

1 **Title**

2 Hand preference in unimanual and bimanual coordinated tasks in wild western lowland gorillas
3 (*Gorilla gorilla gorilla*) feeding on African ginger (Zingiberaceae)

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5 **Short running title**

6 Hand preference in wild western gorillas

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18

Abstract

Objectives: Bimanual coordinated behaviors are critical for detecting robust individual hand preference in non-human primates but are particularly challenging to observe in the wild. This study focuses on spontaneous feeding behavior on African ginger (*Aframomum* sp. and *Renealmia* sp.), which involves a unimanual task (reaching and pulling out a ginger stem) and a bimanual coordinated task (extracting pith from a ginger stem) by wild western lowland gorillas.

Materials and Methods: Study subjects were 21 gorillas in the Moukalaba-Doudou National Park, Gabon. We examined whether they exhibit significant hand preference at the individual and group levels for both tasks.

Results: Sixteen gorillas showed significant hand preference in the unimanual task, whereas all 21 individuals showed significant hand preference in the bimanual coordinated task. Hand preference was significantly stronger in the bimanual coordinated task than in the unimanual task. It is noteworthy that gorillas showed a significant right-hand preference at the group level for the bimanual task (roughly 70% of the subjects).

Discussion: This study confirmed that bimanual coordinated tasks are more sensitive in detecting hand preferences in nonhuman primates. In addition to the bimanual nature of the task, the precision grip for processing and the importance of African ginger as a food resource might influence the expression of hand preference. Evidence of a group-level right-hand preference may support the

37 ‘*postural origins theory*’. Because all wild African great apes feed on the pith of African ginger,
38 comparing this task and its hand preferences can contribute toward a better understanding of the
39 evolution of handedness in Hominidae.

40

41 **Keywords:** African ginger, bimanual task, great apes, hand preference, western lowland gorilla

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43 **Research Highlights**

44 -Twenty-one wild western gorillas showed a strong hand preference for the bimanual coordinated
45 tasks.

46 -Significant group-level right-hand preference was detected.

47 -This behavioral measure can be applicable in other African great ape study sites.

Introduction

That approximately 90% of humans demonstrate right-handedness is a unique and cross-cultural trait in the human population (Perelle & Ehrman, 1994). Historically, it has been considered that the expression of handedness is related to, and coevolved with hemispheric specialization, and especially right-handedness in particular reflects an inherent specialization of the left hemisphere for language skills (Annett, 2002; Falk, 1980; Leask & Crow, 2001). However, recent findings report the existence of hand preference in nonhuman animals, particularly in primate species (Fitch & Braccini, 2013; Hopkins, 2013), thus casting a doubt as to whether language is requisite for the evolution of handedness. As an alternative to evolutionary language links, researchers have proposed that some behavioral traits might be a key driver of right-handedness in humans, such as bipedalism (Braccini, Lambeth, Schapiro, & Fitch, 2010; Westergaard, Kuhn, & Sumoi, 1998), tool-use (Frost, 1980; Greenfield, 1991), and bimanual coordinated actions (Wundrum, 1986; Hopkins, Hook, Braccini, & Schapiro, 2003). However, there is no consensus about when and which factor played an important role in the evolution of population-level right-handedness in humans.

Regarding the closer phylogenetic proximity to humans, nonhuman primates can be important functional models to study the evolutionary origin of handedness (Hopkins, Misiura, Pope, & Latash, 2015). To assess population-level hand preferences in nonhuman primates, identifying

tasks that elicit consistent hand preferences at the individual level should be an important first step (Hopkins, 2013). Formerly, unimanual tasks, such as simple reaching, were the principal measures because of the ease of observation and data collection (Meguerditchian et al., 2015; Papademetriou, Sheu, & Michel, 2005). However, most researchers failed to reveal individual-level hand preferences for unimanual tasks because hand use for this kind of task is influenced by a variety of situational factors such as object position and posture (Hopkins, 1993; Papademetriou et al., 2005). Regarding this issue, Fagot & Vauclair (1991) proposed the ‘task complexity theory’ where primate individuals show strong hand preference in high-level manual tasks (e.g., bimanual, precise, or sequential actions), and thus these tasks can be sensitive measures of population-level hand preference. In particular, bimanual coordinated tasks are not influenced by situational factors because individuals can only perform these tasks when both hands are free. Hand preference in such tasks is therefore considered more likely to reflect hemispheric specialization (Hopkins, 1995; Hopkins, 2013; Meguerditchian, Vauclair, & Hopkins, 2013).

A bimanual coordinated task is represented by the tube task, which was introduced by Hopkins (1995). In the tube task experiment, an individual extracts food from an opaque, polyvinyl chloride tube with the finger of one hand while holding the tube with the other hand. The former hand is considered the dominant hand. Many studies have used this method for the assessment of hand preference in nonhuman primates. Hopkins and his colleagues conducted an extensive

investigation of the tube task with four captive great ape species (*Pan troglodytes*, *P. paniscus*,
Gorilla gorilla, and *Pongo pygmaeus*) in a total of 777 subjects (Hopkins et al., 2011). This method
has been employed with several species of Old World monkey (e.g., *Papio anubis*: Vauclair,
Meguerditchian, & Hopkins, 2005, *Macaca nemestrina*: Zhao, Wang, & Wei, 2016, *M. mulatta*:
Westergaard & Sumoi, 1996) and New World monkey (e.g., *Cebus* spp. and *Sapajus* spp.: de
Andrade & de Sousa, 2018; Lilak & Phillip, 2008; Meunier & Vauclair, 2007; Spinozzi, Gastorina,
& Valentina, 1998, *Saimiri sciureus*: Meguerditchian, Donnot, Molesti, Francioly, & Vauclair, 2012).
The common finding of these studies is that strong hand preference is detected at the individual
level, although some individuals show ambiguousness (reviewed in Hopkins, 2013). In addition to
the tube task, in captivity, there are studies on hand preference for food processing in western
gorillas. Most individuals exhibited robust hand preference in bimanual coordinated feeding but not
in unimanual reaching (Lambert, 2012; Meguerditchian, Calcutt, Lonsdorf, & Ross, 2010).
Bimanual coordinated tasks of primates, especially African great apes, have been focused on animals
in the wild. For instance, bimanual food-processing in chimpanzees at Mahale (Corp & Byrne,
2004), mountain gorillas (*G. beringei beringei*) at Virunga (Byrne & Byrne, 1991), and western
gorillas at Mondika (Salmi, Rahman, & Doran-Sheehy, 2016) all showed strong hand preference at
the individual level.

Although strong hand preference at the individual level was detected in bimanual

coordinated tasks, whether these apes expressed a population or group-level hand preference was inconsistent in inter- and intraspecies comparisons. In an investigation of the tube task by Hopkins et al. (2011), chimpanzees and gorillas exhibited significant population-level right-hand preference whereas orangutans demonstrated significant population-level left-hand preference. As to bonobos, a significant bias toward population-level right-hand preference for tube task was shown in adults (Chapelain, Hogervorst, Mbonzo, & Hopkins, 2011). In captive western gorillas, significant population-level right-hand preference in bimanual feeding was revealed by Meguerditchian et al. (2010), but not by Lambert (2012). In the wild, bimanual feeding of mountain gorillas exhibited a slight right-hand preference at the population level, however this was only significant when using one-tailed significance levels (Byrne & Byrne, 1991). Similar population-level right-hand preference was found in termite feeding of western gorillas although there was no statistical significance due to small sample size (Salmi et al., 2016). There was no significant population-level hand preference for manual processing in chimpanzees in the wild (Corp & Byrne, 2004). Although wild chimpanzees exhibited a strong hand preference at the individual level in tool-using (but see Marchant & McGrew, 2007 for ant-fishing in Mahale), population-level hand preference varied between studies (termite- and ant-fishing left bias: Lonsdorf & Hopkins, 2005, right bias: Humle & Matsuzawa, 2009, no bias: Marchant & McGrew, 2007; Sanz, Morgan, & Hopkins, 2016. Nut-cracking no bias: Boesch, 1991; Humle & Matsuzawa, 2009; Sugiyama, Fushimi, Sakura, & Matsuzawa, 1993).

There tends to be more evidence of population-level right-hand preference for bimanual coordinated tasks than for tool-use (Cashmore, Uomini, & Chapelain, 2008). However, there is a continuing debate about which factor is important for the evolution of population-level right-handedness in humans: tool-use (e.g., Braccini et al., 2010; Hopkins et al., 2017; Moura, 2015; Uomini, 2009) or bimanual coordinated tasks (e.g., Chapelain & Hogervorst, 2009; de Andrade et al., 2018; Meguerditchian et al., 2010; 2013; Salmi et al., 2016). In this regard, further evidence of hand preference in gorillas may be important because gorillas do not customarily use tools (but see Breuer, Ndoundou-Hockemba, & Fishlock, 2005; Kinani & Zimmerman, 2015), but often demonstrate bimanual coordinated feeding in the wild. There is limited research on bimanual coordinated tasks in wild gorillas, and further data accumulation is required (Cashmore et al., 2008; Meguerditchian et al., 2013).

Inconsistency in the tasks that measure hand preferences between studies makes it difficult to conduct direct comparisons. The tube task has been adopted in a large number of primate species in captive settings because of the high specificity for hand preference and the ease of implementation. The versatility of the tube task enables direct comparisons both at inter- and intraspecific level (de Andrade et al., 2018; Hopkins et al., 2011; Meguerditchian et al., 2015). In wild primates, on the other hand, only a few studies used identical measures, and the diversity of tasks is a persistent limitation in making reliable comparisons between studies. Although there is a

study that introduced the tube task to wild primates (Zhao, Hopkins, & Li, 2012), introducing such an artificial task in natural conditions will not always be feasible at all study sites. Considering these situations, a sensitive behavioral measure that is applicable across species and study sites is essential.

In this study, we report hand preference for the feeding behavior on African ginger (Zingiberaceae) under natural conditions in wild western lowland gorillas. Feeding behavior was divided into unimanual tasks and bimanual coordinated tasks, and whether gorillas exhibited stronger hand preference in bimanual coordinated task than in unimanual task at the individual level was investigated. Whether gorillas exhibited a group-level hand preference was investigated and discussed in the context of the evolutionary origin of population-level right-handedness in humans. The potential application of African ginger feeding as a novel measure of hand preference in other African great ape species is discussed.

Materials and Methods

Study site, periods, and subjects

This study was conducted in Moukalaba–Doudou National Park, Gabon. The park has an area of 5,028 km², which consists of a mosaic of forest, savanna, and swamp. The study site (~30 km²) is located in the northeastern part of the Park. There are two distinct seasons in this area; a

rainy season from October to April, and a dry season from May to September. Takenoshita, Ando, and Yamagiwa (2008) provided a more detailed description of this site. Long-term socio-ecological studies of western lowland gorillas at this site started in 2001. Habituation of one gorilla group, named Group Gentil (GG), had been conducted since 2003 (Ando, Iwata, & Yamagiwa, 2008), and all members of GG were identified by 2008 (Inoue et al., 2013).

The study periods were from August to November 2017, February to April 2018, September 2018 to February 2019, and July to December 2019. The study group composition was fluctuated during the study periods because of the disintegration of GG in following the loss of a leading silverback male in 2016 (Takenoshita et al., 2018). At the time of the disintegration, there were in total 19 gorillas in GG, including five adult females, one young silverback male, five blackback males, two subadults, four juveniles, and two infants. From August 2017 to February 2018, we followed some remaining members of GG which kept foraging together without the silverback. From March 2018, we began to habituate and monitor another one-male group, named Group Nidai (GN), which consisted of one silverback male, two adult females, and two infants, as a new study group (Takenoshita et al., 2018). In addition, a suspected disintegration of a neighboring one-male group in 2018 fomented the social upheaval. As a result of the social upheaval, several members of GG and of the disintegrated neighboring group immigrated into GN (Moukalaba Research Team, unpublished data). Eventually, the number of gorillas we observed during the study

periods was 26 in total (male: $N = 15$ including one silverback, one young silverback, seven blackbacks, two subadults, three juveniles, and one infant, female: $N = 11$ including six adults, one subadults, two juveniles, and two infants). Despite this situation, all observations were made in approximately the same area throughout the entire period.

Age of some subjects was determined by reliable birth dates based on observations, and others were estimated by comparing their physical and behavioral maturation with individuals of known age. The age categories we employed followed Breuer, Hockemba, Olejniczak, Parnell, & Stokes (2009): infants (0–4 years old), juveniles (4–7.5 years old), subadults (7.5–11 years old for males, 7.5–10 years old for females), adult females (>10 years old), blackback males (11–14 years old), young silverback males (14–18 years old), and silverback males (>18 years old).

African ginger feeding

African gingers are herbaceous plants that are known as an important staple and a fallback food for wild western lowland gorillas (Doran et al., 2002). The Moukalaba gorillas also feed on these plants throughout the year. At least five species of African ginger were found in the study area, and the gorillas consume mainly two of these species (Tamura, unpublished data), *Aframomum* sp. that grows in sunny places such as relatively wide paths and abandoned plantations, and *Renanthera* sp. that are found in damp places such as riversides and small swamps in a forest (Figure 1).

The African ginger feedings typically consist of two components, *unimanual task* and *bimanual coordinated task*. The unimanual task is an action for pulling a ginger out of the ground in the following manner: a gorilla reaches for and takes a hold of a ginger stem by one hand, and pulls it out with a sitting or tripedal posture (Figure 2a, e). This task is composed of relatively simple manipulations (reaching, grasping, and pulling out) which can be considered as equivalent to food reaching. In rare cases ($N = 266$, 8.9 % of the total feeding events), gorillas fed on ginger by bending the stem without pulling it out, when the stem length was apparently too long and/or the root was too strong to pull out.

Bimanual coordinated tasks are conducted by extracting an edible internal pith after pulling a ginger out. The gorilla holds a ginger in front of its body in an underhand grip with both hands. He/she bites one point of the stem (Figure 2b) and slits the outer layer of the stem by moving both hands to the opposite direction of the head to exposes the internal pith (Figure 2c). The exposed pith is mouthed, and the gorilla keeps holding the root side of the stem or an internal layer in one hand. The opposite hand grips the tip side of the stem with its thumb and fingers, normally the index finger. The gorilla withdraws the pith from the root side to the tip side while sliding the stem by fine movements of the wrist and fingers of the hand on the tip side (Figure 2d). During the movements, the wrist is twisted inward to slide the stem, and the fingers are constantly put on a slightly upper side where the pith comes out to stabilize the pith extraction. The pith is eaten as it comes out, and

the gorilla stops eating it near the tip of the stem (see Supplement 1 and 2 for processing details).

Forrester, Rawlings, & Davila-Ross (2016) provided a simple and comprehensible definition of a dominant hand for bimanual tasks: “one hand holds an object (nondominant hand) while the opposite hand performs any manipulations of the object and brings it to the mouth in the case of feeding (dominant hand)”. According to this definition, the hand on the tip side of the ginger stem that performs the fine movements is regarded as the dominant hand. Extracting a pith was conducted with only one hand in rare cases ($N = 421$, 9.8 % of the total feeding events; Supplement 3 and 4). The manipulating hand moves from the root side to the tip side of the stem and performs the same actions as that of the hand on the tip side during ginger feeding with both hands (Figure 2e–h). This also suggests that the hand on the tip side dose the practical function of extracting the pith (dominant hand), whereas the opposite hand just holds and supports the ginger stem (nondominant hand).

Data collection

Data were collected from any gorillas feeding on African gingers in good view. The hand (left or right) that a gorilla used to pull a ginger out was recorded. When a gorilla began a bimanual coordinated task, the hand (left or right) on the tip side of stem, i.e., the dominant hand was recorded. Data recording was continued until a subject individual terminated ginger consumption or

228 moved out of view. For recoding data, video cameras were used whenever possible (HC-VX985M,
229 Panasonic; SX710 HS, Canon) throughout the study periods. A voice recorder (ICD-PX470F,
230 SONY) was also introduced from July to December 2019.

231 In some previous studies, where an individual transfers an object from one hand to the
232 other before performing a bimanual task is used as a separate measure of hand preference, i.e., hand
233 transfer (Potier, Meguerditchian, & Fagard, 2013; Salmi et al., 2016; Tabiowo & Forrester, 2013). In
234 African ginger feedings, such hand transfers were recorded when a gorilla transferred a ginger stem
235 from the hand that originally pulled it out into the opposite hand, and the latter hand was employed
236 as the dominant hand for the subsequent bimanual coordinated task, (*right to left* or *left to right*;
237 Supplement 5 and 6). Similar behavior occurred when a gorilla fed on a ginger without pulling it out
238 of the ground. For instance, if a gorilla pulled a ginger plant from its right side to the front of its
239 body, the tip of the stem was then on the left side of the body. At the time, he/she may fold back the
240 underpart of the stem and invert the tip side of stem to the right side (Supplement 7). Such a
241 behavior was labelled as *fold-back (to left* or *to right)* and considered as an equivalent measure of
242 hand transfer.

243 In African ginger feedings, when a gorilla finishes eating one ginger, he/she discards the
244 ginger, and both hands are temporarily free each time. The gorilla then begins the next sequence of
245 ginger feeding with both free hands. Given this characteristic of African ginger feeding, hand use in

each successive feeding could be considered independent from the other. Hence, in this study, the feeding sequence of one African ginger was treated as one data point for hand use.

Data analyses

Only individuals that provided at least six data points were included in the analyses (three blackback males and one juvenile female were excluded from the analyses in this procedure). In addition, we excluded one blackback male from the analyses who lost his right forearm. The total number of individuals that met the criteria was 21 (Table 1). Of these 21 subject gorillas, it is revealed that five individuals (one adult female, one young silverback male, and three blackback males) were sired by the same silverback in GG (Inoue et al., 2013). Other five individuals (one subadult male, one subadult female, two juvenile males, and one infant female) were born in GG, but paternity analyses have not been conducted. Two infants (one male and one female) were estimated to be born in GN because they were first identified as infants in the group. Although we were unsure about natal group(s) for three immatures (one subadult male, one juvenile male, and one juvenile female), it is almost certain that they were not born in GG or GN. Also, we did not have any information about natal group(s) for one silverback and five adult females, but it is apparent that they were not born in GG or GN (Table 1). Taken together, it can be said that our subject gorillas originated from more than three social groups in the Moukalaba population.

We measured hand preference for the unimanual task, the bimanual coordinated tasks, and hand transfer and fold-back for each individual using two standard methods: the z-score and Handedness Index (HI). A z-score was calculated by performing a binominal test based on the numbers of left- and right-hand use. The z-score was used to determine whether individuals showed significant directional bias in hand preference as left-hand bias ($z \leq -1.96$), right-hand bias ($1.96 \leq z$), or no hand preference ($-1.96 < z < 1.96$). The HI score was calculated using the following formula: $HI = (R - L) / (R + L)$ where R denotes the number of right-hand usages and L denotes the number of left-hand usages. The score varies on a continuum from -1.0 to 1.0 , and a positive value indicates right-hand bias whereas a negative value indicates left-hand bias. We used absolute HI score (ABS-HI) to characterize the strength of hand preference (independent of direction), with 0 indicating no hand preference and 1.0 indicating the strongest preference.

Statistical analyses

Whether the strength in hand preference was different between the unimanual task and the bimanual coordinated tasks was examined by comparing ABS-HI scores using a paired t-test. A one-sample t-test on HI score was used to assess whether there was significant bias of group-level hand preference. In addition, a chi-square goodness-of-fit test was done to examine whether the group-level bias was detected using the number of right- and left-hand biased individuals based on the

classification by z-score. A Wilcoxon rank-sum test was used to examine sex difference in HI and ABS-HI scores. A Kruskal-Wallis test was used to test the effect of age class on HI and ABS-HI scores. All analyses were conducted in R version 3.3.2 (R Core Team, 2016), and the statistical significance level was set at $\alpha = 0.05$ throughout the study.

Ethics statement

This study conformed to the Guidelines for Field Research established by the Ethics Committee of the Primate Research Institute, Kyoto University. Permission to conduct the research was given by the Centre National de la Recherche Scientifique et Technologique (permission nos. AR0036/17, AR0041/18, AR0050/19) and the Agence Nationale des Parcs Nationaux (permission no. AE17020) in Gabon.

Results

We followed the study groups for 1,806 hours over 331 days. We observed 4,293 African ginger feeding events from 21 gorillas. Bimanual coordinated tasks were recorded for all of these events while unimanual tasks were recorded for only 2,983 events because the initial steps of feeding (i.e., reaching and getting a ginger) were sometimes missed.

Hand preference at individual level

In the unimanual task for African ginger feedings, 13 out of 21 gorillas exhibited significant right-hand preference, three individuals demonstrated significant left-hand preference, and five others did not show any hand preference. In the bimanual coordinated task, all 21 gorillas exhibited significant hand preference, 15 right-handed and six left-handed (Table 1). The percentage of right-handed individual for the bimanual task in our gorilla samples was roughly 70%.

Among the 15 right-handed individuals in the bimanual task, 12 individuals showed significant right-hand preference and three others did not show any hand preference in the unimanual task ($r = 0.641$, Figure 3). On the other hand, among six left-handed individuals in the bimanual task, three individuals showed significant left-hand preference and two individuals did not show any hand preference in the unimanual task. The other, *Sanji*, switched the significant hand preference to right in the unimanual task (Figure 3).

The mean ABS-HI score for the bimanual coordinated task (mean $\pm$ standard error; 0.96 ± 0.017) was significantly greater than that for the unimanual task (0.36 ± 0.045) ($t = -12.64$, $df = 20$, $p < 0.001$, Figure 4). In all subject gorillas except for one individual (*Ukueka*), the ABS-HI scores for the bimanual task exceeded those for the unimanual task ($r = 0.052$, Figure 5a). Also, the absolute values of z-scores for the bimanual task were higher than the unimanual task in all subjects

($r = 0.720$, Figure 5b). These suggest that the hand preferences at an individual level is stronger in bimanual coordinated tasks than unimanual tasks.

Hand preference at the group level

The gorillas demonstrated significant group-level right-hand preferences for both tasks based on the HI scores (unimanual task: mean HI score = 0.234, $t = 3.06$, $df = 20$, $p = 0.006$; bimanual coordinated task: mean HI score = 0.408, $t = 2.10$, $df = 20$, $p = 0.048$). In terms of hand preference classification on the basis of the z-score, the distribution of the number of right-handed and left-handed individuals among lateralized subjects for the unimanual task ($R = 13$ and $L = 3$) showed significant more right- compared to left-handed gorillas ($\chi^2 = 6.25$, $df = 1$, $p = 0.012$). In addition, for the bimanual coordinated task, the distribution of the number of right- and left-handed individuals ($R = 15$ and $L = 6$) differed significantly from chance ($\chi^2 = 3.86$, $df = 1$, $p = 0.049$).

Sex and age class differences

The effects of sex (male: $N = 11$, female: $N = 10$) and age class on hand preference were assessed. The gorillas were categorized into three age classes, 0–5 years old ($N = 5$), 6–10 years old ($N = 5$), and 11 years of age or older ($N = 11$).

There was no significant difference in the preferred hand between sexes for the unimanual

336 task (male: mean HI score = 0.27 ± 0.11 , female: mean HI score = 0.19 ± 0.11 , $W = 50$, $p = 0.76$,
 337 Figure 6) and the bimanual coordinated task (male: mean HI score = 0.26 ± 0.30 , female: mean HI
 338 score = 0.57 ± 0.25 , $W = 60$, $p = 0.75$, Figure 6). Also, there was no significant difference in the
 339 strength of hand preference between sexes for the unimanual task (male: mean ABS-HI score = 0.37
 340 ± 0.08 , female: mean ABS-HI score = 0.35 ± 0.04 , $W = 61$, $p = 0.70$, Figure 7) and the bimanual task
 341 (male: mean ABS-HI score = 0.97 ± 0.02 , female: mean ABS-HI score = 0.94 ± 0.03 , $W = 44$, $p =$
 342 0.44 , Figure 7). In addition, there was no significant difference in the preferred hand between age
 343 classes for the unimanual task (0–5 years old: mean HI score = 0.38 ± 0.09 , 6–10 years old: mean HI
 344 score = 0.09 ± 0.15 , 11 years of age and older: mean HI score = 0.23 ± 0.12 , Kruskal-Wallis chi-
 345 squared = 2.83, $df = 2$, $p = 0.24$, Figure 6) and the bimanual task (0–5 years old: mean HI score =
 346 0.91 ± 0.06 , 6–10 years old: mean HI score = -0.19 ± 0.48 , 11 years of age and older: mean HI score
 347 = 0.45 ± 0.27 , Kruskal-Wallis chi-squared = 2.73, $df = 2$, $p = 0.26$, Figure 6). Also, there was no
 348 significant difference in the strength of hand preference between age classes for the unimanual task
 349 (0–5 years old: mean ABS-HI score = 0.38 ± 0.09 , 6–10 years old: mean ABS-HI score = $0.26 \pm$
 350 0.08 , 11 years of age and older: mean ABS-HI score = 0.40 ± 0.07 , Kruskal-Wallis chi-squared =
 351 2.12 , $df = 2$, $p = 0.35$, Figure 7) and the bimanual task (0–5 years old: mean ABS-HI score = $0.91 \pm$
 352 0.06 , 6–10 years old: mean ABS-HI score = 0.99 ± 0.01 , 11 years of age and older: mean ABS-HI
 353 score = 0.96 ± 0.02 , Kruskal-Wallis chi-squared = 0.037, $df = 2$, $p = 0.98$, Figure 7).

354

355 **Hand transfer and fold-back**

356 The observed number of hand transfers and fold-backs in 21 individuals was 1,077 in total.

357 Data from 18 gorillas with more than six records of these two behaviors were analyzed.

358 Significant hand preference was detected in all 18 individuals. All individuals showed a

359 strong hand preference: ABS-HI scores for 15 gorillas were 1.0 and for three others were 0.98, 0.97

360 and 0.83. The preferred hand was consistent with the selection for bimanual coordinated tasks in all

361 individuals (Table 2).

362

363 **Discussion**

364

365 **Hand preference at the individual level**

366 All 21 gorillas with sufficient data exhibited significant hand preference in bimanual

367 coordinated tasks whereas five individuals showed no hand preference in unimanual tasks. The

368 comparison of ABS-HI scores indicated that the strength of hand preference was significantly higher

369 in bimanual coordinated tasks than unimanual tasks. This result is entirely consistent with the results

370 from many previous studies (Byrne & Byrne, 1991; Lambert, 2012; Meguerditchian et al., 2010;

371 Meunier & Vauclair, 2007; Salmi et al., 2016; Spinozzi et al., 1998; Vauclair et al., 2005). This study

lends support to a widely accepted argument that bimanual coordinated tasks are more sensitive in detecting individual hand preference in nonhuman primates (Fagot & Vauclair, 1991; Hopkins, 2013; Hopkins & Cantalupo, 2004; Meguerditchian et al., 2013; Papademetriou et al., 2005).

The mean ABS-HI score of the bimanual coordinated task in African ginger feeding was 0.96 ± 0.017 . In previous studies, the reported mean ABS-HI score of bimanual tasks was 1.00 ± 0.00 in termite feeding by wild western gorillas (Salmi et al., 2016), 0.50 ± 0.05 in bimanual feeding for provisioning foods by captive western gorillas (Meguerditchian et al., 2010), and 0.81 ± 0.05 and 0.50 ± 0.004 in tube tasks by captive chimpanzees (Llorente, Mosquera, & Fabre, 2009) and bonobos (Chapelain et al., 2011). Compared to these scores, it can be concluded that African ginger feeding is a behavior in which hand preference strongly appears. Hence, this bimanual feeding task will be a novel and sensitive measure to detect hand preference at the individual level under natural conditions.

In addition to bimanual nature of the task, there are two additional explanations, which are not mutually exclusive, as to why the gorillas exhibit strong hand preference in African ginger feeding. First, the grip type of the dominant hand during the bimanual task may affect the expression of hand preference. In previous studies, it is suggested that hand preference in primates including humans becomes strong in grips that demand complex and fine movements, i.e. a precision grip (Christel, Kitzel, & Niemitz, 1998; Hopkins, Russell, Hook, Braccini, & Schapiro, 2005;

Meguerditchian et al., 2015; Pouydebat, Reghem, Borel, & Gorce, 2011). In particular, wild mountain gorillas showed obvious precision grips during defended plant feedings in which strong hand preference was exhibited (Byrne & Byrne, 1991). The gorillas in this study also showed fine finger movements of the dominant hand during the bimanual task with a grip similar to a pencil grip, which is one type of precision grip. Power grips were used for pulling ginger out in the unimanual tasks. Therefore, the difference in the strength of hand preference between these two tasks might be caused by the grip type. Indeed, such a grip type effect in bimanual tasks has been also documented in a study of human infants (Potier et al., 2013).

The second possible explanation is that African gingers are important foods for wild western gorillas. African gingers are well known as super abundant foods and can be fallback foods when fruits are scarce (Doran et al., 2002). White, Rogers, Tutin, Williamson, & Fernandez (1995) mentioned that gorillas could consume hundreds of *Aframomum* stems with rapid processing in a dense patch. The authors also observed gorillas feeding on gingers for a few hours during non-fruiting season. Considering the volume intake of African gingers in a short time, if gorillas cannot extract the edible parts of the pith efficiently, reduction in intake will be huge. There is an idea that unilateral specialization allows fast and effective processing and improves behavioral efficiency for complex tasks (Chapelain & Hogervorst, 2009; Fitch & Barccini, 2013). In line with this argument, motor lateralization may be adaptive in order to consume large numbers of ginger stems efficiently.

These two factors, which are not mutually exclusive, may have accelerated the expression of strong hand preference for the bimanual coordinated task of African ginger feeding in Moukalaba gorillas.

Hand preference at the group-level

The gorillas in this study showed significant group-level right-hand preference in both the unimanual task and the bimanual coordinated task. However, the significant group-level hand preference in the unimanual task might be just a by-product of the tendency in the bimanual task. This view is supported by the fact that 15 of 21 lateralized gorillas in the bimanual task ($R = 12$ and $L = 3$) showed the same direction of hand preference in the unimanual task. Further, the number of lateralized individuals decreased in the unimanual task, and the strength of hand preference was prominently weaker in the unimanual task than the bimanual task. Taken together, these results indicate that the significant group-level right-hand preference in the bimanual coordinated task is more essential than in the unimanual task.

The evidence of significant population-level right-hand preference for bimanual tasks was reported in captive western gorilla groups (Hopkins et al., 2011; Meguerditchian et al., 2010). Similar tendencies were reported in wild populations of mountain gorillas (Byrne & Byrne, 1991) and western gorillas (Salmi et al., 2016), although these results were not statistically significant. Therefore, the current study provides the new evidence that group-level right-hand preference in a

bimanual coordinated task exists in wild gorillas.

More evidence of population-level right-hand preference is available for gorillas than other apes. This reason is unclear, but one explanation might be the high terrestriality of this genus. MacNeilage, Studdert-Kennedy, & Lindblom (1987) proposed the ‘postural origins theory’ as an evolutionary origin of human right-handedness with the following scenario: ancestral arboreal primates used the left hand for visually guided tasks such as reaching foods while supporting the body by the right hand, for example holding a branch. Afterward, when they became more terrestrial, they still used the left hand for reaching actions whereas the right hand, which was liberated from the supporting labor, became specialized for manipulating foods and for other bimanual actions. Although some previous studies have exhibited negative results against the theory (e.g., Papademetriou et al., 2005; Schnoell, Huebner, Kappeler, & Fichtel, 2014), the results of population-level hand preference in the tube task (Hopkins et al., 2011) were consistent with the theory; most terrestrial gorillas showed a strong right-hand preference, semi-terrestrial chimpanzees showed a significant but weaker right-hand preference, and arboreal orangutans showed a left-hand preference. In the investigation of the tube task in great apes, Old World monkeys, New World monkeys, and human infants, arboreal primates exhibited predominance of a left-hand preference, whereas terrestrial primates were predominantly right-handed (Meguerditchian et al., 2013). Given that gorillas are more habitually terrestrial and do not use tools in the wild, the findings from previous

studies and the present study suggest that bimanual coordinated tasks in the terrestrial condition might play an important role in the evolution of human-like right-handedness.

In this paper, we preferred the usage of the term “group-level” to “population-level” because the research was conducted in the small study area. However, as mentioned above, the 21 subject individuals came from more than three social groups. It means that immature subject gorillas are likely to be assigned to three different natal groups. In addition, since both sexes disperse from their natal groups in western lowland gorillas (Stokes, Parnell, & Olejniczak, 2003), the silverback and the adult females in our gorilla samples were likely born in different social groups. In fact, kinship analysis suggested that there were not many kin dyads among silverbacks and adult females, if any, in the same study area at Moukalaba (Inoue et al., 2013). The fact that significant group-level right-hand preference was detected under this situation might indicate that there is a majority of right-hand preference individuals in the Moukalaba population. Thereby, the group-level findings in this study might apply to the population-level.

Although our gorilla samples showed the significant group-level right-hand preference, the percentage of right-handed individuals, roughly 70%, is not equal to human-like handedness bias, ~90% or more. Since there is a continuing debate about the range in application of the word “population-level” hand preference (e.g., Braccini et al., 2010; Cashmore, 2009; Hopkins et al., 2011; McGrew & Marchant, 1997), we cannot conclude that the group-level hand preference in this

study is qualitatively the same as the phenomenon in human populations. However, at least, this study can suggest that gorillas do show significant group- or population-level bias of right-hand preference but the magnitude of expression is lower than that reported in humans (Hopkins et al., 2011). Further, this difference may indicate an occurrence of human-unique adaptation that may have played an important role for a major quantitative shift in right-lateralization in the evolution of human handedness.

Effect of sex and age class

No influence of sex on hand preference was found in this study. In human societies, however, a higher level of right-handedness has been found in females than in males (Oldfield, 1971; Perelle & Ehrman, 1994). Similar sex differences have been reported in some nonhuman primate species (e.g., Colell, Segarra, & Pi, 1995; Corp & Byrne, 2004; de Andrade et al., 2018; Harrison & Nystrom, 2010; Hopkins, Russell, Schaeffer, Gardner, & Schapiro, 2009; Llorente et al., 2011; Spinozzi et al., 1998, but see Sanz et al., 2016), while many other researchers have failed to detect sex differences (e.g., Chapelain & Hogervorst, 2009; Forrester et al., 2016; Hopkins, 1995; Lambert, 2012; Lilak & Phillips, 2008; Meguerditchian et al., 2010; 2012; Meunier & Vauclair, 2007; Vauclair et al., 2005; Zhao et al., 2012; 2016). This study is consistent with the latter results, but further research is necessary to understand the origin of sex difference on the direction of handedness. For

the strength of hand preference, most researchers found no significant effect of sex in nonhuman primates (e.g., Chapelain & Hogervorst, 2009; Forrester et al., 2016; Lilak & Phillips, 2008; Llorente et al., 2011; Meguerditchian et al., 2010; Meunier & Vauclair, 2007; Vauclair et al., 2005; Zhao et al., 2012; 2016). Collectively, these results indicate that one of the common features of hand preference in nonhuman primates is that there is no sex difference in the strength of hand preference, regardless of the direction.

In addition, there is also no consensus on the development of individual hand preference in nonhuman primates. In chimpanzees, for instance, some researchers reported that younger individuals showed a weaker hand preference than older ones, and individual hand preference developed with age (Boesch, 1991; Colell et al., 1995; Hopkins, 1994; 1995; Humle & Matsuzawa, 2009). In contrast, no effect of age on the strength of hand preference was reported in other research (Corp & Byrne, 2004; Sanz et al., 2016; Sugiyama et al., 1993). Harrison & Nystrom (2010) indicated that age did not influence hand preference in western gorillas. It is suggested that gorilla hand preference is fully developed by 4–5 years of age (Fagot & Vauclair, 1988; Salmi et al., 2016). Byrne & Byrne (1991) suggested that hand preference was well established by three years of age in wild mountain gorillas. In this study, there were no significant differences in the strength of hand preference across age classes in wild western gorillas. Significant hand preference was demonstrated even in the two youngest subjects in this study, the two years old (*Petite Randa*) and 3 years old

(*Petite Kojiwa*) infants. Although their ABS-HI scores in the bimanual coordinated task were lower than the other gorillas (0.73 and 0.82, respectively), when considering ABS-HI scores by hand transfer, *Petite Randa* transferred gingers from the left to the right hand 11 times, but from the right to the left hand only once (ABS-HI score = 0.83) indicating a significant right-hand preference. Additionally, *Petite Kojiwa* transferred gingers from the left to the right hand in all four instances. These results suggest that individual hand preferences began to develop strongly at the age of two to three years. A four years old infant (*Petit Ngou*) showed a strong right-hand preference in both ABS-HI scores by the bimanual coordinated task, and hand transfer & fold-back (ABS-HI score = 1.00). In conclusion, hand preference in wild western gorillas for the bimanual coordinated task of African ginger feeding seems to be completely developed by the age of four years.

Application of African ginger feeding

Standardizing the quantification of hand preference across studies is necessary to allow direct comparison of the results between populations and species. A number of investigators have tested for hand preference using the tube task as a common measure in captive settings, whereas, in the wild, limited research has used identical tasks for revealing hand preference. For example, in wild chimpanzees, termite-fishing, ant-fishing, and nut-cracking are observed in several populations (McGrew, 1992), and these tool-use behaviors enable intraspecies comparisons (e.g., Sanz et al.,

2016). However, it is difficult to conduct interspecies comparisons with tool-use because only a few primate species demonstrate tool-uses behavior in the wild. In addition, defended plant foods for wild mountain gorillas reported by Byrne & Byrne (1991) are unique food items in Virunga (Watts, 1984). Termite-tapping behavior by wild western gorillas is a sensitive measure of hand preference (Salmi et al., 2016), and the identical behavior was observed in Bai Hokou (Cipolletta et al., 2007). However, termite feeding was not observed using this identical tapping technique by gorillas in Moukalaba at least during the study periods. On the other hand, consumption of African ginger piths has been reported in western lowland gorillas, eastern lowland gorillas (*G. b. beringei*), and mountain gorillas in several study sites (western lowland gorillas: Mondika in Lodwick & Salmi, 2019, Bai Hokou in Goldsmith, 1999; Remis, 1997, Nouabalé-Ndoki in Nishihara, 1995, Lopé in Rogers, Maisels, Williamson, Fernandez, & Tutin, 1990; Williamson, Tutin, Rogers, & Fernandez, 1990, Rio Muni in Sabater Pi, 1997, Belinga in Tutin & Fernandez, 1985, reviewed in Rogers et al., 2004, and eastern lowland gorillas: Kahuzi-biega in Yamagiwa, Mwanza, Yumoto, & Maruhasi, 1994; Yamagiwa, Basabose, Kaleme, & Yumoto, 2005, and mountain gorillas: Bwindi in Rothman et al., 2006). Furthermore, it is also reported that chimpanzees and bonobos in multiple study sites feed on piths of African gingers in the wild (chimpanzees: Belinga in Tutin & Fernandez, 1985, Bulindi in McLennan, 2013, Kahuzi-biega in Yamagiwa & Basabose, 2006, Kalinzu in Furuichi, Hashimoto, & Tashiro, 2001, Kibale in Potts, Watts, & Wrangham, 2011, Lopé in Tutin & Fernandez, 1993, Mahale

in Nishida & Uehara, 1983, and bonobos: Bolobo in Maloueki, Lutoadio, Ndimbo, & Mbomba, 2016, Lake Tumba in Horn, 1980, Wamba in Ishizuka, Kawamoto, Toda, & Furuichi, 2019, and Yalosidi in Kano, 1983; Uehara, 1990). Whether great apes at other sites show the manipulation described here has yet to be determined, but African ginger feeding has potential as a novel measure of hand preference that enables intraspecies and interspecies comparisons in wild African great apes. Further analysis using this feeding task may elucidate the impact of bimanual coordinated tasks on the evolution of human handedness.

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Conflict of Interest

The authors declare no conflict of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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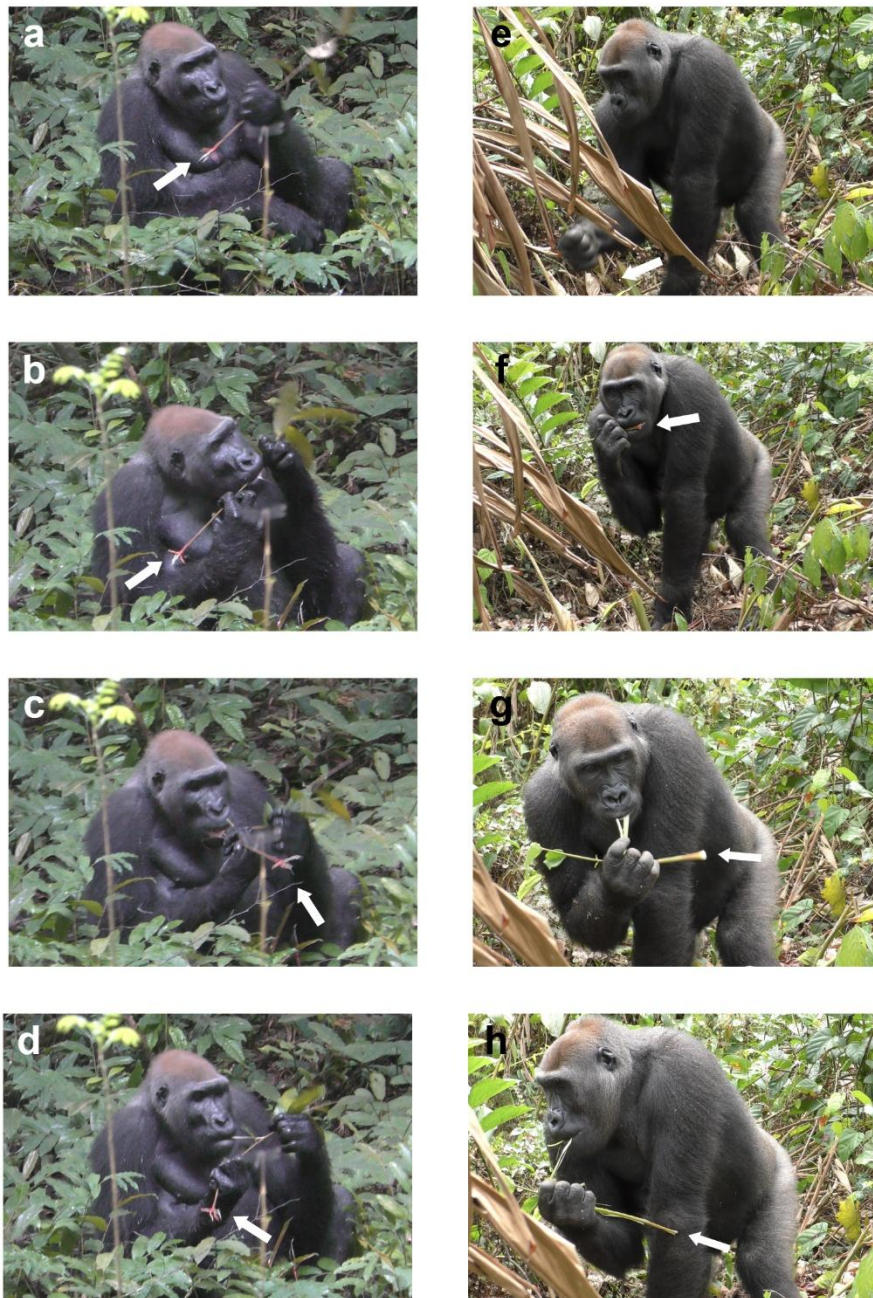
866 **Figure Legends**



867 Figure 1

868 Two genera of African ginger which gorillas mainly feed on at this study site. Left: *Renealmia* sp.

869 Right: *Aframomum* sp.



870 Figure 2

871 Feeding processing of African ginger. Photos on the left in each row indicate ginger processing with
 872 both hands in a sitting posture (a–d). Photos on the right in each row indicate ginger processing with
 873 one hand in tripedal posture (e–h). Photos on the left and right indicate left-hand dominance and
 874 right-hand dominance, respectively. The white arrows indicate the stem ends of the gingers.

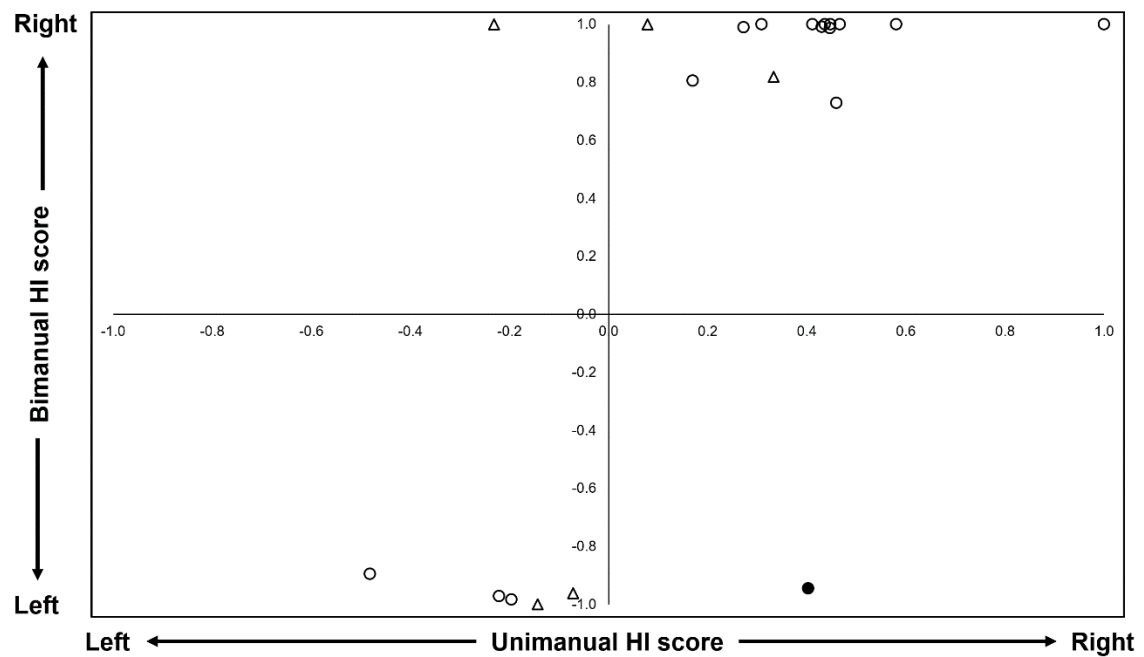
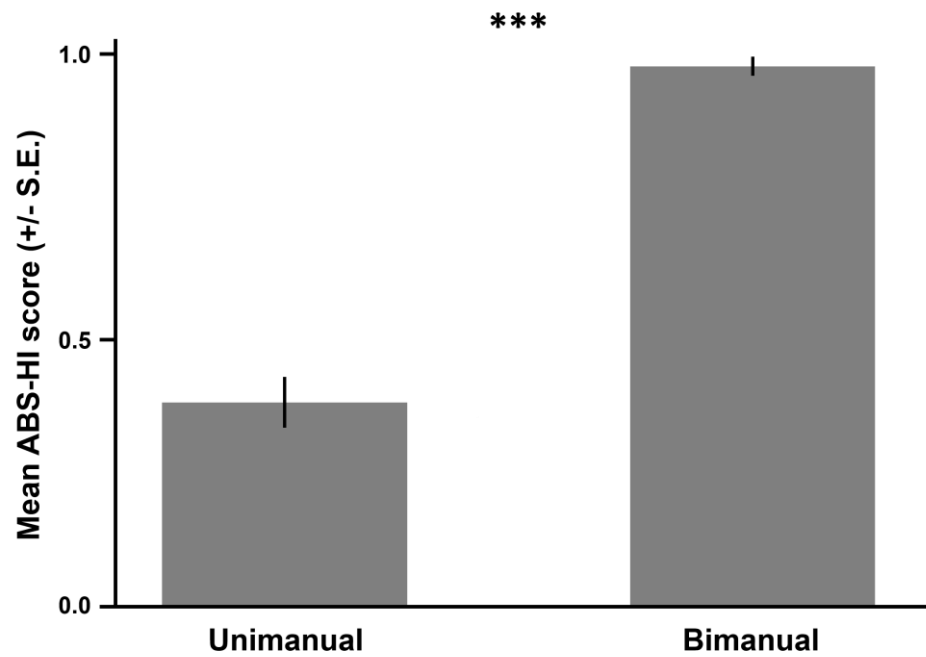
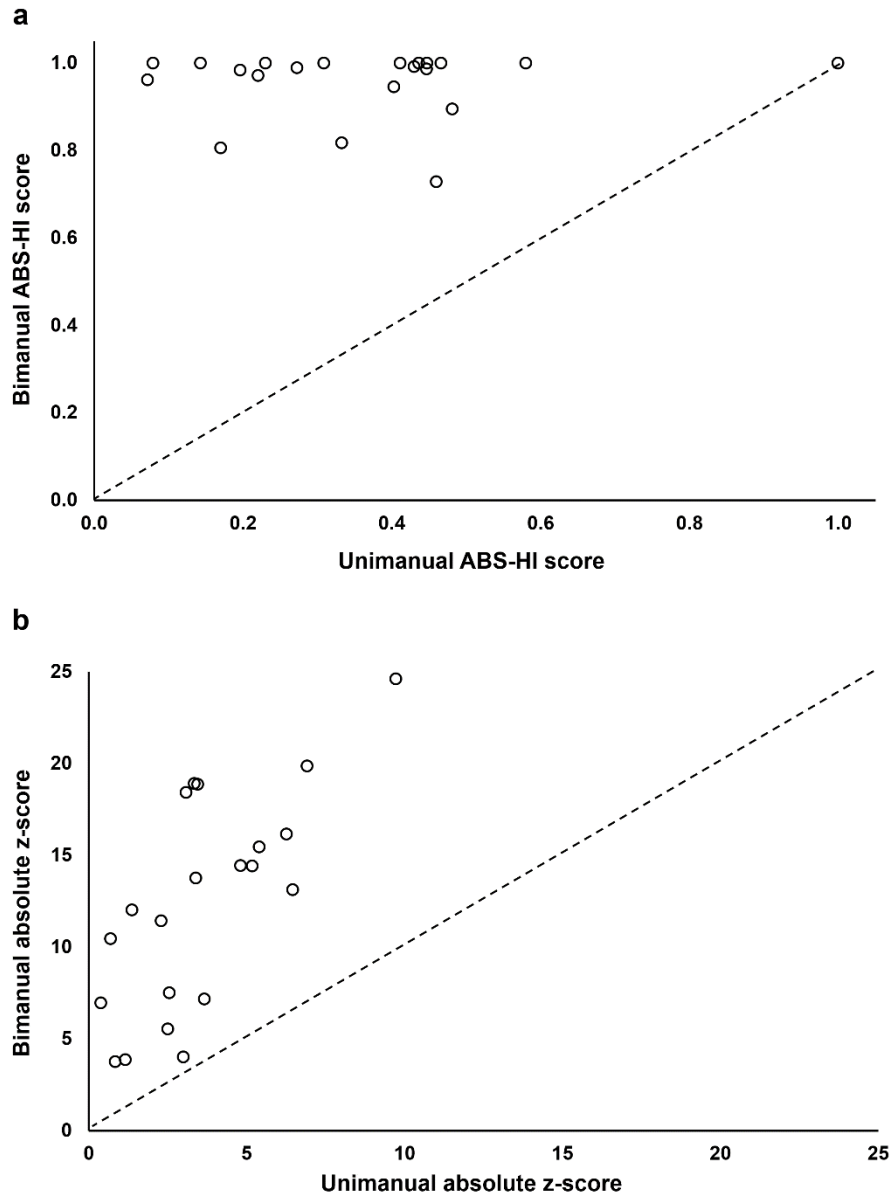


Figure 3

The correlation of HI scores between the unimanual task (x-axis) and the bimanual coordinated task (y-axis). Each plot indicates subject individuals. White circles indicate individuals which exhibit significant hand preference in both tasks. White triangles indicate individuals which exhibit significant hand preference only in the bimanual coordinated task. Black circle indicate individual which switch the direction of significant hand preference between the two tasks.



881 Figure 4
 882 Mean ABS-HI scores (strength of hand preference) in unimanual task ($N = 21$) and bimanual
 883 coordinated tasks ($N = 21$) for African ginger feeding. Significant difference is indicated by *** $P <$
 884 0.001.



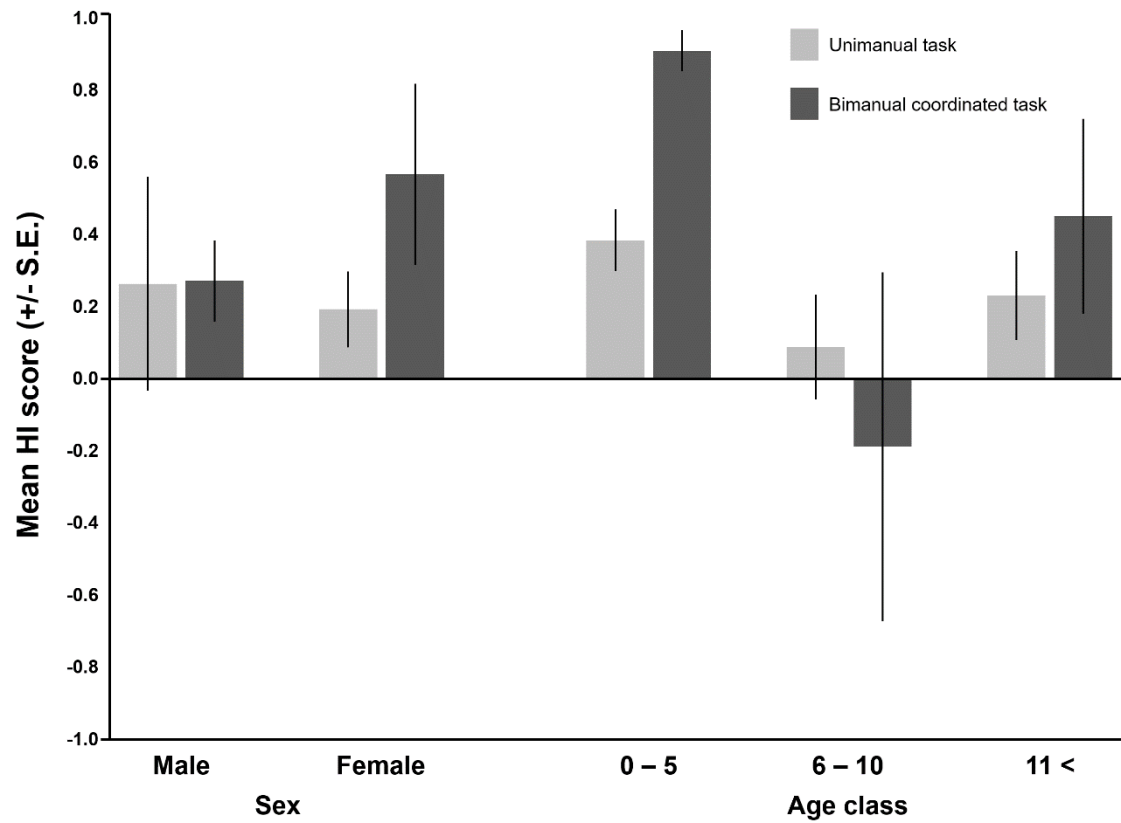
885 Figure 5

886 The correlation of the strength of hand preference between the unimanual task (x-axis) and the

887 bimanual task (y-axis) in each subject gorilla: a) ABS-HI score; b) absolute z-score. Each plot

888 indicates subject individuals. Plots on the upper side of a diagonal dotted line indicate that the score

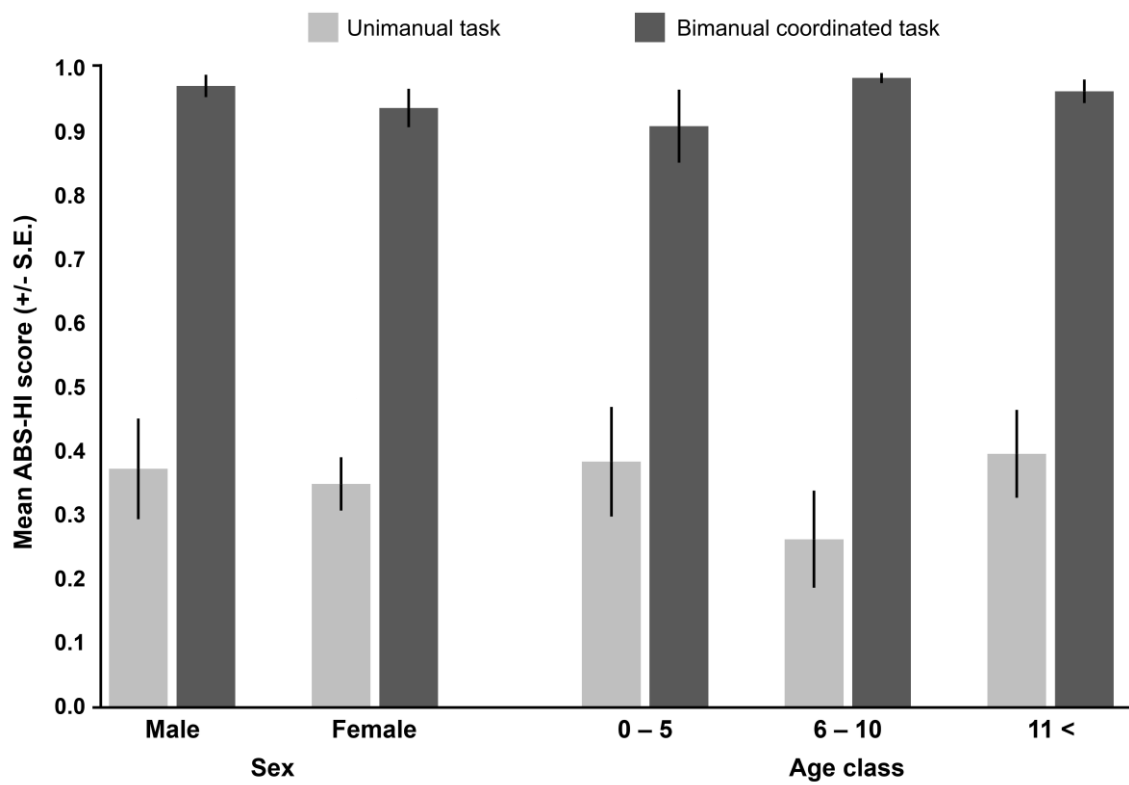
889 for the bimanual task exceeds that for the unimanual task.



890 Figure 6

891 Mean HI score for each sex and each age class on the unimanual task (light grey bar) and the

892 bimanual coordinated task (dark grey bar).



893 Figure 7

894 Mean ABS-HI score for each sex and each age class on the unimanual task (light grey bar) and the

895 bimanual coordinated task (dark grey bar).

Table 1 Individual hand preference for unimanual task and bimanual coordinated task

Subject	Age class	Natal group	Unimanual task						Bimanual coordinated task					
			No. L	No. R	HI score	z-score	<i>P</i> value	Hand preference	No. L	No. R	HI score	z-score	<i>P</i> value	Hand preference
Male														
Nidai	SB	unknown	171	241	0.17	3.45	<0.001	R	53	494	0.81	18.86	<0.001	R
Manbu	YS (15 [†])	GG [‡]	174	117	−0.20	−3.34	<0.001	L	366	3	−0.98	−18.90	<0.001	L
Bengos	BB (14 [†])	GG [‡]	40	96	0.41	4.80	<0.001	R	0	208	1.00	14.42	<0.001	R
Sanji	BB (13 [†])	GG [‡]	88	207	0.40	6.93	<0.001	R	428	12	−0.95	−19.83	<0.001	L
Ukueka	BB (13 [†])	GG [‡]	0	9	1.00	3.00	<0.005	R	0	16	1.00	4.00	<0.001	R
Okame	SA (9 [†])	unknown	52	39	−0.14	−1.36	n.s.	A	144	0	−1.00	−12.00	<0.001	L
Douta	SA (9)	GG [§]	45	113	0.43	5.41	<0.001	R	1	241	0.99	15.43	<0.001	R
Mituty	JV (7)	GG [§]	119	76	−0.22	−3.08	<0.001	L	353	5	−0.97	−18.39	<0.001	L
Petit Ovono	JV (5)	GG [§]	8	22	0.47	2.56	<0.05	R	0	56	1.00	7.48	<0.001	R
Petit Maria	JV (5 [†])	unknown	35	41	0.079	0.69	n.s.	A	0	109	1.00	10.44	<0.001	R
Petit Ngou	IF (4 [†])	GN [§]	26	98	0.58	6.47	<0.001	R	0	172	1.00	13.11	<0.001	R
Female														
Randa	AF (14 [†])	GG [‡]	131	343	0.45	9.74	<0.001	R	4	616	0.99	24.58	<0.001	R
Ngou	AF	unknown	56	98	0.27	3.38	<0.001	R	1	192	0.99	13.75	<0.001	R
Kojiwa	AF	unknown	58	148	0.44	6.27	<0.001	R	0	260	1.00	16.12	<0.001	R
Ovono	AF	unknown	19	36	0.31	2.29	<0.05	R	0	130	1.00	11.40	<0.001	R
Maria	AF	unknown	20	7	−0.48	−2.50	<0.05	L	36	2	−0.90	−5.52	<0.001	L
Mukongu	AF	unknown	8	5	−0.23	−0.83	n.s.	A	0	14	1.00	3.74	<0.001	R
Intsi	SA (8)	GG [§]	37	97	0.45	5.18	<0.001	R	0	207	1.00	14.39	<0.001	R
Tsulime	JV (6 [†])	unknown	15	13	−0.071	−0.38	n.s.	A	51	1	−0.96	−6.93	<0.001	L
Petite Kojiwa	IF (3)	GG [§]	4	8	0.33	1.15	n.s.	A	2	20	0.82	3.84	<0.001	R
Petite Randa	IF (2 [†])	GN [§]	17	46	0.46	3.65	<0.001	R	13	83	0.73	7.14	<0.001	R

Abbreviations of age class indicate as follows: SB = silverback (18 years old <), YS = young silverback (14–18 years old), BB = blackback (11–14 years old), AF = adult female (10 years old <), SA = subadult (7.5–10 years old for females, 7.5–11 years old for males), JV = juvenile (4–7.5 years old), IF = infant (0–4 years old) (referred Breuer et al., 2009). Number in parentheses indicates individual age in 2019 and [†] means estimated age. Abbreviations of natal group indicate as follows: GG = Group Gentil, GN = Group Nidai. [‡] means paternity analyses were conducted in Inoue et al. (2013). [§] means estimation without paternity analyses. Unknown indicates individuals whose natal groups were unsure, but not born in GG or GN. No. L = the number of left-hand uses; No. R = the number of right-hand uses; HI score = Handedness Index score; *P* value = Significances based on binomial test (cf. z-score); n.s. = not significant; L = significant left-hand preference, R = significant right-hand preference, A = no hand preference are indicated in Hand preference column.

Table 2 Individual hand preference for hand transfer and fold-back preceding bimanual coordinated task

Subject	Age class	Hand transfer		Fold-back		HI score	z-score	P value	Hand preference	
		R to L	L to R	to L	to R				Hand transfer & Fold-back	Bimanual task
Male										
Nidai	SB	1	129	0	1	0.98	11.27	<0.001	R	R
Manbu	YS (15†)	116	2	0	0	−0.97	−10.49	<0.001	L	L
Bengos	BB (14†)	0	40	0	3	1.00	6.56	<0.001	R	R
Sanji	BB (13†)	196	0	5	0	−1.00	−14.18	<0.001	L	L
Ukueka	BB (13†)	0	0	0	0	na	na	na	na	R
Okame	SA (9†)	39	0	0	0	−1.00	−6.24	<0.001	L	L
Douta	SA (9)	0	45	0	0	1.00	6.71	<0.001	R	R
Mituty	JV (7)	75	0	9	0	−1.00	−9.17	<0.001	L	L
Petit Ovono	JV (5)	0	8	0	0	1.00	2.83	<0.005	R	R
Petit Maria	JV (5†)	0	35	0	0	1.00	5.92	<0.001	R	R
Petit Ngou	IF (4†)	0	26	0	1	1.00	5.20	<0.001	R	R
Female										
Randa	AF (14†)	0	131	0	2	1.00	11.53	<0.001	R	R
Ngou	AF	0	55	0	0	1.00	7.42	<0.001	R	R
Kojiwa	AF	0	58	0	0	1.00	7.62	<0.001	R	R
Ovono	AF	0	19	0	0	1.00	4.36	<0.001	R	R
Maria	AF	5	0	0	0	na	na	na	na	L
Mukongu	AF	0	8	0	0	1.00	2.83	<0.005	R	R
Intsi	SA (8)	0	37	0	3	1.00	6.32	<0.001	R	R
Tsulime	JV (6†)	12	0	0	0	−1.00	−3.46	<0.001	L	L
Petite Kojiwa	IF (3)	0	4	0	0	na	na	na	na	R
Petite Randa	IF (2†)	1	11	0	0	0.83	2.89	<0.005	R	R

R to L = number of hand transfer from right hand to left hand (a gorilla pulls a ginger out with right hand and uses left hand as dominant hand for subsequent bimanual coordinated task); L to R = number of hand transfer from left hand to right hand (opposite case of R to L); to L = number of fold-back to left hand (a gorilla folds back underpart of a ginger stem and inverts the tip side of stem to left hand); to R = number of fold-back to right hand (opposite case of to L); na = an individual which does not have more than six data points; Bimanual task = individual hand preference based on analysis for bimanual coordinated task. All other abbreviations indicate same meanings as Table 1.