Hand Preferences in Unimanual and Coordinated-Bimanual Tasks by Tufted Capuchin Monkeys (Cebus apella)

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Hand preferences in 26 capuchin monkeys (Cebus apella) were examined in 2 reaching-for-food tasks under 2 postural conditions. In the 1st task (unimanual), monkeys were required to reach for food from both a quadrupedal and an upright posture. A right-hand bias was found for the upright but not for the quadrupedal condition. In the 2nd task (coordinated bimanual), monkeys were required to extract the food from a hanging Plexiglas tube from both a crouched and an upright posture. A right-hand bias was found for both conditions. A significant increase in right-hand use was noted from the unimanual, quadrupedal, reaching task to the coordinated-bimanual task, with females exhibiting a greater right-hand preference than males. In addition, a significant effect of task complexity on strength in laterality was found. Results are discussed in the context of recent theories on primate laterality.

Laterality of manual functions is considered the most conspicuous manifestation of cerebral asymmetries in the human species (Kimura, 1979). Approximately 90% of the human population uses the right hand for most tasks requiring a single hand. Moreover, the right hand assumes a leading role in most activities involving the complementary use of both hands (Annett, 1985; Corballis, 1991; Steenhuis & Bryden, 1989). Such right-handedness is associated with left hemispheric specialization for the organization of manual functions.

Originally, researchers generally argued that population-level laterality in hand use was a uniquely human characteristic. Researchers considered nonhuman primate manual asymmetries to be qualitatively different from the typical human pattern and independent of any asymmetry of cerebral activity (Warren, 1980). In fact, early systematic research with monkeys and apes failed to produce evidence of preferential bias at a population level, even though some individuals in the group were strongly lateralized. Moreover, hand preferences were found to be strongly influenced by certain environmental factors, such as the position of a food reward with respect to the subject, and to be strongly dependent on the task and on practice (Lehman, 1980; Warren, 1980).

MacNeilage, Studdert-Kennedy, and Lindblom (1987) reviewed the published evidence on handedness in nonhuman primates and subsequently claimed that the inconclusive results for hand asymmetries could be explained by researchers’ use of animals that were too young to express stable preferences and by their use of tasks that were too simple to reveal manual laterality. MacNeilage et al. produced evidence that tasks involving single acts of visually guided prehension induce a greater left-hand usage at a population level, whereas tasks requiring a sequence of manipulative acts on an object elicit a stronger right-hand preference. These authors argued that left-hand specialization for visually guided reaching evolved in prosimians and was accompanied by right-hand specialization for postural support. This left-hand superiority remains in monkeys. However, with the emergence of extensive manipulative abilities and the development of the opposable thumb in higher primates, the postural specialization evolved into a right-hand preference for activities requiring fine, sequential manipulations and bimanual coordination (MacNeilage, Studdert-Kennedy, & Lindblom, 1987, 1991).

Recent findings have revealed population-level hand preference for different manipulatory behaviors in numerous nonhuman primate species, from prosimians (Masataka, 1989; Ward, Milliken, & Stafford, 1993) to monkeys (Diamond & McGrew, 1994; Fagot, Drea, & Wallen, 1991; King, 1995; King & Landau, 1993; Kubota, 1990; Lacreuse & Fragaszy, 1996; Masataka, 1990) and great apes (Hopkins, 1993, 1995; Hopkins, Bard, Jones, & Bales, 1993; Hopkins & de Waal, 1995; Olson, Ellis, & Nadler, 1990). However, examination of some reports shows that the evolutionary model proposed by MacNeilage et al. (1987) is not always supported. For example, tasks involving single acts of visually guided prehension, such as reaching for food, do not always induce consistent hand bias in nonhuman primate species. Manual asymmetries for these simple activities are weak and unstable and may depend critically on the posture adopted by subjects when carrying out the actions. In addition, the direction of hand preference is not uniform across species. For example, findings on various prosimian
species indicate a left-hand bias at population level for bipedal posture but not for quadrupedal stance (Larson, Dodson, & Ward, 1989; Sanford, Guin, & Ward, 1984). In New World monkeys, a right-hand bias was noted in capuchin monkeys when a bipedal but not quadrupedal posture was required of them (Westergaard, Kuhn, Lundquist, & Suomi, 1997). Similar results were reported in common chimpanzees, orangutans, bonobos, and gorillas (Hopkins, 1993; Hopkins et al., 1993; Olson et al., 1990). However, the five bonobos examined by De Vleeschouwer, Van Elsacker and Verheyen (1995) showed an increasing trend toward left-handedness when the subjects shifted to a bipedal posture from a seated posture.

However, more pronounced manual asymmetries have been obtained when tasks requiring more complex sensorimotor coordination have been used as handedness measures (Fagot & Vauclair, 1991). Of particular relevance to this study are findings focused on bimanual activity (Boesch, 1991; Brésard & Bresson, 1983; Byrne & Byrne, 1991; Colell, Segarra, & Sabater-Pi, 1995; Fagot & Vauclair, 1988a, 1988b; Hopkins, 1995; Hopkins & de Waal, 1995; Rogers & Kaplan, 1996; Sugiyama, Fushimi, Sakura, & Matsuzawa, 1993; Westergaard & Suomi, 1996). In bimanual tasks, the hands are not involved in locomotor functions but are free to interact and manipulate objects or food items. Performance in these tasks should thus be less dependent on postural factors and may prove a better indication of differences in hand use in nonhuman primate species (see Morris, Hopkins, Bolser-Gilmore, & Washburn, 1993, for comments on this issue). Moreover, according to several theoretical proposals, the emergence of right-handedness and cerebral lateralization during hominid evolution was a consequence of asymmetric use of hands in tool-making and tool-using activities (Prost, 1980; Kimura, 1979; Marshack, 1984).

There is some evidence that tasks requiring the complementary use of both hands elicit population hand bias in some species of great apes; this bias is comparable with that observed in most humans. For example, Byrne and Byrne (1991) observed the manual dexterity of a group of gorillas that were feeding and processing food in their native habitat. They found a trend toward right-handed fine manipulation in a group of bimanual feeding tasks. Similarly, Hopkins (1995) demonstrated a population-level, right-hand bias in a large sample of captive chimpanzees in a feeding task designed to elicit the complementary use of both hands to remove peanut butter from a tube.

In the case of monkeys, only a very small number of studies have been carried out to specifically examine manual bias in tasks requiring the simultaneous coordination of hand movements (Beck & Barton, 1972; Deuel & Dunlop, 1980; Fagot & Vauclair, 1988b; Fragaszy & Mitchell, 1990; Westergaard & Suomi, 1996). In addition, most of these studies usually involved samples composed of too small a number of subjects to allow generalization of the results.

In the present study, we examined and compared hand preferences in unimanual and coordinated-bimanual tasks in a group of 26 capuchin monkeys. Capuchins represent a very interesting species for the study of hand preference. They have the greatest degree of manual dexterity of all New World monkeys (Torigoe, 1985; Visalberghi, 1988). Although their prehensile hand has a pseudo-opposable thumb, they possess both a precise and powerful grip and frequently make use of unimanual and bimanual forms of precision handling (Costello & Fragaszy, 1988; Napier, 1993; Westergaard & Suomi, 1994, 1997). With regard to the laterality of hand function, some findings show that for some complex manipulative acts, capuchins exhibit a significant hand bias. For instance, a right-hand preference at group level has been reported for unimanual reaching actions requiring precision grip (Masataka, 1990), whereas a left-hand preference has been found for haptic searching tasks (Lacreuse & Fragaszy, 1996; Parr, Hopkins, & de Waal, 1997). On the other hand, Anderson, Dagiorgio, Lamarque, and Fagot (1996) found no significant hand bias in a group of 10 capuchins performing a series of tasks of varying complexity. Their data, however, showed that the strength of hand preference was strictly related to the type of manipulation performed. These results are consistent with those reported by Fragaszy and Mitchell (1990), who examined hand preferences in 7 capuchin monkeys during spontaneous activities and in unimanual and bimanual versions of a knob-pulling task. Although no significant hand bias emerged for any of the actions examined, Fragaszy and Mitchell found that the knob-pulling tasks, which were the most demanding in terms of motor requirements, gave rise to the strongest preferences at the individual level.

Our aim in the present study was to examine and compare hand preferences in two reaching tasks of varying levels of complexity with respect to the type of hand use for grasping actions in a captive group of capuchin monkeys. In each task, hand preference for food retrieval was assessed under two postural conditions. We also examined the influence of age and sex on both the direction and the degree of hand preference.

Method

Subjects

The subjects were 26 tufted capuchins (Cebus apella) housed at the Institute of Psychology, Consiglio Nazionale delle Ricerche, Rome. The sample comprised 13 females and 13 males, whose ages ranged from 2 to 25 years. Six of these monkeys were wild born, and the remaining were captive born. The exact age of wild-born monkeys was estimated. The monkeys were housed in five social groups, each in an indoor-outdoor cage (indoor: 1.7 m wide × 3.0 m high × 3.0 m deep; outdoor: 1.7 m × 3.0 m × 2.5 m). None of the subjects had performed these tasks in an experimental situation before.

Design and Apparatus

Unimanual task. This task was designed to elicit single acts of visually guided prehension under two postural conditions: quadrupedal and upright. In both conditions, monkeys were tested individually in their indoor cages, to which they had access through a guillotine door from an adjacent indoor cage.

In the quadrupedal condition, in each trial a single piece of food (a slice of banana or apple) measuring less than 2 cm was placed on
the ground in the center of the experimental cage. The monkey was then allowed to walk into the cage through the guillotine door, pick up the food item, and bring it to its mouth. While reaching for the food, the monkey was positioned quadrupedally. After retrieving the reward, monkeys went back to the adjacent indoor cage, and a new piece of food was again placed on the floor.

In the upright condition, food items were placed on a wooden shelf (15 cm × 7.5 cm) fixed along its longer side to the inside of the wire mesh of the cage. The height of the shelf was approximately 25 cm above the cage floor. In each trial, a single piece of food was placed on the shelf during the monkey’s absence. The monkey was then allowed to enter the testing cage and retrieve the food item. During reaching, the monkey was in an upright stance, keeping both hind feet on the cage floor and using one forelimb to maintain postural support. After retrieving the reward, the monkey went back to the adjacent indoor cage, and a new reward was again placed on the shelf.

Each monkey performed approximately 100 trials (range = 70–109) in each postural condition (20–27 trials a day for 4 days). All trials were recorded in color using video recording equipment placed outside the experimental cage from where it was also operated.

Coordinated-bimanual task. This task was designed to elicit the complementary use of the hands to obtain food. The apparatus was a vertical transparent tube (15 cm long with an inner diameter of 1.5 cm) hanging on an iron chain from the end of a vertical metal bar. The upper end of the bar was fixed to the ceiling of the experimental cage. The entire apparatus was placed in the middle of the cage. A sticky reward (a small piece of ripe banana) was placed inside the tube through a 1.5-cm hole made in the side. To obtain the food, the monkey had to hold the suspended tube with one hand and simultaneously insert the fingers of the other hand into the hole. The hand used to reach for the reward and bring it to the mouth was recorded on each trial. Monkeys were tested individually in the experimental cage. Before a trial started, the tube was baited in the absence of the monkey, who was then allowed to enter the testing cage and manipulate the tube to retrieve the food.

To assess whether the observed effects were caused by the motor requirements of the task or the monkey’s posture, the hand preferences for extracting food from the tube were examined under two postural conditions: crouched and upright. In the first condition (crouched), the distance of the vertical tube from the floor was about 5 cm, so that monkeys had to crouch on the floor to perform the coordinated-bimanual actions. In the second condition (upright), the distance of the vertical tube from the floor was about 25 cm. In this way, monkeys had to stand upright while using both hands in complementary roles.

In each trial, only the initial reaching action was scored. Each monkey performed approximately 100 trials (range = 75–115) in each condition (approximately 25 trials per day for 4 days). All trials were videotaped.

Analysis

Individual frequencies for the use of the left and right hand for each reaching action were analyzed using the two-tailed binomial test. Monkeys with significant positive z scores (z ≥ 1.96, p ≤ .05) were classified as right-handed, whereas individuals with significant negative z scores (z ≤ −1.96, p ≤ .05) were considered left-handed. For each subject, a handedness index (HI) was calculated by subtracting the total number of left-hand reaches (L) from the total number of the right-hand reaches (R) divided by the total number of left- and right-hand reaches: (R − L)/(R + L). The resulting values, ranging from −1.0 to 1.0, differentiated each monkey’s hand preference on a continuum from strongly left-handed to strongly right-handed. The absolute value of the HI (ABS-HI) represents the strength of hand preference, irrespective of the monkey’s direction of hand preference (see Hopkins, 1995). Parametric statistics were used to analyze the HI and ABS-HI data.

Results

Table 1 reports the individual hand-preference data for all 26 capuchin monkeys for unimanual reaching as a function of posture. It also includes the age and sex of each monkey. Table 2 reports the same data for coordinated-bimanual hand use.

Hand Preferences

A one-sample t test was applied to the group data to evaluate whether the mean HI score per subject differed significantly from a chance distribution with a mean of zero. In the unimanual reaching task, the mean HI scores for quadrupedal and upright conditions were .09 and .27, respectively. In the coordinated-bimanual task, the mean HI scores for crouched and upright conditions were .44 and .33, respectively. A significant right-hand bias for the group was evident for unimanual reaching by upright posture, t(25) = −2.91, p < .01, and for coordinated-bimanual hand use in either crouched, t(25) = −3.01, p < .01, or upright, t(25) = −2.13, p < .05, conditions. By contrast, in unimanual quadrupedal reaching, the mean HI score per subject did not deviate significantly from chance (Figure 1).

To assess whether different types of manipulation involved in each task or different postural conditions could affect hand preferences in our monkeys, a mixed-design analysis of variance was performed with sex as the between-subjects variable. The within-subject variables were type of hand use (unimanual vs. coordinated-bimanual) and postural conditions (quadrupedal or crouched vs. upright). The dependent measures included the HI scores and the strength in laterality as determined from the dominance index (ABS-HI).

With regard to the direction of lateral bias, this analysis revealed a significant interaction between tasks and posture, F(1, 24) = 4.79, p < .05 (see Figure 1). Post hoc analysis (least significant difference for planned comparisons) showed that the mean HI score for unimanual reaching by quadrupedal posture (.09) was significantly smaller than the mean HI score for complementary bimanual hand use by crouched posture (.44, p < .01). In contrast, no significant differences were found between the mean HI scores for unimanual reaching (.27) and coordinated-bimanual hand use (.33) by upright stance, p > .10. Thus, when reaching action did not require bipedal standing, a significant right-handedness emerged for the coordinated-bimanual but not for the unimanual task. Moreover, a significant effect for posture was found for the unimanual reaching task: The mean HI scores were greater during upright reaching compared with quadrupedal reaching, p < .05. In contrast, for the coordinated-bimanual task, the mean HI scores did not differ significantly between the two conditions. Taken together, these data suggest that posture clearly influences the direc-
Table 1

Hand Preferences in Unimanual Task by Each Subject, as a Function of Posture

<table>
<thead>
<tr>
<th>Subject</th>
<th>Age (years)</th>
<th>Quadrupedal</th>
<th>Upright</th>
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<tbody>
<tr>
<td></td>
<td>N</td>
<td>L</td>
<td>R</td>
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<tr>
<td>Females</td>
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<td></td>
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<tr>
<td>Rosita</td>
<td>14.10*</td>
<td>100</td>
<td>42</td>
</tr>
<tr>
<td>Pilar</td>
<td>14.10*</td>
<td>100</td>
<td>11</td>
</tr>
<tr>
<td>Consuelo</td>
<td>14.05*</td>
<td>102</td>
<td>95</td>
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<tr>
<td>Pipi</td>
<td>14.00</td>
<td>100</td>
<td>18</td>
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<tr>
<td>Brahms</td>
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</tr>
<tr>
<td>Luna</td>
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<td>60</td>
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<tr>
<td>Carlotta</td>
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<td>108</td>
<td>19</td>
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<tr>
<td>Roberta</td>
<td>9.03</td>
<td>101</td>
<td>64</td>
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<tr>
<td>Rame</td>
<td>8.10</td>
<td>100</td>
<td>28</td>
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<tr>
<td>Paprika</td>
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<td>25</td>
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<tr>
<td>Paquita</td>
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<td>107</td>
<td>34</td>
</tr>
<tr>
<td>Viola</td>
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<td>22</td>
</tr>
<tr>
<td>Robinia</td>
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<td>100</td>
<td>68</td>
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</table>

Males

<table>
<thead>
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<th>Subject</th>
<th>Age (years)</th>
<th>Quadrupedal</th>
<th>Upright</th>
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<tbody>
<tr>
<td></td>
<td>N</td>
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<tr>
<td>Rosso</td>
<td>25.00</td>
<td>109</td>
<td>46</td>
</tr>
<tr>
<td>Cammello</td>
<td>17.03</td>
<td>100</td>
<td>37</td>
</tr>
<tr>
<td>Zapotec</td>
<td>17.00</td>
<td>100</td>
<td>63</td>
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<tr>
<td>Cognac</td>
<td>8.03</td>
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<td>Chopin</td>
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<td>Romeo</td>
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<td>Gal</td>
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<td>Paule</td>
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<tr>
<td>Corto</td>
<td>3.05</td>
<td>100</td>
<td>43</td>
</tr>
</tbody>
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Note. N = number of trials; L = left hand; R = right hand; HI = handedness index; Pref. = hand preference; np = no preference. Positive z scores indicate right lateral bias; negative z scores indicate left lateral bias.

*Estimated age.

*p < .05. **p < .01. ***p < .001. (All ps are two-tailed binomial tests.)

Effect of Age

The relation between age and direction or strength of laterality was examined by correlating the age in years of each monkey with their respective HI or ABS-HI scores. A Pearson product-moment correlation failed to reveal any significant relation between age and direction of laterality, as determined from the HI for unimanual reaching task in either quadrupedal, \( r(26) = .037, p > .10 \), or upright, \( r(26) = .238, p > .10 \), conditions. Likewise, no statistically significant relation was found between the monkeys' ages and direction of laterality in coordinated-bimanual tasks for either the crouched, \( r(26) = .089, p > .10 \), or upright, \( r(26) = .158, p > .10 \), conditions.

With respect to the strength in laterality, no significant correlation was found between age and strength of hand preference as determined from the ABS-HI scores in either the unimanual reaching task for the quadrupedal condition, \( r(26) = -.027, p > .10 \), or the upright condition, \( r(26) = .087, p > .10 \); or the coordinated-bimanual task for the
In the present article, we examined and compared manual preferences by capuchin monkeys in two reaching-for-food tasks of varying levels of complexity with respect to the requirements for grasping-for-food actions. In the unimanual task, capuchins were required to perform single acts of visually guided prehension in either a quadrupedal or an upright posture. In the bimanual task, capuchins were required to use both hands in complementary roles in order to extract food from inside a suspended movable tube. The reaching action involved finely coordinated digit control to obtain food efficiently. In this task, manual preferences were examined while the monkeys were assuming either a crouched or upright posture.

Examination of the unimanual task revealed little evidence of lateral hand bias for simple acts of visually guided prehension from a quadrupedal stance. On the other hand, simple unimanual reaching from a bipedal posture elicited a significant right-hand preference at the group level. The change from quadrupedal to bipedal posture resulted in a significant shift toward a greater preferential use of the right hand.

The lack of an asymmetrical distribution of lateral hand bias for quadrupedal reaching is consistent with a number of recent nonhuman primate studies. In several species of prosimians (see Ward et al., 1993, for a review), monkeys (Fagot & Vauclair, 1991; King & Landau, 1993; Roney & King, 1993) and great apes (see Hopkins, 1996, for a review), simple reaching from a quadrupedal stance elicits individual but not group-level hand preferences. However, a different result for this measure has been reported by Masataka (1990), who found a right-hand group preference for quadrupedal unimanual reaching in three species of capuchin monkeys (Cebus apella, Cebus albifrons, Cebus capucinus). We believe that the discrepancy between the findings is because of differences in the manipulative demands involved in the reaching action. For example, the...
Figure 1. Mean value of handedness index (HI) as a function of posture in unimanual and coordinated-bimanual tasks. HI values range from 0 to 1 and correspond to the percentage of right-hand responses varying between 50 and 100.

Figure 2. Mean value of handedness index (HI) for unimanual and coordinated-bimanual tasks in female and male capuchin monkeys.
capuchin monkeys used in Masataka's study were observed while they were collecting scattered food remnants, which required sophisticated manipulative patterns such as precision grip. By contrast, in our study, a unimanual reaching action from a quadrupedal stance rarely involved any fine prehensile gripping to pick up food items. In most cases, our capuchins grasped food between the surface of fingers and the palm.

Our findings of a significant increase in right-hand use from the quadrupedal to bipedal reaching conditions are consistent with those obtained for several species of great apes (Colell et al., 1995; Hopkins, 1993; Hopkins et al., 1993; Olson et al., 1990). Moreover, they concur with results obtained recently on capuchins by Westergaard et al. (1997), who observed that the adoption of bipedal posture increased the use of the right hand in their subjects. However, studies with prosimians have revealed an opposite pattern. In this species, a bipedal posture elicits a more frequent use of the left hand to reach for food (Larson et al., 1989; Sanford et al., 1984). Taken together, these data suggest that the posture clearly influences the hand bias in nonhuman primates that are performing single acts of visually guidedprehension, but the direction of laterality is not uniform across species.

A different picture emerges when the data on the bimanual tube task are considered. In this task, which required the simultaneous use of both hands in performing two different but coordinated actions, strong preferences were found in almost all capuchins. In both the crouched and upright conditions, the majority of monkeys (73%) preferred to hold and stabilize the tube with their left hand and simultaneously remove the food with their right hand. Thus, when a different posture was required by the task, no change was observed in either the direction or strength of manual preferences.

A tube task designed to elicit coordinated-bimanual hand use was recently used by Hopkins (1995) on a very large sample of chimpanzees (N = 110) and by Westergaard and Suomi (1996) on tufted capuchins (N = 45) and rhesus macaques (N = 55). This task involved baited tubes that were placed on the monkeys' cage floor, which differed from our task (i.e., in our task, the tube was hanging from a chain). These authors reported that their subjects often took the tube with their mouths and sometimes retrieved the tube with either the left or right hand. The animals then walked away from the front of the cage while carrying the tube and before beginning the process of removing food from the hole. A right-hand superiority at a group level was found for chimpanzees and macaques, but no population preference was reported for capuchin monkeys. Our finding of a significant right-hand preference for coordinated-bimanual hand use in tufted capuchins is therefore consistent with findings in chimpanzees (Hopkins, 1995) and macaques (Westergaard & Suomi, 1996) but differs from those noted for just one species by Westergaard and Suomi (1996). Moreover, it should be noted that the percentage of right-handed subjects was higher in our capuchin sample (73%) compared with the chimpanzees (54%) and rhesus macaques (51%) in previous studies. These different results could be explained by analyzing the specific requirements of the two tube tasks. Our bimanual task implied a continuous spatial adjustment of the hand involved in stabilizing and positioning the suspended movable tube. Therefore, a more sustained visual guidance was required for the subject to perform these actions. These constraints were not present in the tube task used in the previously reported findings. It is possible, therefore, that the greater demands of our task may have elicited in our monkeys a stronger lateral bias than the biases reported in chimpanzees and macaques (and capuchins). The replication of our coordinated-bimanual task with both chimpanzees and rhesus macaques as well as other nonhuman primate species would help to clarify these differences.

The interdependence between task complexity and manual preferences has been argued to be a factor pointing to a possible relationship between hemispheric specialization and flexible organization of hand usage in human infants. Young, Segalowitz, Corter, and Trehub (1983) proposed making a distinction between handedness and manual specialization. According to these authors, handedness is related to a prevalence of hand usage in routine, highly practiced, and relatively simple tasks and does not reflect any underlying neurological asymmetry. In contrast, manual specialization refers to a consistent lateralized usage of unpracticed and relatively complex tasks. The same authors suggested that manual specialization, which is most evident in complementary bimanual coordination, is an index of hemispheric specialization of motor functions. Such a distinction was adopted by Fagot and Vauccl (1991) to explain individual and group-level manual lateralization in nonhuman primates. According to their model, simple and familiar behaviors (e.g., single acts of reaching for and grasping food) would not necessarily be expected to induce a consistent bias at the group level (handedness). In contrast, more skilled behaviors involving finely tuned motor patterns required by the spatiotemporal dimensions of the movements would consistently lead to group asymmetries (manual specialization). These authors found that in both gorillas and baboons, simple reaching was not associated with hand asymmetries, whereas in the bimanual tasks, both species consistently used the left hand to move and align a panel and the right hand to reach for and grasp food (Fagot & Vacl, 1988a, 1988b). Our findings on capuchin monkeys seem to fit Fagot and Vauccl's model (1991): Our subjects exhibited stronger hand preferences in more complex manual activity (coordinated-bimanual hand use for grasping food from the tube) compared with that observed in simple reaching behavior (unimanual reaching for food).

As researchers have found for several nonhuman primate species (Hopkins, 1993; Hopkins & Bard, 1993; Lacreuse & Fraguassy, 1996; Rogers & Kaplan, 1996; Ward et al., 1993), we noted a significant effect of sex on the direction of hand preferences. In the coordinated-bimanual tube task, female capuchins exhibited a stronger right-hand bias for fine manipulation than males. Additionally, a significant increase in right-hand preference from the unimanual to the coordinated-bimanual task was observed for females but not for males. Hopkins and Bard found that in infant chimpanzees
females were more likely to have a right-hand preference in hand-to-mouth behavior. Ward et al. (1993) reported a similar effect of gender in prosimians. These authors hypothesized that the greater incidence of left-hand bias in males is related to an early slowing of left hemisphere development, possibly the result of hormonal effects. This hypothesis is supported by anatomical evidence that in the human fetus, the left side of the brain develops later than the right (Geschwind & Galaburda, 1987). Geschwind and Galaburda suggested that testosterone, the male hormone, plays an important role in retarding the development of the left hemisphere. This might explain why there is a high incidence of left-handedness in male humans (Geschwind & Galaburda, 1987) and a stronger right lateral bias in women as compared with men (Porac & Coren, 1981; Seltzer, Forsythe, & Ward, 1990).

The data from this study failed to reveal any significant relationship between age and strength or direction of hand preferences. This negative finding contrasts with the mounting evidence that age is an important factor contributing to the expression of hand preference in primates (Colell et al., 1995; Hopkins, 1995; King, 1995; Rogers & Kaplan, 1996; Westergaard & Suomi, 1993). For example, Westergaard and Suomi (1993) reported a greater incidence of right-hand preference in adult capuchin monkeys than in young monkeys in unimanual food reaching and sponging actions. One possible explanation for the lack of significant findings in the present study is the small number of young subjects. In our sample of capuchin monkeys, 7 subjects were less than 5 years of age, and of those only 2 subjects were less than 4 years of age.

In conclusion, evidence from our study shows that simple unimanual reaching tasks elicit weak forms of handedness: Bias for the use of one hand seems to depend on the posture adopted by animals. In contrast, coordinated-bimanual tasks are more likely to induce asymmetry in the distribution of lateral bias at behavioral levels. Our findings on coordinated-bimanual hand use, however, highlight the necessity to consider the specific task requirements so as to better understand the neural mechanisms controlling the organization of motor patterns in nonhuman primates.

More systematic research using identical testing procedures will perhaps help researchers to resolve the question of whether laterality in hand usage in nonhuman primates is analogous or homologous to that of humans.

References


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