

Lateralized behavior in white-handed gibbons (*Hylobates lar*)

Kiki Spoelstra

Tutor, Matthias Laska
Examinator, Lina Roth

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1. Abstract

The evolutionary origins of human handedness are not yet fully understood as evidence of lateralized behavior in nonhuman primates is inconclusive. In the present study, lateralized behavior in both spontaneously occurring motor patterns and a tube task was examined in 15 white-handed gibbons (*Hylobates lar*). Significant side preferences at the individual level were found within all 15 studied motor patterns. However, no population-level side bias was found for any of the spontaneously occurring or task-related motor patterns and none of the gibbons were consistent in their hand preference across all motor patterns. When only considering the individuals with a significant preference, a significant majority was left-preferent for resting foot. Strength of side preference was significantly higher for the tube task than for all spontaneously occurring motor patterns. Side preferences for manipulation and resting position were significantly stronger than those for supporting hand. Additionally, the preferences for manipulation were significantly stronger than those for leading limb. In the bimanual tube task, females displayed a tendency towards a left-side bias, while males tended to display a bias to the right. Furthermore, females had a significantly stronger hand preference for supporting hand than males. No other sex differences were found. Age, posture, and kinship had no significant effect on lateralized behavior for any of the motor patterns. As in other nonhuman primates, the white-handed gibbons were only consistent in their hand preference across tasks that required similar movements. Altogether, these findings support the notion that population-level handedness may be restricted to human subjects.

Keywords: lateralized behavior, limb/side preference, *Hylobates lar*, white-handed gibbons, nonhuman primates

2. Introduction

Lateral biases for single behaviors, both at the individual and at the population-level, have been reported in a variety of vertebrates, including fish, amphibians, reptiles, birds, and mammals (Hook, 2004; Fitch & Braccini, 2013). Human handedness is considered the most conspicuous form of lateralized brain function (Corballis, 2003; Meguerditchian et al., 2013). However, evidence for handedness at the population-level in other species is inconclusive and thus the evolutionary origins of human handedness are still not entirely understood (Cashmore et al., 2008; Papademetriou et al., 2005). Although laterality has been studied in many species, most studies have focused on nonhuman primates because they are biologically close to humans and are known for their great dexterity (Harris, 1993).

McGrew & Marchant (1997) found that “*laterality in handedness is a gradient, not a dichotomy*”, therefore, the authors proposed a set of definitions to explain the different levels of laterality that occur in nonhuman primates. “Hand preference” is considered the lowest level of laterality, in which an individual displays a significant hand preference in a specific motor pattern. Next, “manual specialization” is defined as an individual being consistent in its hand preference across tasks. On a population-level, “task specialization” is defined as most individuals displaying the same hand preference for a specific motor pattern. Lastly, when most individuals in a population display the same hand preference across an array of tasks this is considered as “true handedness”. So far, this highest level of laterality is still uniquely found in humans.

Despite the definitions proposed by McGrew & Marchant, studies on lateralized behavior remain inconsistent in their findings (Fitch & Braccini, 2013). Mixed results have been found regarding lateralized behavior in nonhuman primates, as most studies only report significant hand preferences at the individual level, but not at the population level (McGrew & Marchant, 1997; Papademetriou et al., 2005). To date, most studies of lateralized behavior in nonhuman primates have focused on our closest relatives, the Great Apes (Caspar et al., 2018). In contrast, only few studies have reported on lateralized behavior in the Lesser Apes, that is, the gibbons. The lack of data on lateralized behavior in this taxon may possibly be explained by their monogamous mating system (Brockelman et al., 1998), which leads to only small captive populations being available. Perhaps for the same reason, all studies on lateralized behavior in gibbons so far included only a limited number of animals (Olson et al., 1990; Fan et al., 2017) or combined data of different species of gibbons (Stafford et al., 1990; McGrew & Marchant,

1997, Morino et al., 2017; Caspar et al., 2018). Furthermore, in all previous studies only one (Barker, 2008; Morino, 2011; Zhao et al., 2019) or, at best, a couple of (Olson et al., 1990; Stafford et al., 1990; Caspar et al., 2018) different behaviors were included, which prevents any conclusions regarding consistency of hand use across motor patterns. Therefore, in the present study, lateralized behavior will be assessed for both a variety of spontaneously occurring motor patterns as well as for the widely used tube task in a sizeable number of individuals of one specific gibbon species: the white-handed gibbon (*Hylobates lar*).

More specifically, it was the aim of the present study:

- to assess lateralized behavior in 15 white-handed gibbons for a variety of motor patterns that are part of their natural behavioral repertoire.
- to assess lateralized behavior of the same animals in a manual tube task that is not part of their natural behavioral repertoire.
- to assess consistency of the preferred hand across tasks per individual.
- to compare the data on spontaneously occurring lateralized behavior to those in a task-related lateralized behavior (tube task).
- to assess whether the gibbons display hand preferences at the population-level.
- to compare the data collected on white-handed gibbons to those reported in earlier studies both on different species of gibbons as well as other species of nonhuman primates.

3. Material and methods

3.1 Study sites

Five different groups of captive white-handed gibbons (*Hylobates lar*) were observed, two were located in Sweden and three in the Netherlands. Data were collected in Kolmården Wildlife Park (Kolmården, Sweden), Parken Zoo (Eskilstuna, Sweden), Wildlands Adventure Zoo (Emmen, the Netherlands), Safaripark Beekse Bergen (Hilvarenbeek, the Netherlands), and Ouwehands Dierenpark (Rhenen, the Netherlands).

3.2 Animals

In the present study, a total of 15 white-handed gibbons (appendix 1) was observed, of which seven were males (age range: 4-47 years; mean age \pm SE: 22.6 ± 6.0 years) and eight were

females (age range: 6-37 years; mean age \pm SE: 19.6 ± 4.3 years). Life history information was collected for every individual (table 1). At all study sites, the gibbons were provided food at least two times a day and water was provided *ad libitum*.

Table 1: Demographic overview of all animals (KM = Kolmården Wildlife Park, PZ = Parken Zoo, WL = Wildlands Adventure Zoo, BB = Safaripark Beekse Bergen, OD = Ouwehands Dierenpark).

Name	Sex	Age (years)	Zoo	Born
Ebbot	M	4	KM	Captive (KM)
Edith	F	6	KM	Captive (KM)
Elliot	F	9	KM	Captive (KM)
Elly	F	32	KM	Captive (PZ)
Lelle	M	33	KM	Captive (KM)
Korak	F	11	PZ	Captive (PZ)
Chili*	M	7	PZ	Captive (PZ)
Tarzan	M	47	PZ	Wild (Laos)
Sheeba	F	38	WL	Captive
Yindee	F	11	WL	Captive (WL)
Ori	M	33	BB	Captive
Muguai	F	20	BB	Captive (WL)
Jindie	F	30	OD	Captive
Tabitha	M	25	OD	Captive (OD)
Gibbi	M	10	OD	Captive (OD)

* *Chili was only observed for a period of three days (14 hours), hereafter he moved to another zoo.*

3.3 Data collection

In total, the gibbons were observed for 209 hours, of which 174 hours were live observation and 35 hours were video footage. Data were collected using an ethogram including both spontaneously occurring behavior as well as the more complex tube task (table 2).

3.3.1 Spontaneously occurring behavior

Hand-use or foot-use in thirteen different, spontaneously occurring motor patterns was recorded (table 2). For four of the five groups, continuous scan sampling was used as the observation method to collect the data for spontaneously occurring behavior. However, in one

of the zoos (Kolmården Wildlife Park) the observed group was too large to use this method exclusively, therefore, continuous focal sampling was used here as an additional observation method. All 15 gibbons were observed for a similar amount of time regardless of the observation method that was used.

Table 2: Ethogram containing all the motor patterns that were observed in the present study.

Motor pattern/category	Description
<i>Manipulation</i>	
Autogrooming hand	Hand used for picking own skin/grooming itself.
Scratching	Hand used for scratching skin.
Feeding hand	Hand used to bring food to mouth
Examining/ picking flat surface	Hand used to examine or pick non-edible objects from flat surfaces.
Unimanual allogrooming	Hand used when grooming conspecifics with one hand.
Bimanual allogrooming	Hand used for fine manipulation when grooming conspecifics with two hands. The hand recorded is the hand used for picking the skin of conspecific. The other hand is used for holding/keeping the fur out of the way.
<i>Leading limb</i>	
Leading hand (brachiation)	Hand used first when initiating brachiation (at least two full arm-swings, Redmond & Lamperez, 2004).
Leading hand (climbing)	Hand used first when initiating climbing vertically.
Leading foot	Foot used first when initiating walking in an upright position (at least two full steps).
<i>Supporting hand</i>	
Supporting hand (hanging still)	Hand used to hang from rope/fence/tree.
Supporting hand (sitting still)	Hand holding object for support while sitting (figure 1a).
<i>Resting hand</i>	
Resting hand	Hand placed on other hand when sitting (figure 1b).
Resting foot	Foot placed on other foot when sitting (figure 1b).
<i>Tube task</i>	
Unimanual tube task	Hand used to get the edible content out of the tube, without holding it with the other hand or while holding it with the feet (figure 2a). Hanging and sitting postures are scored separately.
Bimanual tube task	Hand used to get the edible content out of the tube, while holding it with the other hand (figure 2b).

3.3.2 Tube task

The manual coordinated task used in the present study, the tube task, has previously been used in hylobatids as well as in other nonhuman primate species to determine hand preference (Morino et al., 2017; Caspar et al., 2018). An opaque tube is filled with edible content, which is smeared far enough from the ends of the tubes to discourage tongue use and encourage manual extraction. To extract the content from the inside of the tube, fine manipulation with one hand is required while the other hand or a foot is holding the tube. Because the tube task is considered a complex novel task, it is thought to elicit stronger hand preferences than spontaneously occurring motor patterns, such as picking up food or eating (Fagot & Vauclair, 1991).

The tubes that were used in the present study were made of polyvinyl chloride (PVC), measured either 16 mm (narrow) or 25 mm (wide) in diameter and varied from 165 to 200 mm in length. All gibbons were presented with the tubes in at least three, but in some groups in up to ten sessions (appendix 2). One session per day was carried out, however, two times an extra session was performed on the same day (Wildlands Adventure Zoo). One gibbon, Chili, performed the tube task only once because he was transferred to another zoo during the observation period.

If possible, the tubes were presented in the outdoor enclosures to give the gibbons enough space to interact with the tubes without competition or distraction. To prevent loss of the tubes, these were attached to branches and ropes in the enclosures by short pieces of string. At least the same number of tubes as there were gibbons in the enclosure was provided to prevent competition between individuals (Fan et al., 2017).

As the diet of the gibbons varied between zoos, different types of food (e.g., banana, peanut butter, mashed pellets, figs) were used to fill the tubes. When the gibbons were performing the task, the hand extracting the food from the inside of the tube was recorded. Tube task extraction was categorized as an unimanual or bimanual action. When a gibbon was extracting food from the tube unimanually, hanging, and sitting posture were recorded separately (table 2).

To collect sufficient data points from every individual, a video camera (Panasonic, SDR-H90P) was used to record all tube task sessions where more than one subject interacted with the tubes. To make sure that all gibbons would be visible in the video, the camera was set up first and next the tubes were placed within the frame. The videos were analysed using the same ethogram as used in the live observation sessions. Spontaneously occurring behavior that was recorded in the video sessions was also scored during the video analysis.



Figure 1. Examples of gibbon(s) a) using supporting hand (left hand) while sitting, b) in resting position, both with right resting hand and right resting foot.



Figure 2. Examples of a gibbon doing a) the unimanual tube task (right hand) while hanging, b) the bimanual tube task (right hand).

3.3.3 Definition of the studied motor patterns

As an individual often uses the same hand repeatedly for the same task (e.g., bringing the same food item to its mouth several times in a row), consecutive data points are not necessarily independent of each other. Therefore, all motor patterns were recorded in bouts to ensure that the collected data points were independent. A bout can be defined as a string of non-

independent events and is distinguished from another bout by using a temporal or behavioral criterion (McGrew & Marchant, 1997). In the present study, a three second pause after a specific behavior was used as a temporal criterion and indicated the start of a new bout for all the motor patterns, except for those in the supporting hand and resting limb categories. Behavioral criteria that defined the start of a new bout included a hand switch or a switch to another motor pattern, as well as getting up from a resting position or moving to another part of the enclosure. Regarding the end of a tube task bout, the same criteria applied as for the spontaneously occurring behavior, but also included dropping the tube, holding the tube with two hands, or changing the orientation of the tube (Fan et al., 2017; Morino et al., 2017).

3.4 Data analysis

A two-tailed binomial test was used to assess whether a left or right preference was statistically significant. A subject was classified as significantly left-limb-preferent with a z-score of -1.97 or lower and significantly right-limb-preferent with a z-score of 1.97 or higher ($p < 0.05$). Subjects with z-scores between -1.97 and 1.97 were considered ambidextrous for the motor pattern in question. Additionally, a handedness index (HI) was determined from the raw data for each specific motor pattern in each animal. This HI-score was calculated by subtracting the number of bouts performed with the left limb from the number of bouts performed with the right limb and dividing this by the total number of bouts. Handedness indices varied from -1.00 (strong left-preference) to 1.00 (strong right-preference).

When assessing strength and direction for different types of behavior, all motor patterns were divided into five categories; *manipulation* (hand used for autogrooming, scratching, feeding, examining and uni-/bimanual allogrooming), *leading limb* (hand/foot used to initiate brachiation, climbing or walking bipedally), *supporting hand* (hand used for support when hanging or sitting), *resting hand/foot* (top hand/foot in resting position), and *tube task* (uni-/bimanual tube task) (table 2). To compare the mean (absolute) HI-scores between behavioral categories, a Wilcoxon signed-rank test was performed. For evaluating the differences in lateralized behavior between sexes, a Mann-Whitney U-test was used. The chi-square test was used to assess significant differences between age groups, zoos, and different tube sizes.

4. Results

4.1 Spontaneously occurring behavior

Tables 3-6 summarize the observed left:right ratios and the corresponding handedness indices for all spontaneously occurring motor patterns in the 15 white-handed gibbons.

Manipulation

For *autogrooming hand*, two out of 15 gibbons (13.3%) displayed a significant hand preference, both for the right hand (table 3). Four of the 15 animals (26.7%) had a significant side bias for *scratching hand*, one for the left and three for the right hand (table 3). 13 of the 15 gibbons (86.7%) had a significantly preferred *feeding hand*, of which seven preferred their left and six their right hand (table 3).

Table 3: Left:Right ratios (L:R) and handedness indices (HI) for autogrooming, scratching and feeding in all 15 individuals. Bold numbers indicate ratios that significantly differ from chance ($p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, two-tailed binomial test).*

	Autogrooming hand		Scratching hand		Feeding hand	
	L : R	HI	L : R	HI	L : R	HI
Elly	42 : 42	0.00	71 : 66	-0.04	75 : 205***	0.46
Lelle	5 : 6	0.09	62 : 131***	0.36	192 : 100***	-0.32
Elliot	7 : 9	0.13	83 : 90	0.04	249 : 164***	-0.21
Edith	14 : 21	0.20	70 : 60	-0.08	292 : 151***	-0.32
Ebbot	7 : 6	-0.08	54 : 60	0.05	208 : 277**	0.14
Tarzan	20 : 20	0.00	56 : 37	-0.20	29 : 123***	0.62
Korak	85 : 116*	0.15	233 : 220	-0.03	217 : 167*	-0.13
Chili	4 : 12	0.50	27 : 43	0.23	89 : 132**	0.19
Sheeba	29 : 23	-0.12	63 : 63	0.00	59 : 70	0.09
Yindee	9 : 16	0.28	112 : 79*	-0.17	155 : 33***	-0.65
Ori	14 : 50***	0.56	18 : 84***	0.65	18 : 116***	0.73
Muguai	30 : 28	-0.03	83 : 84	0.01	125 : 85**	-0.19
Jindie	1 : 5	0.67	15 : 31*	0.35	104 : 137*	0.14
Tabitha	3 : 7	0.40	14 : 12	-0.08	138 : 107	-0.13
Gibbi	17 : 8	-0.36	29 : 43	0.19	102 : 60**	-0.26

For *examining hand*, six out of 15 animals (40%) displayed a significant hand preference, three for the left and three for the right hand (table 4). Six out of 13 gibbons (46.2%) had a significant side bias for *unimanual allogrooming*, of which four preferred their left and two preferred their right hand (table 4). For this motor pattern, Ori and Gibbi were disregarded for the assessment of hand preference as less than six data points were collected for these two gibbons. For *bimanual allogrooming*, three out of ten animals (30%) had a significantly side bias and all

three preferred their left hand (table 4). For bimanual allogrooming, Lelle, Ebbot, Ori, Muguai, and Gibbi were disregarded for the assessment of hand preference as less than six data points were collected for these five individuals.

The gibbons displayed no significant population bias for any of the six manipulation motor patterns.

Table 4: Left:Right ratios (L:R) and handedness indices (HI) for examining and allogrooming (unimanual and bimanual) in all 15 individuals. Bold numbers indicate ratios that significantly differ from chance ($p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, two-tailed binomial test). Ratios in italics comprised too few data points to perform statistics ($N < 6$). Hyphens indicate that this specific motor pattern was not observed for this individual.*

	Examining hand		Allogrooming unimanual		Allogrooming bimanual	
	L : R	HI	L : R	HI	L : R	HI
Elly	5 : 6	0.09	52 : 28**	-0.30	92 : 68	-0.15
Lelle	12 : 10	-0.09	5 : 5	0.00	-	-
Elliot	15 : 7	-0.36	27 : 12*	-0.38	23 : 14	-0.24
Edith	31 : 30	-0.02	62 : 39*	-0.23	97 : 59**	-0.24
Ebbot	2 : 5	0.43	9 : 6	-0.20	<i>3 : 1</i>	<i>-0.50</i>
Tarzan	7 : 18*	0.44	74 : 40**	-0.30	37 : 21*	-0.28
Korak	55 : 32*	-0.26	13 : 45***	0.55	46 : 63	0.16
Chili	27 : 31	0.07	3 : 10	0.54	6 : 7	0.08
Sheeba	10 : 21	0.35	38 : 23	-0.25	8 : 2	-0.60
Yindee	32 : 20	-0.23	10 : 17	0.26	14 : 1***	-0.87
Ori	5 : 52***	0.82	<i>1 : 2</i>	<i>0.33</i>	-	-
Muguai	62 : 35**	-0.28	3 : 5	0.25	2 : 2	<i>0.00</i>
Jindie	9 : 53***	0.71	0 : 7*	1.00	4 : 4	0.00
Tabitha	33 : 32	-0.02	10 : 5	-0.33	8 : 5	-0.23
Gibbi	34 : 10***	-0.55	-	-	-	-

Leading limb

Four out of 15 gibbons (26.7%) displayed a significant hand preference for *leading hand in brachiation*, of which two preferred their left and two preferred their right hand (table 5). For *leading hand when climbing*, three of the 15 animals (20%) had a significant preference: two preferred the left hand and one the right hand (table 5). For *leading foot*, five of the 15 gibbons (33.3%) had a significant side bias, of which four were for the left and one for the right side (table 5).

No significant population bias was found for the three motor patterns in the leading limb category.

Table 5: Left:Right ratios (L:R) and handedness indices (HI) for leading limb in all 15 individuals. Bold numbers indicate ratios that significantly differ from chance (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, two-tailed binomial test).

	Leading hand brachiation		Leading hand climbing		Leading foot	
	L : R	HI	L : R	HI	L : R	HI
Elly	37 : 21*	-0.28	48 : 25**	-0.32	61 : 66	0.04
Lelle	63 : 39*	-0.24	23 : 24	0.02	77 : 49*	-0.22
Elliot	63 : 45	-0.17	30 : 35	0.08	83 : 63	-0.14
Edith	95 : 79	-0.09	34 : 64**	0.31	70 : 75	0.03
Ebbot	141 : 164	0.08	59 : 61	0.02	68 : 80	0.08
Tarzan	43 : 57	-0.08	25 : 6***	-0.61	41 : 50	0.10
Korak	45 : 35	-0.13	38 : 22	-0.27	120 : 125	0.02
Chili	54 : 58	0.04	28 : 15	-0.30	80 : 53*	-0.20
Sheeba	49 : 76*	0.22	39 : 33	-0.08	19 : 27	0.17
Yindee	110 : 167***	0.21	34 : 45	0.14	29 : 42	0.18
Ori	49 : 32	-0.21	14 : 25	0.28	137 : 124	-0.05
Muguai	208 : 197	-0.03	39 : 52	0.14	80 : 103	0.13
Jindie	24 : 28	0.08	16 : 8	-0.33	61 : 40*	-0.21
Tabitha	44 : 37	-0.09	14 : 14	0.00	85 : 116*	0.15
Gibbi	58 : 54	-0.04	21 : 11	-0.31	76 : 47*	-0.24

Supporting hand

For *supporting hand when hanging*, eight out of 15 gibbons (53.3%) had a significantly preferred hand, four preferred their left and four their right hand (table 6). Five out of 15 animals (33.3%) displayed a significant side bias for *supporting hand when sitting*, one for the left and four for the right hand (table 6).

There was no significant population bias for either of the two supporting hand motor patterns.

Resting position

For *resting hand*, four of the 14 gibbons (28.6%) significantly preferred to put one hand on top of the other, two preferred their left hand and two their right hand (table 6). Ten of the 14 gibbons (71.4%) had a significantly preferred *resting foot* which was put on top of the other foot, nine preferred their left foot and one its right foot (table 6). Ori was disregarded for the assessment of hand preference for both behaviors in this category, as for this gibbon less than six data points were collected per motor pattern.

For none of the motor patterns a significant population bias was observed. However, nine of the ten individuals with a significant foot-reference significantly preferred to place their left foot to rest on top of the right foot. When only considering the ten individuals that displayed a

significant *resting foot* preference, there was a significant majority of left-preferent individuals ($p=0.021$).

Table 6: Left:Right ratios (L:R) and handedness indices (HI) for supporting hand (hanging and sitting), resting hand and resting foot in all 15 individuals. Bold numbers indicate ratios that significantly differ from chance (* $p<0.05$, ** $p<0.01$, *** $p<0.001$, two-tailed binomial test). Ratios in italics comprised too few data points to perform statistics ($N<6$).

	Supporting hand hanging		Supporting hand sitting		Resting hand		Resting foot	
	L : R	HI	L : R	HI	L : R	HI	L : R	HI
Elly	124 : 71***	-0.27	188 : 115***	-0.24	55 : 90**	0.24	77 : 34***	-0.39
Lelle	92 : 146***	0.23	110 : 132	0.09	40 : 21*	-0.31	24 : 10*	-0.41
Elliot	128 : 218***	0.26	145 : 221***	0.21	54 : 55	0.01	100 : 40***	-0.43
Edith	170 : 322***	0.31	174 : 292***	0.25	43 : 45	0.02	60 : 26***	-0.40
Ebbot	309 : 260*	-0.09	313 : 304	-0.01	35 : 27	-0.13	129 : 39***	-0.54
Tarzan	109 : 68**	-0.23	82 : 63	-0.13	49 : 32	-0.21	6 : 17*	0.48
Korak	62 : 70	0.06	125 : 202***	0.24	71 : 122***	0.26	114 : 66***	-0.27
Chili	62 : 86	0.16	98 : 73	-0.15	27 : 25	-0.04	22 : 26	0.08
Sheeba	105 : 123	0.08	146 : 202**	0.16	10 : 15	0.20	4 : 2	-0.33
Yindee	102 : 148**	0.18	161 : 212**	0.14	22 : 20	-0.05	7 : 2	-0.56
Ori	87 : 111	0.12	105 : 122	0.07	2 : 2	<i>0.00</i>	<i>1 : 3</i>	<i>0.50</i>
Muguai	140 : 110	-0.12	246 : 228	-0.04	38 : 20*	-0.31	42 : 19**	-0.38
Jindie	80 : 29***	-0.47	35 : 35	0.00	88 : 108	0.10	80 : 59	-0.15
Tabitha	82 : 78	-0.03	84 : 97	0.07	28 : 32	0.07	44 : 22**	-0.33
Gibbi	68 : 82	0.09	91 : 82	-0.05	45 : 42	-0.03	68 : 32***	-0.36

4.2 Tube task

For extracting hand in the *unimanual version of the tube task*, 11 out of 14 gibbons (78.6%) displayed a significant side bias, of which seven were for the left hand and four for the right hand (table 7). In the *bimanual tube task*, 13 of the 14 gibbons (92.9%) significantly preferred one hand as the extracting hand, seven preferred their left hand and six their right hand (table 7). Tarzan was disregarded for the assessment of hand preference for both the unimanual and the bimanual tube task, as this gibbon was not interested in participating in the tube task.

For neither the unimanual nor the bimanual tube task a significant population bias was observed.

Table 7: Left:Right ratios (L:R) and handedness indices (HI) for the tube task (unimanual and bimanual) in all 15 individuals. Bold numbers indicate ratios that significantly differ from chance (* $p<0.05$, ** $p<0.01$, *** $p<0.001$, two-tailed binomial test). Ratios in italics comprised too few data points to perform statistics ($N<6$). Hyphens indicate that this specific motor pattern was not observed for this individual.

	Tube task unimanual		Tube task bimanual	
	L : R	HI	L : R	HI
Elly	26 : 32	0.10	21 : 0***	-1.00
Lelle	63 : 16***	-0.59	11 : 22	0.33
Elliot	72 : 13***	-0.69	28 : 3***	-0.81
Edith	145 : 1***	-0.99	38 : 1***	-0.95
Ebbot	58 : 128***	0.38	1 : 29***	0.93
Tarzan	<i>0 : 1</i>	<i>1.00</i>	-	-
Korak	48 : 15***	-0.52	54 : 27**	-0.33
Chili	14 : 7	-0.33	7 : 18*	0.44
Sheeba	69 : 32***	-0.37	102 : 15***	-0.74
Yindee	34 : 7***	-0.66	33 : 9***	-0.57
Ori	9 : 23*	0.44	1 : 16***	0.88
Muguai	35 : 76***	0.37	7 : 44***	0.73
Jindie	4 : 30***	0.76	15 : 96***	0.73
Tabitha	35 : 19*	-0.30	38 : 19*	-0.33
Gibbi	43 : 50	0.08	21 : 47**	0.38

4.3 Consistency of side bias across motor patterns

Summarizing both spontaneously occurring and task-related behavior, I found that among the 15 gibbons the highest number of significant side preferences (two-tailed binomial test; $p<0.05$) per animal was nine (Elly, Edith and Korak). The lowest number of side biases was recorded in Chili, who displayed a significant preference in only three of the 15 motor patterns. However, he was observed for a shorter period of time compared to the rest of the individuals, because he was transferred to another zoo during the observation period. When not taking Chili into account, two gibbons (Tabitha and Sheeba) displayed the lowest number of significant preferences. These gibbons had a significant hand preference in four of the 15 motor patterns.

Table 8: An overview of the number of motor patterns where a significant preference was observed per individual, including the ratio of Left:Right (L:R) preferences.

	Significant preferences (L:R)	No significant bias
Elly	9 (7:2)	6
Edith	9 (6:3)	6
Korak	9 (5:4)	6
Lelle	8 (6:2)	6
Elliot	8 (6:3)	7
Yindee	8 (5:3)	7
Jindie	8 (2:6)	7
Tarzan	7 (4:3)	6
Muguai	6 (4:2)	8
Ori	6 (0:6)	5
Gibbi	5 (4:1)	8
Ebbot	5 (2:3)	9
Tabitha	4 (3:1)	11
Sheeba	4 (2:2)	11
Chili	3 (1:2)	12

None of the 15 gibbons displayed a consistent left- or right-side bias across all 15 motor patterns. Rather, all animals displayed a significant side bias for some of the motor patterns and all except one (Ori) displayed a switch of the preferred side between the observed behaviors.

To investigate if the gibbons displayed a consistent preference across motor patterns that were similar to each other, the consistency between motor patterns was assessed within the behavioral categories.

Manipulation

Of the 15 gibbons, two animals (Tabitha and Sheeba) displayed no significant hand preferences for any of the six behaviors within the *manipulation* category and two animals (Ebbot and Chili) displayed a significant side bias for just one of the six motor patterns. Four gibbons (Elly, Lelle, Tarzan and Korak) had at least one significant preference for the left as well as the right hand and thus displayed a switch of the preferred side within this category. Seven gibbons (Elliot, Edith, Yindee, Ori, Muguai, Jindie and Gibbi) were consistent in their side bias and displayed a significant hand preference for between two and four of the manipulation motor patterns without switching their preferred side (table 3 and 4).

Leading limb

Two of the 15 animals (Elly and Lelle) displayed a significant hand preference for two of the

three motor patterns within the *leading limb* category and both were consistent in the side of their preference. All other 13 gibbons either displayed no significant preference at all or just for one of the three motor patterns (table 5).

Supporting hand

Four of the animals (Elly, Elliot, Edith and Yindee) were consistent in their side bias within the *supporting hand* category and significantly preferred the same hand for holding when hanging or sitting. The other 11 gibbons displayed no significant preference for either of the two motor patterns or just for one of them (table 6).

Resting position

Within the *resting position* category, two of the 15 gibbons (Elly and Korak) displayed a switch of preferred side between the two motor patterns. Two animals (Lelle and Muguai) were consistent in their side bias across the two behaviors. For one gibbon (Ori) no data were available for resting position as he did not cross his hand or feet when resting. The ten remaining animals displayed no significant side bias at all or just for one of the two motor patterns (table 6).

Tube task

Of the 14 gibbons that participated in the *tube task*, ten animals were consistent in their side bias and thus significantly preferred the same hand for both the unimanual and the bimanual tube task. For the four remaining gibbons, consistency across tasks could not be determined, as one gibbon (Lelle) had a significantly preferred hand for just the unimanual tube task and the other three (Elly, Chili and Gibbi) only displayed a significant side bias in the bimanual tube task (table 7). One gibbon (Tarzan) did not participate in the tube task at all.

4.4 Comparison between spontaneously occurring behavior and the tube task

Of all the motor patterns that were observed in the present study, the gibbons had the highest number of significant hand preferences for the bimanual tube task. For this motor pattern, 13 out of 14 gibbons (92.9%) displayed a significant hand preference (figure 3). This proportion was also quite high for the unimanual tube task, as 11 out of 14 gibbons (78.6%) displayed a hand preference for this motor pattern (figure 3). Of the spontaneously occurring behaviors, the gibbons had the highest number of significant side preferences for feeding hand. For this motor pattern, 13 out of 15 gibbons (86.7%) had a significantly preferred hand (figure 3). Because of the high proportion of significant hand preferences for these three behaviors, hand

preferences for feeding were compared to those in the unimanual and bimanual tube task to investigate if the gibbons were consistent in their side bias for spontaneously occurring motor patterns and task-related motor patterns. For all other spontaneously occurring motor patterns, the number of gibbons with a significantly preferred hand was too low, thus these behaviors could not be statistically compared to the tube task.

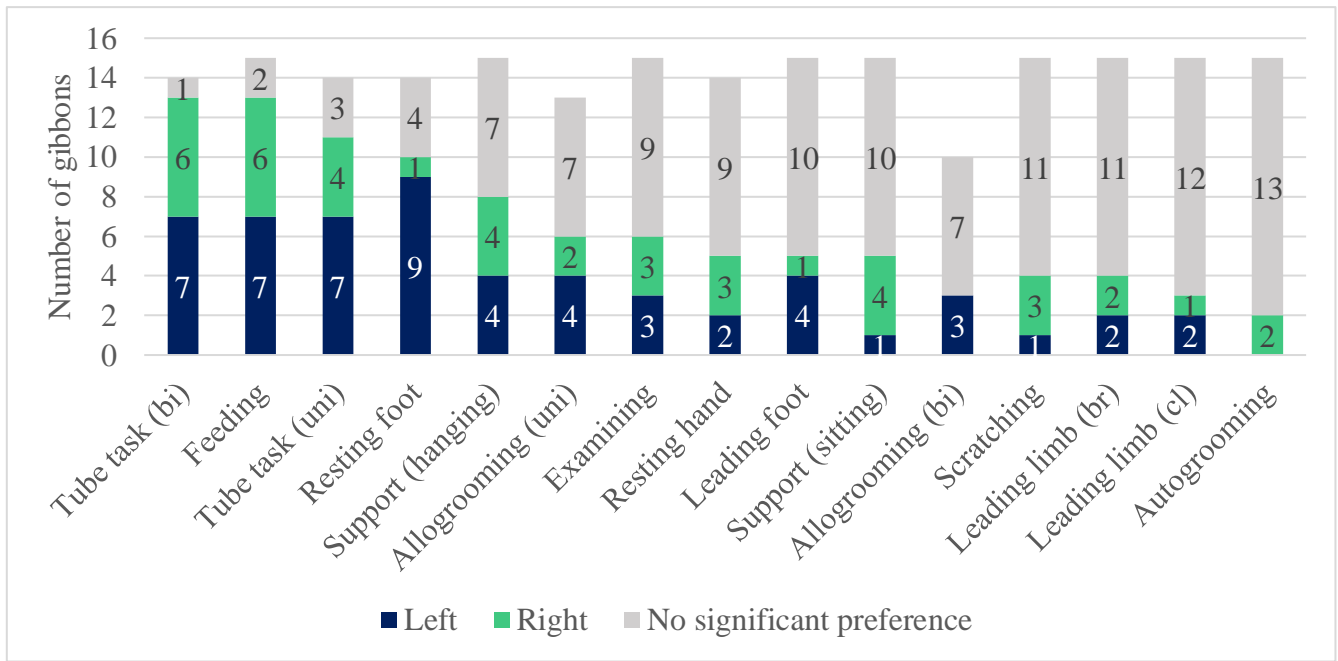


Figure 3: Summary of all left:right proportions for the 15 observed motor patterns. From left to right, the behaviors are arranged by the number of significant preferences (from high to low).

Of the 13 gibbons with a significantly preferred feeding hand, 12 displayed at least one significant hand preference for one of the tube tasks. Nine out of these 12 gibbons significantly preferred the same hand for feeding as for at least one of the tube tasks and three gibbons significantly preferred their opposite hand for feeding (table 9).

Of the eight gibbons that had a significant hand preference for feeding and both versions of the tube task, seven significantly preferred to use the same hand across all three motor patterns. Accordingly, there was a non-significant trend to use the same hand for all three motor patterns ($p=0.070$).

Table 9: An overview of left (L) and right (R) preferences for feeding hand, the unimanual tube task, and the bimanual tube task for 12 of the 15 gibbons. Hyphens indicate that this gibbon had no significant hand preference for this specific motor pattern.

	Feeding hand	Tube task unimanual	Tube task bimanual
Elly	R	-	L
Lelle	L	L	-
Elliot	L	L	L
Edith	L	L	L
Ebbot	R	R	R
Korak	L	L	L
Chili	R	-	R
Yindee	L	L	L
Ori	R	R	R
Muguai	L	R	R
Jindie	R	R	R
Gibbi	L	-	R

4.5 Mean strength and direction of side preference

In order to determine the strength of side bias for the five categories of motor patterns, the absolute HI-scores (absHI) were used to calculate the mean absHI-score (table 10). The category with the lowest mean absHI-scores was *supporting hand*, although for this motor pattern, the females displayed a significantly stronger side bias for this motor pattern ($U=162$, $p=0.039$). The mean absHI-scores for *manipulation* were significantly higher than those for *leading limb* ($V=75$, $p=0.043$) and *supporting hand* ($V=108$, $p=0.0043$). For *resting position*, the mean absHI-scores were significantly higher than those for *supporting hand* ($V=92$, $p=0.014$). Although males had a slightly stronger side bias for motor patterns within the *manipulation* and *leading limb* categories than females, this difference was not significant ($U=23$, $p=0.60$ and $U=16.5$, $p=0.20$, respectively). Overall, the mean absHI-score within the *tube task* category was 0.56, which was significantly higher than the mean absHI-score of those for *manipulation*, *leading limb*, *supporting hand*, and *resting position* ($V=3$, $p=0.0021$; $V=103$, $p=0.00037$; $V=105$, $p=0.0011$; $V=91$, $p=0.00024$, respectively). Although the females tended to display a stronger side bias for the *tube task* than the males, this difference was not significant ($U=138.5$ $p=0.051$).

Table 10: Strength of side preference. Mean absHI-scores \pm SE for the five motor pattern categories calculated for all females, all males, and all gibbons in total.

	Manipulation	Leading limb	Supporting hand	Resting position	Tube task
Females	0.26 \pm 0.04	0.19 \pm 0.04	0.19 \pm 0.03	0.26 \pm 0.02	0.65 \pm 0.06
Males	0.31 \pm 0.07	0.29 \pm 0.06	0.09 \pm 0.02	0.25 \pm 0.05	0.45 \pm 0.07
All	0.28 \pm 0.04	0.24 \pm 0.04	0.14 \pm 0.02	0.25 \pm 0.02	0.56 \pm 0.05

With regard to the direction of side preference, the mean HI-scores (ranging from -1.00 to +1.00) for three of the five motor pattern categories (manipulation, leading limb, and supporting hand) were close to zero, suggesting a lack of side bias at the population level (table 11). In contrast, the mean HI-scores for the motor pattern categories *resting position* and *tube task* deviated from zero, suggesting at least a trend for a side bias towards the left at the population level. For *resting position*, the mean HI-scores were similar in males and females (U=24, p=1.0). Both sexes displayed a non-significant tendency for a left-side bias, however, there was quite some interindividual variation. The mean HI-scores within the *tube task* category were not as close to zero as the means for the other categories and differed more between the sexes. The mean HI-score for the females was -0.31, which indicates a tendency for a left-side bias. In contrast, the mean HI-score was 0.19 for the males, which indicates a slight tendency for a right-side bias. However, a large degree of interindividual variation was found, which is reflected by the high SE-values in this category. Accordingly, this difference between sexes was not statistically significant (U=10, p=0.081).

Table 11: Direction of side preference. Mean HI-scores \pm SE for the five motor pattern categories calculated for all females, all males, and all gibbons in total.

	Manipulation	Leading limb	Supporting hand	Resting position	Tube task
Females	-0.01 \pm 0.22	-0.01 \pm 0.14	0.05 \pm 0.21	-0.15 \pm 0.13	-0.31 \pm 0.62
Males	0.11 \pm 0.30	-0.09 \pm 0.11	0.01 \pm 0.11	-0.14 \pm 0.20	0.19 \pm 0.40
All	0.05 \pm 0.26	-0.05 \pm 0.13	0.03 \pm 0.16	-0.15 \pm 0.15	-0.09 \pm 0.14

4.5.1 Sex differences

For 13 of the 15 motor patterns, no significant sex difference was found for either the number of animals displaying a significant limb preference or the preferred side (chi-square test, $p > 0.05$). However, for *supporting hand when sitting*, significantly more females than males displayed a significant hand preference ($\chi^2_{(2)} = 6.56$, $p = 0.038$). Six of the eight females had a significantly preferred supporting hand (one left, five right) while none of the males displayed

a significant side bias. Furthermore, a non-significant trend ($\chi^2_{(2)}=5.06$, $p=0.080$) for a difference between sexes was found for preferred hand in the *bimanual tube task*. Here, more female gibbons preferred the left hand, whereas more males preferred to use their right hand.

4.5.2 Age differences

Of the 15 gibbons, three were considered juveniles (≤ 8 years old; Reichard, 2003) and the 12 remaining animals were classified as adults. When comparing these age groups, no significant differences for either the number of significant limb preferences or the preferred side were found for any of the observed motor patterns (chi-square test, $p>0.05$).

4.5.3 Differences between zoos

For 14 of the 15 motor patterns, no significant difference for either the number of significant limb preferences or the preferred side was found between the five zoos (chi-square test, $p>0.05$). However, for *leading hand in brachiation*, a significant difference in the direction of side preferences was found between zoos ($\chi^2_{(8)}=19.36$, $p=0.013$). In three of the five zoos no significant preferences were found for this motor pattern, in one zoo (Kolmården Wildlife Park, Sweden) two of the five gibbons preferred to use their left hand and in the remaining zoo (Wildlands Adventure Zoo, the Netherlands) both gibbons preferred their right hand.

4.5.4 Differences in tube diameter

In the first two of the five gibbon groups (Kolmården Wildlife Park and Parken Zoo, Sweden) that were observed for the present study, occasionally two different tube diameters were used. No significant differences in side bias were observed between the two different tube sizes (chi-square test, $p>0.05$).

4.5.5 Differences in posture

For supporting hand and the unimanual tube task both sitting and hanging postures were recorded. In none of the 15 gibbons a significant difference was found between supporting hand in a sitting or in a hanging posture (chi-square test, $p>0.05$). In 13 of the 14 gibbons no significant difference in hand preference was found when comparing the two postures for the unimanual tube task (chi-square test, $p>0.05$). One gibbon (Tabitha) used his left hand significantly more often in the hanging position and his right hand significantly more in the sitting position ($\chi^2_{(1)}=4.69$, $p=0.030$). However, there were only six data points for the sitting position and with a larger dataset, this difference may not be significant.

5. Discussion

The aim of the present study was to assess lateralized behavior for both spontaneously occurring as well as for a task-related behavior. In the 15 white-handed gibbons that were observed, significant lateral biases were found at the individual level for several of the spontaneously occurring motor patterns as well as for the more complex tube task. However, no significant side biases were found at the population-level for any of the 15 studied motor patterns.

In previous laterality studies, not all the motor patterns that were observed in the present study have yet been examined in white-handed gibbons. Therefore, the findings from the present study will also be compared to those from laterality studies in other hylobatids and other nonhuman primates.

5.1 Comparison with other studies in white-handed gibbons

Until now, a study on food-reaching by Olson et al. (1990) is the only study on lateralized behavior that has focused entirely on *Hylobates lar*. Although food-reaching was not examined in the present study, there is an indication that hand preferences for food-reaching and feeding are strongly correlated (Stafford et al., 1993). Therefore, the hand preferences found for feeding in the present study will also be compared with the available data on food-reaching from other studies.

In the present study, 13 of the 15 gibbons (86.7%) had a significant hand preference for feeding, but no population-level hand preference was found. In contrast, Olson et al. (1990) reported a population-level left hand preference for a bipedal food reaching task through a mesh fence. However, the authors reported no population-level hand preference for a simple food-reaching task, which is in line with the findings from the present study. This difference between tasks in Olson et al.'s (1990) results could be due to the different nature of the tasks, as free reaching may differ from reaching through a mesh fence. Additionally, differences in body posture (free choice versus forced bipedal) may have affected hand preferences here.

Similar to the findings for feeding hand of the present study, Stafford et al. (1990) reported no population-level hand preference for spontaneous food reaching. Here, 13 gibbons in a mixed-species (*Hylobates*, *Nomascus* and *Symphalangus*) group of 19 individuals (68.4%) were reported to have a significant hand preference for spontaneous food reaching. Additionally, all four white-handed gibbons in this study had a significantly preferred hand, three for the right

and one for the left hand. Although these findings seem in line with the findings of the present study, the sample size is too small to allow for a more generalizing conclusion. Stafford et al. (1990) also reported a tendency towards a right-hand preference in all five adult females, but no such pattern in juvenile females or males. These findings are in contrast with the results of the present study, as no right-hand preference was found in females for any of the studied motor patterns and the proportion of significant hand preferences reported by Stafford et al. (1990) for food reaching was lower. This may be explained by differences in data analysis, as Stafford et al. used a z-score of 2.55 for significance ($p < 0.01$) instead of 1.97 as in the present study. Additionally, although food reaching and feeding are likely to be similar in the movements that they require, differences between these behaviors may have influenced hand preferences.

In the present study, a high proportion (86.7%) of the white-handed gibbons had a significant hand preference for the tube task, but there was no population-level hand preference. In contrast, Morino et al. (2017) reported a significant left-hand preference at the population-level for the tube task (unimanual and bimanual grouped) in a mixed-species sample of 37 hylobatids. Morino et al. (2017) divided their sample in siamangs (*Symphalangus syndactylus*) and non-siamangs, the latter including eight white-handed gibbons. Interestingly, the left/right proportion in siamangs (10/2) was quite different from the proportion in the non-siamang species (10/7). Also, in the siamangs, the proportion of significant hand preferences was only 12 out of 20 (60%) whereas in the non-siamangs all 17 individuals (100%) had a significant hand preference. Furthermore, when only considering the authors' findings on the eight white-handed gibbons in the study, seven (87.5%) had a significant hand preference and the left/right proportion was 2/5. The results that Morino et al. (2017) reported for non-siamangs (including *H. lar*) are in line with those from the present study but those for siamangs are not, this may be an indication of differences in lateralized behavior between gibbon species, specifically between siamangs and non-siamangs.

Similar to the findings of the present study, Caspar et al. (2018) found no population-level hand preference for the tube task in a mixed-species sample (*Hylobates*, *Nomascus* and *Symphalangus*) of 18 gibbons. Of the 18 gibbons, 15 had a significantly preferred hand (83.3%) for the tube task, nine preferred the left hand and six the right. All three white-handed gibbons in this study had a significant hand preference, two for the left and one for the right hand. Although this is a limited sample size, the proportions are similar to the findings of the present study.

5.2 Comparison with other studies in hylobatids

As studies that have focused on white-handed gibbons exclusively are rare and it is not clear if differences in lateralized behavior exist between gibbon species, findings in other hylobatids may provide extra insight in hand preferences for a few of the motor patterns examined in the present study.

For leading limb in brachiation, four of the 15 white-handed gibbons (26.7%) displayed a significant hand preference, and no population-level side bias was found. Similar to the findings of the present study, Redmond & Lamperez (2004) reported 26.1% of a group of 25 siamangs (*Symphalangus syndactylus*) to have a significantly preferred leading limb when initiating brachiation, accordingly, the authors found no population-level side bias.

Barker (2008) also studied hand preferences for leading limb in brachiation in a mixed *Nomascus* group. Two of the 16 gibbons (12.5%) had a significantly preferred hand to initiate brachiation with and no population-level side bias was found, which is in line with the findings of the present study. Barker also studied leading limb in “level drop” (a downward drop of maximum 1 meter) and found seven of the 16 gibbons (43.8%) to show a significant hand preference; two for the left and five for the right hand. In the present study, all types of brachiation were grouped together, which may explain why the proportion of significant hand preferences for leading limb in brachiation was slightly higher than the 12.5% reported by Barker et al. (2008).

Heestand (unpublished doctoral dissertation, 1986) examined leading limb in brachiation, leading foot, and feeding hand in a group of 13 siamangs. In the present study, I found no population-level side bias for these three motor patterns. Regarding leading foot, five out of 15 gibbons (33.3%) had a significantly preferred foot to initiate terrestrial locomotion, the remaining 10 gibbons had no significant foot-preference. For feeding hand, 86.7% of the white-handed gibbons had a significantly preferred hand. In line with the findings of the present study, Heestand (1986) reported no population-level hand preference for initiating brachiation and feeding hand. Additionally, the majority of the siamangs was reported to present a significant individual hand preference for spontaneous feeding (Heestand, 1986, as cited by Olson et al., 1990). In contrast, the author reported a population-level right-preference for leading foot in terrestrial locomotion (walking/running) (Heestand, 1986, as cited in Stafford et al., 1990). Unfortunately, it is unclear which criteria Heestand used to examine the motor patterns in her dissertation and therefore it remains difficult to explain this contrasting finding.

Regarding examining and touching of inedible objects, six of the 15 white-handed gibbons (40%) in the present study had a significantly preferred hand, and there was no population-level side bias. Zhao et al. (2019a) is the only other study so far that reported findings on hand preference for touching objects in a gibbon species (*Nomascus leucogenys*, or white-cheeked gibbon). For this motor pattern, the authors found two out of 11 gibbons (18.1%) to have a significant hand preference for touching animate objects and only one out of 11 (9.1%) for touching inanimate objects. Zhao et al. (2019a) reported no population-level side bias, which is in line with the findings from the present study. In contrast, Zhao et al.'s (2019a) proportions of significant preferences are much smaller than in the present study. This difference may be due to the authors including touching food and conspecifics instead of only inedible, inanimate objects.

For unimanual grooming, six out of 13 white-handed gibbons (46.2%) had a significant hand preference, and no population-level side bias was found. Another study by Zhao et al. (2019b) examined hand preferences for unimanual grooming in 10 white-cheeked gibbons (*Nomascus leucogenys*) and reported significant hand preferences for three gibbons (30%) in a sitting position and for two gibbons (20%) in a bipedal position. No population-level side bias was found, which is in line with the findings of the present study. In contrast, Zhao et al. (2019b) reported lower proportions of significant hand preferences for unimanual grooming. This may be explained by differences in the design of the study, as Zhao et al. (2019b) recorded hand preferences separately for a sitting and bipedal posture.

In the present study, there was a non-significant trend for the gibbons to be consistent in their hand use for feeding, the unimanual, and the bimanual tube task. Furthermore, no population-level hand preference was found for these three motor patterns. Fan et al. (2017) tested nine white-cheeked (*Nomascus leucogenys*) gibbons for hand preferences and consistency of preference in food-reaching, a box task (reaching for food in a box from a suspensory position), and the bimanual tube task. In line with the findings of the present study, the authors reported no population-level side bias for any of the observed motor patterns. In contrast, Fan et al. (2017) found lower proportions of significant hand preferences for food-reaching (44.4% versus 86.7%) and the bimanual tube task (77.8% versus 92.9%). For the box task, which was not used in the present study, six of the nine gibbons had a significantly preferred hand (67.7%). This proportion was also lower than the proportion for feeding found in the present study. Lastly, the authors reported no consistency between tasks, although in the present study the gibbons tended to be consistent in their hand use across three similar tasks. Perhaps the tasks

used by Fan et al. (2017) were less comparable than those in the present study, which may explain the lack of consistency in hand use.

Even though this motor pattern was not part of the present study, four of the gibbons were occasionally seen drinking with a cupped hand while the others drank water directly with their mouth. One of these four individuals (Tarzan, the only wild-born gibbon in the present study) had a significant right-hand preference, whereas not enough data points were collected for this motor pattern with the other three animals. In a group of 49 wild siamangs, Morino (2011) examined hand preferences for drinking with a cupped hand and found a significant left-hand preference at the population level. Since only a small number of the captive white-handed gibbons in the present study displayed this behavior, it may be interesting to explore if this is a behavior that occurs more in the wild and therefore elicits stronger hand preferences here.

5.3 Comparison with other studies in nonhuman primates

Although studies on lateralized behavior in other nonhuman primates are widely available (Papademetriou et al., 2005; Fitch & Braccini, 2013; Meguerditchian et al., 2013), they often focus on only one or, at best, a few motor patterns within a given study population. As in studies of lateralized behavior in gibbons, population-level hand preferences have rarely been found so far in other nonhuman primates and findings are not consistent between studies (McGrew & Marchant, 1997; Cashmore et al., 2008; Fitch & Braccini, 2013). Furthermore, some motor patterns that were examined in the present study, have not been examined in previous studies and can therefore not be compared to other findings at this moment.

Autogrooming

Of the 15 white-handed gibbons in the present study, only two (13.3%) had a significant hand preference, both for their right hand. Accordingly, no population-level side bias was found.

Similar to the results of the present study, Hopkins et al. (1993) and Hopkins & de Waal (1995) found no significant side bias for self-touch in two groups of 11 and 10 captive bonobos (*Pan paniscus*), respectively. Two out of 11 bonobos (18.1%) displayed a significant left-hand preference (Hopkins et al., 1993) and two out of 10 individuals (20%) significantly preferred the right hand for this motor pattern (Hopkins & de Waal, 1995). The low proportions of significant hand preferences are in line with those from the present study. Marchant & McGrew (1996) also reported no significant hand preference for autogrooming in a group of 42 wild-living eastern chimpanzees (*Pan troglodytes schweinfurtii*), although no precise proportions of significant preferences are available. A contrasting finding has been reported in a study on 20

captive cotton-top tamarins (*Saguinus oedipus*) by Diamond & McGrew (1994). Here, the authors reported a significant population-level right-side bias for autogrooming, although no data was provided on the proportion of significant individual preferences. A possible explanation for this contrasting result may be that the data from all the tamarins in this study were pooled together instead of evaluating the preferences of all the individuals separately.

Scratching

In the present study, no population-level hand preference was found for scratching hand, as only four of the 15 gibbons (26.7%) had a significant hand preference for this motor pattern.

Mixed results have been reported by studies on hand preferences for scratching in nonhuman primates. Marchant & McGrew (1996) reported no population-level side bias for scratching in eastern chimpanzees, which agrees with the results of the present study. Furthermore, in a group of 22 bonobos, Harrison & Nystrom (2008) found no population-level hand preference for this motor pattern. No proportions of individual preferences were provided here but, when applying the same data analysis as in the present study, three of the 22 bonobos would be considered to have a significant (right) hand preference, which is a lower proportion (13.6%) than found in the present study.

Rogers & Kaplan (1996) reported a significant left-side bias in a group of 31 rehabilitated orangutans (*Pongo pygmaeus pygmaeus*) for scratching the head or face, which is in contrast with the findings of the present study. However, no proportions of significant individual preferences were provided for this motor pattern. As the location of the itch was not considered in the present study, the preferred hand may have been biased towards the side of the body that had to be scratched. By only using body parts (head and face) that are located on the midline of the body Rogers & Kaplan eliminated this possible bias, which may explain the difference in results.

Feeding

Feeding is one of the spontaneously occurring motor patterns that has been examined relatively often in studies on lateralized behavior in primates. Although most studies focused on reaching for food and not bringing food to the mouth, these motor patterns are likely correlated (Stafford et al., 1993) and will therefore both be considered in this section.

In the present study, the white-handed gibbons did not display a population-level side bias for feeding, however, a large proportion (86.7%) had a significant hand preference for this behavior.

The absence of a population-level hand preference is in line with the findings from Harrison & Nystrom (2008) in captive bonobos. However, only 14 out of the 22 bonobos (63.6%) had a significantly preferred hand for this motor pattern (calculated using the data analysis used in the present study), which is a smaller proportion than was found in the present study. In another study, in orangutans, Rogers & Kaplan (1996) reported the majority of the individuals to lack a significant hand preference for holding and manipulation of food, accordingly, no population-level side-bias was found. Colell et al. (1995) reported no population-level bias in a group of 31 chimpanzees, two bonobos and three orangutans for food reaching, however, the authors did find a tendency towards a right-hand preference. The absence of a population-level side-bias reported by both Rogers & Kaplan (1996) and Colell et al. (1995) is in line with the results of the present study, although the proportions of individual side preferences seem to vary. Colell et al. (1995) reported a proportion of 80.6% of the apes to have a significantly preferred hand, which is similar to the 86.7% found in the present study. However, Rogers & Kaplan (1996) only found nine of the 18 orangutans (50%) to display a significant hand preference for food holding and manipulation, which is a lower proportion of significant hand preferences than that found in the present study. This lower proportion of significant preferences in orangutans may be due to food holding being included, instead of food manipulation exclusively.

Although most studies found no population-level hand preference for feeding-related motor patterns, some contrasting results have been reported. For example, Diamond & McGrew (1994) reported a significant population-level right hand preference in cotton-top tamarins for holding and carrying food, although proportions of individual preferences were not mentioned here, and thus this finding is based on data that were pooled across individuals. Furthermore, Laska (1996a) reported a significant left-hand preference at the population level in spider monkeys (*Ateles geoffroyi*) for three different food reaching tasks, for all tasks at least 10 of the 13 individuals had a significantly preferred hand. The reported population-level side-biases in both studies disagree with the results of the present study, although the large proportion of individual preferences ($\geq 76,9\%$) found by Laska (1996a) is in line with the proportion found in the present study. The contrasting results in cotton-top tamarins and spider monkeys may be an indication of differences in lateralization between species, however, this may be due to differences in the design of the studies.

Examining

I found no population-level side bias for the hand used to examine non-edible objects, as only two of the 15 gibbons had a significant hand preference for this behavior.

Only a handful of studies on nonhuman primates have focused on spontaneously occurring motor patterns, especially relatively simple tasks such as touching or reaching for non-food items. To the best of my knowledge, Marchant & McGrew (1996) is the only study that examined such motor patterns in chimpanzees. In line with the present study, the authors found no population-level bias, no proportions of individual preferences were available in this study.

Allogrooming

Both unimanual and bimanual allogrooming were observed in the present study. For unimanual grooming, six out of 13 white-handed gibbons (46.2%) displayed a significant hand preference, whereas this was three out of 10 (30%) for bimanual allogrooming. I found no population-level hand preference for either of the two behaviors.

Contrasting findings have been reported in studies examining allogrooming in nonhuman primates. Boesch (1991) found no population-level side bias for unimanual allogrooming in wild chimpanzees (*Pan troglodytes*), which is in line with the results of the present study. However, as reported by Boesch (1991), only five of the 15 chimpanzees (33.3%) displayed a significant hand preference for unimanual allogrooming, which is a lower proportion than found in the present study.

Also, in contrast with the findings of the present study, Diamond & McGrew (1994) reported a significant population-level right-bias for the hand to initiate allogrooming with in cotton-top tamarins, although this result was based on pooled data. Zhao et al. (2010) found a population-level left-bias for bimanual allogrooming (73.1% had a significant hand preference) in wild Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*), but not for unimanual allogrooming (34.6% had a significant hand preference). Hopkins et al. (2007) reported a significant population-level right-side bias in captive chimpanzees for bimanual allogrooming, but not for unimanual allogrooming. However, 124 out of 192 chimpanzees (64.6%) had a significantly preferred hand for unimanual allogrooming while this was only the case for 53 out of 125 individuals (42.4%) for bimanual allogrooming. Although the lack of a population-level side bias for unimanual allogrooming in cotton-top tamarins and chimpanzees is in line with the results of the present study, the significant population-level biases reported by Diamond & McGrew (1994), Zhao et al. (2010), and Hopkins et al. (2007) are not. Furthermore, both Zhao

et al. (2010) and Hopkins et al. (2007) report a significant population-level hand preference for bimanual allogrooming but not for unimanual allogrooming, which disagrees with the findings of the present study. In the present study, more individuals had a significantly preferred hand for unimanual allogrooming (46.1%) than for bimanual allogrooming (30%), which agrees somewhat with the proportions Hopkins et al. (2007) found, but not with those reported by Zhao et al. (2010). The low proportion of significant individual preferences for bimanual allogrooming in the present study may be explained by the relatively small amount of data available, as it was often impossible to distinguish which hand was subordinate to the other in this motor pattern. Possibly, a different observation method may be needed to collect enough data in future studies of bimanual allogrooming in white-handed gibbons.

Leading limb

In the present study, no population-level side biases were found for leading limb in brachiation, leading limb when climbing, and leading foot. Also, the proportions of significant side preferences were relatively low (26.7%, 20%, and 33.3%, respectively).

So far, side preferences for leading limb have been examined in a relatively large number of studies on lateralized behavior in nonhuman primates. Although some studies report findings on side biases for leading foot, the majority focuses on leading limb in brachiation. Hand preferences for leading limb in climbing have not been reported in nonhuman primates so far.

Harrison & Nystrom (2008) found no population-level hand or foot preference for leading limb in bonobos, which is in line with the results of the present study. When applying the same data analysis as used in the present study, four out of 22 (18.1%) bonobos had a significantly preferred leading limb in brachiation, which is slightly lower than the proportion found in the present study (26.7%). Furthermore, for leading foot, the proportion found by Harrison & Nystrom (2008) was considerably lower (one out of 16; 6.3%) than in the present study (33.3%). This may be explained by a difference between species, as gibbons are also considered to be more bipedal than other apes (Hunt, 1991). In contrast, Hopkins et al. (1993) and Hopkins & de Waal (1995) reported a right-hand bias for leading limb in a group of 11 and 10 bonobos, respectively. However, when considering the individual preferences, only five out of 11 (45.5%, Hopkins et al., 1993) and six out of 10 (60%, Hopkins & de Waal, 1995) bonobos displayed a significant right-hand preference. When applying the same data analysis as used in the present study, this would not qualify as a significant population-level right-hand bias, which

partly explains the different outcome reported by Harrison & Nystrom (2008) and the present study.

In six free-ranging orangutans, Peters & Rogers (2008) reported no population-level side bias or significant individual hand preferences for leading limb when brachiating or moving quadrupedally between overlapping trees, which is in line with the results of the present study. However, in the same study, all six orangutans displayed a significant right-limb bias for two other locomotor behaviors (“tree pulling” and “tree swaying”). Even though this seems like a contrasting result, these findings reported by Peters & Rogers (2008) are still largely in line with those of the present study, since the two types of locomotion for which a significant side bias was found are quite different from brachiation in the white-handed gibbons. Nevertheless, it is interesting to note that strength of hand preference in an individual may differ between types of locomotion. Heestand (1986, as cited by Hopkins et al., 1993) also reported a significant population-level right side bias for leading limb in orangutans, as well as in gorillas (*Gorilla gorilla*) and chimpanzees. However, it is unclear what type of locomotion was examined in this study and it is therefore difficult to compare the results to the findings of the present study.

Supporting hand

Regarding supporting hand, I found eight out of 15 white-handed gibbons (53.3%) to have a significant hand preference in a hanging position and five out of 15 (33.3%) to prefer one hand over the other when sitting. However, there was no population-level hand preference for either of the two motor patterns.

To the best of my knowledge, no previous studies on side biases for supporting hand in nonhuman primates exist. So far, postural support has only been considered as a factor that possibly affects the direction of side bias in unimanual tasks, for instance food reaching (MacNeilage et al., 1987). Therefore, the findings that are reported in the present study cannot be compared to other studies at this moment.

Resting position

In the resting position, I found four out of 14 white-handed gibbons (28.6%) to have a significantly preferred resting hand, and ten out of 14 (71.4%) to have a significantly preferred resting foot. No population-level side bias was present, however, of the ten gibbons with a significantly preferred resting foot a significant majority preferred their left foot ($p=0.021$).

Side preferences in a resting position have only been examined in two previous studies. Similar to the findings of the present study, Marchant & McGrew (1996) reported no significant population-level side bias for “chin-resting” (chin was rested on crossed arms, the arm holding the opposite shoulder or arm was recorded) in eastern chimpanzees, no proportions of significant individual preferences were mentioned. Laska & Tutsch (2000) studied tail-wrapping in three species of New World Monkeys (squirrel monkeys (*Saimiri sciureus*), spider monkeys (*Ateles geoffroyi*), and howler monkeys (*Alouatta palliata*)). In this motor pattern, the monkeys wrapped their tails around them, crossing the midline of their body. Although Laska & Tutsch (2000) found no significant population-level side bias in these three species for tail-resting, highly significant individual side preferences were reported for the squirrel monkeys (18 out of 20 individuals, 90%) and spider monkeys (16 out of 20 individuals, 80%), but not for the howler monkeys (two out of 20 individuals, 10%). The lack of significant population-level side biases is in line with the findings of the present study. Furthermore, the high proportion of significant individual side-preferences in squirrel monkeys and spider monkeys is similar to the high proportion of significant side-preferences for resting foot in the white-handed gibbons in the present study (71.4%) but is in contrast with the relatively low proportion of significant hand preferences for resting hand (28.6%). A possible explanation for this difference between resting hand and resting foot may be that the hands are used for more different motor patterns than the feet. Therefore, the hand resting on top may depend on the behavior that was displayed before the resting posture was adopted, whereas the preferred resting foot may be less dependent of the other motor patterns that are displayed.

Tube task

In the present study, I found high proportions of significant hand preferences for both the unimanual (11 out of 14 gibbons, 78.6%) and bimanual (13 out of 14 gibbons, 92.9%) tube task. However, no population-level side bias was present in this sample of white-handed gibbons.

Although many studies used the tube task to examine hand preference in several species of nonhuman primates, the reported findings are far from consistent across studies and species. Chapelain et al. (2011) reported no population-level side-bias for the bimanual tube task in bonobos, however, 68 of the 77 individuals (88.3%, 35 left and 33 right) had a significantly preferred hand for this motor pattern. Lilak & Phillips (2008) reported 10 out of 11 (90.1%) tufted capuchins (*Cebus apella*) to have a significant hand preference for the tube task, however, no population-level side bias was found here as five individuals preferred their left

and five their right hand. In spider monkeys, Motes Rodrigo et al. (2018) found no population-level side-bias for both the unimanual and bimanual tube task. For all three different tasks (for the bimanual tube task, two different tube sizes were used) all 14 spider monkeys had a significant hand-preference. The results reported by Chapelain et al. (2011), Lilak & Phillips (2008), and Motes Rodrigo et al. (2018) are all consistent with the findings of the present study, as all three studies found no population-level hand preference for the tube task. The high proportions of significant hand preferences are also similar to those found for the bimanual tube task in the present study. However, the proportion of lateralized individuals for the unimanual tube task in the present study (78.6%) was slightly lower than reported by Motes Rodrigo et al. (2018) for this motor pattern.

In contrast, population-level side biases have been reported for the bimanual tube task in several species of great apes. In chimpanzees, Hopkins et al. (2003) reported a significant right-side bias in chimpanzees and a proportion of significant individual preferences of 39 out of 46 (84.8%). Furthermore, Hopkins et al. (2011) reported a significant right-bias in a large sample of 534 chimpanzees, however, no proportions of individual side-biases were provided in this study. Hopkins et al. (2003) reported 19 orangutans to display a significant left-side population-level bias, but no population-level side bias in 31 gorillas. In this study, all 19 orangutans (100%) had a significant hand preference, whereas for the gorillas this proportion was 27 out of 31 (87.1%). Furthermore, Hopkins et al. (2011) reported 46 orangutans to have a significant left-side population-level bias, 75 gorillas to display a significant right-side bias, and no population-level side-bias in a sample of 117 bonobos.

Although the high proportions of significant individual preferences (when available) are in line with the present study, the population-level side biases reported in chimpanzees and orangutans are not. However, the lack of population-level biases, or consistency hereof, in gorillas and bonobos agrees with the results of the present study. One other note is that the real proportions from Hopkins et al. (2003) may be lower, as in this study z-scores greater than 1.64 or lower than -1.64 ($p < 0.1$) were already considered significant.

The inconsistency in side biases across species is also apparent in a study by Westergaard & Suomi (1996), as the authors reported a population-level right-bias for the bimanual tube task in rhesus macaques (*Macaca mulatta*), but not in tufted capuchins. In capuchins, 39 of the 45 individuals had a significantly preferred hand (86.7%), whereas this was lower in rhesus macaques (43 of the 55, 78.1%). Although the majority of the rhesus macaques preferred their

right hand (28 out of 43), the population-level side bias that was reported still seems questionable, since individuals with z-scores greater than 1.64 or lower than -1.64 ($p < 0.1$) were already considered to be right- or left-handed, respectively. Lastly, in a study by Zhao et al. (2012), a left-side population-level bias was reported in wild snub-nosed monkeys. Here, 17 of the 24 (70.8%) individuals had a significant hand preference (13 left, four right) for the bimanual tube task. Again, the right-side bias in rhesus macaques and the left-side bias in snub-nosed monkeys are not in line with the results of the present study, only the lack of a population-level side bias in tufted capuchins and the high proportions of significant individual preferences are.

5.4 Spontaneously occurring behavior versus task-related behavior

In the present study, I found the mean absolute HI-scores to be significantly higher in the tube task category than in the four categories of spontaneously occurring motor patterns. So far, only a handful of studies in nonhuman primates have compared side biases for spontaneously occurring motor patterns with those for task-related motor patterns that are not part of an animal's behavioral repertoire in the wild (Chapelain et al., 2006; Schweitzer et al., 2007; Lilak & Phillips, 2008; Motes Rodrigo et al., 2018).

Although spontaneously occurring motor patterns also include complex motor patterns such as termite fishing or nut-cracking, it has been hypothesized that for spontaneously occurring routine tasks (such as unimanual feeding or food reaching) the distribution of hand preferences would be symmetrical in a population (Fagot & Vauclair, 1991). Fagot & Vauclair also suggested that task-related motor patterns, such as the bimanual tube task, are more likely to reveal hemispheric specialization and thus show an asymmetrical distribution of hand preferences. However, this contrasts the findings of the present study, as I found no asymmetrical distribution of hand preferences for the tube task.

Lilak & Phillips (2008) reported a lower mean HI-score for food reaching and invertebrate foraging compared to that of four novel tasks in tufted capuchins, but no asymmetrical distribution of hand preferences was found for any of the motor patterns. In spider monkeys, Motes Rodrigo et al. (2018) reported that the strength of hand preference was significantly lower for simple food reaching than for three different versions of the tube task. Here, too, hand preferences for all the examined motor patterns were symmetrically distributed. The findings from both studies are in line with those of the present study. Chapelain et al. (2006) found Campbell's Monkeys (*Cercopithecus c. campbelli*) to be more strongly lateralized for task-

related motor patterns compared to spontaneously occurring feeding behavior, which agrees with the present study. Schweitzer et al. (2007) reported similar findings in De Brazza's monkeys (*Cercopithecus neglectus*), as the monkeys were more strongly lateralized for the tube task than for spontaneous feeding. Direction of hand preference was not affected by the nature of the task in either study, which is in line with the results of the present study.

5.5 Consistency of hand preference

In the present study, none of the 15 white-handed gibbons were consistent across all motor patterns, and all except one individual displayed a switch of preferred hand between motor patterns. However, within the manipulation category seven gibbons were consistent, four displayed a switch of preferred hand and the four remaining gibbons had no hand preferences for any of the motor patterns or just for one. Regarding the tube task, all ten gibbons that had a preferred hand for both the unimanual and the bimanual tube task were consistent in their preference. Furthermore, I found a non-significant trend ($p=0.070$) between the preferred hand for feeding and the hand used for both tube tasks. The majority of studies on hand preferences in nonhuman primates have focused on only one motor pattern, or sometimes a few in a given study population. Therefore, so far, findings on consistency of hand preference across tasks are rare (Schweitzer et al., 2007; Lilak & Philips, 2008; Motes Rodrigo et al., 2018).

Similar to the findings of the present study, Stafford et al. (1990) reported no consistency in hand preferences for food reaching and leading limb in a mixed-species sample of gibbons. Furthermore, Fan et al. (2017) reported that five out of nine white-cheeked gibbons (*Nomascus leucogenys*) changed their preferred hand from left to right or vice versa between a box task and the bimanual tube task, accordingly, no consistency in hand preference across tasks was found.

Regarding other nonhuman primates, in gentle lemurs (*Hapalemur griseus*), Stafford et al. (1993) reported hand preferences for three components of bamboo leaf shoot feeding to be consistent across tasks. No consistency between the tube task and spontaneous feeding was reported by Schweitzer et al. (2007) in De Brazza's monkeys, however, the authors found a correlation between the different motor patterns that were part of the monkeys' feeding behavior. Lilak & Phillips (2008) reported consistency between hand preferences across two out of four novel, task-related motor patterns (requiring fine precision movements) in tufted capuchins, but not across the two spontaneously occurring motor patterns or the two other novel tasks that were examined. Motes Rodrigo (2018) reported a consistent hand preference in ten

out of 14 spider monkeys for the unimanual tube task, bimanual tube task (big and small tube), and food reaching. Although some consistencies across tasks were reported in all four studies, this was only true for behaviors that were closely related. Considering the results from previous studies as well as from the present study, it is likely that nonhuman primates are only consistent in their hand preference across tasks that are similar in the movements that they require.

5.6 Factors affecting the strength and direction of lateralized behavior

Several factors, such as age (Hopkins et al., 2011; Morino, 2011; Fan et al., 2017), sex (Stafford et al. 1990, Ward et al., 1990; Corp & Byrne, 2004; Redmond & Lamperez, 2004), posture (Olson et al., 1990; Hopkins et al., 1993; Laska, 1996b; Westergaard et al., 1997; Braccini et al. 2010; Laurence et al. 2011), captivity (Hopkins et al., 2007), and kinship (Corp & Byrne, 2004; Hopkins et al., 2009) have been reported to possibly affect strength and/or direction of lateralized behavior in nonhuman primates.

Age

In the present study age was not a factor that significantly affected side bias, however, only three of the 15 white-handed gibbons were considered juveniles. Here, the small sample size may have masked a potential age effect, especially since other studies have reported age to positively affect the strength of lateralized behavior in siamangs (Morino, 2011) and white-cheeked gibbons (*Nomascus leucogenys*, Fan et al., 2017). Hopkins et al. (2011) also reported adult bonobos to be significantly stronger lateralized than juvenile individuals, although in the same study no age effect was found in chimpanzees, orangutans, and gorillas.

Sex

Interestingly, only two differences between sexes were found in the present study. There was a non-significant trend where females tended to be more left-preferent and males more right-preferent in the bimanual tube task, and females were significantly stronger lateralized for supporting hand in a sitting position. For the other motor patterns, no sex differences were found. Mixed findings have been reported regarding the effect of sex on lateralized behavior. Morino (2011) and Morino et al. (2017) both reported no significant sex differences in siamangs for drinking and the bimanual tube task, respectively. Furthermore, Hopkins et al. (2011) found sex to have no significant effect on strength and direction of side preferences for a bimanual tube task in chimpanzees, gorillas, orangutans, and bonobos. In contrast, Corp & Byrne (2004) reported male chimpanzees to be significantly more left-preferent for bimanual feeding, whereas females preferred their right hand more. Males were also reported to be

significantly more left-preferent for food reaching in a mixed-species group of lemurs (Ward et al., 1990) and in siamangs, females tended to be more right-preferent for food reaching (Stafford et al., 1990) and leading limb in brachiation (Redmond & Lamperez, 2004).

Posture

In the present study, posture was only examined for the motor patterns supporting hand and unimanual tube task. Here, hand use in a sitting and hanging posture were recorded separately. For both motor patterns, no significant difference in strength or direction of hand preference was found between the sitting and hanging postures. Although this was not examined in the present study, in previous literature a bipedal posture has been widely reported to positively affect strength of hand preference in, among others, white-handed gibbons (Olson et al., 1990), tufted capuchins (Westergaard et al., 1997), squirrel monkeys (Laska, 1996b), collared mangabeys (*Cercocebus torquatus torquatus*, Laurence et al., 2011), bonobos (Hopkins et al., 1993), chimpanzees (Braccini et al., 2010), and gorillas (Olson et al., 1990). Only McGrew & Marchant (1997) suggested that a hanging posture could induce this same effect, however, to the best of my knowledge, this has not yet been further investigated.

Captivity

A factor that is challenging to examine, is the possibility that living in captivity or in the wild affects lateralized behavior. As the sample of the present study only consists of captive animals, it is not possible to draw any conclusions on this matter, which may be seen as a limitation of the study. In previous literature, it remains unclear if a significant difference in strength or direction of hand preferences exists between captive and wild primates. Hopkins et al. (2007) reported that wild chimpanzees displayed stronger hand preferences for bimanual grooming compared to captive chimpanzees, however, Hopkins et al. (2009) reported no significant differences between HI-scores for termite fishing in captive and wild chimpanzees. Several other studies assessed hand preferences in wild populations of chimpanzees (Boesch, 1991) and snub-nosed monkeys (Zhao et al., 2012), although these were not compared to captive populations.

Kinship

Six mother-offspring pairs were available in the sample of the present study (appendix 3), and no correlation was found between HI-scores for any of the motor patterns. Only few studies have examined the effect of kinship on strength or direction of hand preference in nonhuman primates. For termite fishing in free-ranging chimpanzees, Hopkins et al. (2009) reported a

significant positive correlation between HI-scores in 56 mother-offspring pairs. However, also in free-ranging chimpanzees, Corp & Byrne (2004) examined 11 mother-offspring pairs and reported no overall correlation in hand preference for feeding. However, in contrast to the findings of the present study, the authors did find a pattern in which daughters had the same hand preference as their mothers (four out of four) and sons preferred the opposite hand (six out of seven).

5.7 Outlook

Based on the findings of the present study and the mixed results from previous studies, I have some recommendations for follow-up studies. First of all, it would be a good idea to expand the sample size of this study by visiting other zoos. By increasing the study population, more insight may be gained on the age effect that has been reported in numerous previous studies and possible sex differences for the bimanual tube task. Also, using a similar ethogram in a study with free-living white-handed gibbons would be a very interesting follow-up to investigate the effect of captivity on side bias. Finally, it may be worth to further investigate side biases for resting position in both white-handed gibbons and other nonhuman primate species. This type of motor pattern has barely been investigated in other species and the results of the present study are promising.

6 Societal and ethical considerations

The experiments reported here comply with the *American Society of Primatologists' Principles for the Ethical Treatment of Primates*, with the *European Union Directive on the Protection of Animals Used for Scientific Purposes* (EU Directive 2010/63/EU), with the *European Union Zoos Directive Good Practices Document*, and with current Swedish and Dutch animal welfare laws.

Zoos are required to provide environmental enrichment to zoo-housed animals to enable them to display their natural behavioral repertoires (European Commission, 2015). Often, environmental enrichment includes varying types of food and objects to manipulate. As PVC tubes filled with food are already approved and widely used as enrichment for zoo-housed primates, the present study did not need an extra ethical approval.

The present study was conducted on a purely observational basis, the gibbons participated voluntarily and could leave or ignore the provided enrichment items at any time. The gibbons

were never forced to participate or interact with the provided tubes, additionally, food was never solely provided in the tubes but freely available at the regular feeding times. Based on the noninvasive character of the present study, I have no reason to believe that my study caused any harm or stress to the studied gibbons.

Behavioral studies of captive animals can play an important role in increasing knowledge about the different species that we share our world with. More knowledge on the behavior of animals kept in captivity may help in developing effective measures to increase their welfare. Furthermore, in the case of endangered species, captive animals are often more accessible and easier to study. White-handed gibbons are endangered in the wild, which is mainly due to hunting (for food and pet trade) and deforestation (Brockelman & Geissmann, 2020). *Hylobates lar* is just one of the 16 existing gibbon species, of which half is critically endangered (Lappan & Whittaker, 2009). As little is known yet about the “Lesser Apes”, all knowledge from studies in captive gibbons may contribute to conservation efforts and may help to increase public awareness of the need for research on animal welfare and research on sustainable development of the environment.

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9 Appendix

Appendix 1: All individual gibbons that participated in the present study.



Ebbot (4)



Edith (6)



Chili (7)



Elliot (9)



Gibbi (10)



Yindee (11)



Korak (11)



Muguai (20)



Tabitha (25)



Jindie (30)



Elly (32)



Lelle (33)



Ori (33)



Sheeba (38)



Tarzan (46+)

Appendix 2: Overview of foods used for the tube task and the number of sessions that was performed per zoo

	Food used	Number of sessions
<i>Kolmarden Wildlife Park</i>	Mashed pellets (frozen), paprika, mashed potato, blood pudding	5 for all gibbons
<i>Parken Zoo</i>	Different kinds of fruits	3 for Korak, 1 for Chili
<i>Wildlands Adventure Zoo</i>	Dried figs, banana, pellets, pear, carrots, honey	10 for both gibbons (on two days, a double session was performed)
<i>Safaripark Beekse Bergen</i>	Dried figs, banana, raisins	6 for Muguai, 3 for Ori
<i>Ouwehands Dierenspark</i>	Peanut butter, carrots	6 for Tabitha and Jindie, 5 for Gibbi

Appendix 3: Pedigrees of some of the gibbons in the present study

