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**Hand preferences in two unimanual and two bimanual
coordinated tasks in the black-handed spider monkey,
*Ateles geoffroyi***

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Abstract

Spider monkeys are interesting to study with regard to hand preferences as they are one of the few primate species lacking a thumb and thus unable of performing a precision grip. Further, being platyrrhine primates, they also largely lack independent motor control of the digits and thus have only limited manual dexterity. It was therefore the aim of the present study to assess hand preferences in black-handed spider monkeys (*Ateles geoffroyi*) in four tasks differing in task demand: simple unimanual reaching for food, and three versions of the widely-used tube task, including two bimanual versions which differ from each other in the degree of fine motor control needed, and a unimanual version which does not require coordinated action of the hands. We found that black-handed spider monkeys display significant hand preferences at the individual, but not at the population level. This was true both in the two bimanual coordinated tasks and in the two unimanual tasks. Further, our results show that the majority of animals was consistent in the hand they preferred in these four tasks. Our findings only partially support the notion that task demand positively correlates with strength of hand preference. Finally, we found that the index finger was the most-frequently used digit in all three tube tasks, although the animals also used other digits and two- and three-finger combinations to extract food from a tube. We conclude that limited manual dexterity does not prevent spider monkeys from displaying strong and consistent hand preferences at the individual level.

Keywords: *Ateles geoffroyi*, hand preferences, laterality, spider monkey, tube task

Introduction

Numerous studies on manual laterality in nonhuman primates have found that tasks requiring fine motor skills or bimanual coordination of motor actions are more likely to elicit hand preferences compared to more simple, usually unimanual tasks such as reaching (e.g. Meguerditchian et al., 2013; Hopkins et al., 2015). Some authors even make a distinction between “low-level” and “high-level” tasks, depending on the degree of task demand (e.g. Fagot & Vauclair, 1991; Lilak & Phillips, 2008). However, it is difficult to define a boundary between such categories and it is difficult to define a valid measure of the degree of task demand, particularly when trying to compare between tasks that require different types of fine motor skills (e.g. tool use *versus* precision grip). Furthermore, it should be emphasized that although certain tasks may be more likely to elicit hand preferences than others, all tasks are equally important if we want to make a statement as to whether an individual displays manual specialization or a species displays true handedness according to the now widely accepted definitions introduced by McGrew and Marchant (1997).

The tube task is a frequently used means to assess primate hand preference in a coordinated bimanual motor pattern (e.g. Hopkins et al., 2011, in chimpanzees, bonobos, gorillas, and orangutans; Westergaard & Suomi, 1996, in tufted capuchins and rhesus macaques; Meguerditchian et al., 2012, in squirrel monkeys; Maille et al., 2013, in De Brazza’s monkeys and red-capped mangabeys; Morino et al., 2017, in siamangs and white-cheeked gibbons). In this task, the inner surface of a tube is baited with a sticky food (e.g. peanut butter, honey, or avocado paste) and then presented to an animal. In order to retrieve the food, an animal has to hold the tube with one hand and to insert the other hand, or finger(s) of the other hand, into the tube. By convention, the hand performing the motor pattern requiring the higher degree of precision, that is, the hand whose fingers are inserted into the tube, is recorded. Similar to other tasks that require bimanual coordination and/or fine motor skills,

the tube task has been found to usually elicit *stronger* hand preferences compared to simple unimanual tasks such as unconstrained reaching for food from a flat surface (e.g. Canteloup et al., 2013; Lilak & Phillips, 2008; Schmitt et al., 2008; Spinozzi et al., 1998).

Spider monkeys (genus *Ateles*) are particularly interesting to study with regard to hand preferences as they are one of the few primate species lacking a thumb (Ankel-Simons, 2007). Being platyrrhine primates, they also largely lack independent motor control of the digits (capuchin monkeys being an exception among platyrrhines in this respect) which limits their ability to perform precision grips (Fragaszy & Crast, 2016). Thus, not surprisingly, spider monkeys have been reported to prefer using their mouth rather than their hand to retrieve small food items from the floor when they have the opportunity to choose between these two options (Laska, 1996a). Nevertheless, a recent study found that Colombian spider monkeys (*Ateles fusciceps rufiventris*) are clearly able to perform the tube task and that they display significant hand preferences at the individual, but not at the population level in this task (Nelson et al., 2015). A follow-up study confirmed this finding and further reported that the inner diameter of the tube systematically affected the strength, but not the direction of hand preference which is consistent with the notion that task complexity or the degree of fine motor skills required correlate positively with the expression of hand preference (Nelson & Boevig, 2015).

Only few studies that employed the tube task so far assessed which finger(s) a primate uses for food retrieval when the inner diameter of the tube prevents the animal from inserting its whole hand (e.g. Meunier & Vauclair, 2007, in white-faced capuchins; Vauclair et al., 2005, in olive baboons; Nelson et al., 2015, in Colombian spider monkeys). This, however, should be interesting for at least two reasons: firstly, to further corroborate the presumed correlation between task complexity or fine motor skill and the strength of hand preference, and

secondly, to gain further insight into the role that independent motor control of the digits may play for the expression of hand preference.

It was therefore the aim of the present study to assess hand preferences in black-handed spider monkeys (*Ateles geoffroyi*). More specifically, we compared their performance between a simple unimanual food reaching task and two versions of the coordinated bimanual tube task which differ from each other in the degree of fine motor control needed. Additionally, we assessed whether hand preference in the bimanual tube tasks differed from hand preference in a unimanual tube task, that is, a task that does not require an animal to hold the tube while inserting its finger(s) for retrieving food. In all tasks involving a tube, we also assessed which digits the animals used for food retrieval and the posture that the animals adopted.

Materials and Methods

Subjects

Testing was carried out using 14 adult black-handed spider monkeys (*Ateles geoffroyi*), seven males and seven females. The animals were kept in outdoor enclosures at the UMA Doña Hilda Ávila de O'Farrill (Environmental Management Unit), maintained by the Universidad Veracruzana near Catemaco, Veracruz, Mexico, and were thus exposed to natural environmental conditions concerning ambient temperature, relative humidity, and light.

The animals were fed once a day fresh fruits and vegetables after the daily test sessions described below. The amount of food offered daily was such that left-overs were still present on the floor the next morning and thus it was unlikely that ravenous appetite affected the animals' behavior during the tests.

The experiments reported here comply with the *Guide for the Care and Use of Laboratory Animals* (8th edition, National Research Council, 2011), the *American Society of*

Primatologists' Principles for the Ethical Treatment of Primates, and also with current Swedish and Mexican laws. They were performed according to a protocol approved by the Ethical Board of the Federal Government of Mexico's Secretariat of Environmental and Natural Resources (SEMARNAT; Official permits no. 09/GS-2132/05/10).

Procedure

Each individual was presented with four tasks:

Bimanual Big Tube task: Grasping an opaque PVC tube (length: 20 cm, inner diameter: 23 mm) with one hand the animal introduced any number of fingers of the other hand inside the tube to retrieve the avocado paste placed inside. The tube was connected to a thin rope which allowed the experimenter to retrieve the tube easily. The individuals could adopt any body position they preferred.

Bimanual Small Tube task: Same procedure as the Big Tube task with a smaller tube (opaque PVC, length: 20 cm, inner diameter, 13 mm).

Each task with a big or a small tube was performed as follows: a tube was inserted into a cage at varying locations of the mesh, letting it fall to the floor hanging from the rope, taking care that the experimenter used both hands alternatively. The animals could grasp the tube at any moment (while inserting the tube, while the tube was hanging, or while the tube was lying on the floor). After an animal had grasped the tube and extracted the food reward from its inside, the tube was retrieved from the cage using the attached rope and refilled. A bout started when the animal first grasped the tube and ended when the animal dropped the tube and the experimenter pulled the tube back. The animals completed 100 bouts per task. Twenty bouts, separated in two groups of ten bouts one hour apart, were recorded for each individual on a given day. For each individual, the first 50 bouts with the big tube were recorded at the beginning of the experimental period, while the second 50 bouts were recorded after the

animals had completed their 100 bouts with the small tube. This was done in order to assess if the bouts with the small tube, which required a higher degree of motor control to retrieve the food influenced the performance of the animals with the motorically less demanding big tube.

Unimanual Tube task: One of the big tubes was mounted perpendicular onto the center of a 30 x 30 cm metal plate so that its inner diameter of 23 mm matched an equally-sized hole in the plate. The metal plate was then attached to the outside of the mesh of an enclosure, with the tube protruding towards the experimenter. Care was taken that the opening of the plate, and thus the opening of the tube, matched one of the mesh openings so that an animal could reach into the tube. The animals introduced any number of fingers into the tube to retrieve the avocado paste. No holding of the tube was possible as the animals could not reach around the metal plaque. The plate was relocated in the mesh after every bout in order to ensure body repositioning between bouts.

Unimanual Reaching: Hanging or in a quadrupedal posture, the animals reached for a raisin or a small piece of papaya, banana or grape placed within view on the floor. Food items were thrown into the cages one at a time and at random positions ensuring complete body repositioning between bouts.

The order in which the tasks were tested was: 50 bouts of the Bimanual Big Tube task, 100 bouts of the Bimanual Small Tube task, 50 bouts of the Bimanual Big Tube task, 100 bouts of the Unimanual Tube task, 100 bouts of the Unimanual Reaching task. The animals were tested with the next task as soon as they reached the required number of bouts in the previous task. Therefore there was no time lapse between testing on consecutive tasks.

In all four tasks, the hand retrieving the food was recorded, together with the body posture that the animal adopted while performing the task (except in the unimanual reaching task which always occurred quadrupedally). Additionally, the finger(s) that was/were inserted into

a tube to retrieve the food was/were recorded using numbers (index: 2, middle: 3, ring: 4, pinky: 5). Combinations were recorded using the numbers of all the digits inserted into a tube (e.g. using the index and middle finger was coded as 23).

Body postures were classified as Standing, Sitting or Hanging. Standing required both hindlimbs to be on the floor but not the forelimbs. Sitting was recorded when the buttocks of the animal was touching the floor, and hanging was recorded when three or more limbs were not touching the floor. Only the first hand used and brought to the mouth in a bout of activity was recorded in order to ensure independence of data points (McGrew & Marchant, 1997).

Data analysis

Data were collected in real time, that is, without video recordings. Individual frequencies and proportions of first hand uses per bout were calculated for each task. Proportions were calculated by dividing the frequencies of left and right hand uses by the total frequency of hand uses recorded per individual. To determine individual hand preferences per task and period, binomial z-scores were calculated to classify the individuals into right hand-preferent ($z \geq 1.96$), left hand-preferent ($z \leq -1.96$) or as displaying no hand preference ($-1.96 < z < 1.96$). Binomial tests were used to determine if the differences between left and right proportions of hand use at the individual level were statistically significant. To compare with previous studies, Handedness Index (HI) scores were additionally calculated per individual and task using the formula $(R-L)/(R+L)$ to assess the direction of hand preference, with R being the number of right hand uses and L being the number of left hand uses. HI values vary between -1 (exclusive use of the left hand) and +1 (exclusive use of the right hand). The HI absolute value (AbsHI) was used to assess the strength of hand preference not considering the direction.

One-sample Wilcoxon tests were used to assess hand preferences at the population level using the HI of each task. Two-tailed paired sample Wilcoxon tests were used to compare i) the individual HI and AbsHI between the first 50 and the second 50 bouts recorded with the big tube, ii) the individual HI and AbsHI between tasks, iii) the frequency of each digit combination between pairs of tasks and iv) the individual number of responses performed with a single finger and multiple finger combinations in each tube task. Friedman tests were used to assess if the frequencies of finger use varied as a function of the task and if the strength (AbsHI) and direction (HI) of hand preference varied as a function of the body posture. Two-tailed independent samples Wilcoxon rank sum tests were used to compare the HI and the AbsHI per task between sexes. Effect sizes were calculated using r scores (Rosenthal et al., 1994; $r = Z/\sqrt{N}$) for paired sample Wilcoxon tests and independent samples Wilcoxon rank sum tests. Kendall's τ_b coefficient of concordance was used to estimate the effect size for the Friedman tests and Cohen's d was used to estimate the effect sizes in one-sample Wilcoxon tests. Data were analyzed using R and statistical significance was set at $p < 0.05$.

Results

Bimanual big tube task

All 14 individuals included in the study showed significant hand preferences in the big tube task (Table 1). Eight individuals significantly preferred the right hand and six individuals significantly preferred the left hand. Thus, as a group the animals did not display a significant hand preference at the population level ($N=14$, effect size: $d=0.258$, $W=57.5$, $P=0.775$). The strength ($N=14$, effect size: $r=0.456$, $W=7$, $P=0.140$) and direction ($N=14$, effect size: $r=0.831$, $W=7$, $P=0.140$) of hand preference did not differ significantly between the first and the second 50 bouts of the big tube task.

- Table 1 about here -

Bimanual small tube task

All 14 individuals showed significant hand preferences in the small tube task (Table 2). Nine individuals significantly preferred to use the right hand and five individuals significantly preferred the left hand. Thus, as a group the animals did not display a significant hand preference at the population level ($N=14$, effect size: $d=0.138$, $W=63.5$, $P=0.504$). Karen was the only individual that changed the direction of hand preference between the two bimanual tube tasks, showing a significant left-hand preference with the big tube but a significant right-hand preference with the small tube.

- Table 2 about here -

Unimanual tube task

All 14 individuals showed significant hand preferences in the unimanual tube task. Eight individuals showed a significant right-hand preference and six a significant left-hand preference (Table 3). Thus, as a group the animals did not display a significant hand preference at the population level ($N=14$, effect size: $d=0.139$, $W=55$, $P=0.899$).

- Table 3 about here -

Unimanual Reaching task

Thirteen out of 14 individuals showed a significant hand preference in the unimanual reaching task (Table 4). Seven individuals showed a significant right-hand preference and six a significant left-hand preference. Thus, as a group the animals did not display a significant hand preference at the population level ($N=14$, effect size: $d=0.042$, $W=38$, $P=0.6246$).

All analyses were repeated excluding Karen as some fingers of her left hand were disabled, probably due to improperly healed broken digits. However the results regarding hand preference at the population level did not differ from when Karen was included in the

analysis (N=13, bimanual small tube: effect size: $d=0.204$, $W=53.5$, $P=0.594$; bimanual big tube: effect size: $d=0.185$, $W=51.5$, $P=0.697$; unimanual tube: effect size: $d=0.217$, $W=48$, $P=0.888$; unimanual reaching: effect size: $d=0.044$, $W=38$, $P=0.625$).

- Table 4 about here -

Comparison between tasks

The *direction* of hand preference did not differ significantly between any of the four tasks (big tube versus small tube: $N=14$, effect size: $r=0.3324$, $W=16$, $P=0.261$; big tube versus unimanual tube: $N=14$, effect size: $r=0.103$, $W=19$, $P=0.722$; big tube versus unimanual reaching: $N=14$, effect size: $r=0.151$, $W=54$, $P=0.576$; small tube versus unimanual tube: $N=14$, effect size: $r=0.060$, $W=23.5$, $P=0.953$; small tube versus unimanual reaching: $N=14$, effect size: $r=0.352$, $W=65$, $P=0.184$; unimanual tube versus unimanual reaching: $N=14$, effect size: $r=0.260$, $W=59.5$, $P=0.345$) (Figure 1, left panel).

The *strength* of hand preference, however, differed significantly between tasks: it was significantly lower in the unimanual reaching task compared to all three tube tasks (unimanual reaching versus unimanual tube: $N=14$, effect size: $r=0.839$, $W=90$, $P=0.002$; unimanual reaching versus bimanual small tube: $N=14$, effect size: $r=0.654$, $W=80$, $P=0.018$; unimanual reaching versus bimanual big tube: $N=14$, effect size: $r=0.621$, $W=78$, $P=0.025$). In contrast, no significant differences in the strength of hand preference were found between the three tube tasks (unimanual tube versus bimanual small tube: $N=14$, effect size: $r=0.060$, $W=23.5$, $P=0.953$; unimanual tube versus bimanual big tube: $N=14$, $W=21$, effect size: $r=0.017$, $P=0.906$; bimanual small tube versus bimanual big tube: $N=14$, effect size: $r=0.138$, $W=17$, $P=0.552$) (Figure 1, right panel).

When the analysis was repeated without Karen, the results did not differ.

- Figure 1 about here -

Consistency of hand preference across tasks

Regarding the consistency of hand preference (Table 5), ten of the 14 individuals were completely consistent in the direction of hand preference. Four individuals were only partially consistent. Among those, three individuals (Chavela, Margarita, Neri) were consistent in the direction of hand preference in the three tube tasks, but showed a significant hand preference for the other hand in the unimanual reaching task. One individual (Karen) displayed a left-hand preference in two of the tasks, a right-hand preference in one task, and an ambidexterity in the remaining task (see Table 5).

- Table 5 about here -

Finger use comparisons

The spider monkeys used one, two, three or all four fingers to retrieve the food from the inside of the tubes. A total of ten combinations of single or multiple finger uses were observed. In the bimanual tasks, three-finger combinations (234 and 345) only occurred with the big tube, with 234 being much more frequent (145 uses) than 345 (8 uses). The four-finger combination 2345 only occurred once with the big tube. One- and two-finger use combinations occurred with both the big and the small tube. However, only four of these finger combinations were present in both tasks (2, 3, 4 and 23). The finger combinations 34, 45 and 24 only occurred with the big tube task.

The index finger was the most commonly used single finger in the big tube task (51% of the bouts) as well as in the small tube task (69%). The most common finger combination in the big tube task (18%) was the index and the middle finger (23), and this was also the only combination that was observed in the small tube task. In the big tube task, single fingers were used in a total of 709 bouts (53%), while combinations of more than one finger were used in 640 bouts (47%), although this difference was not significant ($N=14$, effect size: $r=0.125$, $W=57$, $P=0.802$). In the small tube task, single finger uses occurred in 1399 bouts (99.9%) and combinations of more than one finger only occurred once (0.01%). Single fingers were

thus used significantly more often than multiple fingers combined in the small tube task ($N=14$, effect size: $r=0.972$, $W=105$, $P=0.0003$). The index finger (2) and the middle finger (3) were used significantly more often in the small than in the big tube task (index: $N=14$, effect size: $r=0.837$, $W=0$, $P=0.004$; middle: $N=14$, effect size: $r=0.616$, $W=1$, $P=0.021$). However, the combination of index and middle fingers (23) was used significantly more often in the big tube than in the small tube task ($N=14$, effect size: $r=0.859$, $W=78$, $P=0.002$).

Regarding the unimanual tube task, eight combinations of single and multiple finger uses were observed. However, the combination of index and ring finger (24) was not used in this task, whereas the combination of ring and pinky finger (45) was used in one occasion exclusively on this task. Again, the index finger (2) was the most commonly used one (48%). Single fingers were used in 688 bouts (49%) whereas multiple-finger combinations were used in 712 bouts (51%), although this difference was not significant ($N=14$, effect size: $r=0.143$, $W=61$, $P=0.615$). No significant differences were found in the number of finger uses between the unimanual and the big tube task. However, significant differences were found between the unimanual and the small tube task regarding the use of the index ($N=14$, effect size: $r=0.685$, $W=6$, $P=0.0418$), middle ($N=14$, effect size: $r=0.695$, $W=0$, $P=0.022$), and combination of index and middle fingers ($N=14$, effect size: $r=0.837$, $W=66$, $P=0.004$) were used.

A comparison between the three tube tasks (Figure 2) showed that the type of task significantly affected the number of bouts where the index ($N=14$, effect size: $wt=0.486$, $\chi^2=13.682$, $P=0.001$), middle ($N=14$, effect size: $wt=0.192$, $\chi^2=8.194$, $P=0.017$), ring ($N=14$, effect size: $wt=0.256$, $\chi^2=8.824$, $P=0.012$) and the combination of index and middle finger ($N=14$, effect size: $wt=0.246$, $\chi^2=18.136$, $P<0.001$) were used.

When the analysis was repeated without Karen, the results did not differ.

- Figure 2 about here -

Relation between posture and hand use

When solving the bimanual tube tasks, in 47% of the bouts the individuals were hanging, in 44% of the bouts they were sitting and in 9% they were standing. In the case of those individuals which did not use the same hand in 95% or more of the bouts, hand preference did not differ significantly as a function of body posture neither when using the big tube nor the small tube. The *direction* and *strength* of hand preference did not significantly differ as a function of body posture in the big tube task (N=13; direction (HI): effect size: $wt=0.329$, $df=2$, $\chi^2=0.07$, $P=0.96$; strength (AbsHI): effect size: $wt=0.284$, $df=2$, $\chi^2=0.67$, $P=0.72$) or the small tube task (N=11; direction (HI): effect size: $wt=0.31$, $df=2$, $\chi^2=1.09$, $P=0.58$; strength (AbsHI): effect size: $wt=0.326$, $df=2$, $\chi^2=3.27$, $P=0.19$). However, pairwise comparisons using Canover's test showed that the strength of hand preference differed significantly between the sitting and the standing postures in the small tube task ($P=0.007$).

When solving the unimanual tube task, in 45% of the bouts the individuals were hanging, in 39% they were sitting and in 16% the individuals were standing. Again, in the case of those individuals that did not use the same hand in 95% or more of the bouts, hand preference did not differ significantly as a function of body posture. The *direction* (N=9, effect size: $wt=0.431$, $df=2$, $\chi^2=2.29$, $P=0.32$) and *strength* (N=9, effect size: $wt=0.384$, $df=2$, $\chi^2=2.29$, $P=0.32$) of hand preference did not differ as a function of body posture in the unimanual tube task.

Comparisons between males and females

No significant differences in hand use between sexes were found in any of the four tasks regarding *direction* of hand preference (big tube: $N_f=7$, $N_m=7$, effect size: $r=0.052$, $W=23$, $P=0.90$; small tube: $N_f=7$, $N_m=7$, effect size: $r=0$, $W=24.5$, $P=1$; unimanual tube: $N_f=7$,

Nm=7, effect size: $r=0.104$, $W=21.5$, $P=0.75$; unimanual reaching Nf=7, Nm=7, effect size: $r=0.308$, $W=15.5$, $P=0.28$) or *strength* of hand preference (big tube: Nf=7, Nm=7, effect size: $r=-0.054$, $W=26$, $P=0.89$; small tube: Nf=7, Nm=7, effect size: $r=-0.439$, $W=36.5$, $P=0.12$; unimanual tube: Nf=7, Nm=7, effect size: $r=-0.320$, $W=33.5$, $P=0.26$; unimanual reaching: Nf=7, Nm=7, effect size: $r=-0.239$, $W=31.5$, $P=0.41$).

Discussion

The results of the present study demonstrate that black-handed spider monkeys display significant hand preferences at the individual, but not at the population level. This was true both in two bimanual coordination tasks and in two unimanual tasks. Further, our results show that the majority of animals was consistent in the hand they preferred in these four tasks.

Comparison between tasks

Although it is often difficult to properly define whether motor tasks differ in their task demands, it seems plausible to assume that the four tasks employed in the present study clearly differ in this respect: the unimanual tube task can be considered as more demanding than the unimanual reaching task as it required an animal to insert its finger(s) into the tube which necessitates the use of individual fingers rather than a simple power grip plus a higher degree of motor precision than simple food retrieval from a flat surface. Similarly, both bimanual tube tasks can be considered as more demanding than the two unimanual tasks as they required an animal to coordinate the motor actions of both hands and prevented it from using one hand for postural support whereas the two unimanual tasks did not. Finally, the small tube task can be considered as more demanding than the big tube task as it required an

animal to insert its finger(s) into a smaller tube opening which necessitates a higher degree of motor precision compared to a wider tube opening.

Several studies reported a positive correlation between the degree of task demand and the strength of hand preference that nonhuman primates display (e.g. Fagot & Vauclair, 1991; Meunier & Vauclair, 2007; Hook & Rogers, 2008; Lilak & Phillips, 2008). Our findings only partially support this notion: whereas the strength of hand preference was significantly higher in the three tube tasks compared to the simple unimanual reaching task (see Figure 1), no significant differences were found in the absolute HI scores between the three tube tasks. Three explanations, which are not mutually exclusive, might account for this finding: firstly, a ceiling effect may have prevented more clear-cut differences in the strength of hand preferences between tasks. This notion is supported by our finding that, with only few exceptions, all absolute HI scores in the three tube tasks were ≥ 0.80 (see Tables 1, 2, and 3), leaving only little room for between-task differences. Secondly, the effects of presence or absence of postural support (in the unimanual versus bimanual tube tasks) and of the difference in motor precision required (in the big versus small tube task) which have been reported in other studies (e.g. Canteloup et al., 2013; Nelson & Boevig, 2015) may not have been big enough for the spider monkeys to have a significant impact on the strength of hand preference. In this context, it should also be mentioned that success rate, another measure of task demand, was 100% in all three tube tasks, meaning that the spider monkeys always succeeded in retrieving the food from the tubes. Thirdly, there could have been a carryover effect as testing the two bimanual tasks before testing the unimanual task may have affected the performance in the latter. In our view this last possibility is unlikely as we failed to find evidence that performing a more complex task (bimanual small tube task) had a significant effect on the direction or strength of hand preference in a less complex task (bimanual big tube task). Nevertheless, we cannot exclude the possibility that the combined effect of testing

both bimanual tasks before, may have elicited stronger hand preferences in the unimanual task. Therefore, we suggest that future studies should perform tasks in both ascending and descending order of complexity for specifically assessing the above-mentioned carryover effect.

It is interesting to note that even the least demanding one of the four tasks assessed here, unimanual reaching for food from a flat surface, elicited significant hand preferences in all but one of the spider monkeys. This is in contrast to findings from several other species of nonhuman primates which reported a lack of significant hand preferences at the individual level for this motor pattern in at least some, or even in the majority of the studied animals (e.g. squirrel monkeys: Laska, 1996b; capuchin monkeys: Lilak & Phillips, 2008; Tonkean macaques: Canteloup et al., 2013; Barbary macaques: Schmitt et al., 2008; Olive baboons: Vauclair et al., 2005 but see Hook & Rogers, 2000 in common marmosets). The fact that spider monkeys are lacking a thumb might explain this discrepancy as it makes grasping of small food items more difficult for members of the genus *Ateles* than for primates having a thumb. This notion is supported by the finding that spider monkeys prefer to use their mouth rather than a hand for retrieving food from the ground when they have the opportunity to choose between these two options (Laska, 1996a).

Comparison with other tube task studies

Our finding that black-handed spider monkeys display significant hand preferences at the individual level, but not at the population level is in line with the majority of studies that employed the tube task with other species (e.g. rhesus macaques: Bennett et al., 2008; Tonkean macaques: Canteloup et al., 2013; capuchin monkeys: Lilak & Phillips, 2008; squirrel monkeys: Meguerditchian et al., 2012; De Brazza's monkeys and red-capped mangabeys: Maille et al., 2013). Another member of the genus *Ateles*, the Colombian spider

monkey (*Ateles fusciceps rufiventris*) has also been found to only display significant hand preferences at the individual level in this bimanual coordination task (Nelson & Boevig, 2015). Studies that reported population-level hand preferences in the tube task are so far mainly restricted to the Great Apes (chimpanzees, bonobos, gorillas, and orangutans: Hopkins et al., 2011) and the Lesser Apes (siamangs and white-cheeked gibbons: Morino et al., 2017). Whether this reflects a phylogenetic difference between hominoid and non-hominoid primates or is perhaps due to the large sample sizes employed in the studies with hominoids remains an open question.

The few studies so far which tested other species of nonhuman primates with both a big and a small tube or with a unimanual and a bimanual version of the tube task yielded mixed results: whereas Canteloup et al. (2013) – in line with our findings – found no significant difference in the strength of hand preference as a function of tube diameter in Tonkean macaques (*Macaca tonkeana*), Nelson and Boevig (2015) did find such a difference in Colombian spider monkeys (*Ateles fusciceps rufiventris*). Maille et al. (2013) reported that the strength of hand preference in De Brazza's monkeys (*Cercopithecus neglectus*) and red-capped mangabeys (*Cercopithecus torquatus*) was significantly higher in the bimanual than in the unimanual version of the tube task. Future studies including primate species which have not been tested so far with different versions of the tube task might help to elucidate which factors may account for such between-species differences.

Consistency of hand preference across tasks

We found that the majority of animals of the present study were consistent in the hand they preferred across all four tasks (Table 5). Due to their basic similarity, it may not seem too surprising that the three versions of the tube task employed here elicited consistent hand preferences. Accordingly, Tonkean macaques (Canteloup et al., 2013) and Colombian spider

monkeys (Nelson & Boeving, 2015) have also been reported to be consistent in their preferred hand when tested with a small and a wide tube, respectively, and De Brazza's monkeys and red-capped mangabeys (Maille et al., 2013) were consistent in the hand they preferred when tested with a unimanual and a bimanual version of the tube task.

It is interesting to note, however, that ten out of 14 of our animals were also consistent in their preferred hand when comparing between the three tube tasks and simple unimanual reaching. This is in line with findings from Colombian spider monkeys (Nelson et al., 2015) which are closely related to our study species, but in contrast with several other studies which reported that only a minority of animals were consistent in these two tasks (Tonkean macaques: Canteloup et al., 2013; capuchin monkeys: Lilak & Phillips, 2008; squirrel monkeys, Meguerditchian et al., 2012; rhesus macaques: Nelson et al., 2011; De Brazza's monkeys: Schweitzer et al., 2007).

Our finding of consistency in preferential hand use not only across similar tasks, but also across dissimilar ones, raises the question whether black-handed spider monkeys may qualify as displaying manual specialization which has been defined by McGrew and Marchant (1997) as individuals being consistent in their preferred hand across a range of manual tasks. There is no consensus with regard to how many manual tasks should be included and how different these tasks should be in order to assign individual animals as being manually specialized. We feel that four tasks – as assessed in the present study – are definitely not sufficient for assigning such a label, particularly when considering that three of our tasks involved food retrieval from a tube, and thus basically similar tasks.

In this context, it should also be mentioned that a lack of consistency in hand use across tasks may simply reflect that the integrity of one of the hands of an animal may be compromised. Injuries such as broken digits or wrists are frequent in arboreal primates such as spider monkeys and often lead to permanent impairment of the affected hand (Arlet et al., 2009).

This notion fits to at least one of the animals of the present study which was not consistent in her preferred hand: Karen had some fingers of the left hand disabled, probably due to improperly healed broken digits, which made the hand functional for the tasks with the big tube but required the use of the other hand with the small tube. Nevertheless, Karen used both hands and different finger combinations (8 in total including both hands), and displayed hand preferences and finger use preferences, which qualify her for being included in this study. Furthermore, when we repeated the statistical analysis excluding Karen's data we obtained the same significant results in the same tests as when her data were included.

Finger use in the tube tasks

We found that the index finger was the most-frequently used digit in all three tube tasks (Figure 2). This is in line with all previous studies which assessed finger use in the tube task with other species of primates (chimpanzees: Llorente et al., 2009; capuchin monkeys: Meunier & Vauclair, 2007; De Brazza's monkeys and red-capped mangabeys: Maille et al., 2013; rhesus macaques: Westergaard & Suomi, 1996; Olive baboons: Vauclair et al., 2005; Colombian spider monkeys: Nelson & Boevig, 2015). Considering that spider monkeys are rather limited in the independent motor control of their fingers (Fragaszy & Crast, 2016), this is remarkable as it demonstrates that the restricted manual dexterity of *Ateles geoffroyi* nevertheless allows for the deliberate use of single digits. Another platyrrhine primate, the squirrel monkey, has been found unable to insert a single digit into a narrow tube when performing the tube task, and to use the whole hand when the tube's diameter allowed for this option (Meguerditchian et al., 2012). Capuchin monkeys, in contrast, have been shown to display fine motor control of individual fingers in a variety of tasks (Christel & Frigaszy, 2000) including the tube task (Westergaard & Suomi, 1996). This suggests that the degree of

independent motor control of fingers differs considerably among platyrrhine primates, with spider monkeys falling between squirrel monkeys and capuchin monkeys.

However, the spider monkeys of the present study also used digits other than the index finger, either alone or in combination, in a considerable proportion of bouts. Not surprisingly, the use of two- or three-finger combinations occurred much more often with the big tube compared to the small tube (Figure 2), suggesting that the animals used multiple-finger combinations to increase their efficiency in retrieving the food from the inside of the tube.

Although it was not the aim of the present study to collect data on the independence of motor control of individual fingers, we did observe variation in this regard. Some individuals bent the fingers when retrieving food from the tube with one finger while others kept all fingers extended in parallel and oriented the hand so that only one finger was introduced into the tube. We suggest that future studies should conduct systematic observations of individual finger motor control in order to determine if the variation observed is accounted for by individual differences in finger dexterity or if, alternatively, it is the consequence of particular finger or fingers used to retrieve food in the tube task.

Hand preference as a function of sex and body posture

Our finding of a lack of sex differences in both direction and strength of hand preferences in the black-handed spider monkey is in line with the majority of studies that employed the tube task (chimpanzees, bonobos, gorillas, and orangutans: Hopkins et al., 2011; capuchin monkeys: Lilak & Phillips, 2008; De Brazza's monkeys and red-capped mangabeys: Maille et al., 2013; squirrel monkeys: Meguerditchian et al., 2012; Barbary macaques: Schmitt et al., 2008; Olive baboons: Vauclair et al., 2005; Colombian spider monkeys: Nelson et al., 2015). However, Bennett et al. (2008) reported that female rhesus macaques displayed significantly stronger hand preferences in the tube task compared to males. A previous study on hand

preferences in black-handed spider monkeys which assessed visually- and tactually-guided food reaching tasks also failed to find any sex differences in our study species (Laska, 1996a).

Similarly, we found no effect of body posture on the direction or strength of hand preferences in our study population, although we did find significant differences in the strength of hand preference in the most demanding tube task (Binomial small tube task) between the standing and hanging postures. Whereas several studies reported that body posture can significantly affect preferential hand use in a variety of tasks (e.g. Laska, 1996b; McGrew & Marchant, 1997; Cashmore et al., 2008; Hook & Rogers, 2008; Braccini et al., 2010), the few studies so far that considered body posture as a possible variable in the tube task failed to find any effects on both direction and strength of hand preferences (De Brazza's monkeys and red-capped mangabeys: Maille et al., 2013; capuchin monkeys: Spinozzi et al., 1998). Nevertheless, and considering our results, we suggest that future studies on hand preferences employing the tube task should systematically vary body posture and assess its possible effects on preferential hand use.

In summary, we conclude that limited manual dexterity does not prevent spider monkeys from displaying strong and consistent hand preferences at the individual level.

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618 Table 1

619 *Individual hand use frequencies, HI scores, AbsHI scores, and binomial Z-scores in the*
 620 *bimanual big tube task*

	L	R	HI	AbsHI	Z-scores	P value
Brutus	1	99	0.98	0.98	9.7	<<0.001
Cejitas	100	0	-1.00	1.00	-10.1	<<0.001
Colin	0	100	1.00	1.00	9.9	<<0.001
Edgar	100	0	-1.00	1.00	-10.1	<<0.001
Frida	0	100	1.00	1.00	9.9	<<0.001
Karen	92	8	-0.84	0.84	-8.5	<<0.001
Kelly	6	94	0.88	0.88	8.7	<<0.001
Lucas	6	94	0.88	0.88	8.7	<<0.001
Mari	29	71	0.42	0.42	4.1	<<0.001
Paulina	100	0	-1.00	1.00	-10.1	<<0.001
Chavela	94	6	-0.88	0.88	-8.9	<<0.001
Margarita	0	100	1.00	1.00	9.9	<<0.001
Neri	10	90	0.80	0.80	7.9	<<0.001
Yayo	92	8	-0.84	0.84	-8.5	<<0.001

621 *Note.* L: Left-hand use. R: Right-hand use. HI: Handedness Index.

622 AbsHI: absolute value of the HI.

623

624 Table 2

625 *Individual hand use frequencies, HI scores, AbsHI scores, and binomial Z-scores in the*
 626 *bimanual small tube task*

	L	R	HI	AbsHI	Z-scores	P value
Brutus	0	100	1.00	1.00	9.9	<<0.001
Cejitas	100	0	-1.00	1.00	-10.1	<<0.001
Colin	0	100	1.00	1.00	9.9	<<0.001
Edgar	99	1	-0.98	0.98	-9.9	<<0.001
Frida	0	100	1.00	1.00	9.9	<<0.001
Karen	8	92	0.84	0.84	8.3	<<0.001
Kelly	8	92	0.84	0.84	8.3	<<0.001
Lucas	0	100	1.00	1.00	9.9	<<0.001
Mari	18	82	0.64	0.64	6.3	<<0.001
Paulina	100	0	-1.00	1.00	-10.1	<<0.001
Chavela	89	11	-0.78	0.78	-7.9	<<0.001
Margarita	1	99	0.98	0.98	9.7	<<0.001
Neri	9	91	0.82	0.82	8.1	<<0.001
Yayo	100	0	-1.00	1.00	-10.1	<<0.001

627 *Note.* L: Left-hand use. R: Right-hand use. HI: Handedness Index.

628 AbsHI: absolute value of the HI.

629 Table 3

630 *Individual hand use frequencies, HI scores, AbsHI scores, and binomial Z-scores in the*
 631 *unimanual tube task*

	L	R	HI	AbsHI	Z-scores	P value
Brutus	5	95	0.90	0.90	8.9	<<0.001
Cejitas	100	0	-1.00	1.00	-10.1	<<0.001
Colin	0	100	1.00	1.00	9.9	<<0.001
Edgar	100	0	-1.00	1.00	-10.1	<<0.001
Frida	0	100	1.00	1.00	9.9	<<0.001
Karen	91	9	-0.82	0.82	-8.3	<<0.001
Kelly	4	96	0.92	0.92	9.1	<<0.001
Lucas	10	90	0.80	0.80	7.9	<<0.001
Mari	6	94	0.88	0.88	8.7	<<0.001
Paulina	100	0	-1.00	1.00	-10.1	<<0.001
Chavela	84	16	-0.68	0.68	-6.9	<<0.001
Margarita	5	95	0.90	0.90	8.9	<<0.001
Neri	3	97	0.94	0.94	9.3	<<0.001
Yayo	100	0	-1.00	1.00	-10.1	<<0.001

632 *Note.* L: Left-hand use. R: Right-hand use. HI: Handedness Index.

633 AbsHI: absolute value of the HI.

634 Table 4

635 *Individual hand use frequencies, HI scores, AbsHI scores, and binomial Z-scores in the*
 636 *unimanual reaching task*

	L	R	HI	AbsHI	Z-scores	P value
Brutus	34	66	0.32	0.32	3.1	0.002
Cejitas	100	0	-1.00	1.00	-10.1	<<0.001
Colin	6	94	0.88	0.88	8.7	<<0.001
Edgar	96	4	-0.92	0.92	-9.3	<<0.001
Frida	14	86	0.72	0.72	7.1	<<0.001
Karen	50	50	0.00	0.00	-0.1	1.000
Kelly	12	88	0.76	0.76	7.5	<<0.001
Lucas	32	68	0.36	0.36	3.5	<<0.001
Mari	10	90	0.80	0.08	7.9	<<0.001
Paulina	98	2	-0.96	0.96	-9.7	<<0.001
Chavela	26	74	0.48	0.48	4.7	<<0.001
Margarita	67	33	-0.34	0.34	-3.5	<<0.001
Neri	98	2	-0.96	0.96	-9.7	<<0.001
Yayo	79	21	-0.58	0.58	-5.9	<<0.001

637 *Note.* L: Left-hand use. R: Right-hand use. HI: Handedness Index.

638 AbsHI: absolute value of the HI.

639 Table 5

640 *Hand preference of each individual in each of the four tasks*

	Sex	Big tube	Small tube	Unimanual tube	Unimanual reaching
Brutus	M	R	R	R	R
Cejitas	M	L	L	L	L
Colin	M	R	R	R	R
Edgar	M	L	L	L	L
Frida	F	R	R	R	R
Karen	F	L	R	L	A
Kelly	F	R	R	R	R
Lucas	M	R	R	R	R
Mari	F	R	R	R	R
Paulina	F	L	L	L	L
Chavela	F	L	L	L	R
Margarita	F	R	R	R	L
Neri	M	R	R	R	L
Yayo	M	L	L	L	L

641

642 *Note.* R: significant right-hand preference. L: significant left-hand preference.

643 A: ambidexter = no significant preference for either hand

644

646
 647 *Figure 1.* Individual HI scores (left panel) and AbsHI scores (right panel) in the four tasks.
 648 Each line corresponds to one individual and the different data points correspond to the
 649 individual values of direction (left) and strength (right) of hand preference in each of the four
 650 tasks tested.

652 *Figure 2. Comparison of use of the different finger combinations between the three tube*
 653 *tasks. "D2", "D3" and "D4" indicate the index, middle, and ring finger, respectively.*