RESEARCH ARTICLE

Lateralization and Performance Asymmetries in the Termite Fishing of Wild Chimpanzees in the Goualougo Triangle, Republic of Congo

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The nearly universal right hand preference manifested by human populations is one of the most pronounced manifestations of population-level lateralization. Morphological and archeological evidence indicate that this behavioral specialization may have emerged among our hominin ancestors. Whether population-level behavioral asymmetries are evident in non-human animals remains a topic of considerable scientific debate, with the most consistent evidence of population-level trends emerging from studies of chimpanzees (*Pan troglodytes*). However, previous studies of population-level lateralization in wild apes have relied upon data sets pooled across populations to reach adequate sample sizes. Our aim was to test for population-level handedness within a single wild chimpanzee population, and also to determine if performance asymmetries were associated with handedness. To address these questions, we coded handedness and duration of fishing probe insertions from remote video footage of chimpanzee visitation to termite nests (totaling 119 hr) in the Goualougo Triangle, Republic of Congo. Similar to reports from other populations, chimpanzees in the Goualougo Triangle showed robust individual hand preferences for termite fishing. There were 46 right-handed, 39 left-handed, and 4 ambiguously-handed individuals. Though we did not detect an overall significant population-level handedness ($t(88) = 0.83$, n.s.) in this study, males showed a greater right hand preference than females. Further, we found that average dipping latencies were significantly faster for right- compared to left-handed chimpanzees. Possible explanations and evolutionary implications of taxa- and task-specific patterns of population-level laterality are discussed. Am. J. Primatol. 78:1190–1200, 2016.   © 2016 Wiley Periodicals, Inc.

Key words: laterality; handedness; tool use; chimpanzee

INTRODUCTION

Population-level lateralization is defined as the leftward or rightward expression of certain traits or behaviors by a statistical majority of individuals within a sample [Corballis, 1992; Davidson, 1995; Hellige, 1993]. One of the most pronounced manifestations of population-level behavioral lateralization in humans is handedness. Although there is some cultural variation, every human population studied to date exhibits a significant right hand preference, including data from traditional human societies (see Fig. 1) [Marchant et al., 1995; Perelle & Ehrman, 1994; Porac & Coren, 1981; Raymond & Pontier, 2004]. That is to say, a significant majority of individuals prefer to use the right hand for different motor actions. Furthermore, individual differences in hand preference are associated with variation in motor performance or skill [Annett, 2006]. Humans typically perform better with their dominant compared to non-dominant hand, as demonstrated across a variety of tasks including finger tapping, the Annett, or Purdue Peg Board tasks [Brown et al., 2004; Corey et al., 2001; Elliott & Roy, 1996; Peters,
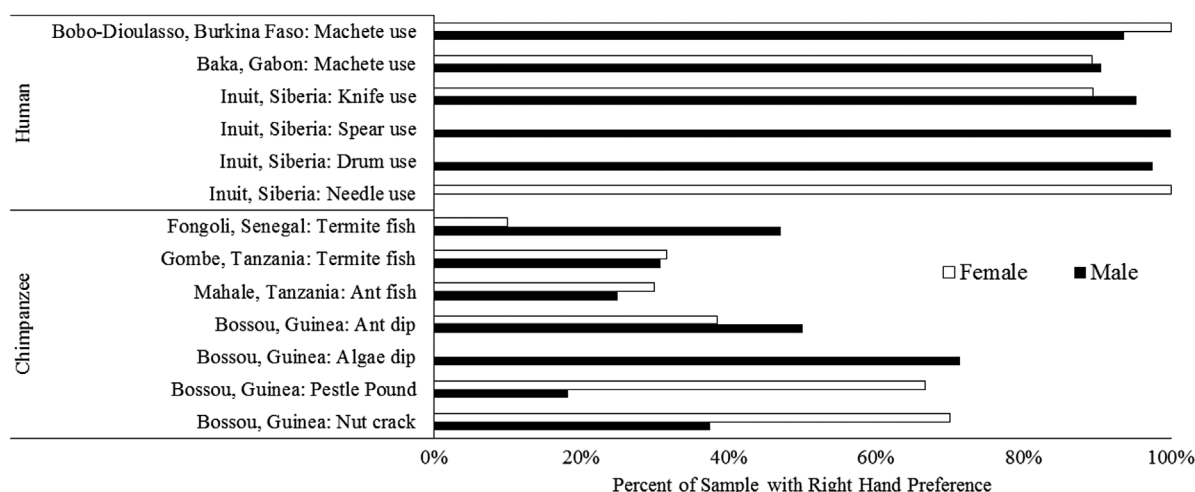
Fig. 1. Comparing sex differences in right hand preference across human and chimpanzee populations. To facilitate comparability, we have only presented information from single tool using tasks assessed in naturalistic contexts. Inuit, Siberia [Faurie et al., 2005]: Needle use ($n = 21$), Drum use ($n = 40$), Spear use ($n = 25$), Knife use ($n = 62$); Bobo-Dioulasso, Burkina Faso [Faurie et al., 2005]: Machete use ($n = 353$); Baka, Gabon [Faurie et al., 2005]: Machete use ($n = 403$); Fongoli [Bogart et al., 2012]: Termite fishing ($n = 27$); Gombe [Lonsdorf & Hopkins, 2005; McGrew & Marchant, 1992]: Termite fish ($n = 32$); Mahale [McGrew & Marchant, 1996]: Ant fish ($n = 18$); Bossou [Humle & Matsuzawa, 2009]: Ant dip ($n = 23$), Algae scoop ($n = 9$), Pestle pound ($n = 20$), Nut crack ($n = 18$).

1980; Steenhuis & Bryden, 1999]. These collective results have led some to suggest that the left hemisphere is dominant for praxic motor control which effectively translates sensory information stored in the brain to motor action [Amunts et al., 1997; Arbib, 2005; Johnson-Frey, 2004; Rizzolatti & Arbib, 1998]. Moreover, because the left hemisphere is dominant for praxic functions, it has been further suggested that neural circuits within this hemisphere were co-opted to control fine motor skills necessary for speech and related control of oro-facial musculature [Arbib, 2005; Corballis, 2002; Rizzolatti & Arbib, 1998].

Whether population-level behavioral asymmetries are evident in non-human animals remains a topic of considerable scientific debate. Though historically population-level asymmetries were considered unique to humans [Cashmore et al., 2008; Crow, 1998; Ettlinger, 1988; Warren, 1980], studies in a variety of vertebrate species in the past 20 years have increasingly challenged this long held view [Hamilton & Vermeire, 1988; MacNeilage et al., 2009; Ocklenburg et al., 2012; Rogers & Andrew, 2002; Strockens et al., 2013]. For example, toads prefer to use their right paw to remove substrates from their head [Bisazza et al., 1996] and a variety of asymmetries in visual discrimination for different classes of stimuli have been found in birds [Andrew et al., 2000; Güntürkün, 1997]. With specific reference to hand preference, there is some evidence of population-level handedness for certain tasks and in some species, though the data are somewhat inconsistent between species [Fagot & Vauclair, 1991; Hook-Costigan & Rogers, 1997; Hopkins, 2006; Marchant & McGrew, 1991; McGrew &

Marchant, 1997]. For instance, 10 nonhuman primates species have been tested on a measure of coordinated bimanual actions referred to as the tube task [Hopkins et al., 2011; Meguerditchian et al., 2013]. When the data are summed across all studies, gorillas, chimpanzees, and baboons show population-level right handedness whereas orangutans, red-capped mangabeys, snub nose monkeys, and spider monkeys show a significant left hand bias [Hopkins et al., 2011; Maille et al., 2013; Nelson & Boeving, 2015; Nelson et al., 2015; Schweitzer et al., 2007; Vauclair et al., 2005; Zhao et al., 2012]. Bonobos, capuchin, squirrel, rhesus, and barbary macaque monkeys fail to show a population-level bias [Bennett et al., 2008; Chapelain et al., 2011; Meguerditchian et al., 2012; Meunier & Vauclair, 2007; Schmitt et al., 2008; Spinozzi et al., 1998].

The most consistent evidence of population-level handedness in nonhuman primates has come from studies in great apes [Meguerditchian et al., 2015] and particularly chimpanzees. In addition to the tube task, significant population-level handedness has been reported in captive chimpanzees for manual gestures, throwing, bimanual feeding, and bimanual grooming [Hopkins, 2013a]. Furthermore, captive chimpanzees show population-level right handedness when characterized across multiple measures of hand use [Hopkins et al., 2013]. In wild chimpanzees, fewer studies with relatively small samples sizes have examined hand preferences, primarily for varieties of tool use [Biro et al., 2003, 2006; Boesch, 1991; Bogart et al., 2012; Humle & Matsuzawa, 2009; Lonsdorf & Hopkins, 2005; Marchant & McGrew, 2007; McGrew & Marchant, 1992, 1996; Nishida et al., 2012; Sugiyama et al.,

1993]. When the data are combined across study sites, wild chimpanzees show a left hand preference for termite fishing and right hand preferences for wadge dipping, and ant dipping (see Fig. 2). There is also some evidence of population-level right handedness for visually guided reaching and grooming [Boesch, 1991; Humle & Matsuzawa, 2009; Marchant & McGrew, 1996; McGrew & Marchant, 2001]. Finally, there is one report of a sex difference in bimanual feeding with males showing a left hand preference and females showing a right hand bias [Corp & Byrne, 2004]. Two studies on hand use for spontaneous behaviors in wild chimpanzees failed to reveal significant hand preferences at both the individual and population-level [Marchant & McGrew, 1996; McGrew & Marchant, 2001]. There is also evidence that posture affects strength of hand preference in tool use [Braccini et al., 2010]. An analysis of tool use and asymmetry using quantitative genetics showed that both tool using skill and handedness were significantly heritable in captive chimpanzees [Hopkins et al., 2015]. However, it is clear that environmental and cultural factors also play a role in expressions of laterality, at least in humans, and perhaps non-human primates.

One aim of the current study was to further examine hand preference for termite fishing in wild chimpanzees. As noted above, studies on termite fishing in wild chimpanzees have reported significant left hand preferences and direct comparison between chimpanzees residing at the east African site of Gombe in Tanzania, and the West African site of Fongoli in Senegal found no significant difference in hand preference [Bogart et al., 2012]. In this study, we sought to examine whether the evidence of left handedness in termite fishing was restricted to the chimpanzees at these two sites or if it would also be evident in the Goualougo Triangle which is located in central Africa's Congo Basin.

A second aim of this study was to assess asymmetries in hand skill for termite fishing. There are remarkably few studies that have examined asymmetries in motor skill performance in nonhuman primates [Andrews & Rosenblum, 2001; Christel, 1994; Christel et al., 1998; Hopkins et al., 1992; Rigamonti et al., 1998]. Field studies of performance are even rarer, with Byrne and Byrne's (1991) study of performance of gorilla food processing being the most notable. In captive chimpanzees, but not capuchin monkeys, there is some evidence that the right hand performs significantly better than the left when grasping small food items [Hopkins et al., 2002; Hopkins & Russell, 2004; Spinozzi et al., 2004]. In captive chimpanzees, performance asymmetries have also been found for tool use. Hopkins et al. [2009] measured hand preference and performance on a simulated termite fishing task in a sample of 192 chimpanzees and found that right- and left-handed subjects had shorter latencies when inserting a small stick into a hole when they used their dominant compared to non-dominant hand. In other words, right-handed subjects took less time to insert the stick on each dip with the right compared to left hand. In contrast, left-handed subjects took less time
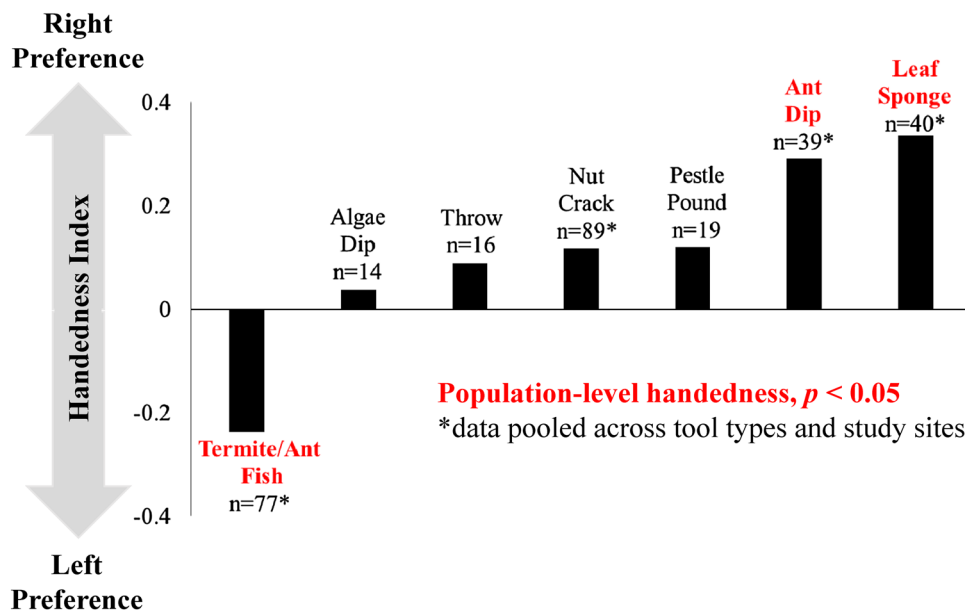

Fig. 2. Summary of handedness data for tool use from wild chimpanzees (Termite Fishing: Bogart et al., 2012; Lonsdorf & Hopkins, 2005; McGrew & Marchant, 1992, 1996; Ant Dipping: Humle & Matsuzawa, 2009; Marchant & McGrew, 2007; Leaf Sponging: Biro et al., 2003; Boesch, 1991; Nut Cracking: Biro et al., 2003; Boesch, 1991; Pestle Pounding: Humle & Matsuzawa, 2009; Algae Dipping: Humle & Matsuzawa, 2009; Sugiyama et al., 1993; Throwing: Nishida et al., 2012). * indicates significant population-level handedness at $P < 0.05$ based on one sample t-tests on the handedness index scores.

to insert the stick with their left compared to right hand. No significant differences were found in the average latency to insert a fishing probe by the dominant and non-dominant hands. Here, we measured the latency to insert a fishing probe into a termite mound in relation to hand use in a sample of wild chimpanzees as a means of assessing performance asymmetries. We hypothesized that wild chimpanzees would have shorter dipping latencies for their dominant compared to non-dominant hand. Further, in light of the assumption that the left hemisphere is dominant for motor skill, we further tested whether latencies in dipping differ between right- and left-handed individuals.

Finally, there is also some evidence of sex differences in motor skill in humans with females performing better than males, though not all studies have reported significant findings [Kimura, 1993; Peters, 1980; Peters et al., 1990]. Therefore, we also tested for sex differences in tool use performance.

METHODS

Study Site

The Goualougo Triangle study area is located along the southern boundary of the Nouabalé-Ndoki National Park (N $2°05' - 3°03'$; E $16°51' - 16°56'$), Republic of Congo. The climate in the northern Republic of Congo can be described as transitional between the Congo-equatorial and sub-equatorial climatic zones. All the field protocols, data collection procedures, and data analyses were conducted in accordance with wildlife research protocols, and ethical standards of the Ministry of Science and Technology of the Republic of Congo, the Ministry of Forest Economy of the Republic of Congo, and the Wildlife Conservation Society of the USA. All research reported in this manuscript complied with the protocols approved by the Animal Care and Use Committee of Washington University in Saint Louis, the legal requirements of the Republic of Congo, and adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non Human Primates.

Data Collection Protocols

Direct observations of the chimpanzees in the Goualougo Triangle have been ongoing since February 1999. Individual chimpanzees were identified from their distinct physical characteristics held in a population history database. The main study group is the Moto community which consisted of 71 individuals at the time of this study, including 12 adult males, and 24 adult females.

This chimpanzee population exhibits a diverse repertoire of tool using behaviors which occur in a variety of contexts [Sanz & Morgan, 2007]. Tool using

behaviors have been documented through direct observation during reconnaissance surveys of chimpanzees since the initiation of research at this site. In 2003, we also began remote video monitoring of tool use sites. Remote video monitoring units consist of video cameras in weatherproof housings that are triggered to record for pre-set intervals by passive infrared sensors [for a more detailed description, see Sanz et al., 2004]. These cameras were placed at termite nests with previous traces or observations of chimpanzee tool use. Video recordings were scored using INTERACT Version 14 (Mangold, 2015). A tool using episode was defined as beginning when the chimpanzee manufactured a tool (or at the first moment after which they were observed with the tool) and ended when the tool was discarded or the task was abandoned. Chimpanzees with a minimum of six observations in hand use were included in the analysis. Across the entire sample, the number of observations ranged from 6 to 2,169 (Mean = 305.56, s.d. = 401.38).

Behavior of Interest

We describe handedness as expressed in termite fishing at the epigeal nests of *Macrotermes muelleri* as this is most comparable to the ecological context of termite fishing which has been reported from chimpanzee populations in East and West Africa [Bogart et al., 2012; Lonsdorf & Hopkins, 2005; McGrew & Marchant, 1992]. A termite fishing probe consists of herbaceous stem with one end modified into a brush-tip [Sanz et al., 2009; Sanz & Morgan, 2007]. Chimpanzees hold the fishing probe in one hand, and insert the brush-tip into an existing termite exit tunnel on the surface of the termite nest. Termites within the nest attack the object invading their nest by closing their mandibles on the fibers of the brush-tip probe. The chimpanzee then withdraws the fishing probe from the nest in one swift motion, sometimes with the tool stalk resting on the opposite arm for support.

Data Analyses

Hand preference

We calculated a handedness index (HI) from the frequency data for each subject using the following formula:

$$HI = \frac{r - l}{l + r}$$

where r denotes the number of probe insertions with the right hand and l denotes the number of probe insertions with the left hand. A positive HI value indicates right-handed bias, with a negative value indicating a left-hand bias. The absolute HI

values indicate magnitude of hand preference. To determine whether individuals showed significant directional bias in hand use, we calculated binomial z scores using the following formula:

$$z = \frac{r - 0.5N}{\sqrt{0.25N}}$$

where r denotes the number of right-hand instances and N is the total number of observations. Following conventional hand-preference criteria in non-humans [Hopkins, 2013b], a z-score above or below ± 1.96 indicated right- or left-handedness, respectively. All others were classified as ambiguously handed.

Performance

The duration of each fishing probe insertion was measured as the time the probe contacted the termite nest until it was completely withdrawn from the nest. The average time per successful dip for each hand was calculated as total time of that hand divided by the total time for that hand divided by the frequency. We chose to examine performance as reflected by dip latencies because 1) faster dips enable a chimpanzee to gather more termites per unit time foraging (particularly when dip insertion depth is not key to success, see discussion section) and 2) dips are distinct units which are directly linked to laterality (as opposed to characteristics of fishing bouts in which handedness may alternate).

Statistical Analyses

Population-level handedness

A one-sample t-test on HI scores was used to assess whether there was significant bias in lateralization within this chimpanzee population.

Sex and age differences

Because of the non-normality in the distribution of HI scores, we used non-parametric statistics. A Mann-Whitney U-test was used to examine sex difference in HI scores. A Kruskal–Wallis was used to test for the effect of age on handedness.

Performance

For this analysis, we performed an analysis of variance (ANOVA) with age (juvenile, sub-adult, adult) and sex (male, female) as independent variables, and mean latency as the dependent measure. To examine the effects of sex and hand preference on tool use latency in termite fishing, hand (left, right) and sex (male, female) were the independent factors while the mean dipping latencies for the dominant hand was the dependent measure. As a follow up analysis, we performed the same ANOVA but used the mean latency scores across all responses (left and right hand) instead of the mean latencies for the dominant hand.

We also sought to conduct a within-subjects analysis for those chimpanzees that made at least 10 dipping responses with both the left and right hands. For this analysis, we compared the mean dipping latencies for the left and right hands in right- and left-handed individuals using a mixed model ANOVA. Mean dipping for each hand (left, right) was the repeated measure while hand preference (right-handed, left-handed) were the between group factors.

Comparisons between termite fishing populations

We used ANOVA to examine whether there was an effect of chimpanzee community and sex on handedness distributions.

RESULTS

Hand Preference

The mean HI scores and distribution in hand preferences are shown in Table I. On the whole, as has been reported in other studies on hand use in termite fishing (and other forms of tool use), the chimpanzees showed robust individual hand preferences for termite fishing. For the entire sample, only four subjects failed to show a significant hand preference and more than half the subjects (53/89) showed exclusive left- or right-hand preferences (Table I and Fig. 3). A one-sample t-test on the HI scores failed to reveal significant population-level handedness $t(88) = 0.83$, n.s. When considering the classification of hand preference, there were 46 right-handed, 39 left-handed and 4 ambiguously handed individuals. There was no significant difference in the number of right- and left-handed chimpanzees. We next considered the potential influence of sex and age on handedness. Males showed a greater right hand preference (Mean $HI = 0.25$) than females (Mean $HI = -0.04$), with a significant sex difference in HI scores (Mann–Whitney U-test, $z = 2.104$, $P < 0.04$). Sixty-two percent of the males showed a significant right hand preference compared to 47% of

TABLE I. Handedness for Epigeal Termite Fishing Among Chimpanzees of the Goualougo Triangle

	Left	Ambiguous	Right	Mean HI
Males	14 (9)	1	24 (20)	0.24
Females	23 (13)	1	21 (10)	−0.04
Unknown	2 (2)	2	1 (1)	−0.17
Total	39 (24)	4	46 (31)	0.08

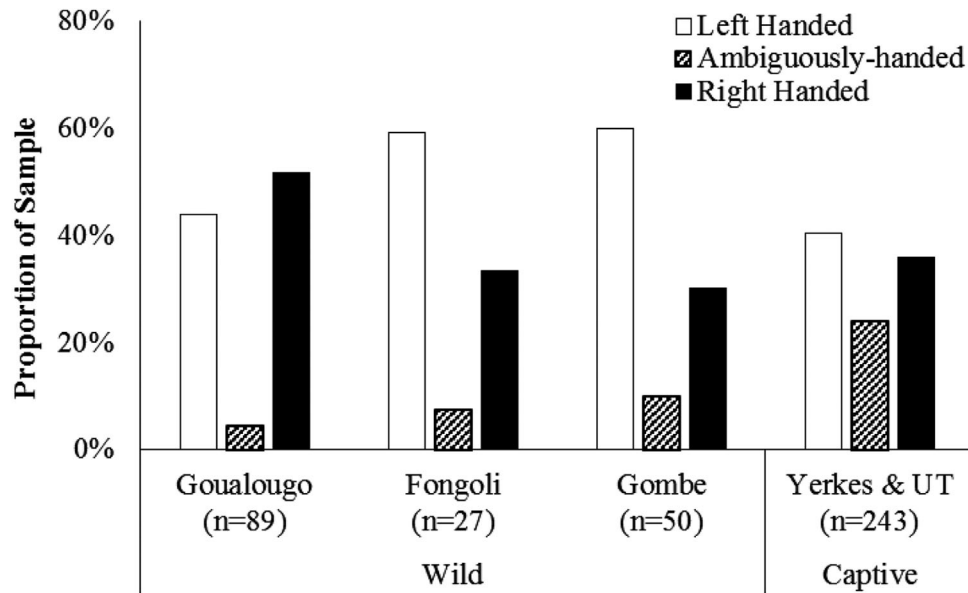Value in parentheses indicate the number of individuals showing exclusive hand preference.

Fig. 3. Handedness for epigeal termite fishing by wild chimpanzee populations compared to asymmetry in captive setting [Hopkins et al., 2015].

the females (see Table I). Age did not show a significant effect on handedness.

Hand Performance

In the initial set of analyses, we examined the influence of sex and age on overall tool use performance. For this analysis, we performed an analysis of variance (ANOVA) with age (juvenile, sub-adult, adult) and sex (male, female) as independent variables, and mean latency as the dependent measure. No significant main effects or interactions were found. Thus, males and females, and adult, sub-adult and juvenile chimpanzees did not differ in their mean dipping latencies. We next considered the effects of sex and hand preference on tool use latency in termite fishing. For this analysis, hand (left, right) and sex (male, female) were the independent factors while the mean dipping latencies for the dominant hand was the dependent measure. The four chimpanzees that did not show a significant hand preference were excluded from this analysis. In addition, two subjects were removed from this analysis because they had latencies scores that were outside the 95% confidence interval for the entire distribution of values (i.e. they were statistical outliers). Thus, this analysis was restricted to the remaining 84 chimpanzees. A significant main effect for hand preference was found $F(1, 78) = 6.726$, $P < 0.01$. The mean latencies for chimpanzees with a right- or left-hand dominance are shown in Figure 4. For both males and females, right-handed subjects had significantly faster dipping latencies scores than left-handed chimpanzees.

Within-Subject Variability in Hand Performance

In the next set of analyses, we sought to test whether performance differences were evident between the hands in chimpanzees classified as left- or right-handed. This analysis was limited to those chimpanzees that were observed to use both hands for termite fishing. Recall that 53 chimpanzees showed exclusive left or right hand use in termite fishing; therefore, these individuals were not included in the analysis. Further, in some cases, there were large differences in the number of left and right hand responses within a subject. Thus, we opted to include only those subjects that made at least 10 dipping responses with both the left and right hands, which lowered our sample size considerably ($n = 22$).
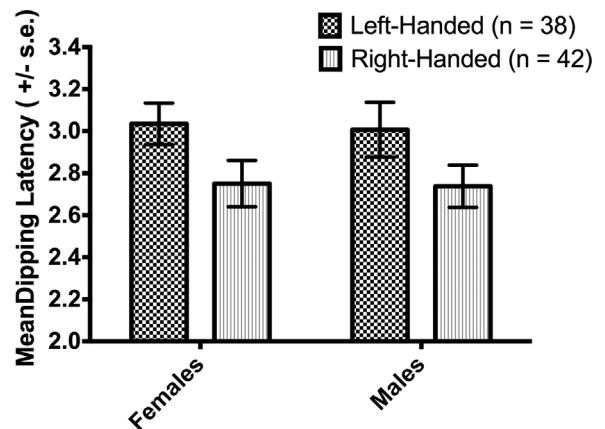

Fig. 4. Performance differences in termite fishing at epigeal nests. Note that fishing with the right hand was faster than with the left hand, across both male and female chimpanzees.
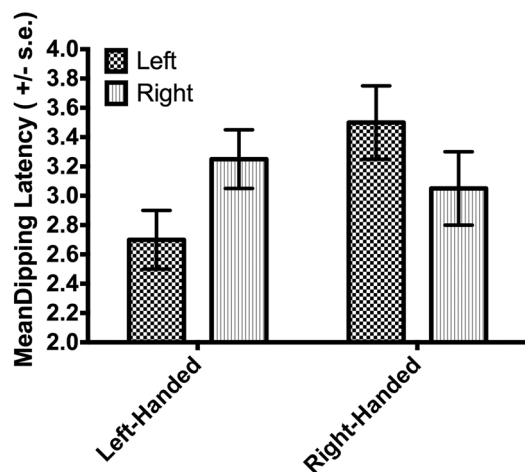
Fig. 5. Performance differences in chimpanzees (categorized by their dominant hand) who exhibited both right and left hand use when fishing. The dominant hand performed better than the non-dominant hand.

For this analysis, we compared the mean dipping latencies for the left and right hands in right- and left-handed individuals using a mixed model AN-OVA. Mean dipping for each hand (left, right) was the repeated measure while hand preference (right- and left-handed) were the between group factors. No significant main effects or interaction were found, though the interaction between hand performance and preference approached conventional levels of statistical significance $F(1, 20) = 4.14$, $P < 0.06$. The mean dipping latency for the left and right hands in right- and left-handed chimpanzees are shown in Figure 5. As would be expected, left-handed chimpanzees had faster latencies for the left compared to right hand whereas right-handed chimpanzees had shorter latencies for their right compared to left hand.

Comparison to Gombe and Fongoli Termite Fishing Handedness

In this final analysis, we compared the handedness data from this sample with the findings on hand preference for termite fishing in chimpanzees at Gombe in Tanzania ($n = 50$) and Fongoli in Senegal ($n = 27$) (see Table II). Bogart et al. [2012] recently

TABLE II. Hand Preferences for Termite Fishing in Three Chimpanzee Communities

	#Left	Ambiguous	Right	Mean HI
Goualougo	39	4	46	+0.104
Fongoli	16	2	9	−0.281
Gombe	50	3	31	−0.242

Note: Five chimpanzees with unknown sex were excluded from the Goualougo sample.
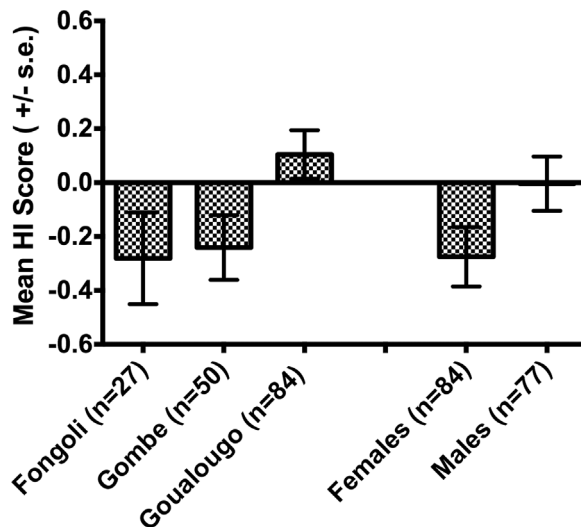

Fig. 6. Comparison of handedness in termite fishing across wild chimpanzee populations.

found no differences in handedness for termite fishing in these two communities and when the data were combined between the Fongoli and Gombe samples, there was a significant sex difference with females showing greater left handedness than males. Thus, we examined the effect of chimpanzee community and sex on handedness distributions in this final analysis. When the data were combined, we found significant main effects for chimpanzee community $F(2, 155) = 3.671$, $P < 0.03$ and a borderline significant effect of sex $F(1, 155) = 3.342$, $P < 0.05$. The mean HI scores for each population (Gombe, Fongoli, Goualougo) and sex are shown in Figure 6. Post-hoc analysis indicated that Goualougo chimpanzees had significantly higher HI scores than the Gombe and Fongoli chimpanzees. Female chimpanzees had a significantly lower HI scores than males. The interaction between community and sex was not significant. Viewing the distribution of handedness in the three chimpanzee communities validates the previous findings. As can be seen, the proportion of left-to-right handed individual is much higher in the Gombe and Fongoli chimpanzees compared the Goualougo apes.

DISCUSSION

The goals of this study were to test for population-level handedness within a single wild chimpanzee population and determine if performance asymmetries were associated with hand preference. The majority of chimpanzees in Goualougo showed strong hand preferences in termite fishing, which is similar to reports from other sites. Chimpanzees at Gombe and Fongoli exhibit left-handed bias in termite fishing whereas chimpanzees in Goualougo showed a right-hand bias at epigeal nests, particularly for the males. There was also a significant sex

difference in chimpanzee handedness in the Goualougo population, with males being more inclined to use their right hand for termite fishing than females. Further, performance asymmetries were detected in that Goualougo chimpanzees who preferred their right hand showed shorter latencies when fishing compared to those that preferred the left hand.

While population-level lateralization in termite fishing was not detected in this sample, the evidence of sex differences in hand preferences are consistent with previous reports on termite fishing in a combined sample of apes from Gombe and Fongoli [Bogart et al., 2012], simulated termite fishing in captive chimpanzees [Hopkins et al., 2009] and for bimanual feeding in the chimpanzees at Mahale [Corp & Byrne, 2004]. The biological or sociological mechanisms underlying the observed sex differences is not clear; notwithstanding there are reports that female chimpanzees use tools more often [Gruber et al., 2010] and learn to acquire their use earlier than males [Lonsdorf et al., 2004] but how this might influence the expression of hand preferences, if at all, it not obvious. Thus, at this point, any potential explanation for the reported sex differences is only speculative but clearly warrants further investigation.

Our comparison of handedness in tool using behaviors across chimpanzee populations and contexts indicated that not all tool tasks are equivalent in eliciting handedness. While termite fishing has previously been considered to be homogenous across different sites, contexts, and species. Our recent research has demonstrated that the structure of the termite mound and defensive behavior of different termite species has a dramatic influence on tool characteristics and gathering technique used by chimpanzees across sites [Sanz et al., 2014]. Similar to differences in ant dipping technique observed among different chimpanzee populations [Sanz et al., 2010], chimpanzees in the Goualougo use different gathering techniques to gather termites from their fishing probes [Sanz et al., 2004]. One variant involves pulling the herb stem through their hand to sweep termites onto their hand and then transferring them to their mouth (also referred to as ant-dip-wipe and pull-through in ant predation), whereas, the other variant involves eating insects directly from the end of the tool (referred to as ant-dip-single and direct-mouthing in ant predation) [Humle & Matsuzawa, 2002; Sanz et al., 2010; Whiten et al., 2001, 1999; Yamakoshi & Myowa-Yamakoshi, 2004]. There is a relatively equal prevalence of these techniques manifested by chimpanzees at epigeal nests of *Macrotermes muelleri*, but a strong bias toward direct mouthing at subterranean nests of *Macrotermes lilljeborgi*. Preliminary analysis indicate that laterality differs between these contexts, which may be due to differences in gathering technique, posture, or performance. More specific

identification of the cognitive, sensory, and motor demands of different tasks may elucidate factors shaping motor execution and performance.

Differences between sites in tool modifications also affect gathering strategies and performance. Competent tool users in Goualougo have a high success rate in gathering termites (95.5% of dips, $n = 561$). In contrast to Gombe, the absolute number of termites in this context is limited by the length of the brush tip on the tool as opposed to fishing probe insertion depth. At Gombe, termites cling along the entire length of the inserted tool and so insertion depth, and extraction speed may affect a chimpanzee's fishing performance. In Goualougo, chimpanzees manufacture brush-tip fishing probes which significantly increase effectiveness in termite gathering compared to a probe without this modification [Sanz et al., 2010]. The termites grasp onto the portion of the tool with the brush fibers and not along the entire length of the tool, and so deeper dip insertion (necessitating more time) is not necessary to be successful or increase yield. In fact, pausing during insertion may result in losing the major soldiers as they release the brush and retreat. In addition, tool using bouts in Goualougo are much shorter than those in Gombe and so maximizing the absolute number termite extractions per unit time is key for this population.

A unique and previously unreported finding from this study was the significant performance asymmetry. When comparing performance by the dominant hand, chimpanzees that preferred to use their right hand performed faster than chimpanzees that preferred the left hand. This would suggest that the left hemisphere exhibits a functional asymmetry in fine motor control or motor planning, a finding consistent with previously published data in human subjects, captive chimpanzees and rhesus monkeys [Annett, 2002; Hopkins & Russell, 2004; Hopkins et al., 1992]. Interestingly, the right hand advantage in skill does not lead to an increased prevalence in right hand preference per se. In other words, if the right hand performs the epigeal termiting more quickly and this presumably has some advantage, then it begs the question why a higher prevalence of right-handed individuals are not evident in the sample? Further, though right hand preferences were more prevalent in male compared to female chimpanzees, the performance differences were evident in both males and females (see Fig. 4). If there is a potential advantage of fishing with the right hand, then one would assume that there is balancing selection to maintain almost equal prevalence of left-handed termite fishing in this population and would help to explain the population-level patterns of left-handed fishing in other chimpanzee populations. It is possible that speed-accuracy trade-offs exist in this context. Chimpanzees that prefer to right hand (and based on the preference data this

would be more males) perhaps feed quickly but with less accuracy. Left-handers (and more prevalently in females) have slower latencies but perhaps capture more prey. Both strategies may yield the same total number of insects but the subjects use different strategies. The slowest dip latencies were associated with right-handed chimpanzees who were using their left hand. They performed more slowly than left-handed chimps when using their right hand. This is consistent with the idea of a left hemisphere dominance for motor skill, at least as defined by latency. An alternative (and not contradictory) assertion is that "perhaps the chimpanzee provides a model for an intermediate phylogenetic state of manual lateralization" resembling a form that evolved after the last common ancestor of living apes and humans, but before emergence of handedness in its more fully developed expression in humans [Marchant & McGrew, 2013]. More information on the links between handedness and foraging efficiency across tasks, and study taxa will shed light on this issue.

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