

RESEARCH ARTICLE

Precise Digit Use Increases the Expression of Handedness in Colombian Spider Monkeys (*Ateles fusciceps rufiventris*)

ELIZA L. NELSON* AND EMILY R. BOEVING

Department of Psychology, Florida International University, Miami, Florida

Decades of research on the hand use patterns of nonhuman primates can be aptly summarized by the following phrase: *measurement matters*. There is a general consensus that simple reaching is a poor indicator of handedness in most species, while tasks that constrain how the hands are used elicit individual, and in some cases, population-level biases. The TUBE task has become a popular measure of handedness, although there is variability in its administration across studies. The goal of this study was to investigate whether TUBE performance is affected by tube diameter, with the hypothesis that decreasing tube diameter would increase task complexity, and therefore the expression of handedness. We predicted that hand preference strength, but not direction, would be affected by tube diameter. We administered the TUBE task using a 1.3 cm tube to Colombian spider monkeys, and compared their performance to a previous study using a larger 2.5 cm diameter tube. Hand preference strength increased significantly on the smaller diameter tube. Hand preference direction was not affected. Notably, spider monkeys performed the TUBE task using a single digit, despite the longstanding view that this species has poor dexterity. We encourage investigators who use the TUBE task to carefully consider the diameter of the tube used in testing, and to report digit use consistently across studies. In addition, we recommend that researchers who cannot use the TUBE task try to incorporate the key features from this task into their own species appropriate measures: bimanual coordination and precise digit use. *Am. J. Primatol.* 77:1253–1262, 2015. © 2015 Wiley Periodicals, Inc.

Key words: handedness; hand preference; laterality; hemispheric specialization; spider monkey

INTRODUCTION

Laterality is defined as a bias for one side of the body over the other. Once thought to be unique to humans, lateralization is a pervasive pattern in both vertebrate and invertebrate brain and behavior [for reviews, see Frasnelli et al., 2012; Frasnelli, 2013; Rogers et al., 2013; Vallortigara & Rogers, 2005]. Handedness, or a preference for one hand over the other, has received considerable attention in laterality research. Approximately 85–90% of human adults are right-handed [Annett, 2002]. Motor lateralization occurs at the level of the brain as well. The motor system is characterized by a pattern of crossed innervation, meaning that the right hand is controlled by the left hemisphere and vice versa. Additionally, each cerebral hemisphere is specialized for motor control mechanisms in each arm [Mutha et al., 2013; Serrien et al., 2006]. Efforts to understand the evolution of motor lateralization and hand use in particular has led to a large body of comparative work [recently reviewed in Rogers, 2014; Versace & Vallortigara, 2015].

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following phrase: *measurement matters*. There is a general consensus that simple reaching is a poor indicator of handedness in most species, while tasks that constrain how the hands are used elicit clear individual, and in some cases, population-level preferences [for reviews, see Cashmore et al., 2008; Fagot & Vauclair, 1991; Hook-Costigan & Rogers, 1996; Hopkins, 2013a; MacNeilage et al., 1987; Marchant & McGrew, 2013; McGrew & Marchant, 1997; Meguerditchian et al., 2013; Papademetriou et al., 2005; Rogers, 2009]. The coordinated bimanual TUBE task is an example of a measure that constrains hand use by requiring the subject to

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*Correspondence to: Eliza L. Nelson, Department of Psychology, Florida International University, 11200 SW 8th Street DM 256, Miami, FL 33199. E-mail: elnelson@fiu.edu

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hold a tube with one hand and extract adhesive food from inside the tube with the opposite hand. First introduced by Hopkins [1995] in chimpanzees (*Pan troglodytes*), the TUBE task has been widely used in all of the great apes [Bardo et al., 2015; Begg-Reid & Schillaci, 2008; Chapelain et al., 2011; Chapelain & Hogervorst, 2009; Hopkins, 1999a; Hopkins et al., 2001, 2003, 2004, 2005, 2011; Llorente et al., 2009, 2011], as well as many monkey species (Table I). Findings from the TUBE task have varied across species, although there is some evidence supporting a pattern of left bias in arboreal species and a right bias in terrestrial species [Meguerditchian et al., 2012].

Despite popular use of the TUBE task, there is variability across studies regarding trial number, tube presentation, setting (i.e., captivity versus wild), recording method (i.e., frequency versus bouts), tube diameter, and digit analysis. Many of these issues have been addressed previously and will not be discussed in detail here [e.g., Hopkins, 1999b, 2013a,b; Hopkins & Cantalupo, 2005; Palmer, 2002, 2003]. However, the range in diameter of the tubes used for testing and the inconsistency in reporting digit use has not received much attention. TUBE studies in monkeys in particular have been highly variable, with tube diameters ranging from 1.4–5.0 cm and roughly only one-third of studies

reporting digit use patterns (Table I). Diameter and digit use may be especially important for understanding *why* the TUBE task is an excellent measure of nonhuman primate handedness. Examining factors that may be linked to the construct validity of the TUBE task is important for two reasons: (1) results could be used towards standardizing the administration of the TUBE task itself, thus facilitating comparisons across studies and (2) identifying the key characteristics of the task could be used for refining other handedness assessments, possibly in species for whom the TUBE task may not be appropriate.

Maille et al. [2013] posed the question of whether the TUBE task is a valid measure of handedness because it elicits precise digit use or because it elicits role-differentiated bimanual coordination where the hands have asymmetric and complementary functions. De Brazza's monkeys (*Cercopithecus neglectus*) and red-capped mangabeys (*Cercocebus torquatus*) were given the standard bimanual TUBE task as well as a unimanual condition where the tube was attached to the cage mesh (i.e., monkeys did not have to hold the tube in order to extract the food). Both the standard bimanual task and the unimanual variation resulted in precise digit use with the index finger, but only the standard task required bimanual

TABLE I. Summary of TUBE Findings in Monkeys

Source	Species	<i>R</i>	<i>L</i>	<i>N</i>	Digit	Diameter
New World						
Nelson et al. [2015]	<i>A. f. rufiventris</i>	3	7	0	N	2.5
Westergaard & Suomi [1996]	<i>C. apella</i>	19	20	6	Y: D2	1.5
Spinozzi et al. [1998]*	<i>C. apella</i>	19 (19)	6 (7)	1 (0)	N	1.5 crouched (upright)
Phillips & Sherwood [2005]	<i>C. apella</i>	3	3	1	N	1.5
Phillips & Hopkins [2007]	<i>C. apella</i>	5	5	1	N	1.5
Phillips et al. [2007]	<i>C. apella</i>	7	5	1	N	1.5
Lilak & Phillips [2008]	<i>C. apella</i>	5	5	1	N	1.5
Phillips & Sherwood [2008]	<i>C. apella</i>	7	5	1	N	1.5
Meunier & Vauclair [2007]	<i>C. capucinus</i>	6	6	1	Y: D2	1.5
Meguerditchian et al. [2012]*	<i>S. sciureus</i>	14	21	2	N	3.0
Old World						
Schweitzer et al. [2007]*	<i>C. neglectus</i>	3	9	0	Y: D2	1.4
Maille et al. [2013]*	<i>C. neglectus</i>	3	7	2	Y: D2	1.4 bimanual
Maille et al. [2013]*	<i>C. torquatus</i>	5	4	6	Y: D2	1.4
Chantagny et al. [2013]*	<i>M. fascicularis</i>	4	4	0	N	5.0
Westergaard & Suomi [1996]	<i>M. mulatta</i>	28	15	12	Y: D2	1.5
Westergaard et al. [1997]	<i>M. mulatta</i>	3	12	4	N	1.5 (infants)
Bennett et al. [2008]	<i>M. mulatta</i>	49	50	25	N	2.5
Nelson et al. [2011]*	<i>M. mulatta</i>	6	6	4	N	2.5 (infants)
Schmitt et al. [2008]*	<i>M. sylvanus</i>	10	14	4	N	4.0
Canteloup et al. [2013]*	<i>M. tonkeana</i>	4 (4)	5 (4)	4 (5)	N	2.8 (1.8) wide (narrow)
Vauclair et al. [2005]*	<i>P. anubis</i>	52	33	19	Y: D2	4.0
Zhao et al. [2012]	<i>R. roxellana</i>	4	13	7	Y: D2	3.0

*Denotes task was modified from the original procedure, but still performed by subjects using a role-differentiated strategy where one hand held the tube and the other hand removed the food. *R* = number with right preference. *L* = number with left preference. *N* = number with no preference. *Digit* denotes whether the study reported digit use, where *N* = no and *Y* = yes. Under *Y*, the digit used most frequently is given. *Diameter* denotes the size of the tube opening used in testing given in centimeters. The study condition is noted in cases where multiple tests were performed in the same subjects.

coordination. Maille et al. [2013] reported stronger hand preferences in the bimanual task, and suggested that role differentiation may increase hand preference by making precise digit use more difficult. Critically, there was no difference in the direction of hand preference (i.e., left or right bias) between the unimanual and bimanual TUBE tasks for either species.

Thus, both role differentiation and precise digit use were implicated as important in the effectiveness of the TUBE task as a handedness measure in De Brazza's monkeys and red-capped mangabeys. However, Maille et al. [2013] did not have a TUBE condition that tested bimanual coordination without precise digit use. The authors noted that females and juveniles in their sample could insert more than one digit into the 1.4 cm diameter tube, although monkeys used the second digit (D2) predominantly on both versions of the task. It is not clear whether enlarging the opening of the tube would change how De Brazza's monkeys and red-capped mangabeys perform the task. However another Old World monkey species, Tonkean macaques (*Macaca tonkeana*), did not differ in hand preference direction or strength when tested with tubes of differing diameters (1.8 cm vs. 2.8 cm) or weights [Canteloup et al., 2013]. There is no agreed upon definition of task complexity, although many researchers have used elements of dexterity including role differentiation and motor precision (for discussion, see Uomini, 2009). In fact, what is considered "difficult" or "complex" may vary by species and taxonomy.

Old World monkeys, like apes, have opposable thumbs and are highly dexterous. Thus, Old World monkeys (i.e., De Brazza's monkeys, red-capped mangabeys, Tonkean macaques) may not be the ideal models for teasing apart these hypotheses regarding the TUBE task. By comparison, the thumb of New World monkeys is only pseudo-opposable with the other digits, which limits grasp types and overall dexterity in many species [Fragaszy, 1998]. In contrast to the findings in Tonkean macaques reported by Canteloup et al. [2013], tube diameter strongly impacted squirrel monkey (*Saimiri sciureus*) performance on the TUBE task [Meguerditchian et al., 2012]. The squirrel monkey has been described as a low dexterity New World species [Rosenbaum et al., 2014]. Meguerditchian et al. [2012] noted that squirrel monkeys were not successful on a 1.1 cm tube because they could not fit their whole hand into the tube, and were unable to insert a single digit. On a larger diameter of 3.0 cm, monkeys could not hold the tube without assistance from their feet. Ultimately, the larger diameter tube was modified to resemble a stem glass, and monkeys were able to perform the task using role-differentiated bimanual manipulation (RDBM) where one hand held a narrow rod while the other hand removed food from the

attached tube. 95% of the squirrel monkeys exhibited a significant hand preference with a trend favoring the left hand on this version of the TUBE task that required bimanual coordination, but not precise digit use [Meguerditchian et al., 2012].

Nelson et al. [2015] observed a similar leftward pattern in Colombian spider monkeys (*Ateles fusciceps rufiventris*) on a 2.5 cm diameter tube. The spider monkey is a unique model species because unlike most primates who have five digits, spider monkeys lack external thumbs and have only four digits. Historically, the spider monkey hand has been described as hook-like with limited independent digit control [Erikson, 1963; Turnquist, 1983]. On the 2.5 cm tube, Nelson et al. [2015] observed that spider monkeys, like the squirrel monkeys tested by Meguerditchian et al. [2012], appeared to try to insert their whole hand into the tube. A limitation of this study was that digit use was not systematically recorded. Nevertheless, 100% of spider monkeys in the sample exhibited a hand preference on the TUBE task with 7 monkeys preferentially using the left hand and 3 monkeys preferentially using the right hand. Although all individual hand preferences were statistically significant, a subset of the monkeys exhibited moderate biases (mean \pm sd percentage of preferred hand use = $69.4 \pm 5.2\%$). An outstanding question is whether the TUBE task could be made more difficult for spider monkeys by decreasing the opening of the tube, and if monkeys are successful on this modification, whether TUBE performance is affected by tube diameter.

In the current study, we asked whether spider monkeys could perform the TUBE task using a smaller diameter tube that would preclude whole hand responses and potentially elicit precise digit use. We hypothesized that task complexity, defined here by the motor constraints placed on hand and digit use, is related to the expression of handedness [e.g., Fagot & Vauclair, 1991; Lilak & Phillips, 2008]. We predicted that role-differentiated action coupled with precise digit use would increase hand preference strength, but would not impact hand preference direction. We reasoned that monkeys' left/right preferences on the TUBE task would be consistent, however we expected the increase in task complexity would elicit stronger hand biases. We administered the TUBE task using a 1.3 cm tube to spider monkeys and recorded hand and digit use. We then compared their performance on the smaller diameter 1.3 cm tube to their prior performance on a larger diameter 2.5 cm tube reported by Nelson et al. [2015].

METHODS

Subjects

Data were collected from 9 Colombian spider monkeys (*Ateles fusciceps rufiventris*) housed at

Monkey Jungle in Miami, Florida, USA from November 2014 to January 2015. The sample consisted of three males and six females who ranged in age from 4 to 32 years old (mean \pm sd = 14 \pm 10 years) and were all captive-born. Testing occurred when monkeys were in their social group, which also included two infants <1 year old, one juvenile female, and one adult male (also all captive-born) who did not participate in the experiment. An additional captive-born infant and one wild-caught adult male showed some interest in the task, but did not contribute sufficient responses for analyses.

The monkeys' main outdoor pen (8.84 m \times 3.96 m \times 4.47 m) was connected to an indoor night house (3.30 m \times 1.09 m \times 2.72 m) through a smaller adjoining outdoor pen (3.30 m \times 1.92 \times 1.77 m). The enclosure was equipped with multiple vertical and horizontal structures for the monkeys. Food and water were freely available throughout the enclosure during testing. Monkeys were fed high protein commercial chow (Purina LabDiet 5045) and a mixture of fruits and vegetables daily at 08:30 and 14:30 hr. Monkeys also received cranberries, raisins, and seeds daily from tourists visiting the wildlife park. The Institutional Animal Care and Use Committees of the DuMond Conservancy and Florida International University approved the research, and the study was conducted in accordance with the laws of the United States. The research adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non Human Primates. The welfare of the monkeys was monitored at all times during data collection by Monkey Jungle staff.

Procedure

The TUBE task was administered to the monkeys according to the procedures described in Nelson et al. [2015]. Briefly, a peanut butter and jelly mixture was smeared on the inside of each end of a poly-vinyl-chloride (PVC) tube measuring 15.24 cm in length and 1.27 cm in diameter. Monkeys held the tube with one hand, and removed food with the other hand. Any response involving stabilizing the tube with a foot was excluded. No monkey stabilized the tube with his or her prehensile tail. Fifteen responses were collected on non-consecutive days until 90 responses per monkey had been obtained. Data were collected in real time by observers who confirmed observations by verbal agreement. Hand (left or right), posture (seated, hanging supported by tail, or bipedal) and digit(s) used by the monkey were recorded for each response where the monkey consumed the food. Digit use was recorded as any single digit or multi-digit combination involving pairs of D2 (index finger), D3, D4, or D5. Spider monkeys do not have an external thumb, which anatomically is denoted as D1.

Data Analysis

A Handedness Index was computed for each monkey using the formula $HI = (R-L)/(R+L)$, where R is the number of right hand responses and L is the number of left hand responses. Since data were not normally distributed, nonparametric tests were used in all analyses. A one-sample Wilcoxon signed-rank test was performed on HI scores to test for population-level bias. Using the cutoffs suggested by Hopkins [2013b], HI scores greater than 0.20 were considered right preference, scores less than -0.20 were considered left preference, and all other HI scores were considered no preference at the individual level. These cutoffs are comparable to z -scores of ± 1.96 when at least 30 responses are collected Hopkins [2013b]. To examine handedness strength, the absolute value of HI scores was computed (ABSHI); a score of 0 indicates no lateralization whereas a score of 1.00 indicates complete lateralization.

Digit use was examined in two ways. A related-samples Wilcoxon signed-rank test was used to compare the percentage of responses performed with a single digit to the percentage of responses performed using multi-digit combinations (i.e., digit pairs). At the individual level, monkeys were classified into one of the two preferred digit patterns that emerged (D2 or D3) using binomial probabilities. Fisher's exact tests were performed on preferred digit (D2 or D3) and hand preference (left or right), and preferred digit and sex (male or female). Mann-Whitney U tests were used to examine the effect of sex on HI, ABSHI, percentage of single digit responses, and the percentage of trials performed while in a suspended posture. Spearman correlations were used to examine relationships between age, direction of hand preference (HI), strength of hand preference (ABSHI), percentage of single digit use, and percentage of trials completed in a hanging posture.

Finally, HI and ABSHI scores on the smaller 1.3 cm tube (denoted in comparisons as HI_{SM} and $ABSHI_{SM}$) were compared to monkeys' previous performance on the large 2.5 cm diameter tube task (Nelson et al., 2015: HI_{LG} and $ABSHI_{LG}$ scores). Related-samples Wilcoxon signed-rank tests were used to compare the direction of hand preferences (HI scores) and the strength of hand preferences (ABSHI scores) across the two tube sizes. The alpha level for all tests was 0.05.

RESULTS

Individual hand use data are given in Table II. HI scores ranged from -1.00 to 1.00 (mean \pm se = -0.33 ± 0.93). A one-sample Wilcoxon signed-rank test on HI scores found no significant group-level bias ($N = 9$, $Z = -0.656$, $P = .512$). Individually, 3 monkeys

TABLE II. Individual Hand Use Data on the 1.3 cm TUBE Task

ID	Sex	Age	#L	#R	HI	Pref. (% use)	#S	#H	#B
Sunday	M	8	90	0	-1.00 (L)	L3 (87.8%)	80	10	0
Molly	F	7	89	1	-0.98 (L)	L3 (65.6%)	7	83	0
Cleo	F	9	89	1	-0.98 (L)	L2 (87.8%)	15	74	1
Carmelita	F	32	89	1	-0.98 (L)	L2 (64.4%)	29	51	10
Mints	F	25	84	6	-0.91 (L)	L2 (95.6%)	58	31	1
Mason	M	4	84	6	-0.87 (L)	L2 (92.2%)	24	65	1
Uva	M	5	13	77	0.71 (R)	R2 (83.3%)	81	9	0
Dusky	F	14	0	90	1.00 (R)	R2 (100%)	14	76	0
CJ	F	25	0	90	1.00 (R)	R2 (92.2%)	32	57	1
					$M = -0.33$		Total = 340	456	14

#L = number of left hand responses, #R = number of right hand response. Preferences 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). Pref. = Preferred digit. S = number of responses while seated. H = number of responses while hanging supported by the tail. B = number of responses while bipedal. M denotes mean.

exhibited a right preference, 6 monkeys exhibited a left preference, and no monkey was classified as having no hand preference. Percentage of single digit use (% single) ranged from 64.44% to 100%. A related-samples Wilcoxon signed-rank test found that monkeys significantly used a single digit over multi-digit combinations ($N = 9$, $Z = -2.677$, $P = .007$; Fig. 1). Interestingly, not all possible one and two digit patterns were observed. The following digit patterns were not used by any of the monkeys: L5, L4/L5, R4, R5, R3/R4, and R4/R5. Individually, three monkeys preferred R2, four monkeys preferred L2, and two monkeys preferred L3 (Table II). A Fisher's exact test found no relationship between preferred digit use (i.e., D2 or D3) and direction of hand preference, or between preferred digit use and sex (all $ps > .05$). Mann-Whitney U tests found no effect of sex on direction of hand preference (HI scores: $U = 10$, $P = 1.00$); strength of hand preference (ABSHI: $U = 13$, $P = .381$); or % single ($U = 6.5$, $P = .548$). Age was not correlated to HI scores ($N = 9$, $R_s = 0.038$, $P = .922$); ABSHI scores ($N = 9$, $R_s = 0.521$, $P = .150$); or % single ($N = 9$, $R_s = -0.222$, $P = .565$).

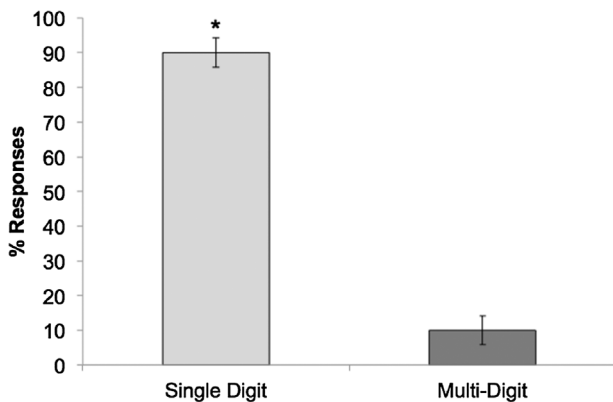


Fig. 1. Mean percent digit use on the small diameter tube. Bars denote standard error. Monkeys preferentially used a single digit over multi-digit combinations.

Performing the TUBE task while hanging from the ceiling or side mesh of the enclosure while supported by the tail accounted for 56% of recorded actions. Performing the TUBE task while seated was the next most common posture comprising 42% of actions. The bipedal posture was rarely observed and accounted for just 2% of all actions. The distribution of responses by posture is given in Table II. Because we could not control monkeys' postures during the experiment and the frequency of the three observed postures varied within and across individuals, our analysis of posture was limited. We calculated the percentage of hanging responses for each monkey (% hanging). A Mann-Whitney U test found no relationship between % hanging and sex ($U = 15$, $P = .167$). There were also no significant correlations found between % hanging and age ($N = 9$, $R_s = -0.050$, $P = .898$); % hanging and % single ($N = 9$, $R_s = -0.077$, $P = .845$); % hanging and HI ($N = 9$, $R_s = 0.094$, $P = .811$); or % hanging and ABSHI ($N = 9$, $R_s = 0.204$, $P = .599$).

We then compared monkeys' performance on the 1.3 cm small diameter TUBE task (current study: HI_{SM} and $ABSHI_{SM}$) with data previously reported by Nelson et al. [2015] using a large diameter 2.5 cm tube (HI_{LG} and $ABSHI_{LG}$). A related-samples Wilcoxon signed-rank test found no difference in hand preference direction between HI_{SM} and HI_{LG} scores ($N = 9$, $Z = 1.363$, $P = .173$). Individually, all monkeys were consistent in hand preference direction across the two versions of the task. Three monkeys who exhibited a right preference on the large diameter task remained right on the small diameter task, and six monkeys who exhibited a left preference on the large diameter remained left on the small diameter. One monkey from this social group who participated on the large diameter TUBE task did not perform the small diameter TUBE task. Notably, a significant difference was found between $ABSHI_{SM}$ and $ABSHI_{LG}$ scores ($N = 9$, $Z = -2.201$, $P = .028$;

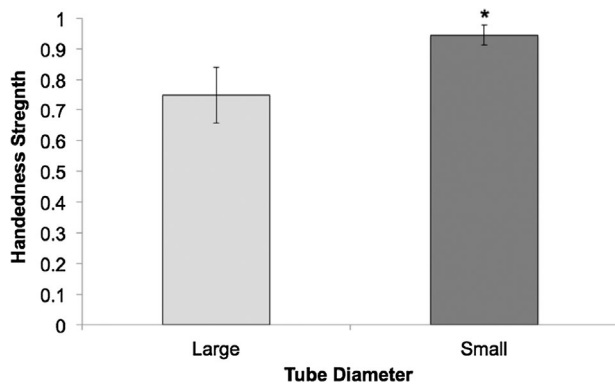


Fig. 2. Mean handedness strength by tube diameter size. Large diameter = 2.5 cm. Small diameter = 1.3 cm. Bars denote standard error. Monkeys expressed stronger hand preferences on the small diameter TUBE task as a group.

Fig. 2). Overall, the strength of hand preference increased as the diameter of the tube decreased. At the individual level, six monkeys were extremely consistent across the two versions of the task with an average difference score ($ABS_{LG} - ABS_{SM}$) of 0.035. The remaining three monkeys showed substantial increase in handedness strength with an average difference score of 0.53 (Fig. 3).

DISCUSSION

The goal of this study was to determine whether Colombian spider monkeys' performance on the TUBE task, a popular handedness measure in nonhuman primates, is affected by the diameter of the tube used in testing. To this end, we administered the TUBE task using a 1.3 cm diameter tube, and compared the results to a prior study conducted with the same group of spider monkeys that had utilized a 2.5 cm diameter tube [Nelson et al., 2015]. We hypothesized that decreasing the tube diameter would make the task increasingly complex for spider monkeys to perform because the smaller tube opening would require precise digit use in addition to role-differentiated bimanual manipulation where one hand holds the tube while the other hand (scored as preferred) extracts the food. We predicted that hand preference strength, but not hand preference direction, would be affected by the change in tube diameter. Our findings supported this prediction. At the group level, hand preference strength was significantly increased on the small (1.3 cm) diameter tube compared to the large (2.5 cm) diameter tube. Data collection for the large and small diameter tubes was separated by more than one year during which time the monkeys did not have any exposure to tubes. It is unlikely that the increase in handedness strength was a result of prior or repeated exposure to the task. Rather, these data support the Maille et al. [2013] hypothesis that role-differentiated bimanual coordination and precise digit use (factors associated

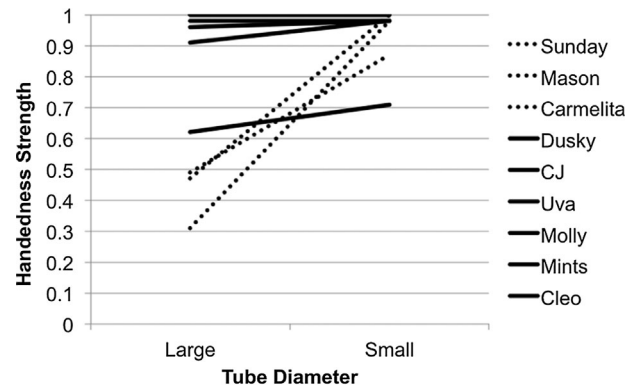


Fig. 3. Individual ABSHI scores for the large and small diameter tubes. Six monkeys were consistent across diameter (black lines), while three monkeys increased in handedness strength on the small diameter TUBE task (dashed lines).

with task complexity) are key features of the TUBE task for detecting handedness in nonhuman primates.

One of the most notable findings from this study was that the spider monkeys were able to successfully insert a single digit into the tube. Moreover, a single digit strategy was used preferentially over a multi-digit strategy at the group level and in each individual monkey. Put another way, monkeys preferred to extract food with one finger even though it was possible to insert two fingers simultaneously (six monkeys utilized a two-digit response at least once during the experiment). Strikingly, three monkeys exclusively made single digit responses (Mason, Dusky, and Mints). This pattern of single digit use is in sharp contrast to squirrel monkeys who were unable to insert a single finger into the tube and used a whole-hand strategy [Meguerditchian et al., 2012]. Both spider monkeys and squirrel monkeys have previously been characterized as less dexterous than other nonhuman primates. Prior to the current study, the only reports of digit use on the TUBE task in New World monkeys were from tufted capuchins [*Cebus apella*: Westergaard & Suomi, 1996] and white-faced capuchins [*Cebus capucinus*: Meunier & Vauclair, 2007]. In both studies, capuchins used the index finger or D2 predominantly. Unlike spider monkeys, capuchins have been characterized as highly dexterous. In studies of Old World monkeys and chimpanzees that have reported digit use, D2 was also the preferred digit [Table I; Hopkins, 1995; Llorente et al., 2009, 2011]. By comparison, D2 was preferred in 7 of the 9 spider monkeys in this study (all right-handers and two-thirds of left-handers). Interestingly, 2 left-handed monkeys preferred D3. To the best of our knowledge, no other study has reported individual preferences for D3, rather than D2. However, the majority of TUBE studies have not reported digit use. A future goal is to characterize grasp morphology in spider monkeys similar to the detailed studies performed in other nonhuman primate species [cf., Byrne et al., 2001; Christel,

1993, 1994; Costello & Frigaszy, 1988; Marzke & Wullstein, 1996; Macfarlane & Graziano, 2009; Pouydebat et al., 2011; Spinozzi et al., 2004]. Interestingly, cortical representation is the largest for D2 in humans [Sutherling et al., 1992], but approximately equal for digits 2–5 in *Ateles* [Pubols & Pubols, 1971]. Examining how the fingers are used independently and in combination at a micro level across a battery of tasks might help to explain our findings on the predominate use of D2 as well as D3 in spider monkeys.

Although the specific single digit used varied (D2 or D3), digit preference was not associated with hand preference direction. Additionally, the change in tube diameter size did not impact hand preference direction as we predicted, which is consistent with prior studies that have compared performance on variations of the TUBE task within the same sample [Canteloup et al., 2013; Maille et al., 2013]. No spider monkey changed from left to right hand preference or vice versa across the two versions of the TUBE task (i.e., large and small diameter). In fact, we observed remarkable consistency between the Nelson et al. [2015] study and the current study. Six monkeys showed virtually no change in HI score. The other 3 monkeys substantially increased in handedness expression from a moderate left preference to a very strong left preference. Given the sample size, we are cautious in our interpretation on the significance of the variability in left-handed monkeys as opposed to right-handed monkeys, who were stable in hand preference strength across the two TUBE tasks. Interestingly, the 3 monkeys affected by tube diameter that exhibited stronger asymmetries in the small diameter task compared to the large diameter task were also monkeys that shifted their pattern of hand use on a unimanual grasping task [Nelson et al., 2015]. Replication in other *Ateles* samples is needed to determine whether there are subgroups in this genus of highly lateralized, task-independent individuals and more variable, task-dependent individuals, and the implications of these different patterns of laterality on other cognitive domains [e.g., Prichard et al., 2013]. For example, tool use and motor planning both require sophisticated hand use where certain laterality patterns may have distinct advantages or disadvantages. Investigating these questions further in an effort to understand the evolution and function of motor lateralization in spider monkeys and other primates remains a goal of future work.

Although the monkeys in our study group were consistent in hand preference direction across administrations of the TUBE task, our findings differed from the only other prior report of hand preference in spider monkeys, *Ateles geoffroyi* [Laska, 1996]. Whether *Ateles fusciceps rufiventris* (this study) is a subspecies of *Ateles geoffroyi* or a separate species is debatable (for discussion, see

Rylands et al., 2006]. Nevertheless, Laska [1996] reported a population-level left hand bias in *A. geoffroyi* on a series of unimanual tasks in a larger sample of 13 monkeys. Although we did not find a bias at the population-level in this study, there was a trend towards the left hand. Larger sample sizes are needed in *A. f. rufiventris* to determine whether the lack of group bias on the TUBE task was simply due to sample size. There is also a need to administer the TUBE task to *A. geoffroyi* for comparison. In both the current study and Laska [1996], there was no effect of sex on hand use, although we caution again that a larger sample is needed. Finally, administering the TUBE task to *Colobus* would also be highly germane, given their similar hand structure to *Ateles*. We are unaware of any studies that have investigated bimanual coordination or precise digit use in *Colobus* (but see Wells 2002 on simple reaching in black and white colobus monkeys, *Colobus guereza*).

In addition to their unique hand structure, spider monkeys also have a powerful prehensile tail. We did not observe any monkeys using the tail to stabilize the tube rather than a hand. However, just over half of the responses made on the TUBE task occurred while monkeys were hanging supported by the tail. There was no relationship between posture and sex, use of a single digit, hand preference direction, or hand preference strength. These findings confirm prior reports that posture does not appear to influence hand use on the TUBE task [e.g., Hopkins, 1995; Maille et al., 2013; Spinozzi et al., 1998]. Posture is an important variable to consider when measuring hand use because it has been implicated in the prevailing evolutionary framework for primate handedness. MacNeilage et al. [1987] introduced what became known as the postural origins theory, which implicated ecological factors including posture and feeding strategies in the origins of handedness. In this account, a division of labor was proposed between the hands for the earliest primates. The right hand was used for postural support, while the left hand became specialized for ballistic smash-and-grab reaching. As primates shifted to terrestrial living, the right hand was freed from its role in posture and became specialized for skilled hand movements. The postural origins theory continues to be a guiding framework for many researchers in the field [MacNeilage, 2007]. Recently, Meguerditchian et al. [2012] implicated the postural origins theory in an evaluation of nonhuman primate performance on the TUBE task. Studies support a general pattern of left hand bias in arboreal species and right hand bias in terrestrial species. Data from this study and Nelson et al. [2015] add some support for this pattern, given the trend for left hand preference observed in spider monkeys on both versions of the TUBE task.

Alternatively, hand use has been characterized by task type rather than species ecology. Fagot and

Vauclair [1991] suggested dividing tasks into the categories of “low-level” and “high-level” manual actions. Low-level tasks include familiar actions such as reaching and foraging, whereas high-level tasks are novel or otherwise challenging. The TUBE task is an example of a high-level task according to Lilak and Phillips [2008] using the Fagot and Vauclair [1991] task complexity framework. Marchant and McGrew [2013] described levels of manual behavioral laterality that are also based on task performance, in addition to subject performance. In this schema, a pattern of hand use that is consistent within a task and within a subject is referred to as hand preference. A pattern that is within a task but across individuals is known as task specialization. A pattern that is within a subject across multiple tasks is manual specialization, while the term “handedness” is used only to refer to a consistent pattern of hand use across subjects and across tasks. Future work should evaluate hand use on multiple tasks that can be considered high-level to further evaluate these frameworks for *Ateles* as well as other primates.

In addition to behavioral studies, advances in neuroimaging have identified links between brain structure and hand preferences measured by the TUBE task in capuchin monkeys and chimpanzees [e.g., Dadda et al., 2006; Hopkins & Cantalupo, 2004; Li et al., 2010; Phillips & Hopkins, 2007; Phillips & Sherwood, 2005]. Recent work in *A. Geoffroyi* using diffusion-tensor imaging found that the structural fibers of the corpus callosum were similar to that of chimpanzees and humans, but differed from that of rhesus monkeys, *Macaca mulatta* [Platas-Neri et al., 2015]. To date, there have been no neuroimaging studies that have examined relationships between brain and behavior asymmetries in *Ateles*. Administering robust measures like the TUBE task in conjunction with neuroimaging methods will advance our understanding of the evolution of motor lateralization in primates, and the evolution of handedness. This type of dynamic approach is needed to supplement theoretical frameworks such as the postural origins theory. We encourage investigators who use the TUBE task to carefully consider the diameter of the tube used for testing, and to report digit use, particularly in species for which there are no information available, as well as to utilize neuroimaging measures whenever possible. In addition, we recommend researchers that currently do not or cannot use the TUBE task to try to incorporate the key features from the task into their own species appropriate measures: bimanual coordination and precise digit use.

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