

Laterality of Grooming and Tool Use in a Group of Captive Bonobos (*Pan paniscus*)

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Abstract

Humans exhibit population level handedness for the right hand; however, the evolution of this behavioral phenotype is poorly understood. Here, we compared the laterality of a simple task (grooming) and a complex task (tool use) to investigate whether increasing task difficulty elicited individual hand preference among a group of captive bonobos (*Pan paniscus*). Subjects were 17 bonobos housed at the Columbus Zoo and Aquarium. Laterality of grooming was recorded using group scans; tool use was recorded using all-occurrence sampling. Grooming was characterized as unimanual or bimanual, and both tasks were scored as right-handed or left-handed. Most individuals did not exhibit significant hand preference for unimanual or bimanual (asymmetrical hand use) grooming, although 1 individual was lateralized for each. For the 8 subjects who engaged in termite fishing enough for statistical testing, 7 individuals exhibited significant laterality and strong individual hand preference. Four subjects preferred their left hand, 3 preferred their right, and 1 had no preference. Grooming, a simple behavior, was not lateralized in this group, yet a more complex behavior revealed a strong individual hand preference, and these results are congruent with other recent findings that demonstrate complex tasks elicit hand preference in bonobos.

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Introduction

While there is some variation across cultures, *Homo sapiens* shows a species-wide bias for the right hand with approximately 90% of individuals exhibiting right-handedness [Marchant et al., 1995; Corballis, 2003; Cavanagh et al., 2016]. This behavioral phenotype is most evident during complex tasks, such as tool use [Fagot and Vauclair, 1991; Annett, 2002; Cavanagh et al., 2016]. Right hand bias has long been associated with hemispheric specialization in the human brain, specifically the left hemisphere, which controls right hand manual functions [Calvin, 1983]. This inferred relationship with brain lateralization has prompted many hypotheses for the origins of potentially unique human behaviors including the evolution of bipedalism [Kimura, 1979], throwing [Calvin, 1983], tool use [Kimura, 1979], language [Corballis, 2003; Vauclair, 2004], and bimanual coordinated actions [Byrne and Byrne, 1991; Fagot and Vauclair, 1991]. These hypotheses and others are explored in greater detail in Cashmore et al. [2008], McGrew and Marchant [1997] and Papademetriou et al. [2005].

In addition to the selective pressure(s) that may have driven manual lateralization, the prehistory of this phenotype is of particular interest. Recent investigations of Neanderthals have suggested that individuals from Regourdou, El Sidrón, and Krapina were predominately right-handed based on directional analysis of tooth striations, particularly incisors [Volpato et al., 2012; Estalrich and Rosas, 2013; Fiore et al., 2015]. Fiore et al. [2015] argue that a similar analysis of all European Neanderthals produces a frequency of 90% of individuals exhibiting right-handedness, congruent with the distribution in extant humans. Data from the archaeological record also suggest that handedness may have been present in humans prior to 2 million years ago [Cashmore et al., 2008; Cashmore, 2009; Uomini, 2009; Frayer et al., 2016]. Combined, these data further support the notion that population-level handedness evolved prior to the evolution of modern humans.

Comparative studies on manual laterality in other animals, particularly primates, can also contribute to understanding the evolution of human handedness. Nonhuman primates are ideal models because of their phylogenetic proximity to humans as well as their shared cognitive capacities [Byrne, 2016]. Following the “postural origins theory” of McNeillage et al. [1987], research on hand use in nonhuman primates intensified (see reviews in Cashmore et al. [2008], Hopkins [2006], Hopkins and Cantalupo [2005], McGrew and Marchant [1997] and Papademetriou et al. [2005]), producing complex and sometimes contradictory findings regarding primate species’ laterality. Indeed, differences in methods and interpretation of results have become a central issue in studying handedness within Primates [Marchant and McGrew, 2013].

Laterality studies use different terminology, which impacts the ability to compare findings across different studies. In the present study, we use the framework outlined by Marchant and McGrew [1994, 2013]. Laterality can be assessed within an individual and across individuals as well as within a behavior/task or across tasks. We use the term *hand preference* to describe significant bias within a subject for a particular task and *task specialization* to describe hand bias across individuals within a single task. *Manual specialization* describes consistent hand bias within an individual across different tasks. Finally, we reserve the term *handedness* to describe consistent directional bias across individuals and across many tasks (e.g., as in *H. sapiens*).

Table 1. Comparative chimpanzee laterality data

Task	Captive or wild	Site	<i>n</i>	AH	LH	RH	Source
Grooming	Captive	Bastrop & Yerkes	200	76	59	65	Hopkins et al., 2007
	Wild	Gombe	34	2	14	18	Marchant and McGrew, 1996
		Mahale	41	34	2	5	McGrew and Marchant, 2001
		Tai	15	10	0	5	Boesch, 1991
Termite fishing	Wild	Fongoli	27	2	16	9	Bogart et al., 2012
		Gombe	17	1	12	4	Lonsdorf and Hopkins, 2005
			15	4	6	5	McGrew and Marchant, 1992
			36	9	16	11	McGrew and Marchant, 1996
	Goualougo	89	4	39	46	Sanz et al., 2016	

n, number of subjects with enough bouts/scans for statistical testing; AH, number of subjects that were ambipreferent; LH, number of subjects with left hand preference; RH, number of subjects with right hand preference.

For this study, we compared manual laterality in 2 different tasks: grooming and tool use. We investigated the laterality of grooming for several reasons. First, grooming is observed in all primate species and occurs at relatively high frequencies as a result of the behavior's social function [McKenna, 1978], and occurs in both the wild and captivity. Additionally, social grooming may involve one or both hands. Several studies have highlighted the necessity of distinguishing between unimanual and bimanual tasks in laterality research (e.g., Hopkins [1995], McGrew and Marchant [1997]). Indeed, if coordinated bimanual actions were a main selective pressure that produced human population-level handedness, it is of critical importance to study these tasks separately. Bimanual tasks are generally considered to be more difficult than unimanual tasks [Hopkins, 1995]. Additionally, tasks that require an asymmetrical use of both hands in complementary roles are considered more difficult than bimanual symmetrical tasks (see Hopkins [1995] and Leca et al. [2011]). Therefore, bimanual asymmetrical grooming can be considered a more complex task than bimanual symmetrical or unimanual grooming. Additionally, to our knowledge, no studies to date have intensively examined the laterality of grooming in either captive or wild bonobos. However, there are 4 publications of manual laterality of grooming in captive and wild chimpanzees [Boesch, 1991; Marchant and McGrew, 1996; McGrew and Marchant, 2001; Hopkins et al., 2007].

One study examined the laterality of grooming among captive chimpanzees [Hopkins et al., 2007]. Researchers examined both unimanual and bimanual asymmetrical grooming. Based on individual *z*-scores, individuals were relatively evenly distributed in overall hand preference (Table 1). When examining unimanual and bimanual asymmetrical grooming separately, there was no significant difference in hand preference for unimanual grooming; however, there was a small yet significant bias toward right-handedness for bimanual asymmetrical grooming. Among wild chimpanzees, the man-

ual laterality of grooming has been studied at 3 different field sites (Table 1). Of the 3 sites it was only at Gombe that a majority of subjects, 32 of 34 individuals, consistently used either their left or right hand [Marchant and McGrew, 1996]. At both Mahale and Tai more than half of the individuals were ambipreferent, yet the greater number of right-handed individuals was interpreted as evidence for a right hand bias despite no significant differences between right- and left-handed individuals. This suggests that wild chimpanzees do not exhibit task specialization during social grooming.

A considerably broader domain of behavior encompasses tool use. Tool use is closely scrutinized given its cultural variation among wild chimpanzees [Whiten et al., 1999] and has also been invoked as a potential selective pressure for human handedness [Kimura, 1979]. In contrast to their sister species, wild bonobos are not known to use tools in food-processing tasks [Furuichi et al., 2011; Koops et al., 2015]; however, their capacity to use tools in captivity is well documented [Gruber et al., 2010; Chapelain et al., 2011; Boose et al., 2013; Bardo et al., 2015]. Thus, studies of tool use laterality in bonobos have focused on captive individuals. Harrison and Nystrom [2008] investigated the laterality of tool use of bonobos at 3 European zoos. Tool use elicited hand preference in some (but not all) individuals in either direction (left and right). However, it is unclear which specific tool use tasks elicited hand preference in some individuals and not others in this study because tool use is broadly defined. Chapelain et al. [2011] examined laterality in a bimanual task, the tube task, among zoo-housed bonobos as well as bonobos at the Lola Ya Bonobo Sanctuary, Democratic Republic of Congo. This task is commonly used to test for manual laterality across various primate species [Hopkins, 1995]. An individual holds a tube (e.g., a short segment of PVC pipe which has been baited with a preferred food like peanut butter) in one hand; the fingers of the other hand reach inside the tube to remove the food. Thus, the hand used to extract the food item is used for the analysis of hand preference. With a combined sample size of 77 individuals, Chapelain et al. [2011] found marked individual hand preference for the tube task but no group-level bias (task specialization). In a separate study, Hopkins et al. [2015] examined the laterality using the tube test at 3 US zoos. Sixteen individuals were right-handed, 4 were ambilateral, and 11 were left-handed for the tube task based on handedness index (HI) scores. Bardo et al. [2015] investigated the effect of the body posture and the complexity of the task on manual abilities in 3 separate tasks, including the tube task, in a group of zoo-living bonobos. Independently of body posture, during the tube task 4 bonobos were left-handed, 3 were right-handed, and 1 did not have a preference. These studies highlight that captive bonobos exhibit strong hand preference for this bimanual complex task but do not show task specialization.

Captive and sanctuary bonobos also exhibit marked laterality in tool use tasks. Neufuss et al. [2017] studied the laterality of nut cracking among the sanctuary bonobos at Lola Ya Bonobo. Of the 15 individuals with 10 or more bouts, 10 exhibited right hand preference, and 5 exhibited left hand preference. This is described by the authors as “group-level bias” and qualifies as task specialization per the framework introduced earlier. Bardo et al. [2015] examined manual laterality in a food extraction task among a group of zoo-housed bonobos. Food was placed inside a central cavity of a log suspended at different heights to investigate the effects of posture. This task is meant to be analogous to termite fishing that is common in some communities of *P. troglodytes*. Seven individuals were right-handed, and 1 individual was left-handed. Thus, this group of bonobos exhibited significant task specialization, biased toward the right hand.

The literature focusing on the laterality of tool use among both captive and wild chimpanzees is more abundant (for example, see Humle and Matsuzawa [2009], Marchant [2015] and McGrew and Marchant [1997]). Patterns of laterality in wild chimpanzees who “fish” for termites are relevant to the present study. Three field sites have produced data on termite fishing laterality: Fongoli, Senegal; Gombe, Tanzania; and the Goulougo Triangle, Republic of Congo (Table 1). Bogart et al. [2012] report on the laterality of termite fishing among the Fongoli chimpanzees. According to the authors, the Fongoli chimpanzees show “a trend toward (left) population-level laterality” [Bogart et al., 2012]. Three studies have investigated termite fishing laterality at Gombe: Lonsdorf and Hopkins [2005] and McGrew and Marchant [1992, 1996]. Both studies of McGrew and Marchant [1992, 1996] found that the Gombe chimpanzees demonstrated strong hand preference with trends toward group bias toward the left hand. Lonsdorf and Hopkins [2005] suggested that left hand preference was more prevalent than right hand preference (task specialization) among the Kasekela community. Central chimpanzees (*P. troglodytes troglodytes*) in the Goulougo Triangle exhibited strong individual hand preference when termite fishing; however, there was no significant overall population-level bias [Sanz et al., 2016]. Collectively, these data suggest that termite fishing elicits strong hand preference. Whereas Western and Central chimpanzees did not exhibit population-level bias, Eastern chimpanzees at Gombe trend toward left hand preference and thus potential task specialization for termite fishing.

The aim of this study was to test for departures from ambilaterality for a simple and a complex behavior. We consider grooming to be a simple or “low-level” task in that it occurs routinely and is not cognitively demanding, whereas tool use constitutes a considerably more complex behavior [Fagot and Vauclair, 1991]. In grooming, unimanual actions are less complex than bimanual tasks, especially bimanual asymmetrical hand use [Hopkins, 1995]. Previous research has highlighted that grooming elicited hand preference among captive chimpanzees [Hopkins et al., 2007] as well as in some wild individuals [Marchant and McGrew, 1996]. Among captive bonobos, we predicted that bimanual asymmetrical grooming would elicit hand preference given its increased complexity, whereas unimanual grooming would not [Fagot and Vauclair, 1991; Hopkins, 1995; Leca et al., 2011]. Based on tool use data from captive bonobos [Chapelain et al., 2011; Hopkins et al., 2011; Bardo et al., 2015; Hopkins et al., 2015] and wild chimpanzees [McGrew and Marchant 1992, 1996; Lonsdorf and Hopkins, 2005; Bogart et al., 2012; Sanz et al., 2016], we anticipated significant individual hand preference for tool use. While Bardo et al. [2015] found task specialization in a food extraction task among captive bonobos, this group bias has only been demonstrated in some studies of wild chimpanzees. Our tool use task more closely resembled chimpanzee termite fishing; therefore, we predicted that task specialization would not occur in this group of bonobos for this task.

Methods

Subjects

Study subjects were 17 bonobos housed at the Columbus Zoo and Aquarium (Powell, OH, USA). Four subjects were wild born, and 13 were captive born. Sex, age, and kinship are displayed for individuals that provided enough data for analysis in Table 2. Bonobos are exhibited in an outdoor exhibit and 2 indoor enclosures (see Boose et al. [2013] and Brand and Marchant [2015]

Table 2. Study subjects

Individual	Sex	Age ¹	Origin	Offspring ²
Ana Neema	F	20	Captive-born	Bila Isia, Gilda
Bila Isia	M	11	Captive-born	
Donnie	M	19	Captive-born	
Gander	M	9	Captive-born	
Gilda	F	6	Captive-born	
Jimmy	M	33	Wild-born	Donnie
Jo-T	F	10	Captive-born	
Lady	F	30	Wild-born	Jo-T
Lola	F	8	Captive-born	
Maiko	M	28	Captive-born	
Susie	F	30	Wild-born	Donnie, Lola
Toby	M	33	Wild-born	Lola
Unga	F	19	Captive-born	Gander

¹ Age as of August 2012. ² Offspring included only if they also had enough bouts or scans for statistical testing.

for exhibit descriptions and dimensions). Individuals form temporary parties that last for 1 or 2 days without compositional changes. These parties range in size from 2 to 9 individuals based primarily on bonobo preferences rather than keeper decisions. This management style emulates the fission-fusion social structure exhibited by wild bonobos [Kano, 1992].

Grooming Data

Data on grooming were collected during 128 h of observation between May and August 2012. We considered a grooming bout a period of investigation using the mouth or hands and considered a bout complete after a pause of 30 s. Laterality was assessed using scan sampling at 5-min intervals during a 15-min sample [Altmann, 1974]. If an individual was socially grooming during the scan, the hand laterality was recorded. For this study we employed scan sampling due to frequent changes in hand use during grooming within a bout. For this analysis, we considered only social grooming bouts.

Following Hopkins et al. [2007], hand use during grooming was categorized in 1 of 6 ways: none, unimanual-right, unimanual-left, bimanual-right, bimanual-left, and bimanual symmetrical. None was recorded when the focal subject was grooming orally rather than manually. Unimanual events described instances of grooming that involved a single hand (left or right) grooming the recipient; in these observations the other hand was not used (idle) or was used as a support. Bimanual grooming designated grooming events during which both hands were in contact with the recipient. Bimanual grooming could be asymmetrical or symmetrical (e.g., Leca et al. [2011]). Asymmetrical bimanual grooming events involved one hand that was actively grooming, i.e., labeled the “dominant” hand (searching through hair, picking at skin) while the other hand was used to press hair down or keep hair in place. Symmetrical grooming events occurred when both hands were actively used in a similar fashion to groom the recipient.

Tool Use Data

Tool use data were collected between June and August 2011. The bonobos were slowly habituated to an artificial termite mound. A full description of the habituation process can be found in Boose et al. [2013]. The mound featured 8 holes formed by PVC pipe that were filled daily with mashed fruit, mashed vegetables, honey, or peanut butter. The bonobos were not provided with

any raw materials to fashion tools. Rather, they exploited available sticks and other vegetation in their enclosure. All tool use was recorded using a video camera and scored at a later time. We stress that while this behavior is ethologically similar to termite fishing that is well documented in chimpanzees, the tool use behavior reported in this study should be treated as an analog to termite fishing, rather than an identical behavioral pattern.

A tool use bout was defined as the time during which an individual continuously fished or attempted to extract bait [Boose et al., 2013]. When an individual departed to a distance of 1 m or more of the mound, or stopped tool use behaviors for more than 30 s but remained within 1 m or more of the mound, the bout was scored as finished [Boose et al., 2013]. While other research on manual laterality has analyzed data at the *unit* level, e.g., a single insertion and withdraw of a probe, these cannot be considered statistically independent of one another, whereas bouts are independent with respect to hand use [McGrew and Marchant, 1992].

Bouts were coded according to the number of units for each hand following McGrew and Marchant [1992]. If the number of left hand units exceeded the number of right-hand units, the bout was considered left-handed. If the number of right hand units exceeded the number of left hand units, the bout was considered right-handed. Finally, if the number of units were equal for both hands the bout was coded as a tie.

Data Analysis

We determined statistically significant deviations from ambilaterality for unimanual grooming, bimanual asymmetrical grooming, and tool use per individual using 2-tailed binomial tests, with a level of significance of 0.05. We also include HI scores, which reflect the direction of hand use [Hopkins, 1999]. HI scores are calculated by subtracting the number of left hand responses from the number of right hand responses and dividing this value by the total number of responses for both hands ($(R - L)/(R + L)$). HI scores range from -1 to 1 ; negative values reflect a left side bias, and positive values reflect a right side bias. We also calculated the absolute value of HI (ABS-HI) scores, which reflect the strength of laterality [Hopkins, 1999]. These values range from 0 to 1, with 0 indicating weak laterality, and 1 indicating strong laterality. We include these statistics for comparison with other studies; however, we strongly note that these statistics are insensitive to sample size unlike binomial tests. As such, we do not calculate HI scores, ABS-HI values, or conduct binomial tests for individuals with <10 bouts or scans. Additionally, grooming scans that were labelled none or bimanual symmetrical were excluded from analyses due to lack of hand use (none) or the inability to distinguish the preferred hand during bimanual symmetrical events. If the number of bouts coded as ties exceeded either left or right hand use during tool use, we considered that individual to exhibit no hand preference, regardless of the HI value, ABS-HI value, or the p value.

We tested for significant variation among HI scores across individuals within a task using repeated G tests of goodness of fit [Sokal and Rohlf, 2011]. We also tested for task specialization using HI scores for each task using 1-sample Wilcoxon signed rank tests. Finally, we compared HI scores across individuals and the 3 tasks using nonparametric correlations. Binomial tests, correlations, and Wilcoxon signed rank tests were run using the software SAS[®], version 9.4 (Cary, NC, USA) while G tests were run using BIOMstat, version 3.3 (E. Setauket, NY, USA).

Results

Laterality of Grooming

We recorded hand use for 12 of the 17 bonobos during grooming for 632 scans. Of these scans, 159 occurred during self-directed grooming and were excluded from analysis. In order to assess bias in hand use, we also excluded 141 scans that did not involve hand use (none) or when the dominant hand could not be determined (bimanual symmetrical hand use). Table 3 presents hand use data for social grooming. HI scores ranged from -0.52 to 0.08 for unimanual grooming ($n = 9$), with only 1 fe-

Table 3. Laterality of social grooming

Individual	Unimanual							Bimanual						
	<i>n</i> (scans)	LH	RH	HI	ABS- HI	<i>p</i>	hand pref- erence	<i>n</i> (scans)	LH	RH	HI	ABS- HI	<i>p</i>	hand pref- erence
Ana Neema	4	4	0	–	–	–	–	29	15	14	–0.03	0.03	0.99	A
Bila Isia	16	12	4	–0.50	0.50	0.08	A	10	5	5	0	0	0.99	A
Donnie	14	8	6	–0.14	0.14	0.79	A	22	10	12	0.09	0.09	0.83	A
Gander	16	10	6	–0.25	0.25	0.45	A	12	4	8	0.33	0.33	0.38	A
Jimmy	11	6	5	–0.09	0.09	0.99	A	8	5	3	–	–	–	–
Jo-T	15	7	8	0.07	0.07	0.99	A	2	2	0	–	–	–	–
Lady	3	0	3	–	–	–	–	5	4	1	–	–	–	–
Lola	13	6	7	0.08	0.08	0.99	A	10	6	4	–0.20	0.20	0.75	A
Maiko	9	6	3	–	–	–	–	10	6	4	–0.20	0.20	0.75	A
Susie	16	8	8	0	0	0.99	A	27	7	20	0.48	0.48	0.02	R
Toby	14	7	7	0	0	0.99	A	0	0	0	–	–	–	–
Unga	25	19	6	–0.52	0.52	0.01	L	33	17	16	–0.03	0.03	0.99	A

–, not enough scans to determine hand preference; A, ambilateral hand preference; ABS-HI, absolute handedness index; HI, handedness index; L, left hand preference; LH, left hand dominant during grooming; *p*, *p* value from 2-tailed binomial test; R, right hand preference; RH, right hand dominant during grooming.

male (Unga) exhibiting a significant left hand preference during unimanual grooming (HI = –0.52, ABS-HI = 0.52, $p < 0.01$). For bimanual asymmetrical grooming, HI scores ranged from –0.20 to 0.48 ($n = 8$). One female (Susie) exhibited right hand preference during bimanual asymmetrical grooming (HI = 0.48, ABS-HI = 0.48, $p < 0.05$) whereas the remaining individuals did not. There was no significant heterogeneity in HI scores for either unimanual ($G = 7.902$, $df = 8$, $p = 0.44$) or bimanual asymmetrical grooming ($G = 7.832$, $df = 7$, $p = 0.35$). Accordingly, individuals did not exhibit task specialization for either unimanual (Wilcoxon signed rank test, $n = 9$, $p = 0.11$) or bimanual asymmetrical grooming ($n = 8$, $p = 0.94$).

Laterality of Tool Use

We recorded and analyzed 1,122 bouts of tool use over the study period. As explored in greater detail elsewhere, the 4 wild-born individuals did not use the artificial termite mound [Boose et al., 2013]. Of the 9 individuals who did use the mound, we excluded 1 individual due to a low number of bouts (Donnie, $n = 3$). One individual (Gilda) had more ambipreferent bouts than either left or right bouts. The remaining 7 individuals exhibited strong hand preference with ABS-HI values ranging from 0.49 to 1 (Table 4). Four individuals exhibited significant left hand preference, and 3 individuals exhibited significant right hand preference. Strong hand preference for both hands resulted in significant heterogeneity ($G = 501.6$, $df = 7$, $p < 0.001$); however, there was no significant group bias (Wilcoxon signed rank test, $n = 8$, $p = 0.2$).

Comparison of Tasks

Only 1 individual exhibited significant hand preference across more than 1 task, Unga. She preferred using her left hand for both unimanual grooming and tool use.

Table 4. Laterality of tool use

Individual	<i>n</i> (bouts)	AH	LH	RH	HI	ABS-HI	<i>p</i>	Hand preference
Ana Neema	68	0	68	0	-1.00	1.00	<0.0001	L
Bila Isia	47	6	32	9	-0.56	0.56	<0.01	L
Donnie	6	3	2	1	-	-	-	-
Gander	65	12	48	5	-0.81	0.81	<0.0001	L
Gilda	311	167	136	8	-0.89	0.89	<0.0001	A
Jo-T	168	23	37	108	0.49	0.49	<0.0001	R
Lola	236	65	20	151	0.77	0.77	<0.0001	R
Maiko	59	12	9	38	0.62	0.62	<0.0001	R
Unga	51	5	45	1	-0.96	0.96	<0.0001	L

-, not enough bouts for statistical testing; ABS-HI, absolute handedness index; A, ambilateral hand preference; AH, the number of insertions using the left hand equaled the number of insertions using the right hand; HI, handedness index; L, left hand preference; LH, a greater number of insertions were completed using the left hand than the right hand in a bout; *p*, *p* value from 2-tailed binomial test; R, right hand preference; RH, a greater number of insertions were completed using the right hand than the left hand in a bout.

When comparing the direction of laterality across tasks, regardless of significant hand preference, unimanual grooming versus bimanual grooming and bimanual grooming versus tool use were both nonsignificant. However, HI scores for unimanual grooming versus tool use were significantly correlated ($n = 5$, $p = 0.03$).

Discussion

Studies of laterality among nonhuman primates are of critical importance to elucidating the evolution of human right-handedness. Our cumulative knowledge is largely drawn from chimpanzees (e.g., Corp and Byrne [2004], Hopkins et al. [2007], McGrew and Marchant [2001]) although the number of studies focusing on bonobos (e.g., Bardo et al. [2015], Chapelain et al. [2011], Harrison and Nystrom [2008], Hopkins et al. [2011, 2015], Neufuss et al. [2017], Shafer [1997]) and other taxa (e.g., capuchins [Lilak and Phillips, 2008], snub-nosed monkeys [Zhao et al., 2010]) are increasing. The present study confirms our prediction that a complex task (termite fishing) would elicit hand preference among captive bonobos whereas a simpler task (grooming) would not. These results also support our original hypothesis that tool use would not elicit task specialization, only hand preference.

Our analysis of grooming did not reveal significant hand preference among this group of captive bonobos. One individual exhibited left hand bias during unimanual grooming, and another exhibited right hand bias during bimanual asymmetrical grooming. This bias may be an artifact of small sample size. What is apparent from Table 3 is that whether we examine unimanual or bimanual asymmetrical grooming, these bonobos are ambipreferent for grooming. We did not detect the effect observed

in Hopkins et al. [2007], where bimanual asymmetrical grooming elicited small but significant task specialization with right hand bias. Our study involved a smaller number of subjects, and thus the absence of the effect may be the product of not enough data points or small sample size. Perhaps grooming requires some manual dexterity and fine motor manipulation, but it is not complex enough to drive the evolution of role differentiation between the 2 hands (e.g., Corp and Byrne [2004]). Our study did not reveal marked laterality; nonetheless, this research highlights the need to investigate unimanual and bimanual asymmetrical grooming across different primate species.

Bonobos are only rarely observed using tools in the wild [White et al., 2008]; however, when presented in captivity with opportunities to perform tool use tasks that are similar to those observed in some well-studied chimpanzee communities, the nature of the tasks elicits hand preference in bonobos [Bardo et al., 2015; Neufuss et al., 2017]. Whatever factors mitigate against the frequent occurrence of tool use in wild bonobos [Furuichi et al., 2015; Koops et al., 2015], these factors do not impede a consistent shared manual response in captive bonobos.

This study highlights that termite fishing elicited strong hand preference among captive bonobos. Laterality was statistically significant in the 8 individuals who used the termite mound with enough bouts for statistical testing. These individuals used their preferred hand during >75% of all fishing bouts. Indeed, 1 individual, Ana Neema, never fished with her right hand ($n = 68$). These findings are consistent with other recent studies that investigated laterality in the tube task [Chapelain et al., 2011; Hopkins et al., 2011; Bardo et al., 2015; Hopkins et al., 2015]. These studies found strong hand preference although a proportion of individuals were ambipreferent. Also concordant with these studies is the lack of a population bias possibly because this tool use task is not difficult enough. The bonobos in this study did not exhibit task specialization for artificial termite fishing unlike the findings of Bardo et al. [2015] although both studies demonstrated strong individual hand preference for this task. While similar, the tasks in this study and that of Bardo et al. [2015] were slightly different. This study used a terrestrial artificial termite mound whereas Bardo et al. [2015] used logs suspended at different heights. This difference may explain why the present study did not reveal task specialization. Additionally, there may be a group effect between these 2 studies; hand preference may be expressed differently despite both groups of bonobos executing similar tasks.

There is considerable discussion regarding the relationship between age and laterality. Previous research on captive bonobos has yielded conflicting results. Shafer [1997] described stronger laterality in adult compared to younger individuals. Chapelain et al. [2011] found no effect of age on the strength of laterality, yet there was a significant effect of age on the direction of laterality. Adults exhibited greater right hand use than nonadults. The authors consider this observation and the occurrence of an age effect in other taxa as support for the maturational hypothesis [Geschwind and Galaburda, 1985]. That is, the slower maturation of the left hemisphere results in an increased use of the right hand as individuals age. Hopkins et al. [2011] found a similar effect; adults exhibited significantly higher HI scores than subadults (reflecting right hand preference). While small, our tool use sample consisted of 3 adults, 4 adolescents, and 1 juvenile. Only 1 adult, Maiko, was determined to exhibit right hand preference while the other 2 adults exhibited left hand preference. Adolescents were equally divided in hand preference: 2 right and 2 left. The juvenile (Gilda) did not

show hand preference during tool use. Our findings are of interest in that these bonobos had never been provided the opportunity to execute this motor action prior to this study. Thus, it appears that experience or practice is not necessary to elicit hand preference in complex tasks. Further studies could explore this question of novelty that is uniquely suited to be answered by studying captive primates. As noted by Chapelain et al. [2011], longitudinal data on a variety of tasks, especially tool use tasks, are needed to adequately address whether age has an effect on the strength or direction of laterality.

Few studies have investigated manual laterality among wild bonobos. Two published abstracts are available on the subject [Ingmanson, 1998, 2005]. Bonobos at Wamba, Democratic Republic of Congo, were reported to consistently use either their right or left hand when peeling sugar cane but there was no group bias. Further study of laterality in wild bonobos is critical, especially of complex bimanual feeding actions that elicit hand preference among chimpanzees [Corp and Byrne, 2004].

Collectively, this study contributes to the understanding of manual laterality in one of our closest living relatives. Using our framework, these data (and that of others) support the hypothesis that certain tasks, such as nut cracking or the tube task, elicit strong hand preference among captive bonobos [Chapelain et al., 2011; Bardo et al., 2015; Neufuss et al., 2017]. Currently available data also demonstrate that bonobos may exhibit task specialization in some contexts (e.g., nut cracking [Neufuss et al., 2017] and food extraction tasks with probes [Bardo et al., 2015]). However, manual specialization or handedness has yet to be demonstrated in this species.

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Disclosure Statement

The authors have no conflicts of interest to declare.

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