RESEARCH ARTICLE

Laterality in Hand Use Across Four Tool-Use Behaviors Among the Wild Chimpanzees of Bossou, Guinea, West Africa

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Population-level right handedness is a human universal, whose evolutionary origins are the source of considerable empirical and theoretical debate. Although our closest neighbor, the chimpanzee, shows some evidence for population-level handedness in captivity, there is little evidence from the wild. Tool-use measures of hand use in chimpanzees have yielded a great deal of variation in directionality and strength in hand preference, which still remains largely unexplored and unexplained. Data on five measures of hand use across four tool-use skills—ant-dipping, algae-scooping, pestle-pounding and nut-cracking—among the wild chimpanzees of Bossou, Guinea, West Africa, are presented here. This study aims to explore age- and sex-class effects, as well as the influence of task motor, cognitive and haptic demands, on the strength and directionality of hand preference within and across all five measures of hand use. Although there was no age- or sex-class effect on the directionality of hand preference, immature ≤10 years old tended to be less lateralized than adults, especially adult females. Nut-cracking, the most cognitively complex of the four behaviors and the only one requiring complementary coordination of both hands, yielded the greatest strength in hand use with all adults expressing exclusive use of one hand over the other, without overall significant directional preference. The least lateralized behavior was pestle-pounding, which required bimanual coordination, but also imposed constraints owing to fatigue. It emerged that only the most hazardous tool use, i.e. ant-dipping, and the sole haptic task, i.e. the extraction by hand of crushed oil-palm heart, were laterally biased and both to the right. Shared motor or grip patterns in tool-use skills failed to reveal any specialization in hand use at the individual level. Finally, Bossou chimpanzees demonstrated a tendency for a population-level right-hand use. Am. J. Primatol. 71:40–48, 2009.   © 2008 Wiley-Liss, Inc.

Key words: chimpanzee; hand use; tool use; laterality; Bossou

INTRODUCTION

The historical view is that population-level handedness is unique to human evolution [Warren, 1980]. Humans across cultures generally exhibit a 77–90% right-hand bias in handedness [Marchant et al., 1995]. Several researchers have proposed that manual specialization was the first step in the evolution of left-hemisphere specialization, which is thought to be crucial to the understanding of the evolution of cognition [Bradshaw & Rogers, 1993; Corballis, 1989] and language in humans [Corballis, 1989, 1991; Frost, 1980; Greenfield, 1991]. In humans, individual hand preference is associated with language hemispheric dominance, with 96% of right-handed individuals and only 70% of left-handed individuals being left-hemisphere dominant for language [Knecht et al., 2000; Rasmussen & Milner, 1977]. This association has resulted in a number of evolutionary and biological theories proposing that hemispheric specialization and language, as well as perhaps other higher cognitive functions, coevolved and are unique characteristics of the human brain [for a review, see Corballis, 1991, 2002]. However, over the past two decades, numerous studies have yielded evidence of population-level hemispheric specialization in a host of nonhuman species ranging from frogs, fish, chickens to chimpanzees for either cognitive, perceptual or motor functions [Bisazza et al., 1998; Bradshaw & Rogers, 1993; Rogers & Andrew, 2002; Ward & Hopkins, 1993]. These findings have therefore shed doubt on whether

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language is a necessary condition for the expression of laterality.

Most major studies of laterality in hand use among large vertebrates have focused on our closest evolutionary neighbor, the chimpanzee (*Pan troglodytes*). The majority of findings in chimpanzees come from captive subjects rather than wild ones in their natural ecological and social setting. Although the captive studies have revealed population-level right handedness across several measures, including reaching [Colell et al., 1995a; Hopkins et al., 2005a], bimanual feeding [Hopkins, 1994], coordinated bimanual actions [Colell et al., 1995b; Hopkins, 1995], throwing [Hopkins et al., 2005b] and manual gestures [Hopkins et al., 2005c], there is still very little to no evidence of population-level handedness among wild subjects. All studies in the wild focusing on simple unimanual nontool-use food acquisition, such as reaching, eating or plucking fruit, have revealed clear ambilaterality in hand use [Boesch, 1991; Marchant & McGrew, 1996; McGrew & Marchant, 2001; Sugiyama et al., 2003]. In addition, no significant population-level handedness emerged from Boesch's [1991] study of handedness among Taï chimpanzees in Côte d'Ivoire. Finally, although termite-fishing is left-hand biased at Gombe, Tanzania [Lonsdorf & Hopkins, 2005], nut-cracking and leaf folding for drinking water at Bossou, Guinea [Biro et al., 2006], nut-cracking and wadge-dipping for drinking water at Taï, Côte d'Ivoire [Boesch, 1991] and ant-fishing at Mahale, Tanzania [McGrew & Marchant, 2007] present a tendency for a right-hand bias.

In spite of the disparities in results emerging from wild or captive studies, there is an emerging consensus that chimpanzees, whether wild or captive, exhibit a high degree of lateralization when performing tool-use [Boesch, 1991; Hopkins et al., 1993; McGrew & Marchant, 2007] or bimanual tasks [Corp & Byrne, 2004; Fletcher, 2006; Fletcher & Weghorst, 2005], which, compared with simple unimanual reaching tasks, present greater motor and cognitive demands. No study among chimpanzees, however, has to date addressed how lateralization in hand use within subjects correlates with differences or similarities between tool tasks in their cognitive, motor or haptic demands. In addition, few have investigated the prevalence of individual hand specialization across tool-use tasks. McGrew et al. [1999] explored laterality at Gombe, Tanzania, within individuals across two tasks—*Strychnos*-pounding and termite-fishing—and found a remarkable congruence in hand use at the individual level. Boesch [1991] also compared individual hand preferences in skilled object manipulation across tasks—hammer use in nut-cracking and wadge-dipping—among 16 Taï chimpanzees. However, he did not find any consistency across tasks. Therefore, although there is some evidence in chimpanzees for

individual hand specialization across tasks, the evidence is weak. In order to ascertain the influence of cognitive, haptic and/or motor requirements of tool tasks on lateral strength and bias in hand use and individual hand specialization, we need data across more than two measures of hand use within a same group of subjects.

This study presents data across four tool-use tasks varying in their cognitive, haptic and motor complexity among the chimpanzees of Bossou, Guinea (*P. troglodytes verus*). First, we investigated differences in the direction and the strength of hand preference between immature subjects (≤ 10 years old) and adults (>10 years old) and between females and males across different tool-use-related measures of hand use. Second, we explored the degree of correlation in the direction of hand preference and differences in the strength of hand preference between the different measures of hand use. Third, we tested the degree of task specialization for each measure, and explored whether this chimpanzee community exhibited a population-level handedness based on the measures of hand use analyzed here. Finally, we discuss these results with respect to the motor, cognitive and haptic demands of each task and emergent patterns of laterality in hand use in chimpanzees.

METHOD

Study Site and Subjects

Bossou ($7°39'N$ and $8°30'W$) is situated in southeastern Guinea, West Africa, 6 km from the foot of the Nimba Mountains on the border with Côte d'Ivoire and Liberia. A small community of chimpanzees inhabits the forest surrounding the village. This community of wild chimpanzees has been habituated to observers, without provisioning, and has ranged in size between 12 and 23 individuals ever since 1976 [Matsuzawa, 2006; Sugiyama, 1981, 1999]. It currently numbers 13 individuals. For further details, refer to Sugiyama [1999], Matsuzawa et al. [2001] and Humle and Matsuzawa [2001, 2004]. We gathered data on a total of 24 individuals between June and August 1995, June and September 1997, August and October 1999, June and September 2000, 2001, June 2003 and March 2004, and July and September 2005, 2006. The subjects included 14 adults (>10 years old, 10 females and 4 males) and 14 immature individuals (≤ 10 years old, 7 females and 7 males) (Table I). We gathered data on four subjects (three females and one male) across both age categories. This study complies with the American Society of Primatology principles for the ethical treatment of nonhuman primates and was approved by the relevant national authorities in Guinea where the research was conducted and by the Primate Research Institute of Kyoto University.

TABLE I. Summary of Number of Responses and Handedness Index (HI) Scores for Each Subject Classed by Age and Sex Across All Five Measures of Hand Use

Subject	Age-class	Sex	No. responses					HI responses				
			AD	NC	AG	PP	EX	AD	NC	AG	PP	EX
Fana[a]	A	F	18	43		25	24	1.00	1.00		1.00	1.00
Fotaiu	A	F	77	33	0	69	92	0.97	1.00		0.45	0.93
Jire	A	F	337	328	22	44	85	−0.48	−1.00	−1.00	0.91	0.98
Kai	A	F	46	49	0	39	39	−1.00	1.00		−0.95	−0.79
Nina	A	F	51	0	0	56	59	0.61			1.00	1.00
Pama	A	F	18	0	4	18	25	0.56		−1.00	−0.78	−1.00
Pili	A	F	0	36	0	11	20		1.00		−1.00	1.00
Velu	A	F	75	43	0	45	48	1.00	1.00		0.47	0.96
Vuavua	A	F	93	118	0	27	36	−0.53	−1.00		−0.85	−0.28
Yo	A	F	582	217	0	0	0	0.91	−1.00			
Foaf	A	M	126	802	180	28	36	0.24	1.00	0.29	0.50	0.72
Na	A	M	46	118	79	40	41	−1.00	1.00	1.00	−0.95	−0.76
Tua	A	M	89	178	147	71	73	0.84	−1.00	0.56	0.04	0.86
Yolo	A	M	236	359	51	0	0	0.96	−1.00	1.00		
Fanle	I	F	263	59	0	208	150	0.44	1.00		0.01	−0.37
Fotaiu	I	F	115	37	0	47	42	0.13	1.00		0.40	0.43
Joya	I	F	36	0	0	0	17	0.61				0.53
Nto	I	F	185	56	0	87	92	0.43	1.00		0.98	0.37
Pili	I	F	0	67	0	29	45		0.97		−0.38	1.00
Veve	I	F	16	0	0	0	0	−0.50				
Vuavua	I	F	89	60	0	18	16	0.19	−0.80		−0.56	−0.13
Fokaye	I	M	27	0	0	15	23	0.41			0.33	0.57
Jeje	I	M	502	318	495	33	22	0.17	−0.96	0.77	−0.33	−0.09
Juru	I	M	227	0	0	122	138	0.52			0.72	0.25
Peley	I	M	237	76	35	124	231	−0.16	−1.00	−0.54	−0.71	0.26
Poni	I	M	84	132	36	26	21	0.81	1.00		0.23	0.90
Vui	I	M	22	203	32	36	51	−0.09	−0.93	−0.75	−0.83	0.29
Yolo	I	M	147	248	0	0	0	0.73	1.00			

Age-class: A, >10 years old; I, ≤10 years old; Sex: F, female; M, male; AD, ant-dipping; NC, nut-cracking; AG, algae-scooping; PP, pestle-pounding; EX, extraction of palm heart.
[a]Fana has a dislocated left shoulder and therefore her HI scores were not used in the data analysis.

MEASURES OF HAND PREFERENCE

On the basis of both video recordings and ad libitum observations, we gathered laterality data in hand use across four tool-use behaviors, i.e. nut-cracking, pestle-pounding, ant-dipping and algae-scooping, and a reaching task required for completing the pestle-pounding task (see below). We recorded both laterality in hand use for bouts and individual responses [McGrew & Marchant, 1996]. On the one hand, a tool-use bout was defined as a period during which an individual is performing a tool-using behavior. A bout ends when no tool is held, the hand performs an intervening activity, such as self-grooming, or when the chimpanzee changes position [McGrew & Marchant, 1992]. A response, on the other hand, failed to consider independence of data points based on the above criteria. For example, if a chimpanzee cracked a series of ten nuts using its right hand for hammering or dipped with its right hand 10 times for ants without changing position, performing an intervening activity or releasing the hammer or stick tool, we considered this to represent

a single right-hand bout and ten right-hand responses. We detail below the measures of hand use retained across each of the four tool-use behaviors recorded. For further description of the tool-use behaviors, refer to Ohashi [2006].

Nut-Cracking

Chimpanzees at Bossou are renowned for their use of a pair of stones, one as a hammer and the other as an anvil, to crack open oil-palm nuts (*Elaeis guineensis*) [Sugiyama & Koman, 1979]. Among all the tool-use behaviors performed by wild chimpanzees, nut-cracking is the most cognitively sophisticated [Matsuzawa, 1999]. Nut-cracking at Bossou requires the combination of three movable objects, i.e. the hammer and anvil stone and the nut, as well as complementary coordination of both hands, with exclusive roles assigned to each hand. Indeed one hand is typically used to place a target nut on the surface of the anvil stone, whereas the other hand is employed for hammering. Similar to previous studies, we used the hammer hand as the measure of

hand use. Several studies have already revealed that adult chimpanzees at Bossou consistently use the same hand for cracking nuts [Fushimi et al., 1991; Sakura & Matsuzawa, 1991; Sugiyama et al., 1993] and that there is high degree of matching between maternal siblings, whereas none between mother and offspring [Biro et al., 2006; Matsuzawa et al., 2001].

Pestle-Pounding

Pestle-pounding consists of several discrete sequential behavioral components [Yamakoshi & Sugiyama, 1995]. This hierarchically complex tool-use behavior, requiring bimanual coordination, is unique to the Bossou community. Pestle-pounding takes place at the center of the crown of an oil palm (*E. guineensis*). First the young fronds and shoots are removed, thus providing access to the apical meristem. A chimpanzee then uses a palm frond, which is often modified by shortening and/or removing the side leaflets, as a pestle to pound at the center of the palm crown. This pounding action results in a softening of the palm heart. When pestling, the chimpanzee either sits at the top of the crown on a palm frond or stands bipedally. After each pounding action, the tool is laid aside and the chimpanzee inserts its arms into the hole to extract the resulting mash of sweet and juicy fibers. For pestle-pounding, we gathered two measures of hand use. The first is the hand used to hold the pestle when pounding. In most cases, chimpanzees used only a single hand, but when two hands were used (30% of subjects), we considered the upper hand as the dominant hand as it is the hand that is used to guide the frond into the cavity and which provides the most downward force during the pounding action. The second measure was the hand used for extracting the palm heart. Extraction required the chimpanzee to insert most of or the whole of its arm up to the shoulder into the deep hole or central cavity to gain access to the pulped apical meristem. The chimpanzee is then obliged to rely on active touch in order to extract the softened palm heart. A bout of extraction typically involved the chimpanzee inserting one arm into the excavated cavity to reach for a handful of crushed palm heart, which it then consumed. The bout ended when the chimpanzee changed position at the top of the oil palm or performed an intervening activity with the hand it had just used. Each insertion of the hand into the cavity was considered as a separate response.

Ant-Dipping

Ant-dipping requires the manufacture and use of a stick or stalk of vegetation as a tool to gather army ants (*Dorylus* spp.). Ant-dipping typically involves a chimpanzee holding the tool between its index and middle finger and performing a back and forth movement of the tool to stimulate the ants to attack the tool [Humle & Matsuzawa, 2002]. While dipping, the chimpanzee may (1) stand tripedally on the ground, (2) sit on the ground or above the ground on a bentover sapling or vine sometimes leaving the free hand idle or employing it for support or (3) hang from above the ground with the nondipping hand serving as support. Ants that climb the tool are then ingested. For ant-dipping, the measure of hand use was the hand used in holding the tool when dipping.

Algae-Scooping

Similar to ant-dipping, algae-scooping requires a chimpanzee to select a stalk or stick, which it breaks off using its teeth. If necessary, it then half-cups one hand at the stem base and strips the leaves off the tool with a swift, upward motion of the hand. A tool more or less devoid of protruding leaves is thus obtained. The tool, held between the index and the middle finger, the type of fine grip also often observed in the cases of ant-dipping, is then inserted, distal end first, into the water. A gentle swiveling action of the wrist usually follows, allowing the chimpanzee to scoop surface algae (*Spirogyra* sp.) from the pond surface [Matsuzawa et al., 1996]. Algae-scooping occurs either while sitting on the ground leaving the nondominant hand idle or tripedally, as also observed occasionally during nut-cracking or more commonly during ant-dipping. For algae-scooping, the hand use measure used was the hand used for manipulating the tool when scooping algae.

Data Analysis

We calculated a handedness index (HI) score for each individual and measure based on both bouts and responses. The HI value was calculated by subtracting the number of right-handed from the number of left-handed bouts or responses and dividing by the total number of bouts or responses: $HI = (R-L)/(R+L)$. Positive values reflected a right-hand bias, whereas negative values reflected a left-hand bias. The paired samples correlation between the HI values based on bouts and the HI values based on responses for each measure yielded in all cases r values greater than 0.96 with $P < 0.0001$. In addition, as all statistical results presented here were the same whether based on bouts or responses, only results based on the analysis of individual HI values based on individual responses are summarized herein.

We used the absolute measure of HI to compare the strength of lateralization in hand use between immature and adult subjects. As appropriate, we systematically checked the data for normality using a normality probability plot and a Kolmogorov–Smirnov test. If the data deviated significantly from normality, we used nonparametric rather than parametric statistics. All tests were two-tailed with an α level set at $P < 0.05$. We carried out within-subjects
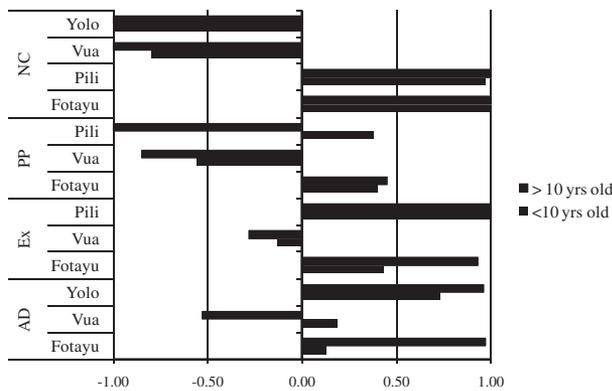
Fig. 1. Within-subject mean HI scores across four measures of hand use (algae-scooping was excluded because of insufficient data; NC, nut-cracking; PP, pestle-pounding; Ex, extraction of palm heart; AD, ant-dipping). HI, handedness index.
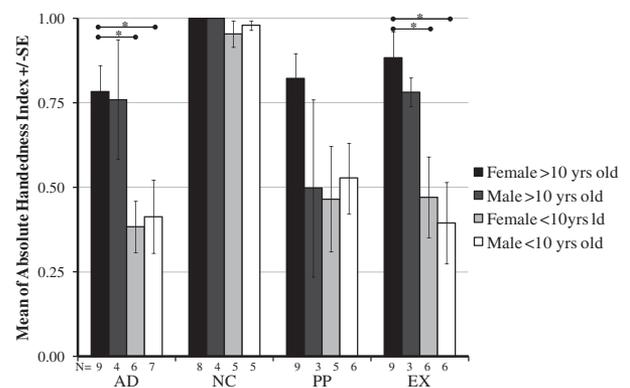

Fig. 2. Mean of absolute handedness index (HI) scores between age- and sex-classes for four measures of hand use across three tool-use behaviors (AD, ant-dipping; NC, nut-cracking; PP, pestle-pounding; EX, extraction).

analysis whenever possible. When conducting between-subjects analyses of the data, we excluded the data for subjects ≤ 10 years old for whom we also had data when mature (> 10 years old).

RESULTS

Hand Preference by Age- and Sex-Classes

Within each of the four measures for which we gathered data for a minimum of three subjects across age-, i.e. ≤ 10 or > 10 years old, and sex-classes (thus excluding algae-scooping), we found no difference in mean HI score between sex- or age-class. In addition, if we analyze the data within subjects between age-classes, there was no significant difference in HI scores (Fig. 1).

However, when analyzing the absolute values of HI scores, we found significant differences between age- and sex-classes for ant-dipping and extraction (analysis of variance: ant-dipping: $F_{3,22} = 4.608$, $P = 0.012$; extraction: $F_{3,20} = 5.699$, $P = 0.005$), whereas none for nut-cracking and pestle-pounding (Fig. 2). A Tukey honestly significant difference post hoc test revealed that, for both ant-dipping and extraction, adult females showed a stronger mean absolute HI score than both female (ant-dipping: $P = 0.036$; extraction: $P = 0.030$) and male (ant-dipping: $P = 0.044$; extraction: $P = 0.009$) subjects ≤ 10 years old (Fig. 2). Therefore, for these two measures of hand use, young ≤ 10 years old were less strongly lateralized than adult females. Although no significant difference emerged in the within-subjects' analysis, there was a clear tendency for subjects to exhibit greater strength in hand preference as adults than as immatures (Fig. 1).

Hand Specialization and Strength of Hand Preference

As there was no significant difference in HI between individuals ≤ 10 years and > 10 years, we pooled those together ensuring a single data point for each subject. We excluded the data on the four subjects ≤ 10 years for whom data were also available as adults. We ran correlations between the different measures. The measures of hand use for ant-dipping, pestle-pounding and palm heart extraction were all positively correlated, whereas there was no correlation between the other measures, i.e. nut-cracking and algae-scooping (Table II). For subjects for whom data were gathered across all five measures, only 1/8 (Foaf, see Table I) matched in the directionality of hand use across all measures. However, for those subjects for whom data were available for ant-dipping, pestle-pounding and palm heart extraction hand use measures, 72% (13/18) matched in the directionality of their hand use across all three measures.

As there was an age effect on the strength of hand preference, we included only data on adults in the following analysis aimed at comparing the strength of the hand preference across all five measures of hand use. The strength of preference in hand use for nut-cracking emerged as the strongest with 100% of subjects exhibiting exclusiveness in hand use. There was no significant difference between nut-cracking and algae-scooping, as 4/6 adult subjects (66%) showed exclusive use of one hand during algae-scooping. However, nut-cracking differed significantly from ant-dipping, pestle-pounding and extraction (Kruskal–Wallis test: $\chi^2(4) = 28.260$, $P = 0.0001$). Indeed fewer adult subjects (range: 25–33%) showed exclusive use of one hand when performing these latter behaviors.

Task Specialization and Population-Level Handedness

A one-sample t-test on the HI scores with only one HI value per subject revealed a significant right-hand bias for ant-dipping and extraction, whereas no bias either to the right or to the left emerged for the other three measures of hand use (one-sample t-test:

TABLE II. Summary of Correlational Statistics Between the Five Different Measures of Hand Use (Statistically Significant Correlations Are Presented in Bold, Adjusted P Level Corrected for Multiple Correlations: $\alpha \leq 0.005$)

Measure	Ant-dipping	Nut-cracking	Algae-scooping	Pestle-pounding	Extraction
Ant-dipping		$r_s = 0.151$, $N = 17$, $P = 0.562$	$r = 0.156$, $N = 9$, $P = 0.688$	$r = 0.614$, $N = 19$, $\boldsymbol{P = 0.005}$	$r = 0.602$, $N = 20$, $\boldsymbol{P = 0.005}$
Nut-cracking			$r_s = 0.193$, $N = 8$, $P = 0.648$	$r_s = 0.130$, $N = 16$, $P = 0.632$	$r_s = 0.106$, $N = 16$, $P = 0.696$
Algae-scooping				$r = -0.085$, $N = 8$, $P = 0.841$	$r = -0.086$, $N = 8$, $P = 0.840$
Pestle-pounding					$r = 0.638$, $N = 20$, $\boldsymbol{P = 0.002}$
Extraction					
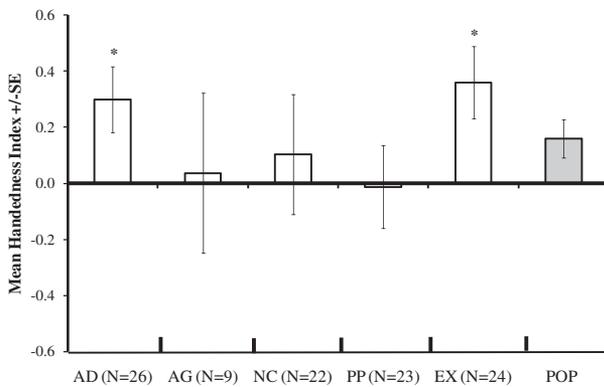
Fig. 3. Mean handedness index (HI) score across five measures of hand use across four tool-use behaviors and population-level mean HI (*$P < 0.05$; AD, ant-dipping; AG, algae-scooping; NC, nut-cracking; PP, pestle-pounding; EX, extraction of palm heart; POP, population-level mean).

ant-dipping: $t_{22} = 2.206$, $P = 0.038$; extraction: $t_{20} = 2.434$, $P = 0.024$; nut-cracking: $t_{17} = 0.489$, $P = 0.631$; algae-scooping: $t_8 = 0.129$, $P = 0.901$ and pestle-pounding: $t_{19} = 0.070$, $P = 0.945$) (Fig. 3). Nevertheless, both nut-cracking and algae-scooping presented a positive mean HI score. Pestle-pounding was the only measure to present a negative mean HI score across subjects, although only marginally so (Fig. 3). If one takes the mean of the mean HI scores for each measure of hand use, to control for unbalanced distribution of data within subjects across all measures, the resulting population mean HI score was positive and tended toward a significant population-level right handedness (one-sample t-test: $t_4 = 2.395$, $P = 0.075$) (Fig. 3).

DISCUSSION

Our findings did not reveal any significant differences between age- and sex-classes in HI scores for the measures of hand use analyzed here. Although, human females tend to be slightly more right handed than males [Kimura, 1993; Springer & Deutsch, 1993], only one study so far among wild

chimpanzees has revealed a similar pattern in sex difference in hand use [Corp & Byrne, 2004]. Corp and Byrne's study of skilled bimanual peeling of the thick-skinned fruit *Saba florida* revealed that males showed a population-level left-hand preference, whereas females exhibited a population-level right-hand preference alongside a stronger lateralization in hand use than males. However, in a compilation of published data on tool use among wild chimpanzees, Lonsdorf and Hopkins [2005] found no effect of sex on population-level handedness. Although our study revealed no difference across age- and sex-classes in the directionality of hand preference in hand use, our results do suggest that adults, especially females, have a significantly stronger preference for using one hand over the other for ant-dipping and palm heart extraction than immature individuals whether male or female. This result corroborates similar findings looking at age-class differences in hand preference in chimpanzees in captivity for simple reaching [Tonooka & Matsuzawa, 1995] and for nut-cracking at Taï [Boesch, 1991]. The stronger preference in hand use in adult females also provides some support for the tendency noted by Corp and Byrne [2004] that female chimpanzees exhibit a stronger lateralization in hand use than males.

Although all four measures of hand use requiring tool manipulation demonstrated a strong degree of lateralization regardless of directionality, exclusive use of one hand was most prevalent for nut-cracking, the most cognitively complex tool-use task of the four, requiring complementary coordinated action of both hands and the spatial and temporal combination of three external objects. The high degree of lateralization for nut-cracking was also extremely high among individuals ≤ 10 years old, compared with the other measures, suggesting that, for cognitively complex behaviors, the establishment of a hand preference arises quite early in development. Although both nut-cracking and pestle-pounding differed in the substrate material used and in the power grip employed in handling the tool, both necessitated a targeted repeated downward power

action and complementary coordination of both hands in action sequence. In spite of these similarities, there was no correlation in the HI scores between these two measures within subjects and pestle-pounding was the least lateralized tool-use measure. However, these two behaviors differ markedly in one respect. Although nut-cracking is performed terrestrially and imposes little postural constraint, pestle-pounding is most often performed bipedally at the crown center of the oil palm, thus requiring both strength and balancing skills. Although previous studies in primates have suggested that postural instability, induced, for example, by a bipedal stance, tends to favor a stronger expression of handedness [e.g. Hopkins et al., 1993; Ward et al., 1993], the added element of fatigue in performing pestle-pounding likely explains the absence of a correlation in HI scores with nut-cracking and its weaker lateral strength.

Our findings do show, however, that haptic tasks, such as extraction, present a high degree of lateralization in hand use. Indeed extraction, a unimanual reaching task entailing no tool manipulation, unlike the other four measures, was strongly lateralized with 38% (8/21) of subjects presenting an absolute HI score ≥ 0.9. Finally, although exclusiveness in hand use was apparent for nut-cracking, exclusiveness in hand use across tasks within a same able-bodied individual was extremely rare (1/20 subjects, i.e. Pili, see Table I), confirming similar results in captivity [Wesley et al., 2002].

Although ant-dipping and algae-scooping both imposed very similar cognitive and motor demands, grip type, i.e. precision grip, and required manipulation of a similar tool type, i.e. stick or stalk of vegetation, hand use and preference also differed significantly between the two. Algae-scooping presented greater lateral strength than ant-dipping. In addition, there was no correlation between these two measures within subjects. However, it must be noted that ant-dipping does differ to some respect from algae-scooping in that, rather than a single twisting and scooping action of the wrist, it requires a more controlled and finer manipulation of the tool most often combined with a localized rhythmic back and forth movement of the tool among biting army ants that induce frequent positional changes not as frequently observed during algae-scooping. Although ant-dipping and algae-scooping do differ in their finer motor details and postural constraints, our results importantly suggest that hand specialization at the individual level does not depend on similitude in tool type being manipulated, grip type being used or general motor performance.

Ant-dipping, pestle-pounding and extraction were the only measures demonstrating a significant correlation within subjects in HI score. Although pestle-pounding was the most ambilateral measure among the five, it is likely that during performance of the entire pestle-pounding activity, there was an individual tendency to employ the same hand for both pestle-pounding and palm heart extraction. Pestle-pounding was the most arboreal of the four tool-use tasks and the pounding action most often performed bipedally at the crown center of the oil palm required strength, as well as balancing skills, a trade-off that might explain the weaker pattern in strength of hand use observed in the performance of this hierarchically and sequentially complex skill. Such a pattern of trade-off provides support for McGrew and Marchant's [2007] proposal that chimpanzees performing tool-use behaviors, such as ant-fishing, which are performed arboreally and require postural support, tend to exhibit less lateralization than those performing other tool-use behaviors.

Ant-dipping and extraction were the only two measures showing a significant bias in hand preference. Both were indeed significantly right handed. The right-hand bias found among the wild chimpanzees of Bossou for extraction supports Lacreuse et al.'s [1999] finding of a similar right-hand preference for an analogous haptic task among captive chimpanzees. This task required the chimpanzees to insert their arms into an opaque bucket enclosed in a metal frame attached to the mesh on the inside of the home cage to recover food contained within. Lonsdorf and Hopkins [2005] also showed that termite-fishing, a haptic tool-use task that requires the insertion of a tool into a narrow hole and is relatively independent of positional constraints, was significantly laterally biased to the left among the wild chimpanzees of Gombe, Tanzania. Haptic tasks in chimpanzees therefore appear to be significantly laterally biased. However, why does termite-fishing differ in directionality from these other haptic measures of hand use? One obvious difference between these tasks is the medium for sensory feedback. The sensory feedback is provided by the hand for extraction and Lacreuse's task, whereas by the tool for termite-fishing. Whether this difference is relevant or not remains to be explored.

Finally, based upon the five measures of hand use presented here, Bossou chimpanzees tend to present a right-hand bias at the population level. If one incorporates additional data on water drinking and nut-cracking from Bossou reported in Biro et al. [2006] and Sousa et al. [in press] 60% (66/110) of individual task-specific data points based on binomial scores were significantly right-hand biased, 10% (11/110) were ambilateral and 30% (33/110) were left-hand biased. These results do suggest that Bossou chimpanzees present a strong population-level right-hand bias for complex tasks, providing support for a similar overall right-hand bias reported among captive chimpanzees and for a tendency also noted in other wild chimpanzee communities [e.g. Taï, Côte d'Ivoire: Boesch, 1991; Mahale, Tanzania: McGrew & Marchant, 2007]. Nevertheless, we need

further data on laterality in hand use across different measures to determine precisely the prevalence of population-level right handedness among wild chimpanzees. In addition, we need to gather more data, especially longitudinal and developmental, on identical manual tasks across chimpanzee communities to test whether emerging patterns in strength and directionality in hand use are consistent between and within communities and what role ontogeny plays in determining mature patterns in hand use. Only then will we be able to shed more light on the evolution and the origins of lateralization in humans and the potential selective roles of genetics, cognition and culture on hand use in humans.

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