



# Short and long-term temporal consistency of hand preference in sanctuary chimpanzees (*Pan troglodytes*) for unimanual and bimanual coordinated tasks



Maria Padrell<sup>a,b,\*</sup>, Carlos Gómez-Martínez<sup>a</sup>, Miquel Llorente<sup>a,b,c</sup>

<sup>a</sup> Facultat d'Educació i Psicologia, Universitat de Girona, Pujada de Sant Domènec 9, 17004, Girona, Spain

<sup>b</sup> Fundació Mona, Unitat de Recerca i Etologia, Carretera C-25, 17457 Riudellots de la Selva, Girona, Spain

<sup>c</sup> Institut de Recerca i Estudis en Primatologia - IPRIM, 17006, Girona, Spain

## ARTICLE INFO

### Keywords:

Bimanual  
Hand preference  
*Pan troglodytes*  
Temporal consistency  
Unimanual

## ABSTRACT

Longitudinal research on manual preferences in humans and non-human primates has mainly been conducted from a developmental perspective, with only a few studies exploring long-term stability of this trait during adulthood. Therefore, we investigated short-term (1 year) and long-term (10 and 11 years) consistency of hand preference in a naturalistic group of 19 juvenile and adult chimpanzees (*Pan troglodytes*) by using two experimental tasks, one unimanual (simple reaching) and one bimanual (tube task). The experimental sessions were conducted in 2007, 2008 and 2018. We found that the direction of hand preference (right vs. left) in the tube task remained stable after both short-time and long-time periods. Conversely, hand preference direction for simple reaching was not consistent after the longest period (11 years), but the handedness indices (HI) between 2007 and 2008 (1-year period) and between 2008 and 2018 (10-year period) were positively correlated. The comparison between tasks confirmed that all the chimpanzees were more strongly lateralised for the tube task. Interestingly, however, the strength of hand preference in the tube task showed an increasing trend in the long term. We hypothesize that this could be a consequence of practice and experience with a particular motor action.

## 1. Introduction

In both humans and non-human primates the development of manual preferences and how they change throughout the lifespan is poorly understood, despite the substantial amount of research conducted on this topic (Prieur et al., 2019). Behavioural lateralisation can already be observed from the first quarter of life for the movements of the right upper limbs (Hepper et al., 1998), and in other behaviours such as thumb sucking (Hepper et al., 2005, 1991) or head turning (Ververs et al., 1994). Furthermore, postural biases in the intrauterine environment or hand motor actions in foetuses can predict later handedness (Porac, 2016; Parma et al., 2017). Hand preference for grasping can be detected as early as 6 months of age (Butterworth and Hopkins, 1993; Michel, 2002; Michel et al., 2014; Nelson et al., 2014), while hand preferences for role-differentiated bimanual actions develop later and can be assessed at approximately 13–14 months of age (Ramsay et al., 1979; Michel et al., 1985; Babik and Michel, 2016). These early preferences for unimanual grasping (Campbell,

Marcinowski, Latta, et al. 2015) influence later preferences for bimanual actions that require greater interhemispheric transfer (Babik and Michel, 2016; Nelson et al., 2013). Nonetheless, these studies also revealed that not all infants were lateralised, thus indicating that hand-use preference is still developing and becomes more evident with age during the first year of life (Campbell, Marcinowski, Babik, et al. 2015). There is also evidence supporting that manual asymmetries for reaching increase in children, with early adolescents experiencing a peak in laterality which slightly decreases as they reach adulthood (Bryden and Roy, 2006). Similarly, it has also been reported that adult chimpanzees exhibit greater strength in hand preference than immatures (Humble and Matsuzawa, 2009).

It is not surprising then that changes in manual preferences across time in humans have been extensively studied from a developmental perspective, with a special focus on infants, whereas only a few studies examine variation in hand preferences during adulthood (Michel, 1981, 2002). Furthermore, the results reported by the authors investigating adult hand preferences are controversial. For example, while some

\* Corresponding author at: Fundació Mona, Unitat de Recerca i Etologia, Carretera C-25, 17457 Riudellots de la Selva, Girona, Spain.

E-mail addresses: [m.padrell@fundacionmona.org](mailto:m.padrell@fundacionmona.org) (M. Padrell), [recerca@fundacionmona.org](mailto:recerca@fundacionmona.org) (C. Gómez-Martínez), [mlllorente@institutprimatologia.com](mailto:mlllorente@institutprimatologia.com) (M. Llorente).

<https://doi.org/10.1016/j.beproc.2019.103911>

Received 21 March 2019; Received in revised form 10 July 2019; Accepted 19 July 2019

Available online 30 July 2019

0376-6357/ © 2019 Elsevier B.V. All rights reserved.

claim that the degree of lateralisation decreases with time and that there is a trend towards ambidexterity (Kalisch et al., 2006), others reported an increase in the use of the preferred hand, at least in right-handers (Coren, 1995; Weller and Latimer-Sayer, 1985). Finally, there is also evidence supporting handedness stability across time (Chua et al., 1995; Gonzalez et al., 2015; Gooderham and Bryden, 2014). A first argument to explain these changes during development suggests that interhemispheric integration due to the *corpus callosum* myelination varies throughout childhood (Salamy, 1978; Scott, 2018). A second model proposes that frontal activity during cognitive or motor performance tends to be less lateralised in older individuals than in young adults; that is, age would favour a tendency towards symmetrical hand use due to the aging of the right hemisphere (Dolcos et al., 2002). Age-related hemispheric asymmetry reduction in older adults is supported by functional neuroimaging evidence in various cognitive domains (Cabeza, 2002). Nevertheless, some other authors argued that developmental changes in manual asymmetries and dexterity are independent from brain aging, and rather they seem to be related to motor experience (Teixeira, 2008) and they are task specific (Sivagnanasunderam et al., 2015). Some of these contradictory findings could also be explained by underpowered studies or inappropriate data collection methods to reliably identify longitudinal trajectories of hand preferences (Campbell, Marcinowski, Latta, et al. 2015; Michel, 2018).

It is also worth noting that studies exploring hand preferences in humans use very different approaches, with some relying on questionnaires (Porac and Coren, 1981; Pietsch and Jansen, 2019; Nelson et al., 2018) while others conduct behavioural assessments of one or several motor tasks (Fagard and Corroyer, 2003; Mouloua et al., 2018; Marchant et al., 1995). Moreover, when evaluating temporal stability the authors usually adopt a cross-sectional approach, comparing groups of different ages (Gonzalez et al., 2015; Gooderham and Bryden, 2014), and the few studies that follow and test the same subjects during different stages of age are limited to infants and toddlers (Jacquet et al., 2012; Nelson et al., 2013). Thus, to our knowledge, no longitudinal study in humans has ever assessed long-term handedness consistency in adults considering the same subjects and the same tasks.

Similarly, research on handedness in great apes has mainly been focused on examining the development of this trait, and therefore it has been mostly conducted in young chimpanzees (Hopkins and Bard, 1993, 2000; Hopkins et al., 2005), whereas temporal consistency in adult subjects has rarely been assessed. Among the few examples we find the study of Hopkins and colleagues (2001) in which a group of 109 chimpanzees, including both juvenile and adults, were tested over a 6-year period using the bimanual tube task (Hopkins, 1995). They found a positive correlation between the original data presented in Hopkins (1995) and the results from the previously mentioned study, thus demonstrating that chimpanzees were consistent in the use of their dominant hand and that the tube task was a reliable measure of hand preference across time.

Besides experimental tasks, spontaneous behaviours have also been evaluated to investigate manual asymmetries and its consistency. For example, in a recent study which evaluates several motor tasks in captive chimpanzees, Motes Rodrigo et al. (2017) reported a temporal stability in a behaviour which was assessed for the first time: manual digging. Nonetheless, the time interval between the different measures of this task was considerably short (less than 6 months). Studies in wild chimpanzees have also explored consistency in hand preference in spontaneous actions, such as tool use during termite fishing. Hand preference direction was found to be stable for this behaviour in Fongoli (Senegal) and in Gombe (Tanzania) considering time periods comprised between 2 and 4 years (Bogart et al., 2012; Lonsdorf and Hopkins, 2005). Other authors have also explored temporal consistency of hand preferences in monkeys by assessing a variety of unimanual and bimanual tasks, both spontaneous and experimental (Meguerditchian et al., 2011; Molesti et al., 2016; Vauclair et al., 2005). These studies, in which animals were retested between 4 months and 5 years after the

first assessment, support a strong stability across time for bimanual tasks, but they revealed discrepancies regarding unimanual actions.

Finally, it should be noted that several authors have raised awareness about the inconsistency in the methodologies for measuring handedness in both humans and non-human primates (Cochet and Byrne, 2013). Some of the factors that have been shown to influence the results are the type of task, the experimental design or the data analysis (Hopkins, 2013a). More importantly, within-task consistency appears to be less robust in chimpanzees than in humans, which also hinders the assessment of handedness in this species (Hopkins et al., 2013).

This study is one of the few examples in literature investigating long-term temporal consistency of hand preferences in chimpanzees which evaluates more than one motor action and considers both hand preference direction and strength. Our purpose is not to provide a global picture of chimpanzee handedness, but rather to specifically address the topic of how manual asymmetries fluctuate across time in this species, as well as to further investigate how the type of task may influence these variations. To do so, we will assess hand preferences in a group of captive chimpanzees (*Pan troglodytes*) in two experimental tasks, one unimanual (simple reaching) and one bimanual (the tube task) over a short-term period (1 year) and two long-term periods (10 and 11 years).

## 2. Materials and methods

### 2.1. Ethics statement

This research was conducted in accordance with all national and institutional guidelines for the care and management of primates established by Fundació Mona, the Association for the Study of Animal Behaviour/Animal Behavior Society and the Spanish Government (RD 53/2013).

### 2.2. Subjects and housing

The study sample consisted of a total of 19 chimpanzees (*Pan troglodytes*), 12 males and 7 females, with ages between 4 and 51 years (mean age  $\pm$  SD = 23.00  $\pm$  12.05) at the time they were first evaluated. They were housed at Fundació Mona (FM) (Girona, Spain), a centre dedicated to the rescue, rehabilitation and resocialisation of former pet and entertainment chimpanzees. One chimpanzee (Pancho) passed away between 2007 and 2008 and another individual (Nico) lost part of his right hand and therefore was not included in the following tests. Another 4 chimpanzees passed away after 2008 and 4 new individuals arrived at Fundació Mona. Finally, one subject (Toni) could not be assessed in 2018 due to health problems. Therefore, consistency of handedness measures in the short-term period (1-year) has been evaluated in 12 chimpanzees, whereas long-term consistency (10-year and 11-year periods) could only be evaluated in 7 subjects (6 males and 1 female, age range in 2018: 15–36 years, mean age  $\pm$  SD = 26.71  $\pm$  8.36). Table 1, adapted from Llorente et al. (2015) contains individual information, characteristics, and background of the 19 chimpanzees.

Under good weather conditions, the chimpanzees spend daytime hours in a 5640 m<sup>2</sup> outdoor enclosure, which is divided into two areas (2420 m<sup>2</sup> and 3220 m<sup>2</sup>). The enclosure is surrounded by a double fence system which includes a steel fence and a 12 V electric fence. It is covered by natural grasses and other Mediterranean herbaceous vegetation subject to seasonal changes. It also contains artificial elements such as wooden platforms, towers and ropes. This naturalistic environment, combined with the integration in a social group, promotes the exhibition of species-typical behaviours and ultimately enhances the welfare of the animals. Besides the outdoor enclosure, the chimpanzees also have a 140m<sup>2</sup> indoor facilities or bedrooms in which they spend the nights and rainy/cold days.

**Table 1**

Demographical information on the 19 chimpanzees housed at Fundació Mona which were tested for hand preferences in at least one of the assessment periods.

Individual				At Mona		Group	
Name	Sex	Year	Place	Rescue Year/ Onset social house	Name	Composition	
Africa	F	1999	wild	2009	BIL > MUT	mix	
Bea	F	1985	wild	2012	BIL	mix	
Bongo	M	2000	captive	2002	BIL > MUT	mix > allM > mix	
Charly	M	1989	captive	2001	MUT	allM > mix	
Cheeta	F	1990	wild	2015	BIL	mix	
Coco	F	1994	wild	2012	BIL	mix	
Julio	M	1979- 2007 <sup>†</sup>	captive	2005	isolated	allM	
Juanito	M	2003	captive	2005	BIL > MUT	mix > allM > mix	
Marco	M	1984	captive	2001	MUT	allM > mix	
Nico	M	2001	captive	2004	BIL	mix	
Pancho	M	1990-2007 <sup>†</sup>	captive	2001	MUT	mix	
Romie	F	1979-2011 <sup>†</sup>	wild	2001	BIL	mix	
Sara	F	1998-2012 <sup>†</sup>	captive	2004	BIL	mix	
Tico	M	1987	wild	2005	BIL	mix	
Tom	M	1985	wild	2011	BIL	mix	
Toni	M	1983	wild	2001	MUT	allM > mix	
Toto	M	1956-2013 <sup>†</sup>	wild	2003	BIL	mix	
Victor	M	1982	captive	2006	BIL	mix	
Waty	F	1997	captive	2002	BIL > MUT	mix	

F: female, M: male, BIL: Bilinga group, MUT: Mutamba group, mix: mixed sex group, allM: all-males group.

### 2.3. Procedure

The chimpanzees were assessed on three occasions using the same tasks and the same experimental design. First, in order to evaluate short-term consistency, the subjects were tested between January and April 2007 and during the same period in 2008 (Llorente et al., 2009, 2011; Llorente, 2011). Second, to investigate long-term consistency, the same animals were reassessed between February and May 2018, which corresponds to 11 years after the first test in 2007 and 10 years after the second test in 2008.

The evaluated tasks were simple reaching and a modified version of the tube task. Simple reaching is a simple motor action, performed unimanually, which implies collecting a piece of food from the floor or other surface. The tube task is a coordinated bimanual task, in which one hand (referred to as the dominant hand) removes food from a PVC tube while the other holds the tube (Hopkins, 1995). As described by Llorente et al. (2009), in this study the PVC tubes were substituted by rubber hoses completely filled with food and of a particular length in order to promote the use of tools (branches, sticks). Although the simple reaching task is considered a poor indicator of handedness, we decided to use it as a low level control task, which could be compared with a complex bimanual task (tube task).

#### 2.3.1. Experiment 1: simple reaching

Manual preference for the simple reaching task was assessed during feeding when subjects were supplied their regular daily snack at 13:30 h. This snack consisted of muesli, sunflower seeds, peanuts, bread, rice flakes and sliced apples. Every item measured 3 × 3 cm maximum, enhancing fine precision manipulation. The food was scattered directly on the ground in the outside facilities, which subjects share with their social group. In order to prevent dominant-subordinate conflicts, enough food was provided and distributed in different spots across the enclosure.

We used continuous focal sampling method (Altmann, 1974), conducting as many observation sessions as needed to compile at least 100 events of simple reaching (Llorente et al., 2009; Vauclair et al., 2005). Individual data was collected in consecutive or non-consecutive days, depending on whether the focal subject was visible. The number of sessions required to reach the minimum of 100 events differed between individuals (mean n<sup>o</sup> of sessions/individual/year ± SD = 3.6 ± 2.6, range = 1–12). We recorded the hand used to collect a food item each

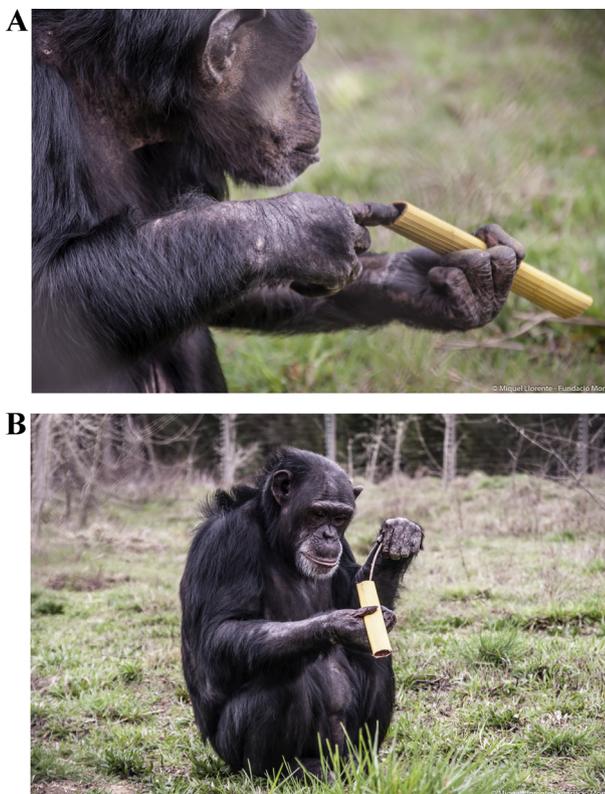
time the subject performed a manual grip, either followed or not by the action of putting it into the mouth, and irrespective of whether the hand already contained another food item. We did not consider grip morphology or posture because in a previous study Llorente et al. (2009) demonstrated that, although these two factors have some impact on hand preferences, no significant differences were found in hand preference direction between the most common grip morphologies and neither between the most common postures. Thus, in order to simplify our analysis we decided not to include this information in the present study. We only registered those events in which the individual picked up an item placed on the central area or on the contralateral side. The central area was defined as the area comprised in a 45° angle from the vertical axis of the subject. Reaching to food items placed on the ipsilateral side was not taken into account, given the fact that it is impossible to determine if this behaviours are reliable indicators of hand preference or merely a consequence of the proximity between the hand and the food item.

Interrater reliability was tested using a 3:30 min videotaped session of a single individual which contained a total of 34 events of reaching. Cohen's kappa coefficients ( $\kappa$ ) (Cohen, 1968) indicated high levels of agreement between raters ( $\kappa \geq 0.90$ ).

#### 2.3.2. Experiment 2: tube task

Cylindrical rubber hoses (length, 25–25.5 cm; diameter, 2.5 cm) filled with preferred foods items (muesli, seeds or chopped fruits) were given directly to the subject or placed on the ground in the outside facilities. Honey or peanut butter was used to maintain the small pieces of food stuck in the inside walls of the hoses. Additionally, the length of the hoses prevented food extraction with the tongue or by hitting them. Therefore, subjects were forced to use either their fingers or tools such as sticks, branches or canes. To avoid dominant-subordinate conflicts in the social groups, we prepared a minimum of 1 hose per individual.

We used continuous focal animal sampling (Altmann, 1974), recording the hand used to extract the food each time the subject inserted its finger or a tool, removed the food and placed its finger/tool in its mouth (Fig. 1). This entire sequence of actions was considered a single event. Several authors have criticized the use of behavioural events versus bouts in the study of hand preference in relation to data independence (McGrew and Marchant, 1997). One of the main concerns is that event recording increases the sample size and consequently the probability of detecting significant differences in hand use



**Fig. 1.** Chimpanzees performing the tube task with their finger (1A) and using a stick as a tool (1B).

(Meguerditchian et al., 2010). However, although some studies have reported an effect of the recording methodology (Chapelain and Hogervorst, 2009), most failed to detect significant differences in recording manual behaviours as events or bouts (Meguerditchian et al., 2010; Hopkins, 2006; Zhao et al., 2016). Therefore, we chose to use events in order to replicate the original test (2007) and to compare our present results with other experimental studies that follow this same procedure.

The session continued until the individual lost interest or left the hose for 1 min. Each individual was assessed 4 times and sessions were separated by at least 2 days. Sessions were only considered valid when the subject completed  $\geq 6$  events of food extraction and they concluded when the subject lost interest and dropped the task for more than 1 min. In total, a minimum of 50 events per subject were recorded (Llorente et al., 2009).

Interrater reliability was evaluated using a 12 min session of one chimpanzee which performed a total of 14 events of finger/tool insertion in the hose. Cohen's kappa coefficients ( $\kappa$ ) (Cohen, 1968) revealed high consistency across raters in all testing periods ( $\kappa \geq 0.90$ ).

**Table 2**

Handedness measures for the unimanual simple reaching task and for the bimanual tube task in 2007, 2008 and 2018.

		2007 (N = 14) <sup>*</sup>	2008 (N = 12)	2018 (N = 12)
SIMPLE REACHING	Lateralised subjects	12 (85.71%)	11 (91.67%)	10 (83.33%)
	%right-handers	64.29	54.55	50.00
	HI (mean $\pm$ SD)	0.22 $\pm$ 0.50	0.02 $\pm$ 0.59	0.19 $\pm$ 0.54
	ABS-HI (mean $\pm$ SD)	0.46 $\pm$ 0.26	0.51 $\pm$ 0.26	0.47 $\pm$ 0.31
TUBE TASK	Lateralised subjects	14 (100%)	12 (100%)	12 (100%)
	%right-handers	71.43	58.33	66.67
	HI (mean $\pm$ SD)	0.35 $\pm$ 0.79	0.09 $\pm$ 0.87	0.37 $\pm$ 0.93
	ABS-HI (mean $\pm$ SD)	0.81 $\pm$ 0.22	0.82 $\pm$ 0.20	0.95 $\pm$ 0.13

\* Previously reported by Llorente et al., 2009.

## 2.4. Data analysis

Independently for each task and period (2007, 2008 and 2018) we calculated the proportion of use of each hand (% Left, % Right), the handedness index (HI), the absolute handedness index (ABS-HI), the z-scores and the P Binomial per individual. The HI was calculated as the number of times the subject uses the right hand minus the number of times he uses the other hand divided by the total number of events. Thus, HI values ranged from -1 (exclusive use of left hand) and +1 (exclusive use of the right hand). Following Hopkins (2013b), we assumed that HI values higher than 0.20 indicated right-hand preferences, whereas HI values lower than -0.20 indicated left-hand preferences. Subjects with HI values between -0.20 and 0.20 were labelled as ambipreferent. The ABS-HI was calculated as the absolute value of the HI and indicated the strength of hand preference. Due to the fact that we recorded 4 sessions of the tube task per subject, the HI and the ABS-HI were calculated considering the sum of the 4 tests. Based on their individual z score, the chimpanzees were categorised as right-handed ( $z \geq 1.96$ ), left-handed ( $z \leq -1.96$ ) or ambipreferent ( $1.96 > z > -1.96$ ). Furthermore, the P binomial value was also considered to determine whether hand preference direction was significant or not: if P binomial  $\leq 0.05$ , the individual was categorised as right- or left-handed (depending on the sign of HI value). Conversely, when P binomial was  $\geq 0.05$ , the subject was considered ambidextrous or ambipreferent (non-lateralised).

All measures were assessed with the Shapiro-Wilk test for normality, which indicated that some data significantly deviate from a normal distribution. Therefore, and also taking into account our small sample size, we chose the more conservative approach by using only non-parametric tests. Differences in hand preference direction (HI) and handedness strength (ABS-HI) between each pair or years were evaluated with a Wilcoxon signed-rank test. Moreover, a Spearman's correlation was calculated to confirm hand use stability over time (Bogart et al., 2012; Hopkins et al., 2001; Lonsdorf and Hopkins, 2005). Consistency in HI and ABS-HI across tasks for each year was also assessed with a Wilcoxon signed-rank test and a Spearman's correlation. Finally, to assess whether there was a manual preference at the population or group level, we used a one-sample Wilcoxon signed-rank test. All analysis were performed with the statistical software JASP (Version 0.9), which uses R-packages. An alpha level of 0.05 was used as cut-off for significance.

## 3. Results

### 3.1. Short-term temporal consistency of hand preference (1year)

Results on all the individuals assessed in 2007 and 2008 for simple reaching and the tube task are presented Appendix Tables A1 and A2. One individual (Pancho) passed away and another suffered a severe hand injury (Nico). A total of 12 chimpanzees were assessed in 2008 compared to the initial 14 subjects in 2007. Table 2 presents a summary

**Table 3**  
Consistency of hand preference direction across time for the simple reaching task. In bold the individuals that could be assessed after both short-time (1-year) and long-term periods (10 and 11-years).

Subject	2007	2008	2018	Consistency
Africa			R	
Bea			R	
<b>Bongo</b>	R	R	R	3/3
<b>Charly</b>	L	L	R	2/3
Cheeta			A	
Coco			L	
Julio	R	R		2/2
<b>Juanito</b>	A	L	L	2/3
<b>Marco</b>	R	R	A	2/3
Nico	R			
Pancho	R			
Romie	L	L		2/2
Sara	R	A		1/2
<b>Tico</b>	R	R	R	3/3
Tom			R	
Toni	L	L		2/2
Toto	R	R		2/2
<b>Víctor</b>	R	R	R	3/3
<b>Waty</b>	A	L	A	2/3

R: right hand preference, L: left-hand preference, A: ambipreferent.

of the handedness measures for each task and year, including the mean values of the handedness index (HI) and handedness degree (ABS-HI).

For simple reaching, 3 chimpanzees (Juanito, Sara and Waty) showed different direction of hand preference between the two assessment periods. They were all classified as ambidextrous in one of the tests and showed a significant direction in hand preference in the other (Table 3). However, no differences were found between HI mean values in 2007 and in 2008 ( $W = 53.00, p = 0.30, 95\% \text{ CI } [-0.08, 0.28]$ ), and neither in the ABS-HI ( $W = 25.00, p = 0.30, 95\% \text{ CI } [-0.29, 0.09]$ ). Significant correlations were found between HI values of these two years ( $r = 0.90, p \leq 0.05, 95\% \text{ CI } [0.68, 0.94]$ ), but not in the ABS-HI ( $r = 0.45, p = 0.15, 95\% \text{ CI } [-0.17, 0.81]$ ).

For the tube task, 1 individual (Juanito) did not maintain handedness direction across time, being categorised as right-hander in 2007 and as left-hander in 2008 (Table 4). Nonetheless, no differences were found between mean values of HI in 2007 and 2008 ( $W = 39.00, p = 0.06, 95\% \text{ CI } [-0.02, 0.79]$ ), and neither in the ABS-HI ( $W = 28.00,$

**Table 4**  
Consistency of hand preference direction across time for the tube task. In bold the individuals that could be assessed after both short-time (1-year) and long-term periods (10 and 11-years).

Subject	2007	2008	2018	Consistency
Africa			R	
Bea			R	
<b>Bongo</b>	R	R	R	3/3
<b>Charly</b>	R	R	R	3/3
Cheeta			L	
Coco			R	
Julio	R	R		2/2
<b>Juanito</b>	R	L	L	2/3
<b>Marco</b>	R	R	R	3/3
Nico	R			
Pancho	R			
Romie	L	L		2/2
Sara	L	L		2/2
<b>Tico</b>	L	L	L	3/3
Tom			R	
Toni	R	R		2/2
Toto	R	R		2/2
<b>Víctor</b>	R	R	R	3/3
<b>Waty</b>	L	L	L	3/3

R: right hand preference, L: left-hand preference.

$p = 0.55, 95\% \text{ CI } [-0.16, 0.16]$ ). Moreover, significant correlations were found between HI in 2007 and 2008 ( $r = 0.96, p \leq 0.05, 95\% \text{ CI } [0.85, 0.99]$ ) and between ABS-HI ( $r = 0.87, p \leq 0.05, 95\% \text{ CI } [0.58, 0.96]$ ).

Population-level handedness was not detected in either of the samples for simple reaching ( $t(13) = 77.00, p = 0.14$  in 2007 and  $t(11) = 39.00, p = 1.00$  in 2008) or for the tube task ( $t(13) = 70.00, p = 0.29$  in 2007 and  $t(11) = 40.00, p = 0.97$  in 2008).

### 3.2. Long-term temporal consistency of hand preference (10 and 11years)

Data on all the individuals assessed in 2018 for both tasks are presented in Appendix Tables A1 and A2. Mean values of handedness measures for 2018 are shown in Table 2, together with the results from previous years. Only seven out of 12 chimpanzees tested in 2007 and 2008 could be assessed in 2018. The majority of the individuals passed away and in some exceptional cases (Nico and Toni), they suffered from health issues that did not allow them to be included them in the study.

Comparing 2007 and 2018 (11-year period), 3 out of 7 chimpanzees (Charly, Juanito and Marco) displayed a change in hand preference direction in the simple reaching task. Similarly, between 2008 and 2018 (10-year period) also 3 out of 7 chimpanzees presented a different direction in hand preference for this task (Charly, Marco and Waty) (Table 3). No significant differences were found between HI values in 2007 and 2018 ( $W = 14.00, p = 1.00, 95\% \text{ CI } [-0.17, 0.40]$ ) and neither between 2008 and 2018 ( $W = 16.00, p = 0.81, 95\% \text{ CI } [-0.34, 0.34]$ ). However, HI in 2007 and 2018 did not correlate ( $r = 0.71, p = 0.09, 95\% \text{ CI } [-0.08, 0.95]$ ), whereas HI in 2008 and 2018 were significantly correlated ( $r = 0.89, p \leq 0.05, 95\% \text{ CI } [0.43, 0.98]$ ). Regarding the strength of hand preference for simple reaching (ABS-HI), no significant differences were found between ABS-HI in 2007 and 2018 ( $W = 13.00, p = 0.94, 95\% \text{ CI } [-0.38, 0.19]$ ) and neither between 2008 and 2018 ( $W = 22.00, p = 0.22, 95\% \text{ CI } [-0.12, 0.46]$ ). The ABS-HI values in 2007 and 2018 were not significantly correlated ( $r = 0.50, p = 0.27, 95\% \text{ CI } [-0.41, 0.91]$ ), but ABS-HI in 2008 and 2018 did correlate ( $r = 0.89, p \leq 0.05, 95\% \text{ CI } [0.43, 0.98]$ ).

In the tube task, 1 chimpanzee (Juanito) showed an opposite direction in hand preference between 2007 and 2018 (11-year period), but no changes were detected between 2008 and 2018 (10-year period) (Table 4). Additionally, they were no significant differences in HI values in 2007 compared to 2018 ( $W = 9.00, p = 0.79, 95\% \text{ CI } [-0.33, 0.76]$ ) and neither between 2008 and 2018 ( $W = 4.00, p = 0.42, 95\% \text{ CI } [-0.38, 0.12]$ ). Moreover, significant correlations in HI were found between each pair of years (2007 vs. 2018:  $r = 0.87, p \leq 0.05, 95\% \text{ CI } [0.35, 0.98]$  and 2008 vs. 2018:  $r = 0.89, p \leq 0.05, 95\% \text{ CI } [0.42, 0.98]$ ). Individual scores in the ABS-HI were higher in 2018 in all the chimpanzees that were not completely lateralised (i.e. ABS-HI = 1.00) in the previous years (Appendix A2). Despite the fact that no differences were found between mean values of this measure, neither between 2007 and 2018 ( $W = 0.00, p = 0.06, 95\% \text{ CI } [-0.58, -0.09]$ ) nor between 2008 and 2018 ( $W = 0.00, p = 0.06, 95\% \text{ CI } [-0.48, 0.12]$ ), in both cases results approached statistical significance ( $p = 0.06$ ), and in the comparison between 2007 and 2018 confidence intervals did not overlap 0. Furthermore, no correlation was found between ABS-HI values in 2007 and 2018 ( $r = 0.34, p = 0.46, 95\% \text{ CI } [-0.56, 0.87]$ ) and neither between ABS-HI values in 2008 and 2018 ( $r = 0.52, p = 0.24, 95\% \text{ CI } [-0.39, 0.91]$ ). Therefore, in the tube task, direction in hand preference remained consistent across time, both considering a 10-year period and an 11-year period, but the strength of this preference tended to increase over time.

In summary, considering both short and long-term periods, only the direction of hand preference for the tube task showed a clear stability across time. Table 5 summarises the results obtained in the statistical tests (Wilcoxon and Spearman correlation) for each pair of years and for each measure (HI and ABS-HI).

Population-level handedness was not detected in 2018 neither for

**Table 5**

Consistency across time in the HI and ABSHI for the two tasks assessed. Checkmarks indicate no significant differences in the Wilcoxon test and significant correlations between pairs ( $p \leq 0.05$ ).

Measure	Year	Simple Reaching		Tube task	
		Wilcoxon test	Spearman correlation	Wilcoxon test	Spearman correlation
HI	2007-2008	✓	✓	✓	✓
	2007-2018	✓		✓	✓
	2008-2018	✓	✓	✓	✓
ABS-HI	2007-2008	✓		✓	✓
	2007-2018	✓		✓*	
	2008-2018	✓	✓	✓*	

\*Results approached statistical significance ( $p = 0.06$ ).

simple reaching ( $t(11) = 56.00, p = 0.20$ ) nor for the tube task ( $t(11) = 56.00, p = 0.19$ ).

### 3.3. Hand preference consistency across tasks

In every assessment year 3 to 4 chimpanzees showed an opposite hand preference direction (right to left, left to right) for simple reaching than for the tube task. Additionally, 1 to 3 subjects changed from ambidextrous in the simple reaching task to lateralised in the tube task (Appendices A1 and A2). Interestingly, two out of seven individuals that were present in all periods (Charly and Tico) exhibited the same pattern each time: Charly was always left-handed for reaching and right-handed in the tube task, whereas Tico was always right-handed for reaching and left-handed in the tube task. The handedness indices (HI) did not differ between tasks in any of the assessment years (Table 6), but no significant correlations were found between HI values (2007:  $r = 0.37, p = 0.19, 95\% \text{ CI } [0.75, -0.2]$ ; 2008:  $r = -0.34, p = 0.28, 95\% \text{ CI } [0.76, 0.29]$ ; and 2018:  $r = 0.12, p = 0.70, 95\% \text{ CI } [0.65, -0.49]$ ). Moreover, in all periods, the mean value of the absolute handedness index (ABS-HI) was higher in the tube task than in the simple reaching task (Table 6) and no significant correlations were found between ABS-HI values in the two tasks (2007:  $r = 0.08, p = 0.79, 95\% \text{ CI } [0.58, -0.47]$ ; 2008:  $r = 0.06, p = 0.86, 95\% \text{ CI } [0.61, -0.54]$ ; 2018:  $r = 0.37, p = 0.23, 95\% \text{ CI } [0.78, -0.25]$ ). Thus, the chimpanzees were more lateralised for the tube task than for simple reaching in every occasion that they were tested.

## 4. Discussion

To our knowledge this is one of the few studies that investigate temporal consistency in manual laterality in chimpanzees assessing the same subjects, using the same tasks, and considering both short (1 year) and long-time periods (> 10 years).

The hand preference direction in the tube task was the only measure which remained stable when considering both short-time (1 year) and long-time periods (10 and 11 years), with only one individual (Juanito) experiencing a switch in this measure between 2007 and 2008. Also, the handedness indices (HI) of all three years were correlated between

each other, thus replicating the results obtained by Hopkins et al. (2001), who also reported positive correlations between HI values from chimpanzees tested over a 6 year-period using the tube task. It is worth noting that Juanito was the youngest chimpanzee (4 years old) in the group and still a juvenile at the beginning of the experimental period, which may be related to the fact that his manual asymmetry could have been still developing. Although juvenile non-human primates have shown to be less lateralised than adults for the tube task (Zhao et al., 2012), our results somehow contradict previous studies in monkeys, chimpanzees and humans which found no effect of age in hand preference for complex bimanual tasks (Vauclair et al., 2005; Humle and Matsuzawa, 2009; Babik and Michel, 2016). However, they are consistent with the study of Hopkins and Bard (2000), in which they determined that asymmetries for the tube task are present in chimpanzees by the age of 5 years. Stability across time in hand preferences for the tube task has also been reported in other primate species, such as white-faced capuchins (*Cebus capucinus*) (Meunier and Vauclair, 2007) and olive baboons (*Papio anubis*) (Vauclair et al., 2005; Molesti et al., 2016), for periods between 8 months and 5 years. Therefore, our findings support the hypothesis that hand preferences for this bimanual task remain consistent over time.

The strength of hand preference in the tube task was consistent between 2007 and 2008 (short-term period), but unexpectedly, there was a lack of correlation in the ABS-HI between these years and 2018 (long-term period). Although no differences were found in the mean values of the ABS-HI in 2007 and in 2008 compared to 2018, the results of the statistical test were close to significance; and all the chimpanzees showed an increase in this measure in 2018 (except for those who already exhibited the maximal strength of lateralisation in the previous years). In addition, the absence of correlations suggests that there was no clear stability in the strength of manual preferences across time. This could be explained by several factors. First, that the individuals from our sample were highly conservative in their hand use and therefore, once they started to perform the task with one specific hand, they didn't change their strategy. In fact, as we were not able to isolate the subjects, in order to avoid quarrels we provided hoses for all individuals in the group every time we conducted the experimental sessions (even if we only evaluated some of the subjects). Therefore, all the chimpanzees

**Table 6**

Wilcoxon signed-rank test for hand preferences across tasks in each period. Significant differences are marked in bold.

Measure	Year	Task 1	Task 2	W	p	Hodges-Lehmann Estimate	95% CI for Hodges-Lehmann Estimate	
							Lower	Upper
HI	2007	SR	-	TT	37.00	0.36	-0.18	0.36
	2008	SR	-	TT	36.00	0.85	-0.05	0.47
	2018	SR	-	TT	29.00	0.47	-0.24	0.48
ABS-HI	2007	SR	-	TT	11.00	<b>0.01</b>	-0.38	-0.18
	2008	SR	-	TT	8.00	<b>0.01</b>	-0.32	-0.09
	2018	SR	-	TT	0.00	<b>0.01</b>	-0.47	-0.30

SR: simple reaching; TT: tube task.

interacted with the hoses repeatedly during all three assessment periods. Additionally, these hoses or similar objects have also been occasionally provided to the chimpanzees as elements of enrichment over the years, which may also contribute to a specialisation in hand use for this particular task. This would fit into the so-called “practice hypothesis”, which predicts an increase in both consistent right-handedness and consistent left-handedness after repeatedly performing a particular motor action (Porac, 1993; Coren, 1995; Teixeira and Okazaki, 2007). However, it would somehow contradict the theory that the more familiar the task, the higher is the tendency to use one hand or the other indistinctly (Fagot and Vauclair, 1991). Finally, another contributing factor to the high degree of lateralisation in the tube task is the fact that it can be considered a high-level or complex task, a feature which has been previously linked to a greater strength of hand preference in non-human primates (Lilak and Phillips, 2008; Laurence et al., 2011; Fagot and Vauclair, 1991).

Although the handedness indices (HI) in the simple reaching task did not correlate between 2007 and 2018 (11-year period), a positive correlation was found between HI in 2007 and 2008 (1-year period) and between HI in 2008 and 2018 (10-years period). However, the ABS-HI for simple reaching only correlated between 2008 and 2018, but not between the other periods. Thus, according to our data, unimanual actions only exhibit a certain degree of stability across time. Previous research in non-human primates using a similar methodology than in the present study (recording 100 events of reaching) have failed to report temporal consistency of hand preference for this behaviour (Vauclair et al., 2005) after 4 months. However, in a later study which replicates the previous experimental design, the authors have reported positive correlations in HI for simple reaching after 5 years (Molesti et al., 2016). Additionally, research on communicational gestures has revealed that hand preferences for a particular unimanual gesture (hand rubbing/slapping) in baboons (*Papio anubis*) also remained stable across time (Meguerditchian et al., 2011). Regarding chimpanzees, Lonsdorf and Hopkins (2005) observed that hand preferences for simple reaching in individuals between 3 and 4 years of age predicted hand use for gestures performed unimanually by the same subjects 10 years later.

Finally, the comparison between tasks revealed that, in each period, between 4 and 6 chimpanzees changed their hand preference direction depending on the task.

Despite the fact that no differences were found in the handedness indices in any of the testing periods, these measures did not correlate. These findings are in line with previous studies in monkeys (Canteloup et al., 2013; Lilak and Phillips, 2008; Meguerditchian et al., 2012) and great apes (Hopkins and Pearson, 2000; Llorente et al., 2009; Hopkins, 2013a,b, Hopkins et al., 2013), which also reported a lack of correlation between HI in reaching or grasping and the tube task. Furthermore, and as expected, the absolute handedness index for the tube task was always higher than for simple reaching, thus supporting the hypothesis that chimpanzees are more lateralised for complementary bimanual tasks than for tasks which can be performed unimanually (Llorente, 2011; Llorente et al., 2011; Meguerditchian et al., 2015; Mosquera et al., 2012). In other words, that the tube task elicited greater hand asymmetries and therefore it constitutes a more reliable measure of hand preference..

It is also interesting to note that two out of the seven chimpanzees assessed in all periods showed opposite hand preferences between tasks (Charly and Tico), but exhibited an obvious intra-task consistency across time. Taken into account the small number of subjects that could be evaluated after long-term periods, these results must be interpreted carefully. Nonetheless, together with the fact that HI and ABSHI between tasks did not correlate, these findings are consistent with the hypothesis that

manual laterality is a multidimensional trait in both humans (Healey et al., 1986) and chimpanzees (Wesley et al., 2002), and therefore hand use for different tasks should not necessarily be correlated.

## 5. Conclusions

In summary, our results indicated a clear consistency in hand preference direction across time in the bimanual complementary action (the tube task), whereas only a certain degree of consistency of this measure was observed for the unimanual task (simple reaching). As expected, all the chimpanzees were strongly lateralised for the bimanual task in all testing periods, thus confirming the hypothesis that role-differentiated bimanual actions elicit greater asymmetries and therefore are more reliable measures of hand preferences. Additionally, the high level of lateralisation for this task in 2018 suggests that the bias towards the use of one hand in a specific motor action could be a result of practice and experience with the task. In order to have a more comprehensive overview of handedness temporal changes in adult chimpanzees and other non-human primates, it would be desirable to assess repeatedly other spontaneous behaviours and experimental tasks, both unimanual and bimanual, and preferably employing the same subjects.

## Author contributions

This study was designed and conceptualized by ML. The original draft was written by MP, CGM and ML. The paper was reviewed and edited before submission by MP and ML. ML coordinated the data collection of 2007 and 2008, and MP in 2018. ML monitored the progress of the study. MP, CGM and ML analysed and interpreted the data. All authors read and approved the final manuscript.

## Declaration of Competing Interest

None.

## Acknowledgments

We would like to thank all the students and researchers who participated in the behavioural observations over the 11 years of the study. We are also grateful to the keepers and the volunteer staff involved in the care of the chimpanzees at Fundació MONA. Finally, we wish to acknowledge the help provided by Phil Guy, who reviewed the English of the manuscript.

## Funding

This work was supported by “la Caixa” Foundation (LCF/PR/PR17/11120020); the Spanish Ministerio de Ciencia e Innovación (HAR2009-07223/HIST); Ministerio de Economía y Competitividad (HAR2012-32548); Generalitat de Catalunya (2009 SGR-188; 2014 SGR-899; 2017 SGR-1040); Fundação para a Ciência e a Tecnologia (PTDC/PSI-PCO/104170/2008); and Universitat Rovira i Virgili (2009AIRE-05).

## References

- Altmann, J., 1974. Observational study of behavior: sampling methods. *Behaviour* 49, 227–267.
- Babik, I., Michel, G.F., 2016. Development of role-differentiated bimanual manipulation in infancy: part 2. Hand preferences for object acquisition and RDBM-continuity or discontinuity? *Dev. Psychobiol.* 58, 257–267. <https://doi.org/10.1002/dev.21378>.
- 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 verus*): Further evidence of a left hand preference. *Am. J. Phys. Anthropol.* 149, 591–598. <https://doi.org/10.1002/ajpa.22175>.
- Bryden, P.J., Roy, E.A., 2006. Preferential reaching across regions of hemispace in adults and children. *Dev. Psychobiol.* 48, 121–132. <https://doi.org/10.1002/dev.20120>.
- Butterworth, G., Hopkins, B., 1993. Origins of handedness in human infants. *Dev. Med. Child Neurol.* 35, 177–184. <https://doi.org/10.1111/j.1469-8749.1993.tb11620.x>.
- Cabeza, R., 2002. Hemispheric asymmetry reduction in older adults: the HAROLD model. *Psychol. Aging* 17, 85–100. <https://doi.org/10.1037/0882-7974.17.1.85>.
- Campbell, J.M., Marciniowski, E.C., Babik, I., Michel, G.F., 2015a. The influence of a hand preference for acquiring objects on the development of a hand preference for unimanual manipulation from 6 to 14 months. *Infant Behav. Dev.* 39, 107–117. <https://doi.org/10.1016/j.infbeh.2015.05.005>.

- [doi.org/10.1016/j.infbeh.2015.02.013](https://doi.org/10.1016/j.infbeh.2015.02.013).
- Campbell, J.M., Marciniowski, E.C., Latta, J.J., Michel, G.F., 2015b. Different assessment tasks produce different estimates of handedness stability during the eight to 14 month age period. *Infant Behav. Dev.* 39, 67–80. <https://doi.org/10.1016/j.infbeh.2015.02.003>.
- Canteloup, C., Vauclair, J., Meunier, H., 2013. Hand preferences on unimanual and bimanual tasks in Tonkean macaques (*Macaca tonkeana*). *Am. J. Phys. Anthropol.* 152, 315–321. <https://doi.org/10.1002/ajpa.22342>.
- Cochet, H., Byrne, R.W., 2013. Evolutionary origins of human handedness: evaluating contrasting hypotheses. *Anim. Cogn.* 16, 531–542. <https://doi.org/10.1007/s10071-013-0626-y>.
- Cohen, J., 1968. Weighted kappa: nominal scale agreement provision for scaled disagreement or partial credit. *Psychol. Bull.* 70, 213–220. <https://doi.org/10.1037/h0026256>.
- Coren, S., 1995. Age and handedness: patterns of change in the population and sex differences become visible with increased statistical power. *Can. J. Exp. Psychol.* 49, 376. <https://doi.org/10.1037/1196-1961.49.3.376>.
- Chapelain, A.S., Hogervorst, E., 2009. Hand preferences for bimanual coordination in 29 bonobos (*Pan paniscus*). *Behav. Brain Res.* 196, 15–29. <https://doi.org/10.1016/j.bbr.2008.07.012>.
- Chua, R., Pollock, B.J., Elliott, D., Swanson, L.R., Carnahan, H., 1995. The influence of age on manual asymmetries in movement preparation and execution. *Dev. Neuropsychol.* 11, 129–137. <https://doi.org/10.1080/87565649509540608>.
- Dolcos, F., Rice, H.J., Cabeza, R., 2002. Hemispheric asymmetry and aging: right hemisphere decline or asymmetry reduction. *Neurosci. Biobehav. Rev.* 26, 819–825.
- Fagard, J., Corroyer, D., 2003. Using a continuous index of laterality to determine how laterality is related to interhemispheric transfer and bimanual coordination in children. *Dev. Psychobiol.* 43, 44–56. <https://doi.org/10.1002/dev.10117>.
- Fagot, J., Vauclair, J., 1991. Manual laterality in nonhuman primates: a distinction between handedness and manual specialization. *Psychol. Bull.* 109, 76–89.
- Gonzalez, C.L.R., Flindall, J.W., Stone, K.D., 2015. Hand preference across the lifespan: effects of end-goal, task nature, and object location. *Front. Psychol.* 5. <https://doi.org/10.3389/fpsyg.2014.01579>.
- Gooderham, S.E., Bryden, P.J., 2014. Does your dominant hand become less dominant with time? The effects of aging and task complexity on hand selection. *Dev. Psychobiol.* 56, 537–546. <https://doi.org/10.1002/dev.21123>.
- Healey, J.M., Liederman, J., Geschwind, N., 1986. Handedness is not a unidimensional trait. *Cortex* 22, 33–53.
- Hepper, P.G., McCartney, G.R., Shannon, E.A., 1998. Lateralised behaviour in first trimester human foetuses. *Neuropsychologia* 36, 531–534.
- Hepper, P.G., Shahidullah, S., White, R., 1991. Handedness in the human fetus. *Neuropsychologia* 29, 1107–1111. [https://doi.org/10.1016/0028-3932\(91\)90080-R](https://doi.org/10.1016/0028-3932(91)90080-R).
- Hepper, P.G., Wells, D.L., Lynch, C., 2005. Prenatal thumb sucking is related to postnatal handedness. *Neuropsychologia* 43, 313–315. <https://doi.org/10.1016/j.neuropsychologia.2004.08.009>.
- Hopkins, W.D., 1995. Hand preferences for a coordinated bimanual task in 110 chimpanzees (*Pan troglodytes*): cross-sectional analysis. *J Comp Psychol* 109, 291. <https://doi.org/10.1037/0735-7036.109.3.291>.
- Hopkins, W.D., 2006. Chimpanzee right-handedness: internal and external validity in the assessment of hand use. *Cortex* 42, 90–93. [https://doi.org/10.1016/s0010-9452\(08\)70326-5](https://doi.org/10.1016/s0010-9452(08)70326-5).
- Hopkins, W.D., 2013a. Independence of data points in the measurement of hand preferences in primates: statistical problem or urban myth? *Am. J. Phys. Anthropol.* 151, 151–157. <https://doi.org/10.1002/ajpa.22248>.
- Hopkins, W.D., 2013b. Comparing human and nonhuman primate handedness: challenges and a modest proposal for consensus. *Dev. Psychobiol.* 55, 621–636. <https://doi.org/10.1002/dev.21139>.
- Hopkins, W.D., Bard, K.A., 1993. The ontogeny of lateralized behavior in nonhuman primates with special reference to chimpanzees (*Pan troglodytes*). In: Ward, J.P., Hopkins, W.D. (Eds.), *Primate Laterality: Current Behavioral Evidence of Primate Asymmetries*. Springer New York, New York, NY.
- Hopkins, W.D., Bard, K.A., 2000. A longitudinal study of hand preference in chimpanzees (*Pan troglodytes*). *Dev. Psychobiol.* 36, 292–300. [https://doi.org/10.1002/\(SICI\)1098-2302\(200005\)36:4<292::AID-DEV4>3.0.CO;2-T](https://doi.org/10.1002/(SICI)1098-2302(200005)36:4<292::AID-DEV4>3.0.CO;2-T).
- Hopkins, W.D., Fernandez-Carrija, S., Wesley, M.J., Hostetter, A., Pilcher, D., Poss, S., 2001. The use of bouts and frequencies in the evaluation of hand preferences for a coordinated bimanual task in chimpanzees (*Pan troglodytes*): an empirical study comparing two different indices of laterality. *J Comp Psychol* 115, 294–299. <https://doi.org/10.1037/0735-7036.115.3.294>.
- Hopkins, W.D., Gardner, M., Mingle, M., Reamer, L., Schapiro, S.J., 2013. Within- and between-task consistency in hand use as a means of characterizing hand preferences in captive chimpanzees (*Pan troglodytes*). *J Comp Psychol* 127, 380. <https://doi.org/10.1037/a0031071>.
- Hopkins, W.D., Pearson, K., 2000. Chimpanzee (*Pan troglodytes*) handedness: variability across multiple measures of hand use. *J Comp Psychol* 114, 126–135.
- Hopkins, W.D., Russell, J., Freeman, H., Buehler, N., Reynolds, E., Schapiro, S.J., 2005. The distribution and development of handedness for manual gestures in captive chimpanzees (*Pan troglodytes*). *Psychol. Sci.* 16, 487–493. <https://doi.org/10.1111/j.0956-7976.2005.01561.x>.
- Humle, T., Matsuzawa, T., 2009. Laterality in hand use across four tool-use behaviors among the wild chimpanzees of Bossou, Guinea, West Africa. *Am. J. Primatol.* 71, 40–48. <https://doi.org/10.1002/ajp.20616>.
- Jacquet, A.Y., Esseily, R., Rider, D., Fagard, J., 2012. Handedness for grasping objects and declarative pointing: a longitudinal study. *Dev. Psychobiol.* 54, 36–46. <https://doi.org/10.1002/dev.20572>.
- Kalisch, T., Wilimzig, C., Kleibel, N., Tegenthoff, M., Dinse, H.R., 2006. Age-related attenuation of dominant hand superiority. *PLoS One* 1, e90.
- Laurence, A., Wallez, C., Blois-Heulin, C., 2011. Task complexity, posture, age, sex: Which is the main factor influencing manual laterality in captive *Cercocebus torquatus torquatus*? *Laterality* 16, 586–606. <https://doi.org/10.1080/1357650x.2010.501338>.
- Lilak, A.L., Phillips, K.A., 2008. Consistency of hand preference across low-level and high-level tasks in Capuchin monkeys (*Cebus apella*). *Am. J. Primatol.* 70, 254–260. <https://doi.org/10.1002/ajp.20485>.
- Lonsdorf, E.V., Hopkins, W.D., 2005. Wild chimpanzees show population-level handedness for tool use. *Proc. Natl. Acad. Sci. U. S. A.* 102, 12634–12638. <https://doi.org/10.1073/pnas.0505806102>.
- Llorente, M., 2011. *Lateralidad Manual y Especialización Hemisférica En Chimpancés (Pan Troglodytes)*. Evaluación Observacional y Experimental. Doctoral Thesis. Facultat de Psicologia, Ciències de l'Educació i de l'Esport Blanquerna, Universitat Ramon Llull, Barcelona.
- Llorente, M., Mosquera, M., Fabrè, M., 2009. Manual laterality for simple reaching and bimanual coordinated tasks in naturalistic housed chimpanzees (*Pan troglodytes*). *Int. J. Primatol.* 30, 183–197. <https://doi.org/10.1007/s10764-009-9338-1>.
- Llorente, M., Riba, D., Ballesta, S., Feliu, O., Rostán, C., 2015. Rehabilitation and socialization of chimpanzees (*Pan troglodytes*) used for entertainment and as pets: an 8-year study at Fundació Mona. *Int. J. Primatol.* 36, 605–624. <https://doi.org/10.1007/s10764-015-9842-4>.
- Llorente, M., Riba, D., Palou, L., Carrasco, L., Mosquera, M., Colell, M., Feliu, O., 2011. Population-level right-handedness for a coordinated bimanual task in naturalistic housed chimpanzees: replication and extension in 114 animals from Zambia and Spain. *Am. J. Primatol.* 73, 281–290. <https://doi.org/10.1002/ajp.20895>.
- Marchant, L.F., McGrew, W.C., Eibl-Eibesfeldt, I., 1995. Is human handedness universal? Ethological analyses from three traditional cultures. *Ethology* 101, 239–258. <https://doi.org/10.1111/j.1439-0310.1995.tb00362.x>.
- McGrew, W.C., Marchant, L.F., 1997. On the other hand: current issues in and meta-analysis of the behavioral laterality of hand function in nonhuman primates. *Am. J. Phys. Anthropol.* 104, 201–232. [https://doi.org/10.1002/\(SICI\)1096-8644\(1997\)25+<201::AID-AJPA8>3.0.CO;2-6](https://doi.org/10.1002/(SICI)1096-8644(1997)25+<201::AID-AJPA8>3.0.CO;2-6).
- Meguerditchian, A., Calcutt, S.E., Lonsdorf, E.V., Ross, S.R., Hopkins, W.D., 2010. Brief communication: captive gorillas are right-handed for bimanual feeding. *Am. J. Phys. Anthropol.* 141, 638–645. <https://doi.org/10.1002/ajpa.21244>.
- Meguerditchian, A., Donnot, J., Molesti, S., Francioly, R., Vauclair, J., 2012. Sex difference in squirrel monkeys' handedness for unimanual and bimanual coordinated tasks. *Anim. Behav.* 83, 635–643. <https://doi.org/10.1016/j.anbehav.2011.12.005>.
- Meguerditchian, A., Molesti, S., Vauclair, J., 2011. Right-handedness predominance in 162 baboons (*Papio anubis*) for gestural communication: consistency across time and groups. *Behav. Neurosci.* 125, 653–660. <https://doi.org/10.1037/a0023823>.
- Meguerditchian, A., Phillips, K.A., Chapelain, A., Mahovetz, L.M., Milne, S., Stoinski, T., Bania, A., Lonsdorf, E., Schaeffer, J., Russell, J., Hopkins, W.D., 2015. Handedness for unimanual grasping in 564 Great Apes: the effect on grip morphology and a comparison with hand use for a bimanual coordinated task. *Front. Psychol.* 6, 1794. <https://doi.org/10.3389/fpsyg.2015.01794>.
- Meunier, H., Vauclair, J., 2007. Hand preferences on unimanual and bimanual tasks in white-faced capuchins (*Cebus capucinus*). *Am. J. Primatol.* 69, 1064–1069. <https://doi.org/10.1002/ajp.20437>.
- Michel, G.F., 1981. Right-handedness: a consequence of infant supine head-orientation preference? *Science* 212, 685–687.
- Michel, G.F., 2002. Development of infant handedness. In: Lewkowicz, D.J., Lickliter, R. (Eds.), *Conceptions of Development: Lessons from the Laboratory*. Psychology Press, New York.
- Michel, G.F., 2018. How might the relation of the development of hand preferences to the development of cognitive functions be examined during infancy: a sketch? *Front. Neurosci.* 11. <https://doi.org/10.3389/fnins.2017.00739>.
- Michel, G.F., Babik, I., Sheu, C.F., Campbell, J.M., 2014. Latent classes in the developmental trajectories of infant handedness. *Dev. Psychol.* 50, 349–359. <https://doi.org/10.1037/a0033312>.
- Michel, G.F., Ovrut, M.R., Harkins, D.A., 1985. Hand-use preference for reaching and object manipulation in 6- through 13-month-old infants. *Genet. Soc. Gen. Psychol. Monogr.* 111, 407–427.
- Molesti, S., Vauclair, J., Meguerditchian, A., 2016. Hand preferences for unimanual and bimanual coordinated actions in olive baboons (*Papio anubis*): consistency over time and across populations. *J Comp Psychol* 130, 341–350. <https://doi.org/10.1037/com0000040>.
- Mosquera, M., Geribàs, N., Bargalló, A., Llorente, M., Riba, D., 2012. Complex tasks force hand laterality and technological behaviour in naturalistically housed chimpanzees: inferences in Hominin evolution. *Sci. World J.* 2012. <https://doi.org/10.1100/2012/514809>. Article ID 514809, 12 pages.
- Motes Rodrigo, A., Hernandez Aguilar, R., Laska, M., 2017. Consistency in preferential hand use by captive chimpanzees (*Pan troglodytes*) in five motor tasks involving tool use and in manual digging. 7th European Federation for Primatology Meeting.
- Mouloua, S.A., Mouloua, M., McConnell, D.S., Hancock, P.A., 2018. Philadelphia, Pennsylvania The Effects of Handedness and Dominance on motor Task Performance, Human Factors and Ergonomics Society Annual Meeting 2018. The Effects of Handedness and Dominance on motor Task Performance, Human Factors and Ergonomics Society Annual Meeting.
- Nelson, E.L., Campbell, J.M., Michel, G.F., 2013. Unimanual to bimanual: tracking the development of handedness from 6 to 24 months. *Infant Behav. Dev.* 36, 181–188. <https://doi.org/10.1016/j.infbeh.2013.01.009>.
- Nelson, E.L., Campbell, J.M., Michel, G.F., 2014. Early handedness in infancy predicts language ability in toddlers. *Dev. Psychol.* 50, 809.
- Nelson, E.L., Gonzalez, S.L., El-Asmar, J.M., Ziade, M.F., Abu-Rustum, R.S., 2018. The home handedness questionnaire: pilot data from preschoolers. *Laterality* 1–22.

- <https://doi.org/10.1080/1357650X.2018.1543313>.
- Parma, V., Brasselet, R., Zoia, S., Bulgheroni, M., Castiello, U., 2017. The origin of human handedness and its role in pre-birth motor control. *Sci. Rep.* 7, 16804. <https://doi.org/10.1038/s41598-017-16827-y>.
- Pietsch, S., Jansen, P., 2019. The relation between mental rotation and handedness is a consequence of how handedness is measured. *Brain Cogn.* 130, 28–36. <https://doi.org/10.1016/j.bandc.2019.01.001>.
- Porac, C., 1993. Are age trends in adult hand preference best explained by developmental shifts or generational differences? *Can. J. Exp. Psychol.* 47, 697–713.
- Porac, C., 2016. *Laterality: Exploring the Enigma of Left-handedness*. Elsevier Academic Press, San Diego, CA, US 232.
- Porac, C., Coren, S., 1981. *Lateral Preferences and Human Behavior*. Springer-Verlag, New York 283.
- Prieur, J., Lemasson, A., Barbu, S., Blois-Héulin, C., 2019. History, development and current advances concerning the evolutionary roots of human right-handedness and language: brain lateralisation and manual laterality in non-human primates. *Ethology* 125, 1–28. <https://doi.org/10.1111/eth.12827>.
- Ramsay, D.S., Campos, J.J., Fenson, L., 1979. Onset of bimanual handedness in infants. *Infant Behav. Dev.* 2, 69–76. [https://doi.org/10.1016/S0163-6383\(79\)80009-0](https://doi.org/10.1016/S0163-6383(79)80009-0).
- Salamy, A., 1978. Commissural transmission: maturational changes in humans. *Science* 200, 1409–1411.
- Scott, K.M., 2018. Split-brain babies? Differences in representation of bilaterally and unilaterally presented visual stimuli in infancy. *Front. Psychol.* 9, 2758. <https://doi.org/10.3389/fpsyg.2018.02758>.
- Sivagnanasunderam, M., Gonzalez, D.A., Bryden, P.J., Young, G., Forsyth, A., Roy, E.A., 2015. Handedness throughout the lifespan: cross-sectional view on sex differences as asymmetries change. *Front. Psychol.* 5, 1556. <https://doi.org/10.3389/fpsyg.2014.01556>.
- Teixeira, L.A., 2008. Categories of manual asymmetry and their variation with advancing age. *Cortex* 44, 707–716. <https://doi.org/10.1016/j.cortex.2006.10.002>.
- Teixeira, L.A., Okazaki, V.H.A., 2007. Shift of manual preference by lateralized practice generalizes to related motor tasks. *Exp. Brain Res.* 183, 417–423. <https://doi.org/10.1007/s00221-007-1148-0>.
- Vauclair, J., Meguerditchian, A., Hopkins, W.D., 2005. Hand preferences for unimanual and coordinated bimanual tasks in baboons (*Papio anubis*). *Brain Res. Cogn. Brain Res.* 25, 210–216. <https://doi.org/10.1016/j.cogbrainres.2005.05.012>.
- Ververs, I.A., de Vries, J.I., van Geijn, H.P., Hopkins, B., 1994. Prenatal head position from 12–38 weeks. I. Developmental aspects. *Early Hum. Dev.* 39, 83–91.
- Weller, M.P., Latimer-Sayer, D.T., 1985. Increasing right hand dominance with age on a motor skill task. *Psychol. Med.* 15, 867–872.
- Wesley, M.J., Fernandez-Carriba, S., Hostetter, A., Pilcher, D., Poss, S., Hopkins, W.D., 2002. Factor analysis of multiple measures of hand use in captive chimpanzees: an alternative approach to the assessment of handedness in nonhuman Primates. *Int. J. Primatol.* 23, 1155–1168. <https://doi.org/10.1023/a:1021114518028>.
- Zhao, D., Hopkins, W.D., Li, B., 2012. Handedness in nature: first evidence on manual laterality on bimanual coordinated tube task in wild primates. *Am. J. Phys. Anthropol.* 148, 36–44. <https://doi.org/10.1002/ajpa.22038>.
- Zhao, D., Wang, Y., Wei, X., 2016. Hand preference during bimanual coordinated task in northern pig-tailed macaques *Macaca leonina*. *Curr. Zoo* 62, 385–391. <https://doi.org/10.1093/cz/zow064>.