

BRIEF REPORT

Hand Preferences on Unimanual and Bimanual Tasks in White-Faced Capuchins (*Cebus capucinus*)

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This study examined hand preference in white-faced capuchins on a unimanual task and on a coordinated bimanual task. For the unimanual task, handedness was assessed by observing simple reaching for small grains. For the bimanual task, tubes lined with chocolate paste inside were presented to the capuchins. The hand and the finger(s) used to remove chocolate paste were recorded. Seven individuals out of eight in the reaching task and 12 out of 13 in the tube task exhibited a hand preference. Moreover, test–retest correlations showed stability in hand use across time for the coordinated bimanual task. We found no significant differences in strength of hand preference between sexes. Finally, as noted in other primate species, the capuchins were more lateralized in the bimanual task compared to the unimanual task. *Am. J. Primatol.* 69:1064–1069, 2007. © 2007 Wiley-Liss, Inc.

Key words: bimanual coordination; *Cebus capucinus*; laterality; New World monkeys; task complexity

INTRODUCTION

Right-handedness and left-hemisphere specialization for language function is one of the strongest manifestations of hemispheric specialization in humans [Annett, 1985]. Recent studies have demonstrated group-level handedness for specific tasks in several nonhuman primates [chimpanzees: Hopkins et al., 2003; olive baboons: Vauclair et al., 2005; rhesus macaques: Westergaard & Suomi, 1996; tufted capuchins: Spinozzi et al., 1998]. However, many findings on handedness are divergent or inconsistent. One difficulty with the interpretation of the available findings on handedness could be due to the lack of common testing procedure and measures of hand use between and within species, which prevents direct comparison of findings. Studies of handedness using the same methods and identical measures are therefore necessary for improving our

Contract grant sponsor: CNRS (OHLL Programme) and the EC Sixth Framework Programme; Contract grant number: ERAS-CT-2003-980409.

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Received 27 November 2006; revised 6 March 2007; revision accepted 7 March 2007

DOI 10.1002/ajp.20437

Published online 3 April 2007 in Wiley InterScience (www.interscience.wiley.com).

understanding of the evolution of handedness. Several authors have begun to test various species in the same experimental tasks: a task of simple reaching (unimanual task) and a coordinated bimanual task (tube task) [e.g., Hopkins, 1995; Hopkins et al., 2004; Phillips & Sherwood, 2005; Spinozzi et al., 1998; Vauclair et al., 2005; Westergaard & Suomi, 1996]. Continuing these efforts, we tested a New World monkey species, the white-faced capuchin monkey (*Cebus capucinus*). To date, only one capuchin species, the tufted capuchin (*Cebus apella*), has been tested on the tube task [Phillips & Sherwood, 2005; Westergaard & Suomi, 1996]. Even although most tufted capuchins tested exhibited hand preferences, no population-level bias was found on the tube task. Hand preferences in white-faced capuchins were studied by Panger [1998] via spontaneous tasks varying in manipulative complexity and postural constraints. One purpose of this study was to compare white-faced capuchins and tufted capuchins in the same tube task to determine if findings could be generalized across the genus *Cebus*. The second purpose was to evaluate the influence of unimanual and bimanual tasks on handedness in white-faced capuchins, two tasks referred to as low-level and high-level manual activities, respectively, by Fagot and Vauclair [1991]. The model proposed by these authors predicts that low-level tasks lead to (a) symmetrical distributions of hand biases for the group and (b) manual preferences that are not indicative of the specialization of the contralateral hemisphere. In contrast, behaviors expressed in high-level tasks (a) show asymmetrical distribution of hand biases for the group and (b) are related to a specialization of the contralateral hemisphere. In addition, Fagot and Vauclair [1991] predicted that the need for coordination between both hands should be a crucial factor influencing strength of laterality. We thus expect that capuchins will be more lateralized for the bimanual than the unimanual task.

METHODS

The subjects were 13 white-faced capuchins (*Cebus capucinus*) housed at the Primate Centre of the Louis Pasteur University, Strasbourg, France. The sample comprised ten adults (three males and seven females) and three immatures (two males and one female). All individuals were mother-raised and all except the oldest female were captive-born. The group was kept in a 1-acre outdoor enclosure with natural vegetation (see Meunier et al. [2006] for details on housing). All capuchins were tested in their social group. Observations were done in real time by H.M. from January 2004 to July 2005. Due to several capuchins' deaths between the experiments, the same number of individuals could not be tested for each task. Observation procedures adhered to the legal requirements of CNRS, France.

Hand preferences on the unimanual task were assessed by observing which hand was used when reaching for food, using a behavior-dependent sampling method [Altmann, 1974]. A response was recorded each time the subject was in a quadrupedal posture, grasped food in front of it in a sagittal median plane and moved between reaches. Small grains of chocolate puffed rice (Coco pops, Kellogg's[®]) were abundantly dispersed in the capuchins' park to minimize competition between subjects. A minimum of 100 responses was required for each subject. As unimanual reaching was usually performed very rapidly, it was not possible to record digit use in this task.

Hand preferences on the coordinated bimanual task were assessed using an opaque polyvinyl-chloride (PVC) tube [see Hopkins, 1995] containing chocolate paste. The tube was 1.5 cm in diameter and 15 cm in length. Four tubes were

given simultaneously to the capuchins to prevent disruptive competition among individuals. Capuchins removed the chocolate paste by holding the tube with one hand and inserting one or several fingers of the opposite hand into one of the two open ends of the tube. The hand and finger(s) used to remove the chocolate paste were recorded each time a capuchin inserted a finger into the tube and brought it to its mouth. Feeding attempts while using the feet to hold the tube were not considered as responses. A minimum of 50 responses were obtained from each subject. Seven capuchins tested on the bimanual task were re-tested 17 months later to assess stability in hand use on this task.

We used *z*-scores to classify capuchins as left-handed ($z \leq -1.96$), right-handed ($z \geq 1.96$) or ambiguously handed ($-1.96 < z < 1.96$). The handedness index (HI = number right responses minus number left responses/total responses), varying from -1.0 to 1.0 , was calculated to quantify the degree of individual lateral biases. Negative values indicate a left-hand bias, positive values indicate a right-hand bias. The absolute values (ABS-HI) reflected the strength of hand preference. Sex differences were tested with the Mann-Whitney *U*-test and the effect of task complexity on handedness with the sign test.

RESULTS

Eight capuchins were tested on the unimanual task. On the basis of individual *z*-scores, two capuchins were classified as right-handed, five left-handed and one as ambiguously handed (Fig. 1). The mean HI score for this task was -0.19 (SE = 0.12). A one-sample *t*-test revealed that overall HI scores do not differ significantly from a chance distribution with a mean of 0 ($t(7) = 1.58$, $P = 0.16$).

Thirteen capuchins were tested on the coordinated bimanual task. On the basis of individual *z*-scores, six subjects were classified as right-handed, six as left-handed and one as ambiguously handed (Fig. 1). The mean HI score for this task was -0.04 (SE = 0.21). A single sample *t*-test revealed that the HI scores do not differ significantly from a chance distribution with a mean of 0 ($t(12) = 0.19$, $P = 0.85$).

On average, 84.5% of the insertions into the tube were made with the index digit, 12.9% with two or three digits simultaneously (including the index digit), 2.2% with the thumb, and 0.4% with the middle finger.

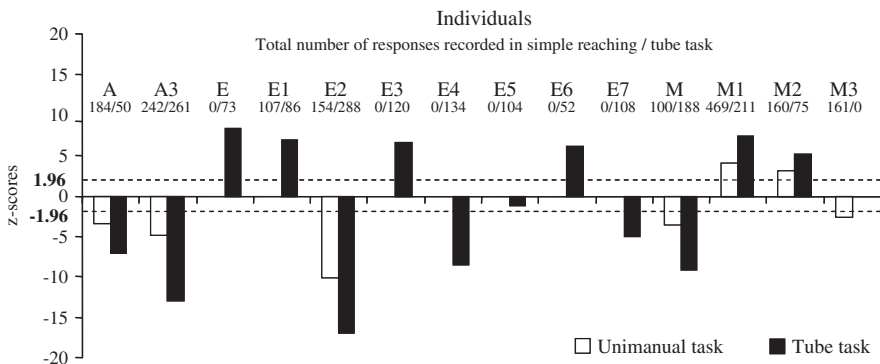


Fig. 1. Individual *z*-scores reflecting hand preference on the unimanual task (white squares) and on the tube task (black squares). The dotted lines indicate significant levels of handedness (left-handed: $z \leq -1.96$, ambiguously handed: $-1.96 < z < 1.96$ or right-handed: $z \geq 1.96$).

Stability in hand use between the two test sessions were assessed by calculating a Spearman correlation on the HI scores of the seven capuchins tested on the tube task in the two sessions. A significant positive correlation was found ($r = 0.941$, $P = 0.005$). This result indicates that hand preferences assessed with the tube task were stable across time in our sample of capuchins.

No difference was found for the tube task between sexes, either in direction of hand preference ($U = 9$; $N1 = 8$; $N2 = 5$; $P = 0.127$; the mean HI score per subject was -0.48 , $SE = 0.28$ for males and 0.24 , $SE = 0.26$ for females), or in the strength of hand preference ($U = 20$; $N1 = 8$; $N2 = 5$; $P = 1.00$; the mean ABS-HI score per subject was 0.72 , $SE = 0.09$ for males and 0.68 , $SE = 0.10$ for females).

The seven subjects tested on both the unimanual and bimanual tasks exhibited the same hand preference for the two tasks but were significantly more lateralized (sign-test: $P = 0.016$, negative ranks = 0; positive ranks = 7; ties = 0) for their hand use in the tube task (mean ABS-HI = 0.76) compared to the reaching task (mean ABS-HI = 0.31). The mean HI scores for the unimanual task (mean = -0.19 , $SE = 0.12$) were not significantly different from the mean HI scores for the bimanual task (mean = 0.17 , $SE = 0.21$) ($t(6) = 0.21$, $P = 0.84$).

DISCUSSION

This study is the first of its kind on white-faced capuchin monkeys. Our results show that seven out of eight capuchins tested on the unimanual task and 12 out of 13 capuchins tested on the bimanual task exhibited a manual preference and that this preference was stronger in the coordinated bimanual task than in the unimanual task. The capuchin monkeys most frequently used their index finger to extract the food from the tube. Sex did not affect the direction or strength of hand preference. Finally, hand preferences for the tube task were stable over time.

Seven of eight tested individuals presented a bias for one hand in the unimanual task. This proportion is unusually high compared to that reported for this task in other species [baboons: Vauclair et al., 2005; tufted capuchins: Frigaszy & Mitchell, 1990; Spinozzi et al., 1998; vervet monkeys: Harrison & Byrne, 2000]. This could be explained by the relative complexity of our unimanual task, in which the grains to reach for and pick up were very small and light, requiring precision grasping. The level of precision of motor acts, and visual guidance [Fagot & Vauclair, 1991] are two determinants of task complexity. The relative complexity of our reaching task could thus explain the high proportion of lateralized individuals. This view is supported by the HI score we obtained for the unimanual task, which is higher than that reported in tufted capuchins by Spinozzi et al. [1998].

Even though the tube task did not reveal a group bias for one hand, all except one of the 13 subjects tested on this task were lateralized. In addition, hand preferences were stable over time. These results are in agreement with previous findings on the same task in tufted capuchins [Westergaard & Suomi, 1996]. We noted increased hand preference strength in white-faced capuchins for the coordinated task, similar to what has been described in tufted capuchins [Westergaard & Suomi, 1996], *Cebus olivaceus* in a bipedal reaching task [Westergaard et al., 1999], and which is higher than that found in rhesus macaques [Westergaard & Suomi, 1996] and baboons [Vauclair et al., 2005]. This result could reflect a greater degree of specialization in *Cebus* for complex manipulation during feeding. Indeed, capuchins are well known for the prevalence of their manual activities, especially their destructive tendency with objects that they manipulate [Frigaszy et al., 2004].

The finding that white-faced capuchins predominantly used their index fingers to remove the food from the tubes matches findings on digit use in chimpanzees [Hopkins, 1995], macaques, capuchins [Westergaard & Suomi, 1996], and baboons [Vauclair et al., 2005]. According to Hopkins [1995], distal movements of the fingers, such as those needed for extracting food from a tube, require greater use of the contralateral hemisphere [Brinkman & Kuypers, 1972] than do gross or ballistic limb movements, such as those involved in simple reaching [Fagot & Vauclair, 1991].

In conclusion, although the size of our sample does not allow us to make strong generalizations about hand preferences in white-faced capuchins, the capuchins we studied appeared lateralized in unimanual and bimanual tasks. Hand preference strength is clearly greater in a coordinated bimanual task than in a unimanual task, which confirms that task complexity could be a crucial factor in the emergence of laterality. Moreover, the tube task offers a reliable procedure for assessing handedness in nonhuman primates due to the stable data it provides. Future research on primate handedness could benefit substantially by focusing on complex tasks requiring bimanual coordination rather than simple, low-level tasks of the kind that have dominated earlier studies.

ACKNOWLEDGMENTS

This work, as part of the European Science Foundation EUROCORES Programme OMLL, was supported by funds from the CNRS (OHLL Programme) and the EC Sixth Framework Programme under Contract no. ERAS-CT-2003-980409. We thank C. Reinhart for language advice. We also thank James R. Anderson and the two anonymous reviewers for insightful comments on the manuscript. Observations were made in accordance with the CNRS guidelines regarding animal care.

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