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RESEARCH ARTICLE

Consistency of Hand Preference Across Low-level and High-level Tasks in Capuchin Monkeys (*Cebus apella*)

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Numerous studies investigating behavioral lateralization in capuchins have been published. Although some research groups have reported a population-level hand preference, other researchers have argued that capuchins do not show hand preference at the population level. As task complexity influences the expression of handedness in other primate species, the purpose of this study was to collect hand preference data across a variety of high- and low-level tasks to evaluate how task complexity influences the expression of hand preference in capuchins. We tested eleven captive brown capuchin monkeys (*Cebus apella*) to determine if they show consistent hand preferences across multiple high- and low-level tasks. Capuchins were expected to display high intertask consistency across the high-level tasks but not the low-level tasks. Although most individuals showed significant hand preferences for each task, only two of the high-level tasks that involved similar hand motions were significantly positively correlated, indicating consistency of hand preference across these tasks only. None of the tasks elicited a group-level hand preference. High-level tasks elicited a greater strength of hand preference than did low-level tasks. No sex differences were found for the direction or strength of hand preference for any task. These results contribute to the growing database of primate laterality and provide additional evidence that capuchins do not display group-level hand preferences. Am. J. Primatol. 70:254–260, 2008.

Key words: capuchin; handedness; complex tasks; laterality; *Cebus*

INTRODUCTION

Nearly 90% of humans are right handed [Annett, 1985; Porac & Coren, 1981], and this is associated with a left hemispheric lateralization for manual control and language. Whether nonhuman primates show such behavioral lateralization has been a subject of much empirical and theoretical debate. There is increasing evidence that captive and wild chimpanzees are similar to humans in expressing a tendency toward population-level right handedness [Hopkins et al., 2003, 2004; Lonsdorf & Hopkins, 2005], albeit to a lesser degree. Baboons display a population-level right-hand preference for a coordinated bimanual task but not a unimanual task [Vauclair et al., 2005]. Westergaard and Suomi [1996] report a population-level right-hand bias in adult macaques but then report a population-level left-hand preference for a sample of nursery-reared infant macaques [Westergaard et al., 1997]. In New World monkeys, squirrel monkeys and cotton-top tamarins do not show population-level hand preferences for simple reaching while in either a quadrapedal or clinging posture [Roney & King, 1993]. In capuchin monkeys some research groups have reported population-level hand preferences for coordinated bimanual tasks [Spinozzi et al., 1998] and others have not [Fragaszy et al., 2004; Westergaard & Suomi, 1996].

MacNeilage et al. [1987] proposed a theoretical model for the development of hand preferences in nonhuman primates for that the right hand was used for postural support, whereas the left hand became specialized for visually guided responses. As nonhuman primates became more terrestrial with less need for a support hand, the right hand became free to use for bimanual activities that required fine precision movements. Thus, this theory proposes that nonhuman primates should exhibit a population-level right-hand preference for tasks that require bimanual actions and a left-hand preference for more simple, unimanual tasks. Laska [1996] found that both posture and whether a task is visually or tactually

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guided, does affect hand preference in squirrel monkeys, thus supporting this theory. However, other studies mostly refute this theory [McGrew & Marchant, 1997; Papademetriou et al., 2005].

Another theory to explain the development of hand preferences in nonhuman primates is the ‘‘task-complexity’’ theory [Fagot & Vauclair, 1991], which proposes that population-level hand preferences should only appear for high-level, or complex, tasks (e.g., bimanual, precise, or sequential actions). Studies across several primate taxa provide support for the notion that more complex tasks elicit a greater strength of hand preference than do low-level tasks such as reaching [*Cebus*: Anderson et al., 1996; Spinozzi et al., 1998; *Cercocebus*: Blois-Heulin et al., 2006; *Pan*: Hopkins & Rabinowitz, 1997; *Papio*: Vauclair et al., 2005; and for a review, see Fagot & Vauclair, 1991]. However, individuals do not always produce consistent hand biases across multiple high-level tasks [Anderson et al., 1996; Colell et al., 1995a; Spinozzi & Truppa, 1999].

Although it is still a matter of debate as to whether capuchins show population-level hand preferences, individual capuchins do display strong and significant preferences for a given hand in specific tasks, particularly in those tasks requiring bimanual coordination [Fragaszy & Mitchell, 1990; Limongelli et al., 1994; Westergaard & Suomi, 1993, 1996]. The TUBE task [Hopkins, 1995] is one of complex bimanual coordination that has been tested in several primate species, including capuchins. This task has been proposed as an ideal measure of hand preference in nonhuman primates, as it is the only task thus far that correlates with neuroanatomical structures associated with cortical motor areas representing hand [Hopkins & Cantalupo, 2004; Phillips & Sherwood, 2005]. The purpose of this study was to collect hand preference data across a variety of high- and low-level tasks to evaluate how task complexity influences the expression of hand preference in capuchins. Capuchins were hypothesized to show a high degree of consistency of hand preference across high-level tasks but not across low-level tasks.

METHOD

Subjects

Eleven brown capuchin monkeys (*Cebus apella*), four females and seven males, were used in this study. Of these 11 capuchins, nine were housed at the Laboratory of Neurobehavioral Investigations at Hiram College (Hiram, OH) and two were housed at Northeastern Ohio Universities College of Medicine (Rootstown, OH). Subjects ranged in age from 3 to 22 years ($M = 9.05$, $SD = 7.16$). Subjects were socially or pair housed in large indoor enclosures enriched with perches, swings, and fresh browse. All subjects were born in captivity and had been socially housed since birth. Data for this study were collected from winter 2005 through summer 2006. This research was approved by the Institutional Animal Care and Use Committee at Hiram College and abided by all applicable US Federal laws governing research with nonhuman primates.

Procedure

Hand preference was measured using six tasks, two low-level and four high-level. Low-level tasks are those that are familiar or do not require fine precision movements [Fagot & Vauclair, 1991] and included simple reaching and an invertebrate foraging activity. High-level tasks imply the need for finely tuned motor actions [Fagot & Vauclair, 1991] and included a coordinated bimanual task known as the TUBE task [Hopkins, 1995], a tool-use task, BOX task [Blois-Heulin et al., 2006; Trouillard & Blois-Heulin, 2005], and a finger log task. Each subject only received one task per day, and there was a minimum of 1 day between task repetitions. A brief description of each task is provided below.

Simple reaching (REACH)

A raisin was tossed to a spot in front of the subject at a distance that required movement of all four limbs to reach. The hand used to retrieve the raisin was recorded as left or right. Each raisin was tossed to a location that required the subject to assume a new position between trials. Each subject completed 50 simple reaching tosses in their home enclosure.

Invertebrate foraging (INVERT)

For this task a piece of commercial astro-turf ($63.5 \times 50.8 \times 50.8$ cm) was placed along the bottom of an individual testing cage ($64 \times 60 \times 60$ cm). Five mealworms (*Tenebrio molitor*) were scattered on top of the astro-turf and covered with woodchips. The subject was then allowed to enter the cage and forage through the woodchips to find the mealworms. The hand used to pick up each of the five mealworms was recorded as left or right. Subjects were tested with this task four times.

Coordinated bimanual task (TUBE)

Each subject was presented with a 6-cm long 1.5-cm diameter piece of PVC pipe that had peanut butter smeared inside. To remove the food, subjects had to hold the tube in one hand and use the fingers of other hand to retrieve the peanut butter. The hand used to retrieve food from inside the tube was recorded as left or right. Every instance where an individual inserted their fingers into the tube, retrieved peanut butter and brought that hand to the mouth was recorded. Data were recorded until the subject lost interest in the tube as indicated by discarding the tube for at least 10 sec. Each subject was tested four times. For this task subjects were tested in their home enclosures.

Tool-use task (TOOL)

A PVC tube, 28 cm in length and 2.5 cm in diameter, was drilled with three holes smaller than the subjects' fingers. Yogurt was placed inside the tube and a cap was secured on each end. To retrieve the yogurt, subjects had to insert straw into one of the holes. Hand use was recorded as left or right when an individual dipped straw into a hole and then brought the straw to the mouth. Each subject was tested four times, with each test session lasting a maximum of 15 min. Subjects were tested in their home enclosures. A session was terminated if the subject lost interest for more than 30 sec.

Box task (BOX)

A wooden box ($17.5 \times 13.5 \times 11$ cm) with a spring-loaded top was held up to the subject by the experimenter [Blois-Heulin et al., 2006; Trouillard & Blois-Heulin, 2005]. The subject was shown a grape and allowed to watch as the experimenter placed the grape into the box and closed the top. For a subject to retrieve the grape, the box top had to be held open with one hand while the second hand was inserted into the box to grab the food. The hand used to retrieve the grape was recorded as left or right. Each subject completed five sessions, with each session consisting of ten separate trials. Testing occurred in the home cage.

Finger log (FINGER)

A solid plastic cylinder (12.7×3.8 cm; Lomir Biomedical, Inc., Malone, NY) had peanut butter inserted into each of six 1-cm curved holes. To retrieve the peanut butter, a subject held the cylinder with one hand and inserted a finger from the other hand into a hole. This task differs from the TUBE task in that it required the subject to use a finger instead of the entire hand. The finger used to retrieve the peanut butter was recorded as right or left, depending upon which hand was used. Each subject was tested four times, with each test session lasting a maximum of 15 min. Subjects were tested individually. A session was terminated if the subject lost interest for more than 30 sec.

For the REACH, INVERT and FINGER tasks, subjects typically were in a quadrapedal position. After subjects took the TUBE from the experimenter they extracted the peanut butter while in a crouched position. Subjects were usually in an upright position while solving the BOX or TOOL task. In all trials across all tasks, subjects were not constrained for hand use.

Data Analysis

The recording of individual hand events has been questioned by some [McGrew & Marchant, 1997], with the objection that these repeated events are not independent of one another. However, Hopkins and colleagues [Damerose & Hopkins, 2002; Hopkins, 1999; Hopkins et al., 2001] have demonstrated there is no empirical support for this position. Therefore, for the TUBE and FINGER tasks we recorded the frequency of individual motor events as opposed to bouts of responses.

Two composite scores, using techniques and terminology devised by Hopkins and Pearson [2000], were calculated to determine if subjects exhibited significant hand preferences. The first measure used to determine hand preferences for each subject was based on z-scores that were calculated for individuals in each task. On the basis of the z-scores, each subject was assigned a -1 for left-hand preference ($z \leq -1.96$), a $+1$ for right hand preference ($z \geq 1.96$), or a 0 for no hand preference ($-1.96 > z < 1.96$) for each task. The assigned numbers of -1, 0, and $+1$ per task were then averaged across all tasks for each individual subject to calculate an overall handedness scores between -1 and 1 (HISUM1). Negative HISUM1 values indicated an overall left-hand preference and positive values indicated an overall right-hand preference. HISUM1 scores were also calculated for each subject across bimanual tasks only (HISUM1b).

Handedness index (HI) scores were determined for each subject in each task by using the hand preference formula (R−L)/(R+L). For each task, excluding simple reaching, the mean handedness index (MHI) was calculated by taking the average HI of all trials for individuals. A second overall hand composite score, HISUM2, was calculated for each individual by averaging the MHIs across all tasks. HISUM2 scores ranged from –1 to 1. Mean handedness indices were also averaged across bimanual tasks only for each subject (HISUM2b).

RESULTS

Descriptive Statistics

Individual MHI scores for each task and corresponding z-scores are shown in Table I. Not all subjects participated in each task: four subjects never performed the TOOL task and six subjects would not complete the INVERT task. These subjects were excluded from these tasks only because they could not perform them (as with the TOOL task) or would not perform them (as with the INVERT task). Of the seven subjects who completed the TOOL task, five displayed a significant left-hand preference, one displayed a significant right-hand preference, and one had no significant hand preference. All subjects completed the TUBE task. Five

TABLE I. Mean Handedness Indices and *z*-Scores for Each Subject in Four High-level and Two Low-level Tasks

			Task												
			High-level								Low-level				
			TOOL		TUBE		FINGER		BOX		REACH		INVERT		
Subject	Sex	Age	MHI	*z*-score	MHI	*z*-score	MHI	*z*-score	MHI	*z*-score	HI	*z*-score	MHI	*z*-score	L/R/NL
Alou	M	3	−0.66	−13.57*	0.81	7.40*	0.76	14.57*	−0.92	−6.50*	0.18	1.29	—	—	2/2/1
Carlos	M	6	−0.52	−4.10*	−0.95	−8.61*	−0.71	−7.24*	−0.84	−5.93*	0.25	1.79	0.44	2.20*	4/1/1
DiMaggio	M	2	−0.90	−7.32*	0.39	10.44*	0.54	3.67*	−1.00	−7.06*	−0.12	−0.83	—	—	1/3/0
Miro	M	13	—	—	1.00	7.02*	0.67	10.87*	−1.00	−7.06*	0.02	0.14	—	—	2/2/1
Shoeless	M	3	—	—	−0.14	−0.68	−0.63	−4.43*	0.68	5.22*	−0.61	−4.34*	−0.68	−3.40*	3/0/3
Sosa	M	4	−0.97	−12.26*	−0.62	−8.64*	−0.97	−20.92*	−0.68	−4.80*	0.20	0.28	—	—	1/2/2
Vincent	M	19	—	—	−1.00	−14.59*	−1.00	−20.94*	−0.56	−4.66*	−0.84	−6.52*	−1.00	−5.00*	1/2/1
DC	F	21	—	—	0.96	5.39*	0.91	7.92*	0.84	5.93*	−0.56	−3.95*	—	—	4/0/2
Georgia	F	7	−0.26	−1.70	−0.75	−9.41*	−0.58	−10.60*	−0.56	−3.95*	0.24	1.69	−0.15	−0.60	3/1/1
LC	F	16	0.64	7.73*	0.85	7.14*	0.28	1.92	−0.64	−4.52*	−0.08	−0.56	—	—	4/0/1
Noel	F	15	−0.78	−13.64*	−0.82	−2.00*	−0.31	−5.97*	0.20	1.41	0.03	0.25	−0.68	−3.40*	5/0/0
L/R/NL				5/1/1		5/5/1		6/4/1		8/2/1		3/0/8		3/1/1	30/13/13

Positive numbers indicate a right-hand preference and negative numbers indicate a left-hand preference.
L, number left-handed; R, number right-handed; NL, number non-lateralized; MHI, mean handedness index; M, male; F, female.
*Significant hand preferences.

TABLE II. Intercorrelations in Hand Preference Across Tasks

Measure	TOOL	TUBE	FINGER	BOX	REACH	INVERT
TOOL	—	.39	.18	−.01	−.25	.47
TUBE	—	—	.92*	−.01	−.05	−.21
FINGER	—	—	—	−.02	.05	.14
BOX	—	—	—	—	−.56	−.54
REACH	—	—	—	—	—	.81
INVERT	—	—	—	—	—	—

*$P < .05$.

displayed a significant left-hand preference, five a right-hand preference, and one had no significant hand preference on this task. On the FINGER task, six had a left-hand preference, four a right-hand preference, and one had no preference. On the BOX task, eight had a significant left-hand preference, two a right-hand preference, and one had no preference. Most subjects did not display a significant hand preference for the REACH task. Of the five subjects to complete the INVERT task, three displayed a left-hand preference and one a right-hand preference.

Intertask Correlations

Intertask correlations for MHI values indicated a strongly positive significant correlation between two high-level tasks, TUBE and FINGER, $r(11) = 0.92$, $P < .001$. The two low-level tasks, INVERT and REACH, were also correlated positively, though this correlation was not significant, $r(5) = .81$, $P = .10$. None of the other tasks were significantly correlated (see Table II).

TABLE III. HISUM Composite Scores for All Subjects (See Text for Calculations of These Composite Measures)

Subject	HISUM1	HISUM2	HISUM1b	HISUM2b
Alou	0.00	0.03	0.00	−0.003
Carlos	−0.50	−0.39	−1.00	−0.76
DiMaggio	0.00	−0.22	0.00	−0.24
Miro	0.25	0.17	0.33	0.23
Shoeless	−0.40	−0.28	0.00	−0.03
Sosa	−0.80	−0.61	−1.00	−0.74
Vincent	−1.00	−0.88	−1.00	−0.85
DC	0.50	0.54	1.00	0.90
Georgia	−0.50	−0.34	−0.75	−0.54
LC	0.20	0.21	0.25	0.28
Noel	−0.67	−0.39	−0.75	−0.43

HISUM scores are based on both low- and high-level tasks, whereas HISUMb scores are based only on high-level tasks. Negative values indicate an overall left-hand preference and positive values indicate an overall right-hand preference.

HISUM1 and HISUM2

HISUM composite scores for all subjects are shown in Table III. The mean HISUM1 score was −.27 (±.48) and the mean HISUM1b score was −.27 (±.67). A one-sample *t*-test indicated that there was not a significant group-level hand preference for HISUM1, $t(10) = -1.83$, $P > .05$. When low-level tasks were excluded from the analysis, there was not a significant group-level hand preference (HISUM1b, $t(10) = -1.31$, $P > .05$). The mean HISUM1 score for males was −.35 (±.46) and for females was −.12 (±.56). The mean HISUM1b score for males was −.38 (±.59) and for females was −.06 (±.85). To determine whether males and females differed in hand preferences, independent samples *t*-tests were performed on HISUM1 composite scores and then for high-level tasks (HISUM1b) only. No significant effect of sex on hand preference was found for either measure (HISUM1: $t(9) = -.75$, $P > .05$; HISUM1b: $t(9) = -.74$, $P > .05$).

The mean HISUM2 score for the group was −.20 (±.40). A one-sample *t*-test indicated there was not a significant group-level hand preference for HISUM2, $t(10) = -1.61$, $P > .05$. The mean HISUM2b score was −.20 (±.54). When low-level tasks were excluded from the analysis, no significant group-level preference was found (HISUM2b, $t(10) = -1.22$, $P > .05$). Male and female composite scores were analyzed using independent samples *t*-tests for all tasks (HISUM2; male $M = -.31 \pm .36$; female $M = .005 \pm .45$) and then for high-level tasks only (HISUM2b; male $M = -.34 \pm .44$; female $M = .05 \pm .67$). Male and female hand preference measures did not differ significantly (HISUM2: $t(9) = -1.29$, $P > .05$; HISUM2b: $t(9) = -1.20$, $P > .05$).

Degree of Hand Preference

The magnitude of hand preference was determined by calculating the absolute MHI (ABS-MHI) for each subject on each task. The mean magnitude of hand preference for the combined low-level tasks and combined high-level tasks was then determined for each subject. The mean ABS-MHI for the low-level tasks was 0.33 (±.28) and for the high-level tasks was 0.72 (±.15). The magnitude of hand preference for the combined high-level tasks was greater than that for the combined low-level tasks (paired *t*-test, $t(10) = 4.11$, $P < .05$; see Fig. 1). Thus, high-level tasks elicited a stronger hand preference than did low-level tasks.

Finally, whether males and females differed in the magnitude of hand preference was determined for each task separately as well as the combined high-level and low-level tasks. The magnitude of hand preference was determined for each sex by calculating the ABS-MHI for each subject for each task, and then calculating the mean for each sex. These summary values are shown in Table IV. There were no sex differences in the magnitude of hand preference for any of these tasks (independent samples *t*-test, TUBE $t(9) = -.83$, $P > .05$; TOOL $t(5) = 1.13$, $P > .05$; FINGER $t(9) = 1.70$, $P > .05$; BOX $t(9) = 1.91$, $P > .05$; REACH $t(9) = .52$, $P > .05$; INVERT $t(3) = 1.01$, $P > .05$; high-level tasks $t(9) = 1.19$, $P > .05$; low-level tasks $t(9) = .27$, $P > .05$).

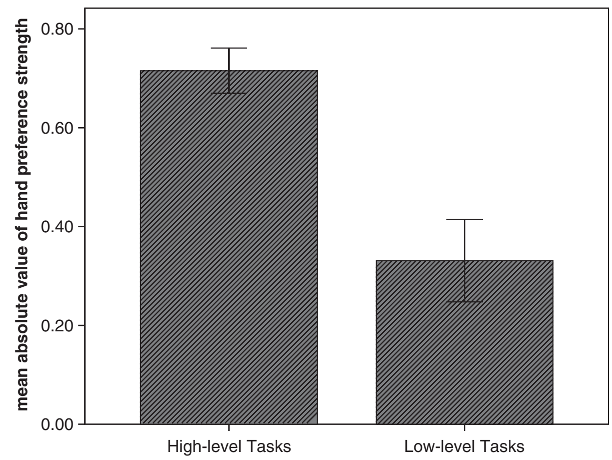

Fig. 1. Mean (±SE) hand preference strength for combined high-level and combined low-level tasks.

TABLE IV. Mean (±SD) Magnitude of Hand Preference (ABS-MHI) for Males and Females for Each Task and the Combined High-and Low-Level Tasks

Task	Sex	Mean ABS-MHI	SD
Tube	M	.70	.33
	F	.85	.09
Tool	M	.76	.21
	F	.56	.27
Finger	M	.75	.17
	F	.52	.29
Box	M	.81	.17
	F	.56	.27
Reach	M	.32	.30
	F	.23	.24
Invert	M	.71	.28
	F	.42	.37
High-level	M	.76	.13
	F	.65	.17
Low-level	M	.35	.32
	F	.30	.21

ABS-MHI, absolute mean handedness index.

DISCUSSION

Several important findings emerge from this study and warrant further discussion. First, individual capuchins displayed consistent hand preferences within tasks, but this group did not display a population-level handedness for any of the tasks, low-level or high-level. Second, capuchins displayed consistency of hand preference across tasks requiring similar motor actions, which include two of the high-level tasks. Finally, high-level tasks elicited greater hand preference strength than did low-level tasks.

The fact that capuchins did not display intertask consistency across all tasks and that no task elicited a population-level hand preference indicates that they show hand specialization and not task specialization or true handedness, according to McGrew and Marchant [1997] model of laterality. This model states that consistency of hand use across tasks, both within and between subjects, indicates the degree of behavioral lateralization. Hand specialization occurs when individuals present hand bias across a range of tasks. Task specialization is indicated when a group or population shows consistency of hand use for a given task, and true handedness is indicated when individuals show consistency of hand use across multiple tasks. Although the sample size tested in this study was small, other studies on capuchins with equivalent sample sizes have yielded similar results [e.g., Anderson et al., 1996]. However, research groups have reached different conclusions with respect to a coordinated bimanual task, the TUBE task, and whether it elicits population-level hand preferences among capuchins. Spinozzi et al. [1998] reported a group-wide right-hand preference for this task in a group of 26 subjects, whereas Westergaard and Suomi [1996] reported no group-wide hand preference for this task in their group of 45 capuchins. The results of this study support the conclusions of Westergaard and Suomi [1996]. This discrepancy may perhaps be explained by differences in postural demands of the task-tested [Colell et al., 1995b; Olson et al., 1990]. Spinozzi et al. [1998] hand preferences under two postural conditions for the tube task: crouched and upright. In the upright condition the tube was hung, requiring subjects to be in an upright position, holding the tube still with one hand and using the other hand to retrieve the peanut butter. In this study and Westergaard and Suomi's [1996] study, the tube was handed to the subjects, and the subjects typically were crouched while extracting the peanut butter. Spinozzi et al.'s [1998] upright condition thus had a multidimensional component and was therefore more complex, perhaps leading to a greater expression of hand preference.

Of the six tasks presented, capuchins displayed consistent hand preferences across both low-level tasks (though not significant), INVERT and REACH, and two of the high-level tasks, FINGER and TUBE. These consistencies are likely because of similar motion required to extract the food. In the FINGER and TUBE tasks, subjects had to use either a finger or the entire hand to extract the food item while holding the apparatus in the other hand. In both cases a similar wrist motion along with a slight twisting motion was used to insert the finger or hand into the apparatus and then bring the hand to the mouth. In the INVERT and REACH tasks, there was also a similar motor action required to retrieve the food. In both tasks subjects extended an arm to retrieve food from a substrate. The tasks are only different in that the subject had to find the mealworm among woodchips in the INVERT task, whereas the raisin was tossed in front of the subject in the REACH task. Hopkins and Pearson [2000] reported similar results in a study of hand preference consistency across multiple tasks in chimpanzees, with correlated tasks requiring similar motor actions.

Capuchins displayed a greater magnitude of hand preference on the complex high-level tasks than the low-level tasks, and all of the high-level tasks elicited similar hand preference strengths. These results are in agreement with other studies on primates showing how task complexity influences manual laterality [Chapelain et al., 2006; Fagot & Vauclair, 1988]. We suggest that this reflects the importance of complex manipulative skills used by capuchins in feeding. In the only extensive field study of capuchin hand preference, white-faced capuchins (*Cebus capucinus*) showed variability in hand preference across feeding tasks both at the individual and population level. Of a variety of feeding behaviors observed, object–substrate use (pounding or rubbing a detached object against a substrate), led to the strongest expression of individual hand preferences [Panger, 1998]. Capuchins are an important species for understanding the interplay of sensorimotor processes underlying the production and use of complex skills and the emergence of handedness.

Our results are noteworthy in that, combined with other published research on laterality in capuchins, they indicate that capuchins do not show population-level hand preferences. However, individuals do display strong hand preferences in specific tasks, and hand preference for tasks requiring similar motor actions is consistent. Future research targeting neuroanatomical correlates of hand use is likely to advance our understanding of associated neurobiological mechanisms. Recent advances in noninvasive neuroimaging, particularly magnetic resonance imaging and functional magnetic resonance imaging, allow researchers to investigate anatomical and behavior asymmetries in the same individual. To date, only a few studies have investigated neural correlates associated with hand preference in nonhuman primates [*Pan*: Dadda et al., 2006; Hopkins & Cantalupo, 2004; *Saimiri*: Nudo et al., 1992; *Cebus*: Phillips & Hopkins, 2007; Phillips & Sherwood, 2005, 2007]. As capuchins display individual but not population-level handedness, they provide an important comparative model for these research efforts.

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