.

RESULTS

Replication: Chimfunshi Wildlife Orphange

Out of the 120 individuals in the sample, 100 obtained the minimum of responses required (n=50). Globally, there were a total of 14,854 manual actions, of which 55.48% (n=8,241) were performed by the right hand and 44.52% (n=6,613) by the left hand. Based on binomial tests, 14 individuals were non preferent, and 86 are lateralized

for this task: 48 are right-handed, and 38 left-handed. The average for SUMHI (M-SUMHI) is 0.107 (SE = 0.064); therefore, subjects expressed a right-hand bias. The MHI value is 0.122 (SE = 0.063). SUMHI and MHI values correlate highly (Rs=0.991; p= 0.000), thus showing that both kinds of handedness characterization were consistent among subjects. Hence we used SUMHI values to minimize type I error. The average for ABSHI for all subjects was 0.573 (SE = 0.030). The ABSHI values among right- (0.676) and left-handed (0.594) subjects were similar (U = 714.500; p=0.086). There were differences between the number of lateralized and non lateralized subjects (χ^2 (1, n=100)=51.840, P=0.000), but there were no differences between the number of right- and left-handed subjects (χ^2 (1, n=86)=1.163, P=0.281).

Regarding the variables associated with the sample, SUMHI showed differences for sex, since females were more right-handed than males (U = 955.000; p=0.047). However, none influence in rearing experience (U=1198.000; p= 0.889), group (Kruskal=2.582; p=0.859) or age class (Kruskal=0.162; p=0.922) were found in the direction of lateralization (SUMHI). Also, we did not find differences in the strength of lateralization in sex (U=1194.500; p=0.743), rearing (U=1114.500; p=0.470), group (Kruskal=2.014; p=0.918) or age class (Kruskal=2.425; p=0.298).

According to the extraction technique, the subjects removed the food 95.66% using their fingers and 4.34% using tools. They performed most of the actions with the index finger (D2; 89.02%), followed by the middle finger (D3; 3.77%), thumb (D1; 1.50%), little finger (D5; 1.31%) and ring finger (D4; 0.07%). We found an effect of extraction technique on the hand (D1; D2; D3; D4; D5; TOOL; χ^2 =217.022, P=0.000). On one hand, the analyses of adjusted residuals showed certain correlations between subjects performing extractions with the index finger (AR=9.3) and preferentially with the right

hand. On the other hand, extractions with the little finger (AR=13.2) and tools (AR=5.7) were correlated with the left hand. There was no difference between digital and tool extraction techniques in direction (HI Finger = 0.103; HI Tool= 0.066; Z= -0.048, p=0.654) or strength (ABSHI Finger = 0.577; ABSHI Tool = 0.588; Z= -0.131, p=0.896) of hand preference.

Four tests showed a high correlation, indicating that preferences were stable and consistent throughout sessions at the individual level (Table 3). The correlation between the values of HI for the first half of the experiment (test 1+2) and the second half of the experiment (test 3+4) was also significant (Rs=0.770; p=0.000). There is a trend for the HI values (direction) to decrease with the experimental tests (Table 4), but these differences are not significant (Friedman Anova= 4.887; p=0.180). Strength (ABSHI) tends to increase from test 1 to test 3, decreasing the value at test 4. However, again the differences are not significant (Friedman Anova=6.486; p=0.090).

Regarding hand preferences at population level, one sample t-test does not point to handedness for the SUMHI value (t (99)=1.678: p=0.097), and we found a borderline right-hand preference for the MHI value (t (99)=1.943: p=0.055). Additionally, we carried out another~~De manera adicional, hemos llevado a cabo otro~~ one sample t test with the ~~con los valores de~~ z-score values, and results were consistent with that obtained for~~ siendo consistente con los obtenidos a través del~~ HI (t (99)=1.621: p=0.108).~~-~~ The evaluation of the population preferences in both parts of the study yielded right asymmetry for the first part (test 1+test2) (t (99)=2.480: p=0.015), but not for the second part (test 3+test4)

(t (99)=1.104: p=0.272) of the experiment. The estimation of the population preferences for each test indicates that test 1 (t (99)= 2.455: p=0.016) and test 2 (t (99)=2.270:

p=0.025) show clear right population asymmetry; test 3 (t (99)=1.795: p=0.076) shows borderline significant right asymmetry; and test 4 (t (99)=0.292: p=0.771) do not show any kind of significant asymmetries at population level.

Regarding the variables associated to the sample at population level, there is a right asymmetry for sex females (t (53)=2.582: p=0.013), but not for sex males (t (45)= -0.255 : p=0.800). The rest of the variables, human reared (t (57)=1.251: p=0.216), mother reared (t (41)=1.104: p=0.276), juveniles (t (35)=0.689: p=0.495), adolescents (t (27)=1.582: p=0.125), adults (t (35)=0.786: p=0.437) and Group 1 to 7 have not shown any population asymmetry, as occur with the actions performed by fingers

(t (99)=1.606: p=0.111) and tools (t (19)=0.413: p=0.684).

Extension: Chimfunshi Wildlife Orphanage + Mona Foundation

In order to evaluate the global pattern of hand lateralization of chimpanzees housed in naturalistic-intermediate environments, we estimate both HI and ABSHI from the Mona Foundation (MF) and Chimfunshi Orphanage (CWO) as a whole. We followed the same methodology used by Hopkins and colleagues [Hopkins 2006; Hopkins et al. 2004] at the USA samples.

The total sample of MF and CWO includes by 114 naturalistic housed chimpanzees (NCh). The mean value for HI is 0.137, so the trend is towards right preferences. There are not significant differences between both colonies (U=532.000; p=0.147). The mean value for the absolute HI (ABS-HI) is 0.603. Here the MF sample showed higher strength than the Zambia sample (U= 359.000; p= 0.003).

At population level, the one sample t-test detected different significant tests (Table 5). Both SUMHI (t (113)=2.220: p=0.028) and MHI (t (113)=2.611: p=0.010) showed clear

right asymmetry. Results of~~Los resultados del~~ the one sample t test with the~~con los valores de~~ z-score values also indicated a right preference at population level ~~también han indicado una preferencia diestra a nivel poblacional~~ (t (113)=2.246: p=0.027). Based on binomial tests, 14 individuals were non preferent, and 100 are lateralized for this task: 58 are right-handed, and 42 left-handed. There were differences between the number of lateralized and non lateralized subjects (χ^2 (1, n=114)=64,877, P=0.000), but there were no differences between the number of right- and left-handed subjects (χ^2 (1, n=100)=2,560, P=0.110).

SUMHI also revealed right population asymmetry for the first part of the study (test 1+2; [t (113)=3.059: p=0.003]) and for the finger use (t (112)=2.070: p=0.041).

DISCUSSION

At Chimfunshi Wildlife Orphanage subjects expressed a right-hand bias. Right and left handedness was consistent among subjects, and the strength of hand preference did not vary between groups. There were differences between the number of lateralized and non lateralized subjects, but there were no differences between the number of right-handed and left-handed subjects.

When taking into consideration data from of Chimfunshi Wildlife Orphanage and Mona Foundation, the samples are right lateralized at individual and population level, without differences between both colonies. However, the MF sample showed higher strength than the Zambia sample, which may be an effect of the bigger sample of the latter.

A similar effect may occur at CWO where sex seems to be the only associated variable

that shows differences both at individual and population level, since females were more right-handed than males. At MF this difference has not been observed. CWO has a sample of 54 females out of 100 individuals, while MF has 3 females out of 14 individuals. This fact makes it difficult to validate the possible effect of the sex variable in MF.

However, the fact that CWO females are more right-handed than males is an outstanding result, since most of studies did not find any difference when evaluating the sex variable. Only the work of Corp and Byrne [2004] on a wild population of chimpanzees at Mahale got similar results at studying bimanual coordinated conducts linked to fruit processing. In that study, males also tended to be more left-handed, while females were clearly more right-handed. In our study at CWO this result is even at population level. Although few studies observe the same pattern, our result is very suggestive for its similarity to humans, since women show higher preference in using the right hand than men [Annett 1985; Annett 2002; Medland et al. 2004]. Medland and colleagues [2004] suggest that this pattern in humans may be conditioned by biological (particularly genetic and hormonal) factors. Therefore, the pattern found in our study may reflect the existence of one common ancestor between chimpanzees and humans regarding sexual differences in hand laterality. Furthermore, some authors support an evolutive continuity for the relation between both variables: sex and hand preference. According to them, this relation may have a very old phylogeny, since some species of prosimians show similar patterns [Ward et al. 1990].

[Ward et al. 1990].

[Ward et al. 1990].

~~las diferencias sexuales en lateralidad manual. De hecho, algunos autores sugieren una continuidad evolutiva en la relación entre las variable sexo y la preferencia manual. Según ellos, ésta podría tener una filogénesis muy antigua ya que en algunas especies de prosimios se han encontrado patrones similares~~ [Ward et al. 1990].

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None of the features involved in the extraction technique were significant at population level at both CWO and MF. Despite this, subjects removed the food 95.66% with their fingers (mostly the index finger) and 4.34% with tools. According to our results, subjects performing extractions with the index finger preferentially did it with the right hand, and extractions with the little finger and with tools, did it with the left hand. Concerning the former, our results are consistent with other studies on chimpanzees [Hopkins 1995] and other primates [Schweitzer et al. 2007b]. It looks like the use of the index finger as an extracting technique seems to encourage the use of the right hand.

Also, there is a relation between the use of the little finger, tools and the left hand. No explanation has been proposed yet. However, it seems that hand laterality is affected by the distal motions of fingers and hands when performing bimanual complementary tasks –where hands differ in their roles. According to Brinkman and Kuypers [1973] distal movements require a frequent use of the contra-lateral brain hemisphere, which may explain our results.

The statistical test used to observe different conducts between human rearing chimpanzees and mother rearing chimpanzees have not revealed significant differences both in direction and degree of preference. Thus the original environment and context where these individuals came from had no specific effect on their hand preference patterns. This conclusion has been also reached in other studies where the sample was

large and varied enough to test this variable [Hopkins 2006]. These results were already shown in an earlier study [Mosquera et al. 2007], where the observation of hand laterality in the MF highly humanized chimpanzees at spontaneous unimanual tasks offered similar results than the wild samples. Unlike that study, here it was possible to evaluate directly the original environment into the MF group. So, results seem to point that the environment can not explain the disparity of results regarding the current pattern of hand preference in non-human primates. If neither the environmental hypothesis nor humanization can explain the results, maybe the complexity of the task does explain it, as suggested by other authors [Fagot and Vauclair 1991; Lilak and Phillips 2008; Riba et al. 2009; Schweitzer et al. 2007b; Vauclair et al. 2005]. Actually, studies focused in tasks requiring bimanual coordination, use of tools and other psychomotor demands have revealed higher degrees and intensities of manual preferences, besides the environment in which they were valued and the humanization degree of the samples.

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Finally, some authors suggested that the functional and neuroanatomical asymmetries are derived features exclusive of ~~De hecho, los estudios focalizados en conductas que requieren una coordinación bimanual, utilización de instrumentos u otro tipo de demanda psicomotora han revelado mayores grados e intensidades de preferencia manual independientemente del ambiente en el que han sido evaluados e, independientemente del grado de "humanización" de las muestras.~~

~~En segundo lugar, a nivel funcional, y tal como sugieren otros autores [Hopkins 2006], pensamos que la tendencia a population right-handedness podría tener unas raíces evolutivas anteriores al punto de divergencia entre los linages *Pan* y *Homo* (6-7 million~~

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