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Evaluating handedness measures in spider monkeys

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Abstract Despite long-standing interest and a vast body of literature, there is still disagreement as to how handedness should be measured in nonhuman primates. The primary goal of this study was to evaluate two common measures of handedness in nonhuman primates using the spider monkey, a unique study species due to its lack of a thumb and limited dexterity. Contrary to our predictions and previous findings in *Ateles*, there was no evidence for group-level hand biases on either the coordinated bimanual TUBE task or a unimanual reaching task. At the individual level, monkeys exhibited preferences on both tasks. There was a leftward trend on the bimanual task and a rightward trend on the unimanual task. Monkeys that were strongly lateralized on the bimanual task showed a comparable hand preference on the unimanual task, whereas monkeys with a moderate preference on the bimanual task shifted to the opposite hand on the unimanual task. Comparing across measures, the two hand-use patterns reported (consistent and shift) might have obscured group-level findings, given the available sample size. Overall, these data reaffirm that task type influences hand use in primates, and multiple measures are needed to fully characterize the construct of handedness. Consideration should be given to the difficulty required between tasks as well as between species.

Keywords Handedness · Hand preference · Laterality · Spider monkey · Nonhuman primate

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Introduction

Despite long-standing interest and a vast body of literature, there is still disagreement as to how handedness should be measured in nonhuman primates (cf., Hopkins 2013a). The issues surrounding measurement are often tied to the prevailing evolutionary framework: the postural origins theory first proposed by MacNeilage et al. (1987). In this account of the origins of handedness, ecological factors such as postural demands and feeding strategies were thought to have driven hand use. In early primates who were arboreal and relied on ballistic movements to catch fast-moving insect prey, the left hand may have become specialized for reaching, while the right hand would have been used in a complementary role for postural support. When later primates became terrestrial, the right hand would not have been needed for posture and may have instead become specialized for manipulation, thus enabling greater food processing such as opening nuts or peeling fruit—actions that require coordination between the hands. As a result of the postural origins theory, many studies have examined whether various nonhuman primate species exhibit preferences for one or both of these two forms of hand use, unimanual reaching, and bimanual coordination. Although it is well known that individuals exhibit hand preferences for particular tasks, evidence for population-level hand preferences has been debated (for reviews, see MacNeilage 2007; McGrew and Marchant 1997; Meguerditchian et al. 2013; Papademetriou et al. 2005).

Nonhuman primate data are often directly compared to the pattern of hand preference observed in human adults, which is strikingly biased. Approximately 90 % of human adults are right-handed (e.g., Annett 2002). Notably, reaching is virtually never used to assess preference in human adults. Rather, standard questionnaire items focus

on *skilled manual actions* such as the hand used for writing, hammering, dealing playing cards, or striking a match (examples taken from the *Edinburgh Handedness Inventory*, Oldfield 1971). As noted by Hopkins (2013a), reaching may not be an inherently poor measure of handedness in nonhuman primates, provided that situational factors are constrained. For example, greater skill is required when vision or posture is challenged. By contrast, studies based on unconstrained reaching tasks have typically not found population-level handedness (e.g., Canteloup et al. 2013; Vauclair et al. 2005). Nevertheless, reaching (constrained and unconstrained forms) is still popularly used as a measure in nonhuman primates, and there is no standard method for collecting this type of data with regard to the number of trials or procedural considerations (for discussions, see Fagot and Vauclair 1991; Hopkins 2013a; Papademetriou et al. 2005; Rogers 2009).

In contrast to unimanual reaching, the coordinated bimanual TUBE task (Hopkins 1995) has become a fairly standard measure for nonhuman primate handedness. Briefly, the TUBE task involves smearing an adhesive food (e.g., peanut butter) into both ends of a tube. Once baited, the tube is given to the test subject and data collection proceeds by observing which hand(s) the subject inserts into the tube to retrieve the food. The TUBE task elicits preferences in a number of different species (New World monkeys: Lilak and Phillips 2008; Meguerditchian et al. 2012; Meunier and Vauclair 2007; Phillips and Sherwood 2005; Spinozzi et al. 1998; Westergaard and Suomi 1996; Old World monkeys: Bennett et al. 2008; Maille et al. 2013; Nelson et al. 2011; Schweitzer et al. 2007; Vauclair et al. 2005; Westergaard et al. 1997; Zhao et al. 2012; Apes: Chapelain and Hogervorst 2009; Chapelain et al. 2011; Hopkins 1995; Hopkins et al. 2001, 2003, 2004, 2011; Llorente et al. 2011). Unlike reaching measures, posture has not been reported to influence hand use on the TUBE task (e.g., Hopkins 1995; Maille et al. 2013; Spinozzi et al. 1998), possibly because of the constraints imposed on each hand to act in complementary roles with one hand stabilizing the tube, while the other hand removes the food.

Efforts to continue to standardize methods for measuring hand preference in nonhuman primates will facilitate comparisons between species and across studies. There are also gaps in our knowledge on particular species that are critical to refining handedness theory. Therefore, the purpose of the current study was to evaluate two common measures of handedness in nonhuman primates, unimanual reaching, and bimanual coordination, in the spider monkey. New World monkeys differ from Old World monkeys and apes in that they lack a saddle joint in the thumb, making the thumb only pseudo-opposable with the other digits (Fragaszy 1998). Within New World monkeys, spider monkeys are further distinguished by lacking thumbs entirely. The spider monkey was selected as the focal species in the current study because of its uncommon hand structure. The spider monkey hand has been characterized as having no functional division, meaning it operates in a hook-like fashion (Erikson 1963; Turnquist 1983). Such a hand is likely a key adaptation for brachiation in this arboreal species but may have consequences for lateralization. Administering the TUBE task to spider monkeys is therefore highly germane given that there are no TUBE data from a nonhuman primate species with this unusual hand structure. The lack of an external thumb also has implications on grasping ability compared to other nonhuman primate species that have been examined using reach and grasp measures. Both the TUBE task and unimanual reaching may be more difficult for spider monkeys to execute compared to other nonhuman primate species. Thus, comparing performance on both tasks in spider monkeys is critical for understanding the evolution of hand-use preferences in primates.

Only one prior study has examined handedness in *Ateles* to date (for comparisons with other New World primates, see Hook-Costigan and Rogers 1996; Smith and Thompson 2011). Laska (1996) reported a population-level left-hand preference in a sample of 13 *Ateles geoffroyi* on three reaching tasks. Spider monkeys grasped raisins from the ground in a quadrupedal posture, from a shelf at eye level in a bipedal standing posture, or from an opaque horizontal tube in a seated posture. The percentage of left-hand use for the group (75–79 %) was consistent across the different unimanual tasks regardless of the varying postural demands. There are no prior data on bimanual hand use in *Ateles*. We hypothesized that spider monkeys would be able to perform the TUBE task despite potential limitations in digit control compared to other primate species that have previously been tested with this measure. We asked whether (1) spider monkeys show individual preferences on the two handedness measures, the TUBE task and a unimanual reaching task; (2) whether spider monkeys show population-level preferences on the two tasks; and (3) whether individual preferences are consistent across the two tasks. Given the previous findings of Laska (1996), we predicted a population-level left-hand preference on the TUBE task and the unimanual reaching task.

Methods

Subjects

Subjects were 10 spider monkeys (*Ateles fusciceps rufiventris;* males = 4, females = 6). Monkeys ranged in age from 3 to 45 years old when the study began

($M = 16 \pm 14$ years). Nine of the monkeys were born in captivity, while the remaining monkey was wild-caught. Monkeys were socially housed in a large indoor/outdoor enclosure containing vertical and horizontal perches at Monkey Jungle, a wildlife park in Miami, Florida, USA. The main outdoor pen measured 8.84 m × 3.96 m × 4.47 m. An adjoining outdoor pen (3.30 m × 1.92 m × 1.77 m) connected the main pen with the monkeys' indoor night house (3.30 m × 1.09 m × 2.72 m) and permitted animals to be separated from the group as needed. Water was freely available in all three areas of the enclosure. Monkeys were fed high protein commercial chow (Purina LabDiet® 5045) and a mixture of fruits and vegetables twice daily at 0830 and 1430 hours. Tourists also fed monkeys dried cranberries, raisins, and seeds daily. The Institutional Animal Care and Use Committees of Florida International University and the DuMond Conservancy approved the research, and the study was conducted in accordance with the laws of the USA. Monkeys were tested in their social group whenever possible, which also included an adult male (28 years old) and three infants (<1-year-old) who did not participate in the experiment.

TUBE task

Monkeys were given the coordinated bimanual TUBE task to measure handedness for role-differentiated bimanual manipulation (Hopkins 1995; Fig. 1). In this task, a peanut butter and jelly mixture were smeared on the inside of both ends of a poly-vinyl-chloride (PVC) tube measuring approximately 23 cm in length and 2.5 cm in diameter. Tubes were given directly to focal monkeys through openings in the mesh of the enclosure (15.24 cm × 4.45 cm). Monkeys were required to hold the tube with one hand and insert one or more fingers of the opposite hand into the tube to retrieve the food substrate. Each entry into the tube where the hand was brought to the mouth to eat was scored as left or right. Entries that did not result in food being consumed were not scored. Any response that included the monkey holding the tube with a foot and removing food with one of the hands was not scored. While it is possible that monkeys could have stabilized the tube with their prehensile tail and removed food with one hand, this combination was never observed during data collection. Although often debated, there is no evidence that using frequency of responses as opposed to bouts as the unit of analysis affects interpretation on the TUBE task (for a recent discussion, see Hopkins 2013b). The first 15 responses per monkey per session were recorded in real time by two observers who confirmed observations by verbal agreement. Monkeys were thereafter permitted to access the tubes until they lost interest, or until the tube dropped through the floor mesh of the enclosure.

Additional tubes were provided to reduce competition among monkeys. Subjects were tested individually if the monkey voluntarily isolated from the social group or was isolated for a medical reason not related to the use of their hands. We observed that subordinate animals would occasionally sit near a dominant individual and attempt to access the tube from the opposite end. These responses were not recorded since hand use by the subordinate animal in this context could be influenced by the situational factors. If a dominant animal dropped the tube and a subordinate animal recovered it, data were then collected from the subordinate animal. Monkeys moved freely within their enclosure and could complete the task seated or suspended by the tail. Animal care staff retrieved tubes at the end of each session. Sessions occurred on non-consecutive test days throughout the experiment, and sampling continued until 90 data points had been obtained for each monkey.
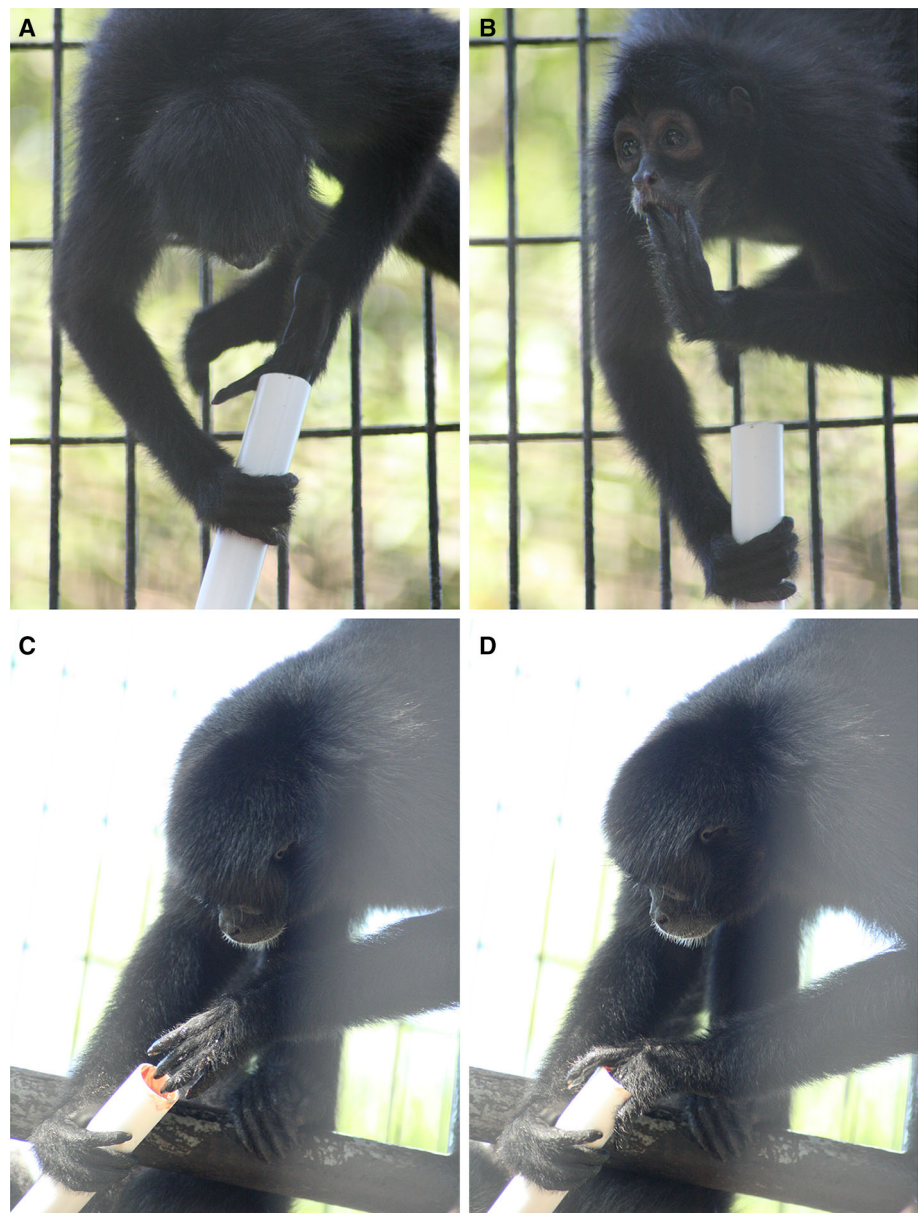
REACH task

Hand preference was measured from a unimanual reaching task, which involved monkeys picking up a raisin or similarly sized small food object on separate trials (Fig. 2). In this task, the food stimuli were presented on a table outside of the home cage that was adjoining the enclosure at approximately floor height because of housing constraints (i.e., the elevated pen coupled with the diameter of the floor mesh precluded presentations of small objects inside the subjects' enclosure). A trial consisted of a single food item presented at the focal animal's midline within arm's reach. Monkeys were required to locomote between trials to ensure independence of data points. The first 15 trials per monkey per session were recorded in real time by two observers who confirmed observations by verbal agreement. Additional feeding stations were provided to reduce competition among monkeys. Sessions occurred on non-consecutive test days throughout the experiment, and sampling continued until 90 data points had been obtained for each monkey. All monkeys were tested in their social group on this task. Data were collected for the REACH task after all data had been collected for the TUBE task.

Data analysis

Hand preferences on the TUBE and REACH tasks were characterized at the individual level in two ways: direction (left, right, or no bias) and degree (strength of bias). To determine the direction of bias, a Handedness Index (HI) was calculated by subtracting the number of left-hand responses from the number of right-hand responses and then dividing by the total number of responses, $HI = (R - L)/(R + L)$. HI scores range from -1.00 (only left-hand responses) to 1.00 (only right-hand responses). HI

Fig. 1 Examples of spider monkeys performing the TUBE task. **a**, **b** Molly (female) using digits 2–4 in a suspended posture. **c**, **d** Sunday (male) using digits 3–4 in a crouched posture. Posture was not constrained in monkeys, and both postures were common during data collection. Illustrative photographs were obtained after data collection was complete

scores were calculated separately for each measure (HI_{TUBE}, HI_{REACH}). Using the cutoff guidelines suggested by Hopkins (2013b), HI scores greater than 0.20 were considered right bias, HI scores less than −0.20 were considered left bias, and all other HI scores were considered to represent no bias. These cutoff values correspond to two-tailed binomial probabilities for the data set collected (90 data points per monkey per measure). To determine the strength of bias, the absolute value of each HI was computed ($ABSHI_{TUBE}$, $ABSHI_{REACH}$). ABSHI scores range from 0 (not lateralized) to 1.00 (completely lateralized). Since data were not normally distributed, nonparametric tests were used in all analyses. Group data were examined with one-sample Wilcoxon signed-rank tests on HI values using a test value of 0 and two-tailed binomial probabilities

on the counts of left, right, or no bias monkeys on each measure. The effect of sex on HI and ABSHI scores was examined with independent-samples Mann–Whitney U tests. Spearman correlations were used to examine the relationships between age, direction of bias (HI scores), and degree of bias (ABSHI scores) for both handedness measures. All statistical analyses were conducted in IBM® SPSS® Statistics 20 using an alpha level of 0.05.

Results

Individual hand-use data and HI scores by task are given in Table 1. On the TUBE task, 7 monkeys were classified as having a left bias, 3 monkeys were classified as having a
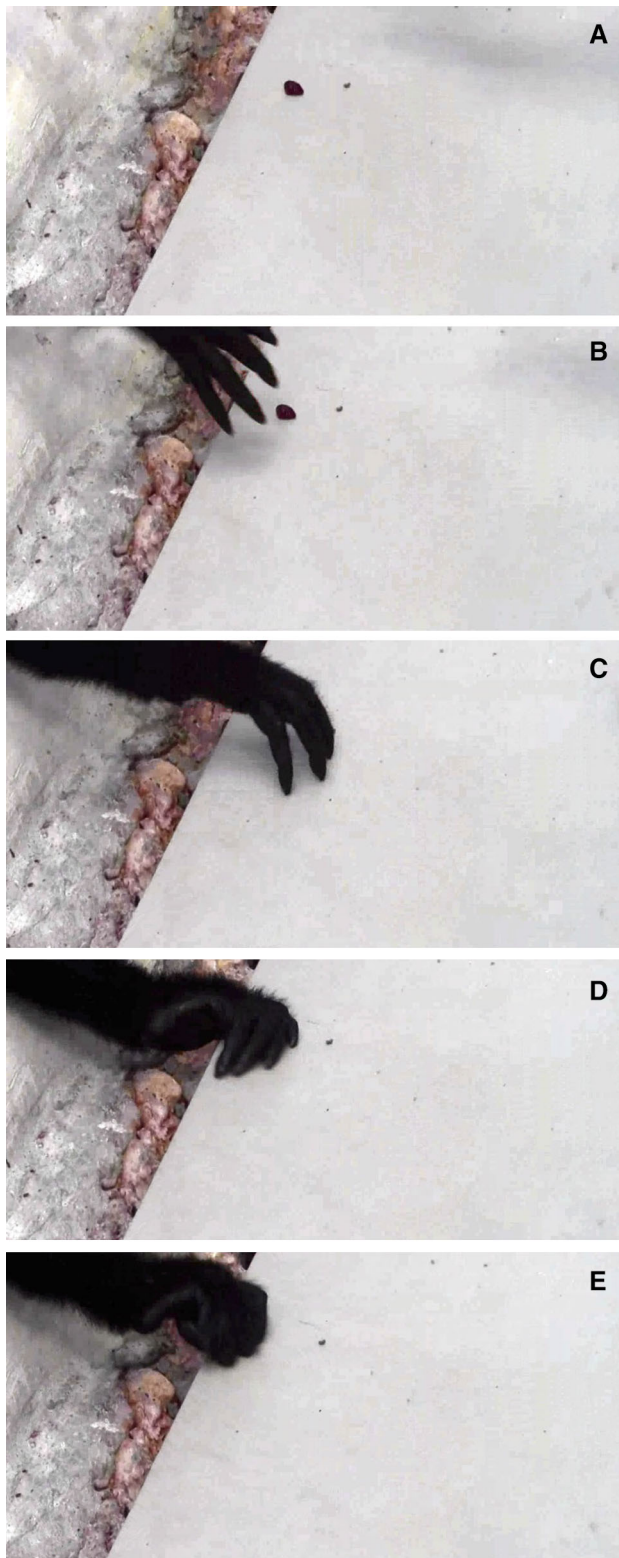
Fig. 2 Sequence of Sunday (male) performing the REACH task with the right hand

right bias, and 0 monkey was classified as having no bias. The number of monkeys showing a left or right preference did not differ (two-tailed binomial probability, $p = .344$).

HI_{TUBE} scores ranged from -0.98 (very strongly left) to 1.00 (exclusively right). A one-sample Wilcoxon signed-rank test on HI_{TUBE} scores found no significant group-level bias ($N = 10$, $Z = -0.357$, $p = .721$). There was no sex difference on HI_{TUBE} scores ($U = 10$, $p = .762$). Degree of lateralization for the TUBE task was measured by taking the absolute value of HI scores. $ABSHI_{TUBE}$ scores ranged from 0.29 to 1.00. Males and females did not differ on $ABSHI_{TUBE}$ scores ($U = 21$, $p = .067$). Age was not correlated with either direction ($N = 10$, $Rs = 0.250$, $p = .486$) or degree of bias on the TUBE task ($N = 10$, $Rs = -0.110$, $p = .763$).

By comparison on the REACH task, 3 monkeys were classified as having a left bias, 6 monkeys were classified as having a right bias, and 1 monkey was classified as having no bias. The number of monkeys showing a left- or a right-hand preference did not significantly differ (two-tailed binomial probability, $p = .754$). HI_{REACH} scores ranged from -0.71 (strongly left) to 1.00 (exclusively right). A one-sample Wilcoxon signed-rank test on HI_{REACH} scores found no significant group-level bias ($N = 10$, $Z = 0.664$, $p = .507$). There was no sex difference on HI_{REACH} scores ($U = 4$, $p = .114$). Degree of lateralization for the REACH task was measured by taking the absolute value of HI scores. $ABSHI_{REACH}$ scores ranged from 0.20 to 1.00. Males and females did not differ on $ABSHI_{REACH}$ scores ($U = 12$, $p = 1.00$). Age was not correlated with either direction ($N = 10$, $Rs = -0.146$, $p = .687$) or degree of bias on the REACH task ($N = 10$, $Rs = -0.345$, $p = .329$). There was a marginal correlation between the direction of hand-use bias on the TUBE task and the direction of hand-use bias on the REACH task ($N = 10$, $Rs = 0.579$, $p = .079$; Fig. 3). There was no relationship between the degree of hand-use bias on the two measures ($N = 10$, $Rs = 0.197$, $p = .586$).

Discussion

The primary goal of this study was to evaluate two common measures of handedness in nonhuman primates using the spider monkey, a unique study species due to its lack of a thumb and limited dexterity. We administered the classic bimanual TUBE task to spider monkeys for the first time and compared performance on the TUBE task with performance on the unimanual REACH task. We collected 90 responses per monkey on each of the two measures to allow for valid statistical comparisons. At the individual level, monkeys exhibited preferences on both tasks. On the TUBE task, monkeys trended toward left-hand use. There were seven monkeys with a left-hand preference and three monkeys with a right-hand preference. By contrast on the REACH task, monkeys trended toward right-hand use.

Table 1 Individual hand-use data and HI scores on the TUBE and REACH tasks

ID	Rearing	Sex	Age	TUBE			REACH		
				#L	#R	HI$_{TUBE}$	#L	#R	HI$_{REACH}$
Dusky	Captive-bred	F	12	0	90	1.00 (R)	0	90	1.00 (R)
CJ	Captive-bred	F	24	0	90	1.00 (R)	19	71	0.58 (R)
Uva	Captive-bred	M	3	17	73	0.62 (R)	9	81	0.80 (R)
Butch	*Wild-caught*	*M*	*45*	*58*	*32*	*−0.29 (L)*	*6*	*84*	*0.87 (R)*
Carmelita	*Captive-bred*	*F*	*30*	*59*	*31*	*−0.31 (L)*	*36*	*54*	*0.20 (N)*
Sunday	*Captive-bred*	*M*	*6*	*66*	*24*	*−0.47 (L)*	*5*	*85*	*0.89 (R)*
Mason	*Captive-bred*	*M*	*3*	*67*	*23*	*−0.49 (L)*	*1*	*89*	*0.98 (R)*
Molly	Captive-bred	F	5	86	4	−0.91 (L)	90	0	−1.00 (L)
Mints	Captive-bred	F	23	88	2	−0.96 (L)	90	0	−1.00 (L)
Cleo	Captive-bred	F	7	89	1	−0.98 (L)	77	13	−0.71 (L)

#L = number of left-hand responses, #R = number of right-hand response. Scores calculated with the formula $HI = R − L/R + L$, where HI = Handedness Index, R = Right response, L = Left response. HI values > 0.20 = Right bias (R). HI values < −0.20 = Left bias (L). All other HI values = No preference (N). Italics indicates monkeys that changed in hand-use bias between measures

There were three monkeys with a left preference, six monkeys with a right preference, and 1 monkey with no statistically significant preference. Contrary to our predictions and previous findings in *Ateles*, there was no evidence for population-level preferences on either the TUBE or REACH tasks. When the measures were compared, two distinct patterns emerged. Monkeys that exhibited near-exclusive use of one hand on the TUBE task showed comparable levels of hand use with the same preferred hand on the REACH task, regardless of whether the preferred hand was the left or the right (Table 1). Three of the monkeys who exhibited this consistent pattern preferred the left hand, and three monkeys consistently preferred the right hand (Fig. 3). Interestingly, four monkeys with moderate left preferences on the TUBE task (HI$_{TUBE}$ scores from −0.29 to −0.49) shifted hands on the REACH task, preferring the right hand instead for grasping (HI$_{REACH}$ scores from 0.20 to 1.00; Table 1; Fig. 3). Age was not related to either direction or strength of preferences on either task.

Our results differed from that of Laska (1996), who reported a population-level left bias in spider monkeys on a series of unimanual tasks, including picking up raisins from the ground (comparable to our REACH task) and taking raisins from an opaque tube (unlike our TUBE task, the tube was horizontal and did not require that the hands worked together in a coordinated fashion). One factor that may have contributed to the difference observed between the two studies is that the taxonomy of *Ateles* is contentious, with some experts classifying *Ateles fusciceps rufiventris* (this study) as a subspecies of *Ateles geoffroyi* (Laska 1996 study). Other experts consider the two to be separate species (for discussion, see Rylands et al. 2006). If indeed *Ateles fusciceps rufiventris* is a distinct species from *Ateles geoffroyi*, this might explain in part the difference in
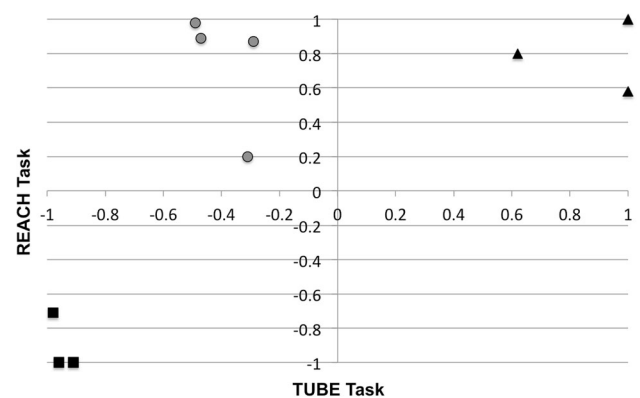

Fig. 3 Direction of hand-use bias on the TUBE and REACH tasks was marginally correlated, Rs = 0.579, p = .079. *Black shapes* indicate monkeys with a consistent strong bias on both tasks (*squares* consistent left-hand bias; *triangles* consistent right-hand bias). *Gray circles* indicate monkeys who shifted their direction of hand bias between handedness measures

hand use observed across the two studies. Similar to Laska (1996), however, we did not find sex differences on direction of hand bias on the TUBE or REACH tasks (HI scores) or the strength of hand bias on the TUBE or REACH tasks (ABSHI scores). Whether sex plays a role in primate handedness remains uncertain, as reports have been mixed. For example, Meguerditchian et al. (2012) reported a left trend for males on the TUBE task, and a right preference for females on a unimanual task in squirrel monkeys. Other investigators have reported no sex effect in primate handedness (see McGrew and Marchant 1997). The possible influence of sex on handedness remains a target for future studies with large sample sizes.

This study may serve as a first step in using the TUBE task with spider monkeys. As illustrated in Fig. 1, we

observed that spider monkeys appeared to attempt to insert the whole hand into the tube. Sometimes, this resulted in one or two fingers jutting out to the sides. This result was unexpected, given prior descriptions of a "hook-like" hand in spider monkeys and poor independent digit control (Erikson 1963; Turnquist 1983). Squirrel monkeys, another New World monkey species, were only able to perform the TUBE task when given a modified tube with a diameter larger enough to accommodate the whole hand (Meguerditchian et al. 2012). A next step may be to explore whether differences in the diameter of the tube may similarly alter findings in spider monkeys (cf., Canteloup et al. 2013). For spider monkeys, a smaller opening may impede their ability to perform the task. Alternatively, a smaller opening may increase the complexity of the task in as so much that it increases the percentage of preferred hand use among individuals with moderate preferences. Future work might explore other bimanual tasks that would increase the motoric demand placed on spider monkeys to further examine the notion that role-differentiated action coupled with increased difficulty elicits robust preferences (cf., Maille et al. 2013).

A number of other researchers have similarly discussed the notion of task complexity as it relates to measurement in handedness. For example, Fagot and Vauclair (1991) introduced the terms "low-level" and "high-level" to refer to categories of manual actions. Low-level tasks include familiar and practiced everyday kinds of actions, whereas high-level tasks are novel and cognitively and/or motorically challenging. Lilak and Phillips (2008) characterized reaching and foraging as low-level tasks, and measures such as tool use and the TUBE task as high-level tasks. Although appropriate for most primates, the notion of low-level versus high-level may need to be redefined for spider monkeys to reflect the greater difficulty in reaching and grasping due to the lack of the thumb. As illustrated in Fig. 2, spider monkeys were observed to invert the hand to grasp the raisin with the index finger touching the grasping surface. The inverted grip is presumably less efficient for picking up small objects, although investigating grip morphology in any meaningful detail in spider monkeys remains a goal for future work. An additional caveat is needed for when reaching may serve as a valid indicator of handedness. Aside from situational demands such as posture or vision, reaching may be a good measure *if reaching to grasp is difficult* for the test population. Nevertheless, population-level preferences were not found on the REACH task or the TUBE task, even though both tasks were presumably challenging. Additional work is needed to understand why some monkeys were consistent across tasks while others shifted direction in hand preference, and whether there are advantages or disadvantages to either hand-use strategy (i.e., consistent or shift) for spider

monkey ecology. These questions are particularly salient given that the spider monkey can use the tail to support its body, entirely freeing both hands, as well as using the tail to extend reach to acquire objects. The role of the tail in lateralization, particularly in conjunction with how the hands are used, will be explored in future studies.

In addition to measurement, these findings also have implications for understanding the evolution of handedness in nonhuman primates. The postural origins theory (MacNeilage et al. 1987; MacNeilage 2007) continues to be used as a framework for many researchers and has overall increased interest in the topic of handedness in primates. To briefly summarize, a left preference was proposed for the earliest arboreal primates and it was not until the shift to ground living that a right preference was thought to be established. Using data from the TUBE task across different studies, Meguerditchian et al. (2012) laid out a general pattern for a leftward preference in arboreal species (i.e., orangutans, snub-nosed monkeys, De Brazza's monkeys, squirrel monkeys) and a rightward preference in terrestrial species (i.e., rhesus monkeys, baboons, bonobos, chimpanzees, gorillas). These results do not fit entirely with the original conception of the postural origins theory, which is based on evolutionary continuity, given the split in the ape taxonomy. Nevertheless, we can now add spider monkeys to the arboreal grouping of species that show a leftward trend on the TUBE task.

But what does it mean to observe a different trend on another hand-use measure within the same population? Similar to the squirrel monkeys studied by Meguerditchian et al. (2012), there was a rightward trend for spider monkeys on the unimanual reaching task. McGrew and Marchant (1997) described four levels of manual laterality that vary within and across tasks and subjects (see also Marchant & McGrew 2013). According to this framework, the hand preferences of six of the monkeys tested in this study would be characterized by the term *manual specialization*, where hand use is consistent across tasks within subjects. The other four monkeys tested in this study that shifted hand preference between tasks would be better characterized by the term *hand preference*, where hand use is biased within a task within an individual. Data collected in this study do not meet McGrew and Marchant's requirement for *task specialization*, as there was no population-level bias across subjects within a task. Finally, these data also do not meet their definition of *handedness*, as there was no pattern of consistency across all individuals across all tasks. However, we want to caution that there are very little data on spider monkeys in general, and it would be premature to draw conclusions without extending the sample size and number of manual tasks.

It is also worth considering that there may be an advantage to using one hand on a particular type of task

related to information processing efficiency in the corresponding hemisphere at the individual level (Rogers et al. 2013). The functional implication of such individual preferences is a critical question for future work in this field, as is whether there is an advantage for an individual to be consistent across tasks (e.g., Prichard et al. 2013). A take-home message from the current study and other recent work is to critically consider the tasks used to measure the construct of handedness, broadly defined, with particular attention toward actions that demand *skilled manual actions* as relevant to the species of study. Only through such careful attention to methodology will we further our understanding of the patterns of hand use across species, and brain–behavior relationships in primates.

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