RESEARCH ARTICLE

Manual preference, performance, and dexterity for bimanual grass-feeding behavior in wild geladas (*Theropithecus gelada*)

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Abstract

We assessed whether wild geladas, highly specialized terrestrial grass eaters, are lateralized for bimanual grass-plucking behavior. According to the literature, we expected that complex motor movements in grass feeding would favor the emergence of a population-level hand bias in these primates. In addition, we described geladas' manual behavior based on systematic observations of several individuals. Our study group included 28 individuals belonging to a population of free-ranging geladas frequenting the Kundi plateau, Ethiopia. We filmed monkeys while feeding on grass, and hand preference and performance were coded. Geladas performed more plucking movements per second with their left hand (LH) compared to the right one and preferred their LH both to start and finish collection bouts. Also, the rhythmic movements of each hand had a significant tendency toward isochrony. Finally, geladas used forceful pad-to-pad precision grips, in-hand movements, and compound grips to pluck and collect grass blades, considered the most advanced manual skills in primate species. The LH's leading role suggests an advantage of the right hemisphere in regulating geladas' bimanual grass-feeding behavior. The tactile input from the hands and/or rhythmic hand movements might contribute to explaining this pattern of laterality. Our findings highlighted the importance of adopting multiple laterality measures to investigate manual laterality. Moreover, the need to speed up the execution time of manual foraging might be a further important factor in studying the evolution of manual laterality and dexterity in primates.

KEYWORDS
bimanual behavior, geladas, manual dexterity, manual laterality, rhythm

1 | INTRODUCTION

In the last decades, many studies have shown lateralized behaviors in a wide range of vertebrate species, thereby supporting the idea of continuity in the evolution of lateralization, which does not place humans apart from other species on this particular characteristic (Rogers, 2009; Wiper, 2017). Not surprisingly, the vast majority of the comparative studies conducted to evaluate laterality in other species have been focused on measuring hand preference in nonhuman primates, especially for prehensile behaviors (for reviews,

see Fagot & Vauclair, 1991; Hopkins, 2018; MacNeilage et al., 1987; Meguerditchian et al., 2013).

Manual laterality for grasping movements in nonhuman primates has been studied in unimanual tasks and bimanual activities. In their seminal work on hand laterality in primates, McGrew and Marchant (1997) argued that there are four forms of bimanual activities: (1) Both hands operate simultaneously and identically on the same object, for example, simultaneous grasping with the two hands on the same fruit; (2) both hands operate alternately but identically, for example, alternate movements during locomotion; (3) both hands operate simultaneously, but complementarily on the same object, for example, one holds a fruit while the other tears some of its pieces apart; (4) both hands operate simultaneously but do different tasks, for example, one hand holds a fruit while the other hand is used for climbing.

The third type of bimanual task has received particular attention because the two hands play different roles on the same object, that is, one hand performs the most complex motor movements (dominant hand), while the other hand acts as a support (nondominant hand). Measuring hand preference in other bimanual tasks is impossible (type 1) or much less frequent (types 2 and 4). McGrew and Marchant (1997) pointed out that the second type rarely occurs in primates, except for locomotory gaits when limbs are repeatedly moved in sequence, and it is possible to look at the "leading limb," such as the forelimb leading off a bout of quadrupedal walking (e.g., Hopkins et al., 1993) or brachiation (e.g., Stafford et al., 1990). The study of laterality for quadrupedal walking has shown contrasting results. For example, a right-hand (RH) preference emerged in bonobos (Hopkins & de Waal, 1995; Hopkins et al., 1993) and chimpanzees (Morcillo et al., 2006), whereas no preference emerged in gorillas (Harrison & Nystrom, 2010) and marmosets (Hook & Rogers, 2002). According to the model proposed by Fagot and Vauclair (1991), leading limbs in quadrupedal walking can be considered a low-level task because it is a familiar activity that does not involve skilled manual actions. As such, walking would be a less sensitive measure for evaluating hand preferences associated with the contralateral hemisphere's specialization.

We believe that geladas' bimanual grass-feeding behavior is a rare example of a complex motor foraging activity that can fall into the second type of bimanual task proposed by McGrew and Marchant (1997) in their classificatory framework. Similarly to leading limb behavior for locomotion, geladas' bimanual grass-plucking involves bouts of alternate movements of their limbs. However, unlike locomotion, this task is associated with complex finger movements. Therefore, assessing if geladas have a leading limb during bimanual feeding on grass can be relevant to understand the interplay between hand use and hemispheric specialization in primates.

Grass-plucking represents the main foraging activity of *Theropithecus gelada*, a primarily herbivorous primate species endemic to Ethiopia (Dunbar, 1977; Fashing et al., 2014). Its diet consists of 50%–60% (or more in heavily disturbed ecosystems) graminoid leaves, with seasonal shifts to forb leaves, tubers, corms, and roots in the dry season (Fashing et al., 2014). *Geladas* usually feed on graminoids by collecting and storing plants manually before bringing them to their mouth. Although the search for graminoids involves visual information, careful observation of bimanual grass-feeding behavior suggests that, during this activity, geladas also strongly rely on tactile information processing. First, they usually keep their forelimbs in pronation to the ground and use the volar aspect of the hands, which faces downwards, to move the grass blades within their hands (see Supporting Information S1: Video S1). Thus, geladas rely heavily on finger movements regulated by tactile input and proprioceptive information from different manual segments. Second, tactile input from the mechanoreceptors of their hands constantly informs the central nervous system regarding the volume of blades gradually stored in each hand. Evidence in human and nonhuman primates shows that the right hemisphere might play a major role in processing spatial information, including proprioceptive and tactile input from the thoracic limb. These findings have been mainly reported in object/food discrimination tasks using experimental procedures designed to prevent subjects from using visual guidance (*Homo sapiens*, Fagot et al., 1997; Flanery & Balling, 1979; *Macaca mulatta*, Fagot et al., 1991; *Ateles geoffroyi*, Laska, 1996; *Sapajus* spp., Lacreuse & Fragaszy, 1996; Parr et al., 1997; Spinozzi & Cacchiarelli, 2000; but see Lacreuse et al., 1999 for different results in *Pan troglodytes*). Thus, it would be interesting to assess geladas' manual laterality for grass-plucking, being this an extensive foraging activity distinctive of the species and characterized by a critical tactile component.

The fact that the two forelimbs/hands move regularly while geladas are feeding on grass is another characteristic that deserves attention. Evidence in human literature suggests that the right hemisphere has an advantage in processing the regular pace of both perceptual stimuli (e.g., Geiser et al., 2008) and motor behaviors (e.g., Chieffi et al., 2017). Therefore, an analysis of the temporal regularity between the onsets of plucking movements (i.e., isochrony) of each of the two hands in grass feeding might help to clarify a possible contribution of the rhythmic movements to the manual laterality pattern of geladas in this manual foraging activity. The potential rhythmic component of the task and the tactile processing discussed above are not mutually exclusive factors that converge in providing a line of reasoning for our expectation of a right hemisphere/left-hand (LH) advantage in geladas' grass-feeding behavior.

Following a different line of argument on the evolution of manual laterality in primates, a left hemisphere/RH advantage has been suggested for mainly terrestrial catarrhines in unimanual and bimanual coordinated tasks that require complex finger movements (MacNeilage et al., 1987; Meguerditchian et al., 2013). MacNeilage et al. (1987) argued that primates evolved first an LH preference for visually guided reaching accompanied by an RH preference for postural support. When postural demand decreased and with the emergence of extensive manipulative abilities in terrestrial primates, the postural specialization evolved into an RH preference for activities requiring fine, sequential manipulations and bimanual coordination. As discussed above, geladas' bimanual grass feeding,

differently from bimanual coordination, involves bouts of identical movements of both hands. However, according to the first descriptions reported in the literature, they use complex hand movements during this foraging activity (Dunbar, 1977; Maier, 1993).

According to the literature, opposing predictions can be made about the direction of hand preference in geladas' bimanual grass-plucking behavior. On one side, given the noticeable role of tactile input and rhythmic movements, one might expect an LH advantage. On the other side, complex finger movements might also favor the leading role of the RH.

As far as geladas' manual dexterity is concerned, according to Napier and Napier (1967), the selective advantage of a high opposability index is apparent in the behavior of ground-living monkeys in which grass-plucking is an essential feature of the feeding repertoire. In particular, geladas possess short index fingers, and the high ratio in the thumb size relative to the index finger (i.e., opposability index) suggests well-developed index finger and thumb dexterity (Napier & Napier, 1967). In line with this, during grass-plucking, geladas have been reported to use skilled hand movements (Dunbar, 1977). However, it is unclear to what extent the descriptions reported in the literature result from systematic observations of several individuals in a similar foraging context.

The main aim of this study was to assess whether wild geladas (T. gelada) have a population-level hand bias in bimanual grass-plucking. For this purpose, we evaluated (1) the number and time intervals of grass-plucking actions performed by each hand within-bout as a measure of hand performance, (2) the number of actions in which each hand had a leading role in starting as well as finishing grass-plucking bouts as a measure of hand preference, (3) the rhythmic structure with which geladas performed these plucking behaviors and whether they tended to isochrony. Moreover, we provided a detailed description of finger movements during grass plucking based on systematic observations conducted on several individuals. Particular attention has been paid to the ability to move the grass blades within the hand and perform simultaneously more than one grip within one hand. This allowed us to establish if there were interindividual differences within our study group and to compare our data with those available from the first descriptions reported in the literature.

2 | METHODS

2.1 | Site

The study area is located on the Kundi highland (North Shewa Zone, Amhara Region, Ethiopia 9_40.4020N, 39_45.0600E). The Kundi plateau (26 ha) is surrounded by cliffs and characterized by crop (approx. 12 ha) and pasture areas (approx. 14 ha), which have the same visibility conditions. This area is regularly frequented by 19 one-male breeding units (OMUs) of geladas (we knew the full composition for 14 of them; Caselli et al., 2021; Gallo et al., 2021).

2.2 | Study group

This study was conducted on 28 individuals belonging to 9 OMUs of geladas (T. gelada) frequenting the Kundi plateau (see Table 1). They included 11 males (7 adults: >6 years and 4 subadults: 4–6 years) and 17 females (all adults). Individual identification was achieved by previous observations and based on sex and distinctive external features. Age classes of individuals were estimated on the basis of physical characteristic and behavior (Dunbar, 1980) when they were first encountered by the research team of the project "Geladas to understand humans, herps to understand their environment."

2.3 | Data collection

Data collection was carried out from January to May 2019 and from December 2019 to February 2020 daily, spanning the dry season (December–March) and the beginning of the small rainy season (April–May). Data were collected 5 days per week (excluding days with heavy rain or mist), from around 9:30 to 17:00 (for a total of 94 full days and a total of 658 h). Each day, four observers (M. C., A. Z., C. D., A. G., C. D. G.) went to the Kundi plateau and split into two groups to search for and follow the gelada groups. Videos were recorded with two video cameras (Panasonic HC-V180, full-HD, 50 fps, optical zoom 50×) for 120 h.

2.4 | Data coding

Data were coded from videos in slow motion and frame-by-frame by one observer (R. T.) using Behavioral Observation Research Interactive Software, an open-source software for video/audio coding (Friard & Gamba, 2016). Only videos that allowed individual identification were coded. When necessary, we zoomed in on the frames to center the view on the hands. A second observer (V. T.) coded 24% of the videos to assess interobserver reliability (Cohen's κ = 0.87).

We coded feeding behavior in which geladas collected grass blades using bouts of alternate movements of both hands. We considered a storage bout as a complete sequence of grass-plucking actions, from the first contact of one hand with the grass to bringing the collected blades to the mouth. In particular, concerning manual performance, we coded for 28 individuals the number of grass-plucking actions performed by each hand (right and left) in 10 grass-storage bouts and the duration of each bout. In addition, on three out of those 10 bouts, we coded for each hand the time the grass-plucking actions took place to measure the time between onsets of consecutive movements.

Moreover, regarding manual preference, we coded the hand (right or left) used to start and finish a bout, respectively. Manual preference was coded for those 23 monkeys (14 females, nine males; 20 adults, three subadults) for which at least 30 bouts were available. Finally, we selected the best quality video (i.e., constantly in focus, without objects or individuals interfering with the vision of the upper

TABLE 1 Sex, class of age, and individual manual laterality scores of geladas in the study group.

Subjects	Age class	OMU	Performance		Preference Start bout					End bout				
			RH	LH	RH	LH	HI	z	cutoff	RH	LH	HI	z	cutoff
Males														
Pol	A	17	1.6	1.7	12	18	−0.2	np	L	3	27	−0.8	L***	L
Occ	A	16	1.7	1.5	9	21	−0.4	L*	L	4	26	−0.7	L***	L
Gio	A	10	1.4	1.6	18	12	0.2	np	R	16	14	0.1	np	np
Ped	A	15	1.3	1.4	10	20	−0.3	np	L	11	19	−0.3	np	L
Zam	A	6	1.3	1.5	-	-	-	-	-	-	-	-	-	-
Feg	A	15	1.2	1.3	13	17	−0.1	np	np	17	13	0.1	np	np
Cer	A	3	1.1	2	2	28	−0.9	L***	L	1	29	−0.9	L***	L
Wal	SA	15	1.6	1.6	10	20	−0.3	np	L	8	22	−0.5	L*	L
Dex	SA	10	1.5	1.6	13	17	−0.1	np	np	14	16	−0.1	np	np
Coc	SA	16	1.2	1.1	14	16	−0.1	np	np	11	19	−0.3	np	L
Jac	SA	15	1.3	1.5	-	-	-	-	-	-	-	-	-	-
Females														
Gin	A	15	1.3	1.3	8	22	−0.5	L*	L	9	21	−0.4	L*	L
Bra	A	15	1.5	1.3	16	14	0.1	np	np	14	16	−0.1	np	np
Span	A	15	1.8	1.9	13	17	−0.1	np	np	10	20	−0.3	np	L
Pan	A	15	1.5	1.6	16	14	0.1	np	np	10	20	−0.3	np	L
Fin	A	1	1.2	1.4	5	25	−0.7	L***	L	11	19	−0.3	np	L
Jas	A	16	1.5	1.6	11	19	−0.3	np	L	12	18	−0.2	np	L
Fri	A	10	1.7	1.8	6	24	−0.6	L***	L	6	24	−0.6	L***	L
Bia	A	16	1.3	1.2	17	13	0.1	np	np	18	12	0.2	np	R
Gar	A	15	1.6	1.8	5	21	−0.6	L***	L	6	24	−0.6	L***	L
Won	A	16	1.3	1.4	18	12	0.2	np	R	16	14	0.1	np	np
Spal	A	16	1.3	1.4	18	12	0.2	np	R	28	2	0.9	R***	R
Lom	A	10	1.7	1.7	10	20	−0.3	np	L	14	16	−0.1	np	np
Tor	A	16	1.5	1.7	11	18	−0.2	np	L	11	19	−0.3	np	L
Enn	A	1	1.3	1.2	14	15	−0.03	np	np	19	11	0.3	np	R
May	A	18	1.6	1.9	-	-	-	-	-	-	-	-	-	-
Lun	A	12	1.3	1.4	-	-	-	-	-	-	-	-	-	-
Nap	A	6	1.8	1.9	-	-	-	-	-	-	-	-	-	-

Note: A, adult; cutoff, preference according to cut-off points HI ≥ +0.20 and HI ≤ −0.20 (Hopkins, 2013); HI, handedness index; L, left handed; LH, left hand; np, nonpreferent; OMU, one-male breeding unit; R, right handed; RH, right hand; SA, subadult; z, preference according to binomial z scores (Binomial test).

*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

limbs, in which the animal maintained a position that allowed the view of the upper limbs for the duration of the video) for each of the 28 individuals to code manual behaviors to pluck and store grass blades within the hands, with particular attention to the ability of geladas to use finger movements and simultaneous grips within one hand.

2.5 | Data analysis

The assessment of manual laterality was based on hand preference and performance. Hand preference refers to a difference in the frequency of using the RH or LH to start or finish grass-plucking bouts. Hand performance in our study referred to a difference in

speed between hands, that is, in the number of single plucking actions off each hand within-bout. Inter-movement intervals were also analyzed as an additional measure of performance, which was informative for evaluating the regularity of movements of the two hands.

To evaluate laterality in performance (hand speed), we calculated for each individual the number of plucking actions performed with each of the two hands within the same bouts. The number of actions was then normalized to the bout's duration in seconds. To assess the direction of hand preference at the individual level, we calculated the handedness index (HI), using the formula $(R − L)/(R + L)$, where R and L are the total number of RH and LH actions, respectively. This measure varies from 1.0 (totally right-handed) to −1.0 (totally left-handed). We used the absolute value of the HI (ABS-HI) to examine the strength of manual preference independent of direction.

Moreover, we calculated a binomial z score for each subject based on the total frequency of RH and LH leading actions. According to this classification, monkeys with z scores higher than 1.96 or less than −1.96 are right- or left-handed, respectively. Besides, we classified right- and left-handed individuals according to HI cut-off points of +0.20 and −0.20, respectively, whereas all others would be classified as nonpreferent. This second classification follows the criterion suggested more recently by Hopkins (2013), who found that HI values of +0.20 and −0.20 roughly correspond to z scores of ±1.96 when a minimum of 30 responses are obtained to measure hand preference. However, the advantage of adopting this approach is that HI scores are not sensitive to variation in the sample size.

The Kolmogorov–Smirnov test showed that hand speed and preference data distributions did not significantly deviate from normality. Therefore, we used a mixed-model Analysis of Variance to compare RH and LH scores for manual performance, including RH and LH scores as repeated measures, whereas Sex was introduced as the grouping variable. Mixed-model Analyses of Variance were also used to analyze HI and ABS-HI values. In both cases, we use the values observed at the bouts' start and end as repeated measures and the Sex as the grouping variable. Moreover, we used one-sample t tests to evaluate whether the mean HI values of the sample differed from a chance distribution with a mean of 0. Finally, we used a Pearson correlation coefficient to determine the direction and rate of statistical dependence force between manual performance (hand speed) and preference.

Data on the onsets of successive hand movements were collected as inter-onset intervals t_k (De Gregorio et al., 2023; Raimondi et al., 2023) and were not normally distributed. Considering the two hands separately, we calculated t_ks, (i.e., the time between the onset of a hand-plucking movement) and then calculated the rhythm r_k using the formula in Roeske et al. (2020). To evaluate the occurrence of isochrony (following De Gregorio et al., 2021; Raimondi et al., 2023), we centered the on-isochrony ratio range around 1:1 and divided the ratio distribution into on-isochrony and off-isochrony (see De Gregorio et al., 2023 for details). After counting all ratios that fell in each on- and off-isochrony ratio range for each session of each individual, we test whether the counts into the on-isochrony ratio range differed from the off-isochrony ratio range using

a paired-data Wilcoxon test in R (R Core Team, 2023). We used paired-data Wilcoxon test in R also to test possible differences in the regularity of the movement between the two hands.

Statistical significance was set at $\alpha = 0.05$. All tests were two tailed.

3 | RESULTS

3.1 | Hand performance

3.1.1 | Hand speed

Table 1 reports individual mean scores of 28 monkeys (11 males, 17 females), for which 10 videos of bimanual bouts were available, making it possible to count the number of plucking actions performed by the monkeys with each of the two hands.

On average, geladas performed a total of 44 grass-plucking actions per bout. They carried out a significantly higher mean number of plucking actions per second with their LH compared to their RH (LH: mean = 1.6, SE = 0.04; RH: mean = 1.4, SE = 0.04; $F(1, 26) = 8.24$, $p = 0.008$, $\eta_p^2 = 0.241$; Figure 1a). Males and females did not significantly differ neither in terms of overall mean number of actions (males: mean = 1.5, SE = 0.05; females: mean = 1.5, SE=0.05; $F(1, 26) = 0.76$, $p = 0.39$, Figure 1b), nor in terms of laterality patterns ($F(1, 26) = 0.80$, $p = 0.38$).
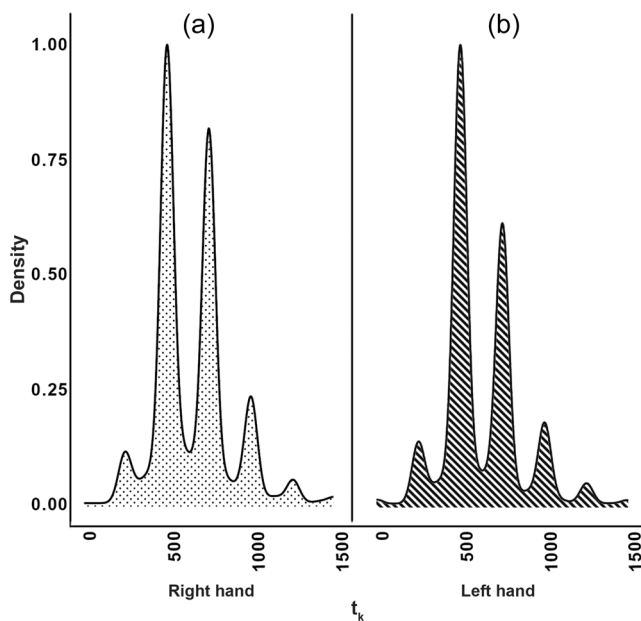
3.1.2 | Interonset intervals

The plots of the t_ks are informative of the degree of occurrence of the different tempi (Figure 2). First, we found similar tempi across the two hands, with most plucking movements occurring every 500 ms. Second, we analyzed the rhythmic categories (r_k) to evaluate how the intervals of the plucking movements followed one another. The probability density functions of rhythm ratios reported in Figure 3 show that both the RH and LH had prominent peaks corresponding to isochrony, thus indicating that there was a regular gap between the onsets of plucking movements. Therefore, we assessed the presence or absence of isochrony (ratios 1:1) on each hand. Wilcoxon signed rank tests with continuity correction showed that isochrony was significant for both the right ($V = 390$, $p = 2.119e−05$) and the LH ($V = 395.5$, $p = 1.217e−05$). Finally, we compared the rhythmic regularity of the two hands. For each hand, we calculated the coefficient of variation per session and then averaged it across individuals, and a Wilcoxon test indicated that the degree of rhythmic variation of the two hands did not significantly differ ($W = 343$, $p = 0.43$).

3.2 | Hand preference

Table 1 reports individual HI and ABS-HI scores of 23 monkeys (9 males, 14 females), for which 30 videos of bimanual grass-plucking
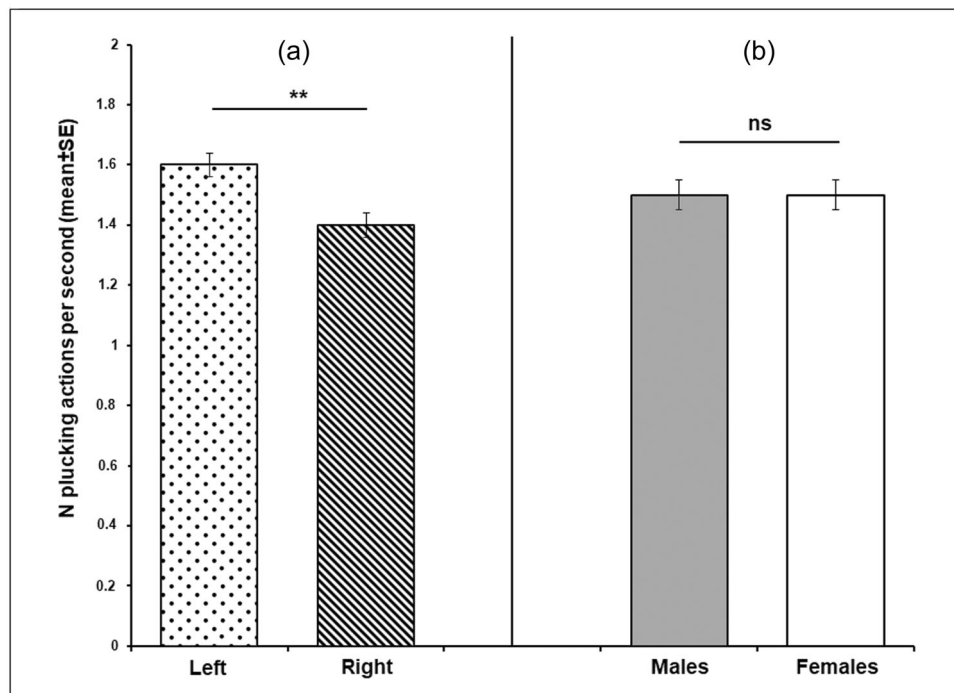
FIGURE 1 Number of plucking actions per second (mean ± SE) of the whole sample performed with the right and left hand (a) and mean number of plucking actions per second performed by males and females (b).

FIGURE 2 Interonset intervals (t_k) distribution for the right (a) and left hand (b) movements of geladas. Interonset intervals were measured as the time between the beginnings of successive plucking actions. The probability density functions of t_ks show two prominent peaks for both hands.
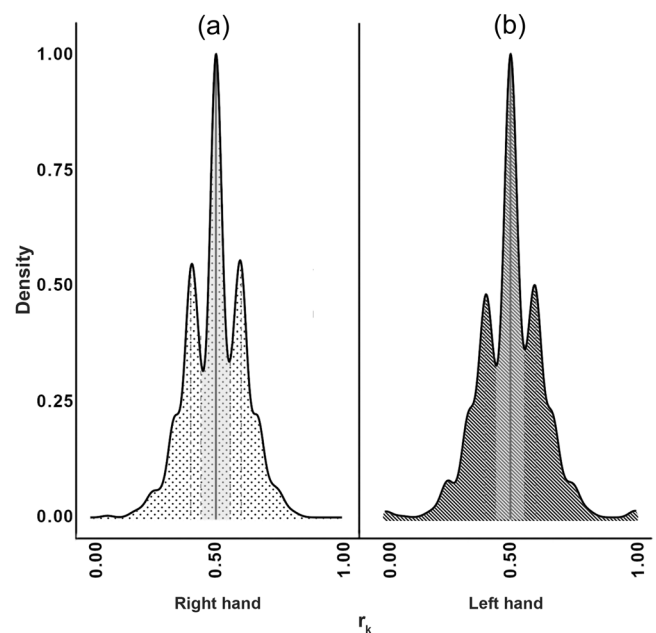
FIGURE 3 Rhythm ratio (r_k) distribution for the right (a) and left hand (b) movements of geladas. Probability density functions of r_ks also show on-isochrony areas (gray shading) and adjacent off-isochrony ratio ranges. Dotted lines denote the borders of the on-isochrony and off-isochrony ratio ranges. The solid gray lines indicate perfect isochrony (i.e., 0.5), which occurs significantly more often in the study individuals for both hands.
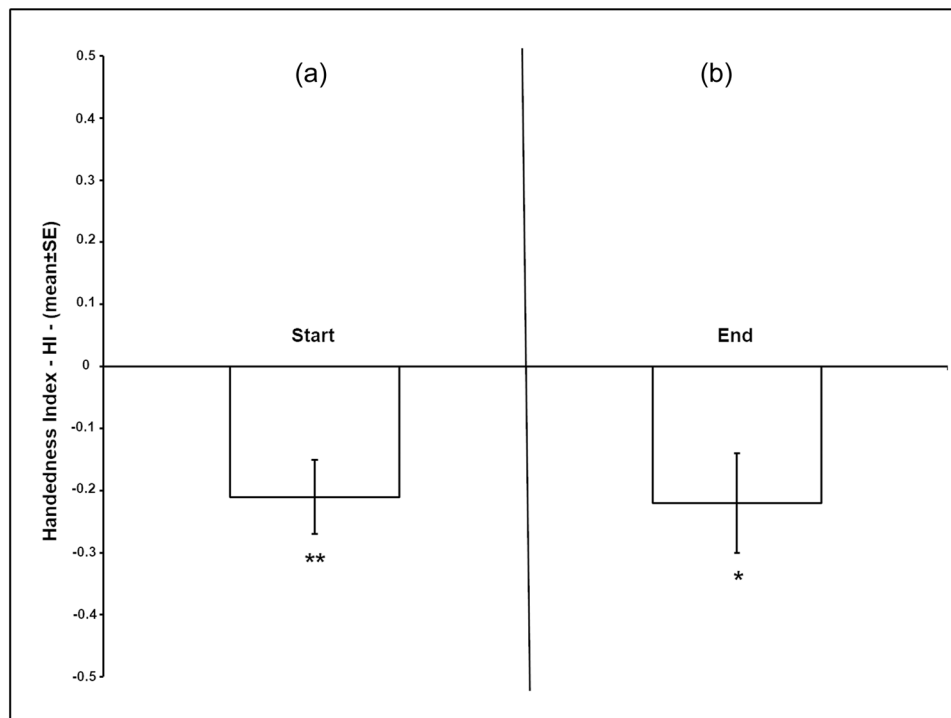
FIGURE 4 Handedness index (HI) scores (mean ± SE) for starting (a) and ending (b) bimanual bouts of plucking actions. The mean HI score were compared to a chance distribution with a mean of zero (HI = 0.0); *p < 0.05, **p < 0.01 (one sample t test).

bouts made it possible to identify the hand used by geladas to start and finish a bout. Preferences at the individual level are also reported in Table 1.

Geladas showed a significant preference at the group level for using their LH to start (mean HI = −0.21, SE = 0.06; one-sample t test, t(22) = −3.27, p = 0.003; Figure 4a) a plucking bout. Likewise, at the end of a bout, the first hand preferentially used to bring the grass blades to the mouth was the LH [mean HI = −0.22, SE = 0.08; one-sample t test, t(22) = −2.66, p = 0.014; Figure 4b].

No significant difference emerged in the geladas' manual laterality patterns when they started and ended grass-plucking bouts, neither in terms of direction [Start: mean HI = −0.21, ES = 0.06; End: mean HI = −0.22, SE = 0.08; F(1, 21) = 0.38, p = 0.543], nor in terms of strength of hand preference [Start: mean ABS-HI = 0.29, SE = 0.05; End: mean ABS-HI = 0.37, SE = 0.05; F(1, 21) = 3.08, p = 0.094]. Moreover, the mean HI and ABS-HI values of the males in our study group did not significantly differ from those of the females [males: mean HI = −0.31, SE = 0.11; females: mean HI = −0.15, SE = 0.09; F(1, 21) = 1.27, p = 0.272; males: mean ABS-HI = 0.35, SE = 0.09; females: mean ABS-HI = 0.31, SE = 0.05; F(1, 21) = 0.23, p = 0.336], regardless of whether we considered the start or the end of plucking bouts [HI: F(1, 21) = 3.14, p = 0.091; ABS-HI: F(1, 21) = 0.64, p = 0.434].

Finally, HI values were negatively correlated with the frequency of plucking per second performed by geladas with their LH; this was found when we considered either the start (r = −0.46, N = 23, p = 0.028) or the end of the bout (r = −0.54, N = 23, p = 0.008). Given

that negative HI values reflect LH bias, this result indicates that the more frequent the use of the LH to start or end the bimanual plucking bout, the more efficient the LH is in the number of plucking actions per second.

3.3 | Manipulative patterns to pluck and store grass blades

We conducted a qualitative analysis of the manual behavior used by geladas in our study group to pluck, store, and bring to the mouth grass blades. Grass-plucking bimanual sequences were performed by geladas with their hands while standing in a sitting posture and moving forward with small movements of their hind limbs/feet. All 28 individuals showed the same manual pattern in which the hands approached the grass with all the fingers flexed at the level of the metacarpophalangeal and proximal interphalangeal joints (Figure 5a), then the index finger and the thumb of each hand were extended to grasp one or few blades of grass using a pad-to-pad precision grip (Figure 5b). Based on several attempts by our research team to pluck blades of grass using precision grips, it was possible to establish that precision grips need to be forceful to pluck blades of grass in our study site effectively (A. Z., personal observation). After the blades were torn off, geladas moved the volar aspects of the index finger and thumb against each other to slide the blades toward the palm at the level of the metacarpophalangeal joints (Figure 5c). Adduction/abduction and rotational movements of the thumb were also
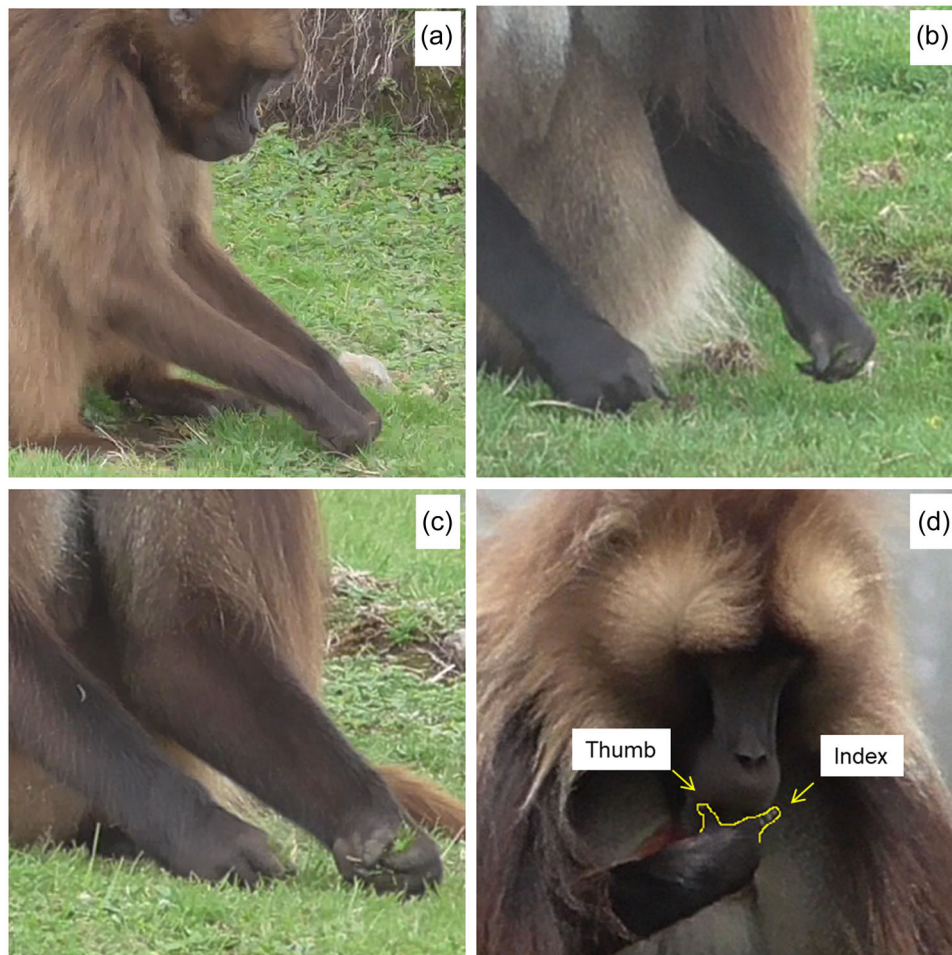
FIGURE 5 Geladas approach the grass with the fingers flexed at the level of the metacarpophalangeal and proximal interphalangeal joints (a), then the index finger and the thumb are extended to grasp one or few blades of grass using a pad-to-pad precision grips (b), once the blades are torn off, geladas move the volar aspects of index finger and thumb against each other to move the blades toward the metacarpal-phalangeal joints (c), after the steps b and c are repeated several times to collect a bundle of grass blades, the radial aspect of the hand is brought to the mouth, and the thumb and index fingers are extended to allow the incisors to grab the blades (d).

performed to adjust the blades' storage position. Hence, an effective collection of grass blades entailed the ability to perform both in-hand movements and compound grips.

The above action sequence was repeated until a bundle of grass blades was collected. Then, the radial aspect of the hand—from where the blades of grass protruded—was brought to the mouth, and the thumb and index fingers were extended to allow the incisors to grab the blades (Figure 5d). Usually, the two hands were brought to the mouth in rapid succession.

4 | DISCUSSION

To our knowledge, this is the first systematic study on manual laterality of free-ranging *T. gelada*. We found a significant leading-limb asymmetry in geladas during bimanual collection of graminoid plants: (i) Within a collection bout, they performed more plucking actions per second with their LH compared to the right one; (ii) they

preferred their LH to start and finish a collection bout. Our results also showed that hand performance and preference were correlated. Both these measures coherently suggested a right-hemisphere/LH advantage in geladas for bimanual grass-feeding behavior, the technique typically used by this species when foraging for grass blades (Dunbar, 1977); (iii) geladas moved their hands following an isochronous rhythm (ratio 1:1) and used precise fine motor functions of individual digits, such as forceful pad-to-pad precision grips, in-hand movements, and compound grips, which are considered to be the most advanced manual skills in primate species.

4.1 | Manual laterality

Manual performance has been scarcely considered as a measure of laterality compared to manual preference. Also, the relationship between these two measures of manual asymmetry is still largely unexplored. The main reasons for this lack of knowledge are partly

due to the extensive use of indirect laterality measures in the human literature (i.e., questionnaires on hand preference). Moreover, manual performance is usually more challenging to measure, even when adopting direct behavioral measures. Our study represents a step forward in understanding the connection between these two measures in a very dexterous catarrhine species. We found not only that manual performance in geladas was an effective measure to bring out the presence of a hand bias but also that it was consistent with manual preference, with both measures indicating a leading role of the LH. In line with the literature, we considered the hand that moves faster as the one that is superior in terms of performance. However, we cannot exclude that other analyses on manual movements, which were not possible to carry out in our study, could reveal that the RH is better in other respects during bimanual grass plucking.

An advantage of the right hemisphere/LH system was found in other primate species when manual laterality was assessed in haptic discrimination experimental tasks. Baboons (*Papio papio*) exhibited an LH preference to discriminate the shape of 3D objects haptically and explored objects longer with the LH than RH (Lacreuse, 1995). Rhesus monkeys (*M. mulatta*) showed an LH bias. At the same time, they reached inside an opaque box to discriminate haptically between peanuts and rocks (Fagot et al., 1991), with left-handed individuals that learned to solve a tactile discrimination task faster than right-handed ones (Hörster & Ettlinger, 1985). An LH preference has been found in robust capuchin monkeys (*Sapajus* spp., formerly identified as *Cebus*) in haptic discrimination and visual-tactual tasks (Lacreuse & Fragaszy, 1996; Spinozzi & Cacchiarelli, 2000). Furthermore, capuchins' accuracy in discriminating between food and nonfood items, when they mainly or exclusively relied on tactile input, was significantly higher when they used their LH (Spinozzi & Cacchiarelli, 2000). Similar findings have been found in humans as well. For example, Fagot et al. (1993) showed that when subjects had to explore meaningless cubes monohaptically, their LH simultaneously touched more cubes than the right one. In addition, a more recent study showed that haptic discrimination for not verbally identifiable shapes is better for the LH than the right one in humans (Stoycheva et al., 2020). According to Bradshaw and Nettleton (1981), the LH advantage of humans for haptic discrimination might reflect a greater involvement of the right hemisphere for spatial processing. Manual grass feeding performed by geladas is not a typical haptic task because these monkeys can use visual guidance to explore the ground and detect the patches of grass. However, all the in-hand movements performed by the fingers to pluck and especially to store the blades appear to mainly rely on tactile input from the volar part of their hands. Moreover, finger movements are performed by the two hands in a very fast alternation and sometimes even simultaneously; this leads to thinking of an activity greatly based on tactile input in support of visual guidance.

An alternative, nonmutual exclusive explanation for the right-hemisphere/LH advantage could be related to the rhythmic movements of each hand. We found that, in geladas' bimanual grass plucking, movement ratios of each hand matched the rhythmic

category 1:1, isochronous, that is, similar to the pace of a metronome. A right hemisphere advantage for timing tasks is consistent with some evidence from humans in both motor and perception domains. Evidence of a right hemisphere/LH advantage emerged in blindfolded right-handed individuals who were required to perform a sequence of hand movements to temporally adhere to an auditory rhythm (Chieffi et al., 2017). Moreover, Geiser et al. (2008) found a right-lateralized activation of basal ganglia (neostriatum), as well as of inferior frontal gyrus, related to the performance of rhythm processing in speech perception. In particular, only explicit processing of isochronous sentences revealed activation in the right posterior superior temporal gyrus, the right supramarginal gyrus, and the right parietal operculum. Interestingly, perception and actions can be coupled in rhythm processing. Listening to musical rhythms recruits motor regions of the brain, and a perceptual event can still engage the motor system even when it is dissociated from action processes (Chen et al., 2008).

4.2 | Manual dexterity and manipulative patterns

Geladas' manual grass feeding involves behaviors that are recognized as cornerstones of advanced hand skills in humans and other primates:

1. They grasp grass blades using precision grips involving the volar aspect of their thumb and forefinger. Having made some attempts, we know that such precision grips need to be forceful for an individual to tear off blades of grass in our study site successfully.
2. Geladas simultaneously use power grips to store the blades within their hands and precision grips to continue collecting blades with their thumbs and forefingers.
3. They use in-hand movements to move the collected blades of grass to store them within the hand and make the thumb and forefinger free to carry on collecting additional blades.

Accuracy and strength appear to set apart the finger grips of primate species such as humans and geladas. Geladas' forceful precision grip is possible thanks to a very short index finger and a well-developed thumb, whose movements are supported by a strong thumb musculature and a differentiation of the radial tendon of the deep flexor muscle of the forearm subdivided into three portions, the medial of which gives origin to the thumb tendon (Maier, 1993). These features enhance the thumb's mobility and ensure a firm grip between the thumb and index finger. A forceful pad-to-pad precision grip is one of the main characteristics distinguishing most dexterous catarrhines from other primates. Among platyrrhines, for instance, capuchin monkeys can perform precision grips. However, they do not seem to be able to apply much force besides precision in this grasping action, often opting to use power-grip techniques to pick up very small food items (Spinozzi et al., 2004; Truppa et al., 2019).

Our results also confirm the importance of compound grips in geladas. Among nonhuman primates, compound grips have been

described in macaques (*M. mulatta*; Macfarlane & Graziano, 2009) and more recently in capuchin monkeys (*Sapajus libidinosus* and *Sapajus* spp.; Jones & Fragaszy, 2020). Besides, as pointed out by Jones and Fragaszy (2020), descriptions of this grasping ability have been also reported in great apes such as gorillas (Byrne et al., 2001) and chimpanzees (Boesch & Boesch, 1993; Corp & Byrne, 2002; Marzke et al., 2015), although it was not specifically identified as a compound grip. Our systematic observations confirmed and expanded the first description reported by Dunbar (1977). Similarly, to what was reported by Macfarlane and Graziano (2009) in macaques, geladas are capable of grasping an object with one grip and storing it with a second grip, all within the digits of one hand and using in-hand movements. Furthermore, geladas can perform compound grips with both hands simultaneously.

Initially described in human literature (Elliott & Connolly, 1984; Exner, 1992), in-hand movements have been investigated only more recently in nonhuman species (for a review, see Fragaszy & Crast, 2016). In wild geladas, we observed movements of the index and thumb in opposite directions to slide the blades of grass toward the base of the index. These movements resemble the reciprocal synergies described in humans by Elliott and Connolly (1984). According to these authors, a reciprocal synergy involves the simultaneous movement of two or more digits in opposite directions to turn an object about one of its axes, as in turning a screw. Moreover, the way geladas accumulate the blades of grass toward the metacarpophalangeal articulation of the index finger in a storage position reminds the translation movement described by Exner (1992), where the object is moved to be "hidden" in the palm of the hand.

As Maier (1993) pointed out, geladas have ranges of daily activities distinctly shorter than other related species like baboons (*Papio* spp.), and, during all seasons, their diet mainly consists of grass. Such a graminoid-based diet may encompass challenging problems. Geladas are large monkeys whose diet is based on small-sized and relatively low-energy blades of grass, hence the need to develop morphological, physiological, and behavioral adaptations to optimize the collection and processing of the maximum amount of grass per unit of time. Geladas' dental morphology, including enlarged molars and deeply crenellated and high-crowned cheek teeth (Jablonski, 1993), allows particle size reduction of tough foods without highly specialized digestive physiology (Venkataraman et al., 2014). The same ecological pressures might have also contributed to the evolution in geladas of hands capable of performing forceful precision grips, compound grips, and in-hand movements; manual skills that are usually associated with cognitively advanced primate activities, such as extractive foraging and tool use (Fragaszy & Crast, 2016; Marzke & Shackley, 1986).

5 | CONCLUSIONS

The evolution of skilled thoracic limbs equipped with prehensile hands strongly contributed to the adaptive success of primates by shaping how they interact with the surrounding environment, especially their foraging techniques. Therefore, the study of the manual skills of primates appears to be crucial for understanding their

evolution. This study represents a step forward in this respect, trying to shed light on key aspects of manual dexterity in geladas, whose neuroanatomical characteristics of the hand have made this species count as one of the most similar to human beings.

Our findings highlighted the importance of including measures of hand performance when possible. This seems particularly suitable for the study of bimanual behaviors, especially those in which the two hands perform similar actions with neither having a clear dominant role. Hand preference and performance measures together can return a more complete picture of manual laterality.

The origin of manual dexterity is often traced back to the ability to solve complex cognitive and/or motor tasks such as extractive foraging. Indeed, using the hands dexterously is a considerable advantage when translating cognitive capabilities into actions. In addition, here we observed a highly sophisticated use of the hands by geladas for feeding on grass, a foraging activity that does not necessarily require skilled cognitive and motor capabilities. The way these monkeys have developed to optimize grass collection is associated with those manual behaviors that most characterize manual dexterity in primates. Thus, the need to increase the movement execution time of forelimbs, hands, and single digits might be a crucial factor in the evolution of primate manual behavior, a factor capable of transforming a seemingly simple activity into a motorically challenging task.

country in which the work took place and adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Nonhuman Primates.

CONFLICT OF INTEREST STATEMENT

DATA AVAILABILITY STATEMENT

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