

Cite as: Cubí, M., & Llorente, M. (2021). Hand preference for a coordinated bimanual task in captive hatinh langurs (*Trachypithecus hatinhensis*) and gray-shanked douc langurs (*Pygathrix cinerea*) at the Endangered Primate Rescue Center (Vietnam). *Behavioural Processes*, art.num. 104393. <https://doi.org/10.1016/j.beproc.2021.104393>

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Hand preference for a bimanual coordinated task in captive hatinh langurs (*Trachypithecus hatinhensis*) and grey-shanked douc langurs (*Pygathrix cinerea*)

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Highlights

- We evaluated hand preferences in hatinh and grey-shanked douc langurs for the first time.
- Both species present clear individual lateralisation.
- No group level hand preferences were detected.
- The strength of hand preferences was greater in hatinh than in douc langurs.
- No sex differences were detected within species.
- The tube-task is sensitive tool to evaluate hand preferences in these primates.

Abstract

Right-handedness in humans reflects the functional brain specialisation of the left hemisphere. To better understand the origins of this population-level tendency, it is crucial to understand manual lateralisation in other non-human primate species. The aim of this article is to present a first approach to the hand preference of two primates from Vietnam, the endangered hatinh langur (*Trachypithecus hatinhensis*) and the critically endangered grey-shanked douc langur (*Pygathrix cinerea*). Eighteen individuals from each species (N=36) were evaluated by means of the bimanual coordinated tube task and their responses were recorded in terms of manual events and bouts. Our results showed that subjects presented strong individual-level preferences but not lateralisation at the group-level. No sex differences were detected within species. The index finger was used in all of the extractions during this bimanual task, alone (86%) or in combination with other fingers (14%). In addition, hatinh langurs exhibited a greater strength of hand preferences than grey-shanked douc langurs, pointing to a possible higher manual specialisation during the leaf-eating process. These findings help to broaden our scarce knowledge of manual laterality in Asian colobine monkeys and

confirm the bimanual tube task as a sensitive measure for assessing manual laterality in non-human primates.

Keywords: Asian colobine monkeys, handedness, bimanual coordinated task, tube task, endangered primate species, manual lateralisation

1. Introduction

Brain asymmetries in non-human animals have been detected over the last four decades in the brains of fish, amphibians, reptiles and mammals (Bisazza et al., 1998; Braitenberg and Kemali, 1970; Denenberg, 1981; Nottebohm et al., 1976; Rogers et al., 2013; Rogers and Anson, 1979). Nevertheless, it has only recently been accepted that the human brain is not the only lateralised one in the animal kingdom (Corballis, 2020; Miletto Petrazzini et al., 2020; Rogers et al., 2013). Results in this area indicate that there are a significant number of vertebrate species (Hori et al., 2017; Lippolis et al., 2002; Vallortigara et al., 1998; Wiper, 2017), and even some invertebrates (Duistermars et al., 2009; Frasnelli, 2017, 2013; Rogers and Vallortigara, 2019, 2008; Suzuki et al., 2008; Vallortigara and Versace, 2017), that present this characteristic.

Non-human primates have been proposed as a potential model for understanding the evolution and development of human brain asymmetries (Fitch and Braccini, 2013). Some functional asymmetries are particularly suitable to explain human handedness phylogenesis (Cochet and Byrne, 2013). The comparative approach applied to the study of manual laterality helps us understand those processes that led to the strong left-hemisphere brain specialisation observed in modern humans (Hopkins and Cantero, 2003). Socioecological lifestyle, postural characteristics and demands, task-level

complexity and tool use have been proposed as factors that could shape the evolution of manual preferences in human and non-human primates (Prieur et al., 2019).

For many years, there has been a strong interest in whether population-level handedness is human-specific or a characteristic also present in non-human animals (Bradshaw and Rogers, 1993; Güntürkün et al., 2020; Rogers and Andrew, 2002). It is now widely accepted that humans are right-handed at the population level, as an estimated 90% of the population presents this trait (Annett, 2002; Porac and Coren, 1981). Recently, Marcori and Okazaki (2019) reviewed current hypothesis on the origins of human handedness evaluating the effects of genetic, neural asymmetries, pregnancy and socio-cultural influences on human manual laterality. Although most of the reviewed studies did not reject the influence of both genetic and environmental factors, the exact mechanisms responsible for human brain laterality still remain unknown. For this reason, it is believed that a comparative perspective may help unravel the evolution and origins of human cerebral lateralisation (Bradshaw and Rogers, 1993; Hopkins et al., 2015; Llorente et al., 2009; Rogers, 2014; Ward and Hopkins, 1993) and are crucial to understand the functions and pathologies of the asymmetric brain (Güntürkün et al., 2020).

Historically speaking, findings on manual laterality in non-human primates have been inconsistent between and within species (Hopkins, 2006; Papademetriou et al., 2005). Some potential explanations have been proposed to address these issues, including the research setting, statistical approach or task used (Hopkins, 2013a, 2013b). Given that bimanual tasks are cognitively demanding, these tasks are generally more successful in eliciting manual asymmetries than simpler unimanual tasks (Hopkins et al., 2003). These tasks are complex and cognitively demanding, providing more efficiency in detecting manual asymmetries than simple unimanual tasks (Blois-Heulin

et al., 2006; Maille et al., 2013). It was Hopkins (1995) who first described the “tube task”, a bimanual coordinated complex device for testing manual preferences in non-human primates. The task involves the provision of a tube containing a preferred food to a primate in order to observe which is the non-dominant hand (used to hold the tube) and which is the dominant hand (used to extract the food from the tube and bring it to the mouth; Hopkins, 1995). According to the task complexity hypothesis (Fagot and Vauclair, 1991), the tube task can be classified as a high-level task, forcing specialised use of the dominant hand to extract the food. Accordingly, the tube task has become a recognised method, which to date has been used to test around 20 different primate species, including cercopithecines (Maille et al., 2013), *Rhinopithecus roxellana* (Zhao et al., 2012), *Ateles geoffroyi* (Motes Rodrigo et al., 2018), hylobatids (Morino et al., 2017), as well as great apes (Hopkins et al., 2011). Although most tube task experiments have been conducted in captivity (Canteloup et al., 2013; Meunier and Vauclair, 2007; Zhao et al., 2016), some authors have applied this task in wild (Zhao et al., 2012) and semi-wild settings (Llorente et al., 2011). Despite the above, there are still many species which hand preferences have not been investigated. Such investigations could prove helpful in tracing the evolutionary history of primate handedness and the ecological pressures that shape manual use in the primate lineage.

The Asian colobine monkeys or langurs of the Presbytini tribe (Old World monkeys) are medium-sized, generally arboreal monkeys that follow a folivorous diet and whose multi-chambered stomachs have adapted to digest leaves (Brandon-Jones, 2004; Mittermeier et al., 2013; Nadler and Brockman, 2014). Most of the laterality studies conducted on these primates include observations on spontaneous unimanual and bimanual activities during different daily behaviours (Ahamed and Dharmaretnam, 2015; Miller and Paciulli, 2002; Mittra et al., 1997; Pan et al., 2011; Roy and Nagarajan,

2018; Zhao et al., 2010, 2008). For example, 11 red-shanked douc langurs (*Pygathrix nemaeus*) at the Cologne Zoo were evaluated for hand function based on the degree of fine motor skills required for the behaviours observed. The results yielded four individuals with right-hand preferences and four with left-hand preferences, leading the authors to conclude an absence of population-level handedness (Smith and Scollay, 2001). Zhao and colleagues (2012) performed a study using the tube task on wild Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) and found tentative evidence of group-level left-handedness in this species of Cercopithecoidea. Our study constitutes a first approach to measuring manual laterality among hatinh langurs (*Trachypithecus hatinhensis*) and grey-shanked douc langurs (*Pygathrix cinerea*) using the coordinated bimanual tube task. Our main objectives were to: (1) determine whether these langurs present individual hand preferences and/or group level handedness, (2) assess whether sexes or species differed in the strength and/or direction of hand preferences, and (3) evaluate finger use on food extraction. Based on previous reports we predicted that langurs would present clear individual hand preferences but fail to show group-level handedness (Miller and Paciulli, 2002; Zhao et al., 2016), that no sex or species differences would be detected (Fu et al., 2019; Zhao et al., 2007), and finally, that the index finger would be the one most recurrently used in this bimanual task (Maille et al., 2013; Zhao et al., 2012).

2. Material and methods

2.1. Statement of ethics

This project followed the protocols approved by the European Parliament and Council's Directive 2010/63/EU of 22 September 2010 on the protection of animals used for scientific purposes. It also followed the institutional guidelines for the care and

management of primates established by the Endangered Primate Rescue Center and the International Primatological Society.

2.2. Study site and subjects

The Endangered Primate Rescue Center (EPRC, <https://www.eprc.asia>) houses more than 180 non-human primates from around 15 different endangered Vietnamese species belonging to the Ceropithecidae, Hylobatidae and Lorisidae families. It is located in Cuc Phuong National Park (20°14'40.2"N 105°42'56.0"E), in Ninh Binh province, Vietnam. In recent decades, most of the country's wildlife has been struggling to survive the many different threats it faces. Unfortunately, most of Vietnam's 25 species of primates are endangered or critically endangered. This was the reason why Tilo Nadler and the Cuc Phuong National Park established the rescue centre in 1993, with the collaboration of the Frankfurt Zoological Society. Later, from 2013 until the present day, Leipzig Zoo became the main sponsor of the center. From the outset, the centre's main objectives have been to rescue, rehabilitate, breed, release and study some of these endangered Vietnamese primates.

The species investigated in this study were the hatinh langur (*T. hatinhensis*) and the grey-shanked douc langur (*P. cinerea*), since these were the most abundant langur species at the centre. The centre was designed with different enclosures of the same size (10m x 5m x 3m) housing one to eight individuals. It also has two semi-wild hills, of 2 ha and of 5 ha, for those individuals participating in a release programme. The hatinh langurs (*T. hatinhensis*) stay outdoors all year round, while the grey-shanked douc langurs (*P. cinerea*) have indoor access during the winter. Over 100 different local species of leaves are delivered each day during the three feedings (6.30 a.m., 11.00 a.m. and 4.00 p.m.) and the cages are cleaned twice a day (6.30 a.m. and 3.30 p.m.). The centre provides different enrichment devices made from local materials (bamboo, sticks,

bottles, ropes, swings, food, boxes, etc.). However, nearly all of the enrichment devices are delivered to the gibbons. That is, it is very rare to see any of these toys or objects in the langur enclosures. The langurs receive some fresh branches to climb on time to time.

The study sample initially comprised 19 hatinh langurs (*T. hatinhensis*) and 20 grey-shanked douc langurs (*P. cinerea*) (Table 1) distributed in 22 enclosures. However, Minni (hatinh langur), Tonic and Eric (two grey-shanked douc langurs) were excluded from the final analysis due to their lack of motivation to participate in any tube task sessions. During the observation period, some individuals were transferred from one enclosure to another. Eco, Sung and Mr. Bean were moved on October 29th 2018, while Phuong, Naomi, Claus and Falk changed enclosures on November 6th 2018. Finally, Seba was moved on December 12th 2018 and again on January 12th 2019 (Table 1). Only adult individuals were tested in order to avoid undefined manual laterality in immature individuals. Thus, only sexually mature subjects were included, females over four years of age and males over five (Agmen, 2014; Insua-cao et al., 2012; Nadler et al., 2003)

<INSERT TABLE 1>

2.3. Data collection

We follow the same procedure used to evaluate hand preference in complex bimanual tasks applied in previous studies (Hopkins, 2013b; Llorente et al., 2011). The bimanual tube task proposed by Hopkins (Hopkins, 1995) is considered sensitive in determining hand motor bias, because it may remove or minimise those postural factors that could influence the use of one hand or another in simple unimanual tasks. For the tube task device, an empty piece of plastic water pipe of 7 cm length and 3 cm in diameter was used, filled with preferred food inside (steamed and raw sweet potato). To complete the task, it was necessary to hold the tube with one hand, introduce one finger

of the other hand, extract the food and ingest it (Figure 1). The food needed to be placed far enough inside the tube to avoid the possibility of the animals licking it instead of using their fingers to remove it.

<INSERT FIGURE 1>

A focal untimed-event/bout recording strategy was deployed (Bakeman and Quera, 2011). The hand (right, R or left, L) and finger (D1 to D5) that the individual used to remove the food from the tube were recorded. The sessions were live-coded. Events and bouts were considered in all cases (see definitions in table 2). During the observation period (October 2018 to March 2019), two experimental sessions were carried out in the morning (between 9 a.m. and 11 a.m.) and two more in the afternoon (between 1.30 p.m. and 3.30 p.m.). One single observer (MC) performed the data collection. To ensure the observer did not directly influence the individuals, data were collected from outside the enclosures at a fixed distance of 1 to 2m and after a habituation period of 30 days. During this first 30 days animals were habituated to the observer and to the empty enrichment device (tube task) to avoid reactivity and neophobia during the experimental phase. Animals were randomly exposed to the tubes inside the enclosure. No systematic observations of behaviours or hand use were made during this period.

Although only one individual was observed in each session, several plastic water pipe tubes baited with food were delivered by the keepers to the rest of the group to avoid fights or monopolisation of the task by dominant individuals. Sessions did not have a predetermined length and were individual-specific. The session began when the subject took the tube and performed a first food extraction. A session was considered valid if the individual completed at least six events of food extraction, and the session

concluded when the subject finished the food or lost interest in the task for more than one minute, in line with previous studies (Llorente et al., 2011; Padrell et al., 2019). If the experimental subject did not perform a minimum of six events the session were discarded. We carried out a total of 379 experimental sessions. Seventy-seven sessions (20%) were discarded for having less than 6 events. The minimum responses by session were six and the maximum 317 (Mean=51.55; SD=44.47). The minimum duration by session were one minute and the maximum 45 minutes (Mean=6.07; SD=5.46). In total, a minimum of 104 events and a maximum of 999 events by subject were recorded across sessions (Mean=465.20; SD=284.90). Sessions for the same subject were separated by at least 2 days. Each individual participated in 1 session minimum and 9 sessions maximum (Mean=7.85; SD=2.11). If the tube from the observed individual had no food left or was stolen by another individual, the session was stopped to deliver a new tube and continue with the observation (de Andrade and de Sousa, 2018).

Four to five enclosures were tested on a daily basis, following a random plan to allow hand preference data collection of all individuals each week. The variables recorded in each session are represented in Table 2.

<INSERT TABLE 2>

An intra-rater reliability test was performed to ensure the quality of the collected data. Three per cent (n=11) of all the tube task sessions (n=379) were video recorded and observed at two different times by the same observer in order to check for point-by-point agreement. Cohen's Kappa coefficients (Cohen, 1968) obtained for each session were excellent and ranged from 85% to 100%.

2.4. Data analysis

The handedness index (HI) was used to calculate individual handedness from the events and bouts, following the formula of subtracting the number of left events/bouts from the number of right events/bouts and dividing by the total number of events/bouts for both hands (Hopkins, 1995). The results range from -1 to +1. The absolute values (ABSHI) indicate strength of preference in hand use, values close to 1 being the most asymmetric and values close to 0 the most ambidextrous. Z-score values were used to classify the subjects' hand preference. Individuals with Z-score values higher than +1.96 were classified as right-handed, those with values lower than -1.96 as left-handed, and all other subjects with results between these two values were classified as ambiguously handed (Hopkins et al., 2003; McGrew and Marchant, 1997). A binomial test was also performed to double-check the individual hand-preference results obtained from the Z-score (Llorente et al., 2011). Descriptive statistics were used to evaluate finger use preference based on the total number of actions recorded, while to compare the HI and ABSHI scores obtained by the two different measurement methods (events and bouts) we used a Spearman's correlation test. The later test was also used to obtain the correlation between both measurement methods in the total number of responses acquired for the HI and ABSHI. Group level preferences were analysed via the Wilcoxon one-sample t-test, with individual HI-event and HI-bout scores for the whole sample and for each species (Hopkins, 1999; Zhao et al., 2016). Independent Mann-Whitney test samples were used to assess species or sex differences regarding the HI and ABSHI. Finally, we used the Spearman correlation to test the relationship between the number of data points (events and bouts) per subject and the HI and ABSHI scores (Fu et al., 2020; Hopkins and Cantalupo, 2005). All analyses were performed with the

JASP statistical software (Version 0.14.1), which uses R-packages. Means are reported as mean \pm SE. An alpha level of 0.05 was used as cut-off for significance.

3. Results

3.1. Description of collected data

A total of 19,537 events and 4,661 bouts were obtained on hand preference in the tube task (Table 3). Globally, 10,884 events (55.71%) were performed with the left hand and 8,653 (44.29%) with the right. As for bouts, 2,593 bouts were performed with the left hand (55.63%) and 2,068 (44.37%) with the right. Referring to events, each individual performed a mean number of 542.69 ± 39.41 manual actions (range: 104 to 999), with a mean HI score of -0.04 ± 0.12 (range: -1 to 0.99), and a mean ABSHI of 0.66 ± 0.06 (range: 0 to 1). With regard to bouts, each individual performed a mean number of 129.47 ± 12.12 manual actions (range: 34 to 382), with a mean HI score of -0.06 ± 0.11 (range: -1 to 0.98) and a mean ABSHI of 0.52 ± 0.06 (range: 0.011 to 1). No correlation was found in the number of responses between either the HI or ABSHI values obtained ($P > 0.12$ in all cases).

3.2. Data consistency

A significant positive correlation was detected between the HI ($r=0.98$, $P < 0.01$, 95% CI [0.96, 0.99]) and ABSHI ($r=0.94$, $P < 0.01$, 95% CI [0.89, 0.97]) scored for event and bouts methods (Figure 2).

<INSERT FIGURE 2>

3.3. Individual handedness

We used the Z-score and binomial test to define the hand preference of each individual (Table 3). Regarding individual hand preferences, different results were

obtained depending on the measurement method used. With regard to events, 91% of the sample was lateralised: 17 left-handed (47%) and 16 right-handed (44%), while three ambidextrous individuals (8%) were detected. Despite the difference in the number of lateralised and non-lateralised subjects ($\chi^2=(1, n=36)=25.00, P<0.01$), no differences were found in the number of right- and left-handed subjects ($\chi^2=(1, n=33)=0.30, P=0.86$). As for the bout scores, 81% of the sample was lateralised: 14 left-handed individuals (39%) and 15 right-handed (42%), while seven ambidextrous (19%) langurs were detected. Despite the difference in the number of lateralised and non-lateralised subjects ($\chi^2=(1, n=36)=13.44, P<0.01$), no differences were found in the number of right and left-handed subjects ($\chi^2=(1, n=29)=0.34, P=0.85$). As neither method presented significant differences, only the HI scores based on events were taken into consideration for this analysis.

<INSERT TABLE 3>

3.4. Population-level handedness

Referring to population-level preferences, a one sample t-test did not point significantly to handedness in either the total tube task observations or when separated by species i.e. *T. hatinhensis* and *P. cinerea* (Table 4).

<INSERT TABLE 4>

3.5. The influence of species and sex on manual laterality

A comparison of the two species revealed no significant differences in direction of hand preference (HI) (event: $U=208.00, P=0.15, 95\% \text{ CI } [-0.08, 0.99]$; bout: $U=210.00, P=0.13, 95\% \text{ CI } [-0.11, 0.87]$). Nevertheless, *T. hatinhensis* displayed a significantly greater strength of hand preference than *P. cinerea* in terms of both event

($U=80.50$, $P=0.01$, 95% CI [-0.62, -0.03]) and bout ($U = 94.00$, $P=0.03$, 95% CI [-0.55, -0.02]) indices.

No significant differences were detected between the sexes in *T. hatinhensis*, using either the HI (event: $U=28.00$, $P=0.31$, 95% CI [-1.72, 0.08], bout: $U=26.00$, $P=0.24$, 95% CI [-1.43, 0.22]) or the ABSHI (event: $U=34.00$, $P=0.63$, 95% CI [-0.15, 0.31]; bout: $U=37.00$, $P=0.83$, 95% CI [-0.06, 0.41]). Equally, no differences were found with regard to sex in *P. cinerea* in terms of hand preference direction (event: $U=45.00$, $P=0.60$, 95% CI [-0.42, 0.95], bout: $U=41.00$, $P=0.86$, 95% CI [-0.42, 0.77]) or strength (event: $U=24.00$, $P=0.21$, 95% CI [-0.67, 0.20]; bout: $U=28.00$, $P=0.38$, 95% CI [-0.67, 0.10]).

3.6. Finger use

An analysis was also conducted of the digit (D1, D2, D3, D4, or D5) used to extract the food from the tube. This was mostly found to be done with the index finger (D2; 86%), while the other times comprised a combination between the index finger and one or a combination of other fingers (((D2+D3)+D4)+D5); 14%). The thumb was not recorded in any of the actions.

4. Discussion

To the best of our knowledge, this is the first report on manual laterality in both *T. hatinhensis* and *P. cinerea* tested by means of the bimanual coordinated tube task. It also constitutes one of the first studies to use the tube task with colobine monkeys. In accordance with our first prediction, the subjects in our study presented a strong individual manual laterality (event: 91% lateralised; bout: 81%), which reinforces the validity of the tube task as a valid tool to detect manual asymmetries (Maille et al.,

2013). However, no evidence was found of population-level handedness in our target population. This absence of group-level manual laterality is in line with the findings of previous studies conducted on similar species in both unimanual and bimanual activities (e.g. *Simias concolor*, uncoordinated feeding: Miller and Paciulli, 2002; *Pygathrix neamaeus*, combined dominant behaviours and eating behaviours: Smith and Scollay, 2001; *Colobus guereza*, feeding: Wells, 2002; *Rhinopithecus roxellana*, nipple preferences and maternal cradling: Zhao et al., 2008, *Rhinopithecus roxellana*, quadrupedal and bipedal actions: Zhao et al., 2007). Prior research on the bimanual coordinated tube task in wild *Rhinopithecus roxellana* showed the first evidence of left-handed population preferences in Asian colobine monkeys (Zhao et al., 2012). This agreed with the Postural Origin Theory (MacNeilage et al., 1987), which could play an important role when defining hand preference in these species. This theory states that in arboreal primates the left-hand preference evolved for visually guided reaching, whereas the right hand was favoured for postural control and locomotion in trees (Meguerditchian et al., 2013; Zhao et al., 2012). The non-consistency of our results with this theory and with wild *R. roxellana* could be related to ecological differences between species, artefactual variables (e.g. experimental factors such as learning by induced practice with the experimental device) and environmental differences between captive and wild settings (e.g. being raised by humans, artificial activity conditions, stress, environmental stress) versus wild settings (McGrew and Marchant, 1997; Prieur et al., 2019). Further research is required on this issue in order to increase data consistency and gain a better understanding of the brain asymmetries and manual specialisation in these understudied primates.

Our data were recorded following both the event and bouts methodology for the direction and strength of manual preferences. Although the results regarding the

direction of hand preference did not differ based on the unit of measurement employed (events or bouts), the strength of hand preferences differed between both types of measures. According to Hopkins (Hopkins, 2013b), events are more sensitive than bouts in detecting strength of lateralisation. That said, the measures exhibited an extremely high correlation (of almost 1.00) in both cases. In both measures, individual hand preferences (left-handed, right-handed and ambidextrous) coincided in almost all individuals (86%). This may suggest that both measurement methods were similar enough, at least referring to the HI, to quantify almost the same hand preference (Hopkins, 2013). However, divergences in some individuals' observations differed from the results of studies conducted by Zhao and colleagues (Zhao et al., 2016, 2012), which quantified the two measures as being equivalent. In our case, different results between events and bouts could show that some individuals presented more extractions within one bout than other subjects (asymmetries in bout length), as suggested in Hopkins (2013). Hopkins (1999) recommended the use of both methods to avoid skewed distributions.

In the current study, we compared the hand preferences of two species of langurs (*T. hatinhensis* and *P. cinerea*) as well as of the males and females of each species. Our second prediction, that no sex or species differences would be detected, was confirmed by the absence of population-level preferences in this study. This is also supported by previous findings (Chapelain and Hogervorst, 2009; Meguerditchian et al., 2010; Meunier and Vauclair, 2007; Zhao et al., 2016, 2007), which revealed similarities between female and male hemisphere specialisations among non-human primates (Fu et al., 2019). That being said, some studies have detected significant differences between the sexes in this regard. For instance, in the study by Spinozzi, Castorina and Truppa (1998) and by de Andrade and de Sousa (de Andrade and de Sousa, 2018), some of the

results showed that brown capuchin monkey females (*Sapajus apella*) presented a stronger right-hand preference than that in males in coordinated-bimanual tasks. The same preferences were demonstrated in a tool-using context, nut cracking and in hunting behaviours (Hellner-Burris et al., 2010; Westergaard and Suomi, 1993). Similar results were obtained by Pan and collaborators (2011) who investigated sex differences in hand preference of black-and-white snub-nosed monkeys (*Rhinopithecus bieti*). Hand preferences in these species would therefore seem to be related to the selective pressure each sex has been subjected to in foraging (Hellner-Burris et al., 2010; Pan et al., 2011). With regard to the langur species, more data are required to determine whether the similar results between sexes depend on the type of task used, the sexual dimorphism of each species, or any other brain-related factors yet to be studied, in both wild and captive settings.

Aside from tube task experiments with wild golden snub-nosed monkeys (Zhao et al., 2012), ours is the only study to have used this device with Asian colobine monkeys. It is therefore of great importance to consider the results from the perspective of comparing the two species tested (*T. hatinhensis* and *P. cinerea*). The handedness index (HI) evidenced no differences between species in any of the measurement methods. However, the species comparison revealed differences concerning strength of laterality (ABSHI), it being greater in hatinh langurs (*T. hatinhensis*) than in grey-shanked douc langurs (*P. cinerea*). This may be explained by the possibility of hatinh langurs (*T. hatinhensis*) presenting a greater hand specialisation in the leaf-eating process, despite being closely related to grey-shanked douc langurs (*P. cinerea*). As a matter of fact, some studies identified differences between hatinh and douc langurs in terms of food selection, ingestive behaviour, dental and mandibular morphology and gut physiology, which may be related to different manual strategies during leaf-eating

manipulation (Caton, 1999; Wright et al., 2008a, 2008b). That being said, these differences could also be related to each individual's previous life experience and prior experiences with bimanual coordinated tasks. More comparative studies on these two species would be needed to confirm this first approach to explaining the different hand preference intensities found between the two species.

Both *T. hatinhensis* and *P. cinerea* displayed a strong preference for exclusively using the index finger (D2) when extracting food during the tube task, regardless of which hand was used. Moreover, all other responses combined the index finger with the middle, annular and/or small finger. This finding was in line with those of the first tube task study (Hopkins, 1995), as well as many other similar studies in bimanual coordinated primate hand preferences (e.g. Chapelain et al., 2011; Llorente et al., 2011; Maille et al., 2013; Vauclair et al., 2005). These findings lend support to the belief that the tube task is a highly complex device sensitive to detecting manual specialisation in primates, since it requires not only use of the dominant hand but also precise finger usage (Zhao et al., 2016). Further large-sample-size studies on hand preference will be needed with other close-related species using the tube task to compare and delve deeper into the evolutionary implications of manual laterality in Asian colobine monkeys.

5. Conclusions

The results of this study are the first to evidence clear individual manual laterality in *T. hatinhensis* and *P. cinerea* and will serve as further evidence on hand preferences in arboreal Asian colobine monkeys. Although most of the subjects presented individual hand preferences when using the tube task, no population-level handedness (following McGrew and Marchant, 1997) or differences between sexes were found. The significant differences detected in the greater strength of handedness

among hatinh langurs in comparison with grey-shanked douc langurs needs to be confirmed in future research. Finally, the coordinated bimanual tube task has again proved to be useful in measuring manual laterality and finger use, confirming the validity of the method to study hand preferences in langur monkeys.

Acknowledgements

We would like to thank Elke Schwierz, head-keeper at the EPRC, for sharing her guidance, passion for good animal care and knowledge related to the studied species. We also appreciate the daily support and help provided by the EPRC staff, together with all of the volunteers and interns. Special gratitude to Adam Davies, the EPRC director at the moment. We thank the Fundació UdG: Innovació i Formació and Endangered Primate Rescue Center for their cooperation in signing the agreement and giving us the opportunity to participate in this research. The manuscript was greatly improved thanks to the thoughtful feedback provided by the journal editor and one anonymous reviewer.

Funding

This work was partially supported by La Caixa Foundation (LCF/PR/PR17/11120020); Generalitat de Catalunya (2017 SGR-1040); Universitat Rovira i Virgili (2019PFR-URV91); and Universitat de Girona (Programa d'Ajuts de Suport a la Recerca 2020).

Author contributions

Martina Cubí: Validation, Formal analyses, Investigation, Data curation, Writing - Original Draft, Visualization; **Miquel Llorente:** Conceptualization, Methodology, Formal analyses, Writing - Review & Editing, Supervision, Project administration, Funding acquisition

REFERENCES

- Agmen, F.L., 2014. Conservation strategies for Delacour's langur (*Trachypithecus delacouri*) in Vietnam: Behavioural comparisons and reviewing a release. The Australian National University. <https://doi.org/10.25911/5D7392C55DAD3>
- Ahamed, A.M.R., Dharmaretnam, M., 2015. Hand preference in wild Hanuman langurs (*Presbytis entellus*). *Int. J. Biol. Pharm. Sci.* 2, 40–46. <https://doi.org/15.1026/BR022046052>
- Annett, M., 2002. Handedness and brain asymmetry: The right shift theory. Psychology Press, Hove, UK.
- Bakeman, R., Quera, V., 2011. Sequential analysis and observational methods for the behavioral sciences. Cambridge University Press, Cambridge, MA. <https://doi.org/10.1017/CBO9781139017343>
- Bisazza, A., Rogers, L.J., Vallortigara, G., 1998. The origins of cerebral asymmetry: a review of evidence of behavioural and brain lateralization in fishes, reptiles and amphibians. *Neurosci. Biobehav. Rev.* 22, 411–426. [https://doi.org/10.1016/S0149-7634\(97\)00050-X](https://doi.org/10.1016/S0149-7634(97)00050-X)
- Blois-Heulin, C., Guitton, J.S., Nedellec-Bienvenue, D., Roparts, L., Vallet, E., 2006. Hand preference in unimanual and bimanual tasks and postural effect on manual laterality in captive red-capped mangabeys (*Cercocebus torquatus torquatus*). *Am. J. Primatol.* 68, 429–444. <https://doi.org/10.1002/ajp.20239>
- Bradshaw, J.L., Rogers, L.J., 1993. The evolution of lateral asymmetries, language, tool-use and intellect. Academic Press, San Diego.
- Braitenberg, V., Kemali, M., 1970. Exceptions to bilateral symmetry in the epithalamus of lower vertebrates. *J. Comp. Neurol.* 138, 137–146. <https://doi.org/10.1002/cne.901380203>
- Brandon-Jones, D., 2004. A taxonomic revision of the langurs and leaf monkeys (Primates: Colobinae) of South Asia. *Zoos' Print J.* 19, 1552–1594. <https://doi.org/10.11609/JoTT.ZPJ.971.1552-94>
- Canteloup, C., Vauclair, J., Meunier, H., 2013. Hand preferences on unimanual and bimanual tasks in Tonkean macaques (*Macaca tonkeana*). *Am. J. Phys. Anthropol.* 152, 315–321. <https://doi.org/10.1002/ajpa.22342>
- Caton, J.M., 1999. Digestive strategy of the asian colobine genus *Trachypithecus*. *Primates* 40, 311–325. <https://doi.org/10.1007/BF02557555>
- Chapelain, A.S., Hogervorst, E., 2009. Hand preferences for bimanual coordination in 29 bonobos (*Pan paniscus*). *Behav. Brain Res.* 196, 15–29.
- Chapelain, A.S., Hogervorst, E., Mbonzo, P., Hopkins, W.D., 2011. Hand preferences for bimanual coordination in 77 Bonobos (*Pan paniscus*): Replication and extension. *Int. J. Primatol.* 32, 491–510. <https://doi.org/10.1016/j.bbr.2008.07.012>
- Cochet, H., Byrne, R.W., 2013. Evolutionary origins of human handedness: evaluating contrasting hypotheses. *Anim. Cogn.* 16, 531–542. <https://doi.org/10.1007/s10071-013-0626-y>

- Cohen, J., 1968. Weighted kappa: Nominal scale agreement provision for scaled disagreement or partial credit. *Psychol. Bull.* 70, 213–220.
<https://doi.org/10.1037/h0026256>
- Corballis, C.M., 2020. Bilaterally symmetrical: To be or not to be? *Symmetry (Basel)*. 12, 326. <https://doi.org/10.3390/sym12030326>
- de Andrade, A.C., de Sousa, A.B., 2018. Hand preferences and differences in extractive foraging in seven capuchin monkey species. *Am. J. Primatol.* 80, e22901.
<https://doi.org/10.1002/ajp.22901>
- Denenberg, V.H., 1981. Hemispheric laterality in animals and the effects of early experience. *Behav. Brain Sci.* 4, 1–21.
<https://doi.org/10.1017/S0140525X00007330>
- Duistermars, B.J., Chow, D.M., Frye, M.A., 2009. Flies require bilateral sensory input to track odor gradients in flight. *Curr. Biol.* 19, 1301–7.
<https://doi.org/10.1016/j.cub.2009.06.022>
- Fagot, J., Vauclair, J., 1991. Manual laterality in nonhuman primates: A distinction between handedness and manual specialization. *Psychol. Bull.* 109, 76–89.
<https://doi.org/10.1037/0033-2909.109.1.76>
- Fitch, W.T., Braccini, S.N., 2013. Primate laterality and the biology and evolution of human handedness: A review and synthesis. *Ann. N. Y. Acad. Sci.* 1288, 70–85.
<https://doi.org/10.1111/nyas.12071>
- Frasnelli, E., 2017. Lateralization in invertebrates, in: Rogers, L., Vallortigara, G. (Eds.), *Lateralized Brain Functions. Neuromethods*, Vol. 122. Humana Press, New York, NY, pp. 153–208. https://doi.org/10.1007/978-1-4939-6725-4_6
- Frasnelli, E., 2013. Brain and behavioral lateralization in invertebrates. *Front. Psychol.* 4, 1–10. <https://doi.org/10.3389/fpsyg.2013.00939>
- Fu, W.-W., Ren, Y., Wang, C.-L., Wang, X.-W., Li, B.-G., 2020. Hand preference in *Rhinopithecus roxellana* infants: Is it influenced by familial inheritance? *Symmetry (Basel)*. 12, 1905. <https://doi.org/10.3390/sym12111905>
- Fu, W.-W., Wang, X.-W., Wang, C.-L., Zhao, H.-T., Ren, Y., Li, B.-G., 2019. Effects of age, sex and manual task on hand preference in wild *Rhinopithecus roxellana*. *Zool. Res.* 40, 129–138. <https://doi.org/10.24272/j.issn.2095-8137.2019.023>
- Güntürkün, O., Ströckens, F., Ocklenburg, S., 2020. Brain lateralization: a comparative perspective. *Physiol. Rev.* 100, 1019–1063.
<https://doi.org/10.1152/physrev.00006.2019>
- Hellner-Burris, K., Sobieski, C.A., Gilbert, V.R., Phillips, K.A., 2010. Prey capture efficiency in brown capuchin monkeys (*Cebus apella*) is influenced by sex and corpus callosum morphology. *Am. J. Primatol.* 72, 502–508.
<https://doi.org/10.1002/ajp.20800>
- Hopkins, W.D., 2013a. Comparing human and nonhuman primate handedness: challenges and a modest proposal for consensus. *Dev. Psychobiol.* 55, 621–636.
<https://doi.org/10.1002/dev.21139>
- Hopkins, W.D., 2013b. Independence of data points in the measurement of hand

- preferences in primates: Statistical problem or urban myth? *Am. J. Phys. Anthropol.* 151, 151–157. <https://doi.org/10.1002/ajpa.22248>
- Hopkins, W.D., 2006. Comparative and familial analysis of handedness in great apes. *Psychol. Bull.* 132, 538–599. <https://doi.org/10.1037/0033-2909.132.4.538>
- Hopkins, W.D., 1999. On the other hand: statistical issues in the assessment and interpretation of hand preference data in nonhuman primates. *Int. J. Primatol.* 20, 851–866. <https://doi.org/10.1023/A:1020822401195>
- Hopkins, W.D., 1995. Hand preferences for a co-ordinated bimanual task in 110 chimpanzees (*Pan troglodytes*): Cross-sectional analysis. *J. Comp. Psychol.* 109, 197–291. <https://doi.org/10.1037/0735-7036.109.3.291>
- Hopkins, W.D., Cantalupo, C., 2005. Individual and setting differences in the hand preferences of chimpanzees (*Pan troglodytes*): A critical analysis and some alternative explanations. *Laterality* 10, 65–80. <https://doi.org/10.1080/13576500342000301>.
- Hopkins, W.D., Cantero, M., 2003. From hand to mouth in the evolution of language: the influence of vocal behavior on lateralized hand use in manual gestures by chimpanzees (*Pan troglodytes*). *Dev. Sci.* 6, 55–61. <https://doi.org/10.1111/1467-7687.00254>
- Hopkins, W.D., Hook, M., Braccini, S., Schapiro, S.J., 2003. Population-level right handedness for a coordinated bimanual task in chimpanzees: replication and extension in a second colony of apes. *Int. J. Primatol.* 24, 677–689. <https://doi.org/10.1023/A:1023752816951>
- Hopkins, W.D., Phillips, K.A., Bania, A., Calcutt, S.E., Gardner, M., Russell, J., Schaeffer, J., Lonsdorf, E. V, Ross, S.R., Schapiro, S.J., 2011. Hand preferences for coordinated bimanual actions in 777 great apes: Implications for the evolution of handedness in Hominins. *J. Hum. Evol.* 60, 605–611. <https://doi.org/https://doi.org/10.1016/j.jhevol.2010.12.008>
- Hopkins, W.D., Reamer, L., Mareno, M.C., Schapiro, S.J., 2015. Genetic basis in motor skill and hand preference for tool use in chimpanzees (*Pan troglodytes*). *Proc. R. Soc. B Biol. Sci.* 282, 20141223. <https://doi.org/10.1098/rspb.2014.1223>
- Hori, M., Nakajima, M., Hata, H., Yasugi, M., Takahashi, S., Nakae, M., Yamaoka, K., Kohda, M., Kitamura, J., Maehata, M., Tanaka, H., Okada, N., Takeuchi, Y., 2017. Laterality is universal among fishes but increasingly cryptic among derived groups. *Zool. Sci.* 34, 267–274. <https://doi.org/10.2108/zs160196>
- Insua-cao, P., Hoang, T.M., Dine, M., 2012. Conservation status and needs of François ' s Langur in Vietnam. People Resources and Conservation Foundation, Hanoi, Vietnam.
- Lippolis, G., Bisazza, A., Rogers, L.J., Vallortigara, G., 2002. Lateralisation of predator avoidance responses in three species of toads. *Laterality* 7, 163–183. <https://doi.org/10.1080/13576500143000221>
- Llorente, M., Mosquera, M., Fabr e, M., 2009. Manual laterality for simple reaching and bimanual coordinated task in naturalistic housed *Pan troglodytes*. *Int. J. Primatol.* 30. <https://doi.org/10.1007/s10764-009-9338-1>

- Llorente, M., Riba, D., Palou, L., Carrasco, L., Mosquera, M., Colell, M., Feliu, O., 2011. Population-level right-handedness for a coordinated bimanual task in naturalistic housed chimpanzees: replication and extension in 114 animals from Zambia and Spain. *Am. J. Primatol.* 73, 281–290.
<https://doi.org/10.1002/ajp.20895>
- MacNeilage, P.F., Studdert-Kennedy, M.G., Lindblom, B., 1987. Primate handedness reconsidered. *Behav. Brain Sci.* 10, 247–263.
<https://doi.org/10.1017/S0140525X00047695>
- Maille, A., Belbeoc'h, C., Rossard, A., Bec, P., Blois-Heulin, C., 2013. Which are the features of the tube task that make it so efficient in detecting manual asymmetries? An investigation in two Cercopithecine species (*Cercopithecus neglectus* and *Cercocebus torquatus*). *J. Comp. Psychol.* 127, 436–444.
<https://doi.org/10.1037/a0032227>
- Marcori, A.J., Okazaki, V.H.A., 2019. A historical, systematic review of handedness origins. *Laterality* 25, 87–108. <https://doi.org/10.1080/1357650x.2019.1614597>
- McGrew, W.C., Marchant, L.F., 1997. On the other hand: Current issues in and meta-analysis of the behavioral laterality of hand function in nonhuman primates. *Am. J. Phys. Anthropol.* 104, 201–232. [https://doi.org/10.1002/\(SICI\)1096-8644\(1997\)25+<201::AID-AJPA8>3.0.CO;2-6](https://doi.org/10.1002/(SICI)1096-8644(1997)25+<201::AID-AJPA8>3.0.CO;2-6)
- Meguerditchian, A., Calcutt, S.E., Lonsdorf, E. V, Ross, S.R., Hopkins, W.D., 2010. Captive gorillas are right-handed for bimanual feeding. *Am. J. Phys. Anthropol.* 141, 638–645. <https://doi.org/10.1002/ajpa.21244>.
- Meguerditchian, A., Vauclair, J., Hopkins, W.D., 2013. On the origins of human handedness and language: A comparative review of hand preferences for bimanual coordinated actions and gestural communication in nonhuman primates. *Dev. Psychobiol.* 55, 637–650. <https://doi.org/10.1002/dev.21150>
- Meunier, H., Vauclair, J., 2007. Hand preferences on unimanual and bimanual tasks in white-faced capuchins (*Cebus capucinus*). *Am. J. Primatol.* 69, 1064–1069.
<https://doi.org/10.1002/ajp.20437>
- Miletto Petrazzini, M.E., Sovrano, V.A., Vallortigara, G., Messina, A., 2020. Brain and behavioral asymmetry: A lesson from fish. *Front. Neuroanat.* 14, 11.
<https://doi.org/10.3389/fnana.2020.00011>
- Miller, C.T., Paciulli, L.M., 2002. Patterns of lateralized hand use in an arboreal primate, *Simias concolor*. *Am. J. Primatol.* 56, 231–236.
<https://doi.org/10.1002/ajp.1077>
- Mittermeier, R.A., Wilson, D.E., Rylands, A.B., 2013. Handbook of the mammals of the world. Volume 3: Primates. Lynx Edicions, Bellaterra (Spain).
- Mitra, E.S., Fuentes, A., McGrew, W.C., 1997. Lack of hand preference in wild hanuman langurs (*Presbytis entellus*). *Am. J. Phys. Anthropol.* 103, 455–461.
[https://doi.org/10.1002/\(SICI\)1096-8644\(199708\)103:4<455::AID-AJPA3>3.0.CO;2-M](https://doi.org/10.1002/(SICI)1096-8644(199708)103:4<455::AID-AJPA3>3.0.CO;2-M)
- Morino, L., Uchikoshi, M., Bercovitch, F., Hopkins, W.D., Matsuzawa, T., 2017. Tube task hand preference in captive hylobatids. *Primates* 58, 403–412.

<https://doi.org/10.1007/s10329-017-0605-z>

- Motes Rodrigo, A., Ramirez Torres, C.E., Hernandez Salazar, L.T., Laska, M., 2018. Hand preferences in two unimanual and two bimanual coordinated tasks in the black-handed spider monkey (*Ateles geoffroyi*). *J. Comp. Psychol.* 132, 220–229. <https://doi.org/10.1037/com0000110>
- Nadler, T., Brockman, D.K., 2014. *Primates of Vietnam*. Endangered Primate Rescue Center, Cuc Phuong National Park, Vietnam.
- Nadler, T., Momberg, F., Dang, N.X., Lormee, N., 2003. Vietnam primate conservation status review 2002. Part 2: Leaf monkeys. *Fauna and Flora International*, Hanoi, Vietnam.
- Nottebohm, F., Stokes, T.M., Leonard, C.M., 1976. Central control of song in the canary, *Serinus canarius*. *J. Comp. Neurol.* 165, 457–486. <https://doi.org/10.1002/cne.901650405>
- Padrell, M., Gómez-Martínez, C., Llorente, M., 2019. Short and long-term temporal consistency of hand preference in sanctuary chimpanzees (*Pan troglodytes*) for unimanual and bimanual coordinated tasks. *Behav. Processes* 167, 103911. <https://doi.org/10.1016/J.BEPROC.2019.103911>
- Pan, J., Xiao, W., Zhao, Q.K., 2011. Hand preference by black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) in captivity: Influence of tasks and sexes. *Laterality* 16, 656–672. <https://doi.org/10.1080/1357650X.2010.506713>
- Papademetriou, E., Sheu, C.-F., Michel, G.F., 2005. A meta-analysis of primate hand preferences, particularly for reaching. *J. Comp. Psychol.* 119, 33–48. <https://doi.org/10.1037/0735-7036.119.1.33>
- Porac, C., Coren, S., 1981. *Lateral preferences and human behavior*. Springer-Verlag, New York.
- Prieur, J., Lemasson, A., Barbu, S., Blois-Heulin, C., 2019. History, development and current advances concerning the evolutionary roots of human right-handedness and language: Brain lateralisation and manual laterality in non-human primates. *Ethology* 125, 1–28. <https://doi.org/10.1111/eth.12827>
- Rogers, L.J., 2014. Asymmetry of brain and behavior in animals: Its development, function, and human relevance. *Genesis* 52, 555–571. <https://doi.org/10.1002/dvg.22741>
- Rogers, L.J., Andrew, J.R., 2002. *Comparative vertebrate lateralization*. Cambridge University Press, Cambridge, UK.
- Rogers, L.J., Anson, J.M., 1979. Lateralisation of function in the chicken fore-brain. *Pharmacol. Biochem. Behav.* 10, 679–686. [https://doi.org/10.1016/0091-3057\(79\)90320-4](https://doi.org/10.1016/0091-3057(79)90320-4)
- Rogers, L.J., Vallortigara, G., 2019. Complementary specializations of the left and right sides of the honeybee brain. *Front. Psychol.* 10, 280. <https://doi.org/10.3389/fpsyg.2019.00280>
- Rogers, L.J., Vallortigara, G., 2008. From antenna to antenna: lateral shift of olfactory memory recall by honeybees. *PLoS One* 3, e2340.

<https://doi.org/10.1371/journal.pone.0002340>

- Rogers, L.J., Vallortigara, G., Andrew, R.J., 2013. Divided brains. The biology and behaviour of brain asymmetries. Cambridge University Press.
- Roy, D., Nagarajan, R., 2018. Patterns of hand use in golden langur (*Trachypithecus geei*) during feeding in a fragmented habitat of Western Assam, India. *Clarion- Int. Multidiscip. J.* 7, 10–16. <https://doi.org/10.5958/2277-937x.2018.00002.3>
- Smith, C., Scollay, P.A., 2001. Evidence for laterality of hand function in red-shanked douc langurs (*Pygathrix nemaeus*) at the Cologne Zoo. *Am. J. Primatol.* 54, 47.
- Spinozzi, G., Castorina, M.G., Truppa, V., 1998. Hand preferences in unimanual and coordinated-bimanual tasks by tufted capuchin monkeys (*Cebus apella*). *J. Comp. Psychol.* 112, 183–191. <https://doi.org/10.1016/j.cogbrainres.2005.05.012>
- Suzuki, H., Thiele, T.R., Faumont, S., Ezcurra, M., Lockery, S.R., Schafer, W.R., 2008. Functional asymmetry in *C. elegans* taste neurons and its computational role in chemotaxis. *Nature* 454, 114–117. <https://doi.org/10.1038/nature06927>
- Vallortigara, G., Rogers, L.J., Bisazza, A., Lippolis, G., Robins, A., 1998. Complementary right and left hemifield use for predatory and agonistic behaviour in toads. *Neuroreport* 9, 3341–3344. <https://doi.org/10.1097/00001756-199810050-00035>
- Vallortigara, G., Versace, E., 2017. Laterality at the neural, cognitive, and behavioral levels., in: *APA Handbook of Comparative Psychology: Basic Concepts, Methods, Neural Substrate, and Behavior*. American Psychological Association, Washington, pp. 557–577. <https://doi.org/10.1037/0000011-027>
- Vauclair, J., Meguerditchian, A., Hopkins, W.D., 2005. Hand preferences for unimanual and coordinated bimanual tasks in baboons (*Papio anubis*). *Cogn. Brain Res.* 25, 210–216. <https://doi.org/10.1016/j.cogbrainres.2005.05.012>
- Ward, J.P., Hopkins, W.D., 1993. Primate laterality : current behavioral evidence of primate asymmetries. Springer-Verlag.
- Wells, D.L., 2002. Hand preference for feeding in captive *Colobus guereza*. *Folia Primatol.* 73, 57–59. <https://doi.org/10.1159/000060421>
- Westergaard, G.C., Suomi, S.J., 1993. Hand preference in capuchin monkeys (*Cebus apella*) varies with age. *Primates* 34, 295–299. <https://doi.org/10.1007/BF02382624>
- Wiper, M.L., 2017. Evolutionary and mechanistic drivers of laterality: A review and new synthesis. *Laterality* 22, 740–770. <https://doi.org/10.1080/1357650X.2017.1291658>
- Wright, B.W., Prodhan, R., Wright, K.A., Nadler, T., 2008a. Mandibular morphology as it relates to ingestive and digestive folivory in *Trachypithecus* and *Pygathrix*. *Vietnamese J. Primatol.* 2, 25–32.
- Wright, B.W., Ulibarri, L., O'Brien, J., Sadler, B., Prodhan, R., Covert, H.H., Nadler, T., 2008b. It's tough out there: Variation in the toughness of ingested leaves and feeding behavior among four Colobinae in Vietnam. *Int. J. Primatol.* 29, 1455–1466. <https://doi.org/10.1007/s10764-008-9294-1>

- Zhao, D., Gao, X., Li, B., 2010. Hand preference for spontaneously unimanual and bimanual coordinated tasks in wild Sichuan snub-nosed monkeys: Implication for hemispheric specialization. *Behav. Brain Res.* 208, 85–89.
<https://doi.org/10.1016/j.bbr.2009.11.011>
- Zhao, D., Gao, X., Li, B., Watanabe, K., 2008. First wild evidence of neonate nipple preference and maternal cradling laterality in Old World monkeys: A preliminary study from *Rhinopithecus roxellana*. *Behav. Processes* 77, 364–368.
<https://doi.org/10.1016/j.beproc.2007.10.004>
- Zhao, D., Hopkins, W.D., Li, B., 2012. Handedness in nature: first evidence on manual laterality on bimanual coordinated tube task in wild primates 148(1), 36–44.
<https://doi.org/10.1002/ajpa.22038>
- Zhao, D., Ji, W., Watanabe, K., Li, B., 2007. Hand preference during unimanual and bimanual reaching actions in Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*). *Am. J. Primatol.* 70, 1–5. <https://doi.org/10.1002/ajp.20509>
- Zhao, D., Wang, Y., Wei, X., 2016. Hand preference during bimanual coordinated task in northern pig-tailed macaques *Macaca leonina*. *Curr. Zool.* 62, 385–391.
<https://doi.org/10.1093/cz/zow064>

Figure 1: Hatinh langur (left) and grey-shanked douc (right) performing the bimanual tube task at the Endangered Primate Rescue Centre (Vietnam). Credit: Martina Cubí.



Figure 2: Spearman correlation scatter plots between event and bout values for handedness index (HI; direction of preference) and absolute handedness index (ABSHI; strength of preference). Confidence intervals (95%; blue lines) and prediction intervals (95%; green lines) are indicated.

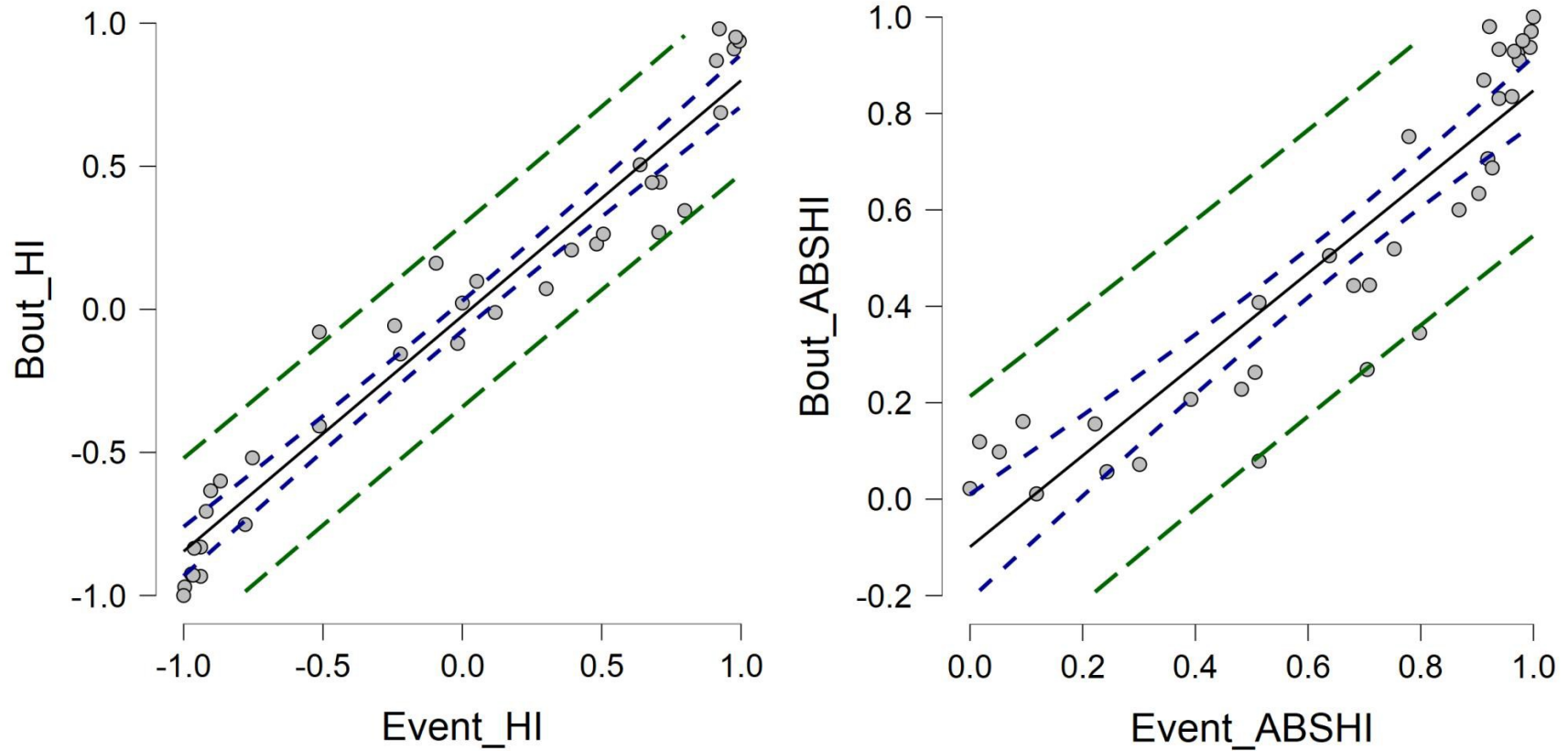


Table 1. List of names and characteristics of individuals in the study sample at EPRC. Note: DOB = day of birth; DOA = day of arrival at the centre.

Name	Species	Sex	DOB	DOA	Source	Origin	Cage
Minni	<i>T.hatinhensis</i>	F	1994	1994	Confiscated	Unknown	22
Kurt	<i>T.hatinhensis</i>	M	1995	1996	Priv. Own.		22
Roland	<i>T.hatinhensis</i>	M	1997	1997	Born EPRC		6B
Uli	<i>T.hatinhensis</i>	F	1994	1997	Tourist		6B
Katie	<i>T.hatinhensis</i>	F	1995	1998	Tourist		6B
Cuc	<i>T.hatinhensis</i>	F	2001	2001	Born EPRC		13B
Hanh	<i>T.hatinhensis</i>	F	2002	2002	Born EPRC		13B
Willy	<i>T.hatinhensis</i>	M	2004	2004	Born EPRC		3B
Kristin	<i>T.hatinhensis</i>	F	2004	2005	Tourist		2B
Kumi	<i>T.hatinhensis</i>	M	2005	2005	Born EPRC		2B
Mia	<i>T.hatinhensis</i>	F	2006	2006	Born EPRC		3B
Heinrich	<i>T.hatinhensis</i>	M	2006	2006	Born EPRC		6A
Knut	<i>T.hatinhensis</i>	M	2006	2006	Born EPRC		18A
Ami	<i>T.hatinhensis</i>	F	2008	2008	Born EPRC		6A
Khang	<i>T.hatinhensis</i>	M	2010	2010	Born EPRC		2A
Quyet	<i>T.hatinhensis</i>	M	2010	2010	Born EPRC		21
Hau	<i>T.hatinhensis</i>	M	2011	2011	Born EPRC		27
Ma	<i>T.hatinhensis</i>	F	2011	2011	Born EPRC		2A
Chau	<i>T.hatinhensis</i>	M	2011	2011	Born EPRC		17
Phuong	<i>P.cinerea</i>	F	1997	2001	Confiscated	An Lão, Bình Định province	13A, 4B
Eco †	<i>P.cinerea</i>	M	1998	2002	Confiscated	An Lão, Bình Định province	24, 18B († 14/2/19)
Naomi	<i>P.cinerea</i>	F	2004	2004	Born EPRC		13A, 10B
Sung	<i>P.cinerea</i>	M	2000	2004	Confiscated	Bình Định province	18B, 24
Claus	<i>P.cinerea</i>	M	2003	2006	Confiscated	Bình Định province	4B, 19
Falk	<i>P.cinerea</i>	M	2003	2007	Confiscated	Unknown	19, 24
Ines	<i>P.cinerea</i>	F	2007	2008	Confiscated	An Lão, Bình Định province	4B
Gin	<i>P.cinerea</i>	M	2005	2009	Confiscated	Unknow	11B
Tonic	<i>P.cinerea</i>	M	2004	2009	Confiscated	An Lão, Bình Định province	12B
Pip	<i>P.cinerea</i>	F	2009	2009	Born EPRC		11B
Eric	<i>P.cinerea</i>	M	2010	2010	Confiscated	Quảng Nam province	18A
Cactus	<i>P.cinerea</i>	M	2010	2010	Born EPRC		28
Lychee	<i>P.cinerea</i>	F	2011	2011	Born EPRC		11B
Manh	<i>P.cinerea</i>	M	2011	2011	Born EPRC		28
Mr. Bean	<i>P.cinerea</i>	M	2011	2011	Born EPRC		24, 18B
Omo	<i>P.cinerea</i>	F	2011	2011	Confiscated	Quảng Nam province	12B
Barack	<i>P.cinerea</i>	M	2012	2012	Born EPRC		28
Michelle	<i>P.cinerea</i>	F	2012	2012	Born EPRC		10B
Seba	<i>P.cinerea</i>	M	2013	2013	Confiscated	Unknown	17, 20-22, 18B
Ronaldo	<i>P.cinerea</i>	M	Adult	2016	Confiscated	Ba To	10B

Table 2. Variables considered in the statistical analysis.

Predictor variables	Definition
Species	Defined by: (1) <i>Trachypithecus hatinhensis</i> and (2) <i>Pygathrix cinerea</i> .
Sex	Defined by: (1) females and (2) males.
Subject	Unique ID of each individual from the centre.
Response variables	Definition
Events	Every time the sequence of actions starting with the individual inserting a finger inside the tube and ending with the individual putting the food in the mouth was completed.
Bouts	Set of events until the individual dropped the tube, changed the holding hand, rotated the tube or spent more than 60 seconds holding the tube without performing the task.
Finger use	The finger that the individual used in each event. Defined by: (D1) thumb, (D2) index finger, (D3) middle finger, (D4) ring finger, and (D5) little finger.

Table 3. Individual data on hand preference in hatinh langurs (*Trachypithecus hatinhensis*) and grey-shanked douc langurs (*Pygathrix cinerea*). Note: Confis. = Confiscated; HI = handedness index; ABSHI = absolute handedness index.

Subject	Sex	Species	Event data							Bout data						
			Left	Right	HI	ABS-HI	z-score	P-binomial	Preference	Left	Right	HI	ABS-HI	z-score	P-binomial	Preference
Kristin	F	Hatinh	603	19	-0.94	0.94	-46.83	<0.01	Left	141	13	-0.83	0.83	-20.63	<0.01	Left
Ami	F	Hatinh	142	10	-0.87	0.87	-21.41	<0.01	Left	28	7	-0.6	0.6	-7.10	<0.01	Left
Uli	F	Hatinh	448	14	-0.94	0.94	-40.38	<0.01	Left	145	5	-0.93	0.93	-22.86	<0.01	Left
Katie	F	Hatinh	142	6	-0.92	0.92	-22.36	<0.01	Left	29	5	-0.71	0.71	-8.23	<0.01	Left
Hanh	F	Hatinh	432	22	-0.9	0.9	-38.49	<0.01	Left	58	13	-0.63	0.63	-10.68	<0.01	Left
Ma	F	Hatinh	306	38	-0.78	0.78	-28.90	<0.01	Left	106	15	-0.75	0.75	-16.55	<0.01	Left
Cuc	F	Hatinh	837	118	-0.75	0.75	-46.53	<0.01	Left	164	52	-0.52	0.52	-15.24	<0.01	Left
Mia	F	Hatinh	122	706	0.71	0.71	40.59	<0.01	Right	61	106	0.27	0.27	6.96	<0.01	Right
Heinrich	M	Hatinh	900	2	-1	1	-59.80	<0.01	Left	133	2	-0.97	0.97	-22.55	<0.01	Left
Kurt	M	Hatinh	927	13	-0.97	0.97	-59.62	<0.01	Left	179	7	-0.93	0.93	-25.22	<0.01	Left
Hau	M	Hatinh	999	0	-1	1	-63.21	<0.01	Left	126	0	-1	1	-22.45	<0.01	Left
Khang	M	Hatinh	292	94	-0.51	0.51	-20.16	<0.01	Left	41	35	-0.08	0.08	-1.38	0.57	No
Chau	M	Hatinh	186	426	0.39	0.39	19.40	<0.01	Right	94	143	0.21	0.21	6.37	<0.01	Right
Kumi	M	Hatinh	185	529	0.48	0.48	25.75	<0.01	Right	44	70	0.23	0.23	4.87	0.02	Right
Quyet	M	Hatinh	36	163	0.64	0.64	18.01	<0.01	Right	26	79	0.51	0.51	10.35	<0.01	Right
Willy	M	Hatinh	17	451	0.93	0.93	40.12	<0.01	Right	13	70	0.69	0.69	12.51	<0.01	Right
Roland	M	Hatinh	4	319	0.98	0.98	35.05	<0.01	Right	3	64	0.91	0.91	14.91	<0.01	Right
Knut	M	Hatinh	2	662	0.99	0.99	51.23	<0.01	Right	2	61	0.94	0.94	14.87	<0.01	Right
Lychee	F	Grey-sh	399	254	-0.22	0.22	-11.35	<0.01	Left	115	84	-0.16	0.16	-4.40	0.03	Left
Michelle	F	Grey-sh	290	290	0	0	0.00	1.03	No	132	138	0.02	0.02	0.73	0.76	No
Pip	F	Grey-sh	206	199	-0.02	0.02	-0.70	0.77	No	47	37	-0.12	0.12	-2.18	0.33	No
Ines	F	Grey-sh	171	318	0.3	0.3	13.30	<0.01	Right	58	67	0.07	0.07	1.61	0.47	No
Naomi	F	Grey-sh	107	326	0.51	0.51	21.05	<0.01	Right	42	72	0.26	0.26	5.62	0.01	Right
Phuong	F	Grey-sh	75	441	0.71	0.71	32.23	<0.01	Right	20	52	0.44	0.44	7.54	<0.01	Right
Omo	F	Grey-sh	25	544	0.91	0.91	43.52	<0.01	Right	14	199	0.87	0.87	25.35	<0.01	Right
Gin	M	Grey-sh	574	11	-0.96	0.96	-46.55	<0.01	Left	78	7	-0.84	0.84	-15.40	<0.01	Left
Cactus	M	Grey-sh	342	6	-0.97	0.97	-36.02	<0.01	Left	109	4	-0.93	0.93	-19.76	<0.01	Left
Barack	M	Grey-sh	726	234	-0.51	0.51	-31.76	<0.01	Left	269	113	-0.41	0.41	-15.96	<0.01	Left
Ronaldo	M	Grey-sh	322	196	-0.24	0.24	-11.07	<0.01	Left	56	50	-0.06	0.06	-1.17	0.63	No
Mr. Bean	M	Grey-sh	297	246	-0.09	0.09	-4.38	0.03	Left	78	108	0.16	0.16	4.40	0.03	Right
Seba	M	Grey-sh	367	407	0.05	0.05	2.88	0.16	No	46	56	0.1	0.1	1.98	0.37	No
Falk	M	Grey-sh	291	369	0.12	0.12	6.07	<0.01	Right	88	86	-0.01	0.01	-0.30	0.94	No
Manh	M	Grey-sh	47	248	0.68	0.68	23.41	<0.01	Right	27	70	0.44	0.44	8.73	<0.01	Right
Sung	M	Grey-sh	45	400	0.8	0.8	33.66	<0.01	Right	19	39	0.35	0.35	5.25	0.01	Right
Claus	M	Grey-sh	19	469	0.92	0.92	40.74	<0.01	Right	1	99	0.98	0.98	19.60	<0.01	Right
Eco	M	Grey-sh	1	103	0.98	0.98	20.00	<0.01	Right	1	40	0.95	0.95	12.18	<0.01	Right

Table 4. Wilcoxon signed-rank test for population-level hand preferences and descriptive statistics in event and bout data, separated by species.

	Mean	SE	V	p	Hodges-Lehmann Estimate	95% CI for Hodges- Lehmann Estimate		Rank-Biserial Correlation
						Lower	Upper	
Event	-0.04	0.21	284.00	0.62	-0.04	-0.29	0.23	-0.10
Bout	-0.06	0.10	309.00	0.72	-0.04	-0.30	0.17	-0.07
<i>P. cinerea</i> Event	0.17	0.14	98.00	0.32	0.21	-0.14	0.52	0.28
<i>P. cinerea</i> Bout	0.12	0.13	113.00	0.25	0.11	-0.12	0.41	0.32
<i>T. hatinhensis</i> Event	-0.25	0.19	54.00	0.18	-0.18	-0.87	0.05	-0.37
<i>T. hatinhensis</i> Bout	-0.23	0.16	52.00	0.15	-0.24	-0.72	0.10	-0.39

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