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Manual Function in *Cebus apella.* Digital Mobility, Preshaping, and Endurance in Repetitive Grasping

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Manual dexterity varies across species of primates in accord with hand morphology and degree of fine motor control of the digits. Platyrrhine monkeys achieve less direct opposition between thumb and index finger than that of catarrhine primates, and many of them typically whole-hand grip. However, tufted capuchins (Cebus apella), *exhibit a degree of independent control of the digits and effective thumb–forefinger opposition. We report how capuchins prehended small objects, with particular attention to the form of sequential fine movements of the fingers, choice of hand, and differences between the two hands in the temporal properties of reaching and grasping. We compare these actions across tasks with differing demands for fine motor control. For tasks that required all the digits to flex in synchrony, capuchins displayed smooth, fast, and efficient reach-to-grasp movements and a higher endurance than for tasks requiring more complex digital coordination. These latter tasks induced a slightly differentiated preshaping of the hand when approaching the objects, indicating preparation for grasping in advance of contact with the object. A right-hand preponderance for complex digital coordination was evident. The monkeys coordinated their fingers rather poorly at the substrate, and they took longer to achieve control of the objects when complex coordination was required than when simultaneous flexion was sufficient. We conclude that precise finger coordination is more effortful and less well coordinated, and the coordination is less lateralized, in capuchins than in catarrhine primates.*

KEY WORDS: dexterity; movement coordination; hand asymmetry; precision grips; capuchin monkeys.

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INTRODUCTION

Dexterous manual activity is a defining characteristic of primates (Schultz, 1956; Napier, 1962), and a prime element in recent human evolution (Susman, 1994). Therefore, understanding the diversity of manual capabilities among primates is an integral part of a biological understanding of primates. We focus on the manual capabilities of capuchins (*Cebus* spp.) Field researchers described capuchins using their hands dexterously during extractive foraging (Fragaszy, 1986; Panger, 1998). Laboratory studies confirm a high degree of manual dexterity in capuchins (Costello and Fragaszy, 1988; Fragaszy *et al.,* 1989; Lacreuse and Fragaszy, 1997). Capuchins stand out among New World monkeys in this domain, prompting interest in the details of their unusual capacities and the neuromuscular correlates of their dexterity. Capuchins provide an independent phylogenetic comparison for ideas about the origins and organization of manual dexterity in Old World primates.

The various taxa of nonhuman primates show differences in hand morphology and the movements of their fingers, which affect manual activity. Along with those of all other New World monkeys, capuchin thumbs lack the saddle-shaped carpometacarpal joint typical of catarrhines (Erickson, 1948; Napier, 1962), possessing instead a hinge-shaped joint separated by a deep interdigital cleft. Their thumbs can be abducted from the index finger by 45° and flexion in this position enables pseudo-opposability with the index finger (Napier and Napier, 1967). Napier (1962) proposed that the saddle joint is necessary to achieve opposition of the thumb to forefinger, which defines a functional precision grip. His view shaped the consensus for decades afterward that no New World monkey could display dexterity equivalent to that of catarrhine primates, because a precision grip was impossible for them to achieve. Moreover, Old World monkeys, apes, and humans display movements of a single digit, as well as complementary movements of digits in opposition to one another (Napier and Napier, 1967; Schieber, 1990, 1991). Digital individuation is a prerequisite to adjust and to synchronize fingers for a grip (Landsmeer, 1984, 1993; Schieber, 1990, 1991).

Subsequent observations of several genera of New World monkeys confirmed that they exhibit only whole-hand grips and presented no evidence of single-digit coordination (Bishop, 1964; Fragaszy, 1983). However, Costello and Fragaszy (1988) observed that capuchins clearly achieved precision grips in spontaneous activity by touching the thumb to the index finger (as well as other digits), and thus claimed that capuchins have functionally opposable thumbs, a distinction that has not been demonstrated for any other New World genus. Bortoff and Strick (1993) confirmed that a dense neuronal substrate of direct corticospinal motoneurons innervates the fingers of Cebus apella, as it does in macaques, though this pattern of innervation is not present in squirrel monkeys (Saimiri sciureus). Morphological studies of white-faced capuchins, (*Cebus capucinus*) documented that the deepest layer of the *M. flexor digitorum profundus* clearly divides into a radial and an ulnar portion, with the radial fingers being supplied by *Nervus medius* (Erickson, 1948). Thus capuchins have both neuronal and muscular anatomy that can support differentiated postures and movements of the radial and ulnar digits. However, we still know little about how capuchins organize sequential finger movements in precision grasping. Describing the form of capuchin grasping actions, with attention to the degree of independent control of the digits and the form of opposition in precision grasping, was an aim of our study.

A second aim was to define the form of reach-to-grasp movements in capuchins, and particularly preshaping the hand, as they have been defined for macaques and humans (Jeannerod, 1984; Christel, Weiss, Bavar, 1998b; Roy *et al.,* 1998). Macaques and humans share many kinematic properties during reaching, though they preshape the hand differently (Christel, 1993b). Humans are able to spread, flex and abduct the ulnar fingers while the thumb and index finger perform a precision grip. Chimpanzees do this also, but monkeys do not (Christel, 1993a; Christel, Kitzel, Niemitz, 1998a). Rhesus monkeys and pig-taileded macaques move the thumb to oppose the index finger, while the 3rd, 4th, and 5th fingers move in concert (Muir and Lemon, 1983; Brinkman, 1984; Christel, 1993b). When the thumb and index finger show no clear opposition space and all fingers act in concert before contact with the object to be prehended, the preshaping is undifferentiated. Like prosimians (Bishop, 1964), *Cebus apella* and *Saimiri sciureus* also display this pattern (Costello and Fragaszy, 1988). The quality of video recordings and the comparative database on prehensile activity in primates have both improved substantially since Costello and Fragaszy (1988) completed their study.

Repetitive reach-to-grasp actions are smooth, fast and efficient—routinized—movements in humans and macaques, for example, picking up a small object from a flat surface (Thelen, 1994; Lee, 1998; Walter, 1998). During reaching for the object, an opposition-space between thumb and index appears before contact with the object. The shape of the opposition space is influenced by the visually and tactilely perceived characteristics of the object (Jeannerod, 1981, 1984; Arbib *et al.,* 1985). Additionally, the intended activity with the object affects the kinematics of reaching, such as the timing of the onset of hand preshaping and its size (Marteniuk *et al.,* 1990). Human and macaque abilities to routinize the demanding cycles of reaching and grasping small objects therefore reflect sophisticated perceptuomotor functioning. We were interested in (a) the extent of preshaping of the hand before contact with the object and (b) the temporal pattern of repetitive activity in picking up small objects by capuchins, as these variables serve as co-indicators of capuchin ability to routinize repetitive precise grasping actions.

We intended our study to shed light on lateral asymmetry in capuchins. The neurological correlates and phylogenic origins of manual asymmetries in humans and other primates are decidedly unclear at this time. In most humans the left cerebral hemisphere appears to be specialized for fine-tuned sequential motor tasks, whereas the right-hemisphere dominates for visuospatial functions (Bryden, 1982; Geschwind and Galaburda, 1985). Right-handers are typically faster with the right than with the left hand when performing rapid sequences of visually guided movements (Bradshaw *et al.,* 1990). The dominant (right) hand also exhibits considerably better control of acceleration and deceleration during fine movements (Fitts, 1954). For right-handers, the movements of the left hand tend to be more variable in time than those of the right hand (Annett, 1992). In individuals with strongly expressed left or right preferences, the dominant and nondominant hands are differentially skilled at hand writing and finger-tapping speed. However, arguing against strong hemispheric specialization for manual activity, individuals without strong manual preferences do not show large asymmetries in such tasks (Peters, 1990; Provins and Magliaro, 1993). Kimura and Vanderwolf (1970) found that isolated digital flexion was performed better with the nondominant hand in right-handers, and Carey and colleagues (1994) showed that subjects performing an index-tracking task are more accurate with their nondominant hand than with the dominant one.

Several authors have suggested that the right hand/left hemisphere system is faster and more efficient in correcting movement errors on the basis of response-produced feedback (Elliott and Chua, 1996). These ideas are based on a long tradition in hand asymmetry research in humans (Woodworth 1899; Fitts, 1954; Annett *et al.,* 1979; Todor and Doane, 1977; Jeannerod, 1981, 1984). Moreover, Elliott and Chua (1996) propose that the right hand system is more elaborated to regulate timing and to specify the precise muscular forces required for fine finger adjustments. Thus actions with fine sequential finger movements should be more likely to produce lateral asymmetries in performance than simpler actions would.

We do not understand whether or when nonhuman primates exhibit asymmetries in choice or performance of the hands. MacNeilage, *et al.,* (1987) proposed an evolutionary model for handedness in primates, accompanied by brain asymmetry for increasing manual skills. According to their model, in catarrhine primates demanding manual tasks should reveal a right-hand preference. Many studies in the last 10 years indicate that manually demanding tasks enhance individual hand preferences (Hopkins and Morris, 1993; McGrew and Marchant, 1996), but few indicate a populationwide bias in any task. Several recent studies with captive capuchins indicate a left-hand group bias for some haptic tasks and tasks permitting vision but requiring precise spatial orientation of the hand, while other tasks requiring haptic search simply enhanced individual hand preferences (Lacreuse and Fragaszy, 1996, 1997, 1999; Parr, Hopkins, and deWaal, 1997). Similarly, tasks with increasing demands on manual strategies (Anderson *et al.,* 1996) and presenting a tool (Westergaard and Suomi, 1993; Limongelli, Sonetti and Visalberghi, 1994) induced increasing individual manual asymmetries but did not produce a consistent bias at the population level. Accordingly we are less concerned with the direction of bias than in its correlates with performance, particularly of finer digital movements.

Reaching and grasping movements incorporate neuronal asymmetry at different levels (Jeannerod, 1994). During reaching, the coarser proximal muscle groups coordinate the acceleration of the arm and stabilize it. The ipsilateral hemisphere controls them. During the deceleration phase, finger muscle groups are finely adjusted for a proper grip. They are controlled contralaterally (Kuypers, 1985), and kinematics of their actions is evidently lateralized in humans (Marteniuk *et al.,* 1990; Castiello, Bennett, and Stelmach, 1993). Given that, like macaques and humans, capuchins display differentiated corticospinal innervation of contralateral and ipsilateral nerve tracts, it seems plausible that they would also have hemispheric specialization for movements involving contralateral control. We sought to determine if performance of contralaterally controlled movements varied between the hands in capuchins.

In sum, our principal aim in this study was to describe manual dexterity in capuchins during prehension of small objects; i.e., in conditions demanding precise coordination of the digits. We expected the extent of preshaping to correlate with dexterity, measured as movement duration and regularity, and by posture of the fingers. Secondarily, we sought to characterize the relation between dexterity and degree of lateral asymmetry in performance within subjects. Finally, we wanted to document the relation between asymmetry and task difficulty. We expected a stronger bias for use of one hand and stronger performance asymmetries when demands for digital coordination were greatest.

METHODS

Subjects

Five young adult male tufted capuchins (*Cebus apella*) between 5 and 13 years old, participated. The monkeys are housed socially but were tested singly. Subjects had participated in a variety of other manipulation tasks but were naive about the particular testing conditions that we used. The study location is the University of Georgia.

Apparatus

During testing, subjects remained in a cage (50 × 27 × 40 cm) with a clear Plexiglas front panel and metal mesh sides (Fig. 1). The front panel had a centered rectangular 8 × 9 cm opening 20 cm above the bottom (about subject breast height), permitting them freedom to adjust the forelimb while reaching and grasping. The subjects reached from a seated position. Reaching through the panel aperture required lifting the forelimb, which induced abduction and elevation of the arm. The forearm was flexed and pronated, and simultaneously the wrist rotated and the fingers achieved particular positions.

Procedure

We used small objects at standardized locations to encourage preshaping during reaching. We proffered small pieces of currants and grapes in a randomized order on transparent acrylic boards (20 × 10 × 1.5 cm), modeled after those of Brinkman (1984), centered in front of the opening. Standardized distances of the object support spatial accuracy in grasping objects (Carlton, 1994). We presented the food items (a) in hemispheric shallow wells—shallows— 1 cm in diameter × 5 mm deep, (b) on the top of 4-cm sticks (screws mounted in the acrylic panel), and (c) in grooves (150 mm long × 4 mm deep), or (d) on a flat surface. The grooves were angled at 0°, 45°, 90°, or 135° with respect to the subject. Each board contained 20 food items per presentation at distances from 10 to 20 cm from the front of the cage. The angle of the grooves was balanced by left-right position and by distance. We designated the shallows easy to handle as they allowed for the use of all finger tips in parallel. The flat boards and the sticks also were easy, as they allowed all kinds of grips, including a whole-hand grip with the palm. The food pieces were lightly attached to the sticks, and they required a soft and accurate grip without the passive support of the hand provided by the solid board. The angled grooves required the use of one finger, or the extreme tips of both the thumb and index finger. Thus, the grooves were difficult to handle.

We conducted two test series, one year apart. In the first series, we tested 4 subjects with flat boards and grooves. In the second series, we

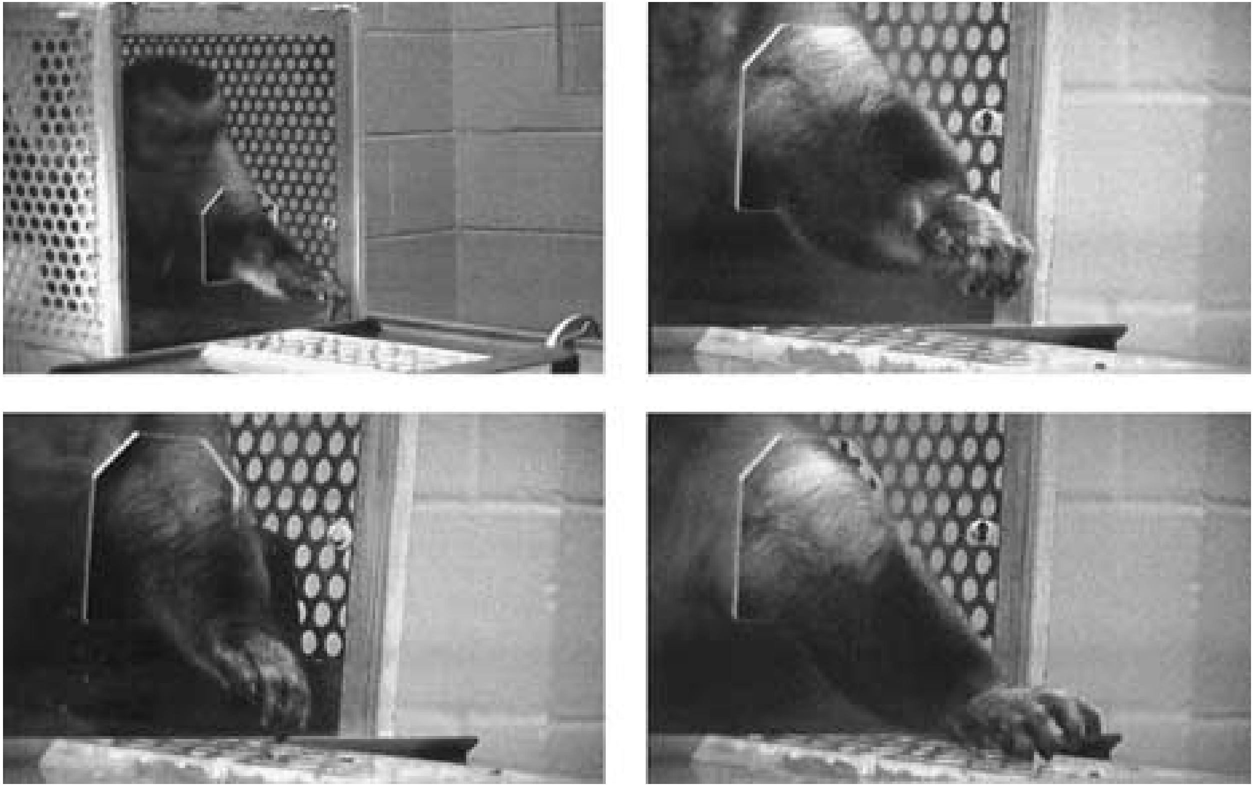

Fig. 1. Types of preshapings, and actions during grasping. *Left side above,* the index finger showed a slight differentiation during preshaping for touching the objects at grooves; *right above to left below,* less differentiated preshapings for shallows, in which the thumb was adducted or flexed. *Right below,* finger in grasping from grooves appeared uncoordinated.

tested the same 4 subjects and one additional subject with shallows, sticks, and grooves. Each test session lasted between 15 and 30 min. The monkeys were tested once a day. Before we presented the boards to the monkeys, we blocked their vision of the testing area with an opaque panel. When the test board was installed, the opaque panel was removed, allowing the monkey access to the test board. We randomized the presentation of the different kinds of boards. The experimenters approached the test cage from the left or right side. All trials were recorded with two cameras (Panasonic AG 346) set to a shutter of 1/1000 sec. We arranged the cameras to capture the ulnar and radial aspect of the hand.

Scoring

Two observers scored all the videos concurrently using the Observer 3.1 (Noldus Inc.) to collect the data. We scored 2008 reaching cycles; 1349 for 4 subjects with flat boards and grooves in Test Series 1, and the remainder during Test Series 2 with 5 subjects. We scored samples in Test Series 2 from the last third of testing, after the subjects had practiced with all the boards for several sessions.

We first scored all unimanual reaching actions for choice of hand. We then separated each prehensive event into three components. Reaching is the period following movements away from the mouth (start) to contact the object. Grasping is the period from first contact to when the hand lifted off the board holding the food. Retrieval is the period of movement off the board until first contact of the fingers with the mouth. Subjects often made multiple attempts to get the food item out of the grooves, sometimes unsuccessfully. In the case of failed attempts, we ignored the whole action cycle. If the two scorers did not agree about onset points of the submovements, they checked each video frame to reach consensus. Third, we identified bouts of actions and which hand was used in each cycle of prehension within the bout, for example, left, right, left, left, right, right, right. We noted which hand the subject used to initiate his first action at each new board—initial hand—and the hand used to initiate each new bout of action a board: bout hand.

Finally, we scored the first 10 scoreable instances per board of preshapings and grips, noting for each digit whether it was abducted or adducted, flexed or extended. We identified three patterns of preshaping during reaching (Fig. 1 a–c): (a) The thumb adducts toward the index finger and flexes slightly at the metacarpophalangeal (MCP) joint as the index extends and the other fingers flex slightly; (b) the thumb abducts from the index finger and flexes at the MCP joint as the other fingers flex and abduct slightly, and (c) the thumb adducts toward the index finger and extends as the other fingers extend and adduct. During grasping we noted whether the tip of the thumb touched the tip of another finger on the dorsal, ulnar, or volar aspect. We report the proportional occurrence of the different patterns.

We scored hand preference and configuration for all subjects and both test series, and movement times for the various components of reaching from five trials per subject and task during test series 2. We derived several variables for each subject from these data concerning preference, interest, endurance, and duration of movement for different segments of the action cycle.

Preference

We calculated the degree and the direction of intermanual differences within subjects using a preference index and a performance index. A positive preference index (calculated as [(right - left)/(sum)]*100) (Annett, 1992) indicates that the right hand performed more actions than the left. A preference index of zero indicates that both hands performed the same number of actions, and 100 indicates that only one hand performed. A positive performance index (calculated as [(left - right)/(sum)]*100) indicates that the right hand required less time per reach-grasp-retrieve cycle than the left hand did. Thus, a preference index of 50 indicates that the right hand was used twice as often as the left hand, and a performance index of 50 indicates that the right hand completed the action cycle in half the time taken by the left hand.

Interest and Endurance

We characterized the overall activity of each subject in two ways: as the average number of acts per board (an index of interest in the task), and as the average number of acts per bout (an index of endurance). We calculated both these values for the left and right hand separately.

Regularity of Movement Times

We characterized each subject's regularity of movement time as the fraction [Quotient of regularity = $(MT-SD)/(MT+SD)$], where in MT =

movement time and SD = standard deviation. Values close to 1 indicate a small standard deviation in relation to the mean movement time.

Analysis

We evaluated preference for bout hand within subjects with the binomial test (two-tailed, alpha set at 0.05). Via nonparametric tests, the Wilcoxon or Kruskal–Wallis matched pairs signed ranks we tested intermanual differences in submovement time, movement regularity, interest, and endurance among subjects, using 5 scores each for sticks, shallows, and grooves (total $N = 15$) per subject.

RESULTS

Preshaping

We identified three forms of preshaping during reaching for food. Figure 1a shows a preshaping that we termed slightly differentiated. This pattern was evident in 11% of reaches at grooves. It is distinctive in that the index finger led the action as it extended in parallel with an adducted thumb. All other fingers (III-V) flexed slightly. The functional consequence of this posture is that the index finger touched the object first. We did not observe an active abduction of the thumb simultaneously with a flexion of fingers III-V with this preshaping.

The second preshaping, accounting for 79% of reaches, is ‘‘flexed undifferentiated’’ (Fig. 1b). Subject used it with the easy boards: shallows and sticks. In this pattern, the thumb is abducted and flexed slightly at the metacarpophalangeal (MCP) joint or interphalangeal (IP) joint. All other fingers were also abducted and flexed slightly.

The third pattern of preshaping—stretched undifferentiated—was the least differentiated (Fig. 1c), and occurred in 9% of reaches. The thumb was extended and adducted and all other fingers hooked, as they were flexed slightly. The subjects also used this pattern with the flat boards, shallows and sticks.

When capuchins extended their forelimbs to grasp objects at longer distances, we occasionally observed a cleft either between digits II and III, or between III and IV, formed by the abduction, while the others remained adducted, e.g. II/III- cleft -IV/V).

The Grasping Pattern

The monkeys often made several attempts to grasp the food from the grooves. When doing so, the radial fingers (I-II, III) acted in concert while the ulnar digits (IV-V) moved asynchronously (Fig. 1c). In contrast, at the shallows or sticks, all fingers acted more or less in concert to apply a precision grip with the tips of the thumb and index finger. The movements appeared relatively uniform. The thumb usually adducted and flexed at the MCP and IP joints. When grasping food on the sticks, where in the food was fixed loosely, typically all fingers flexed slightly in the MCP joints and strongly in the IP joints, and occasionally all finger tips enclosed the object.

Achieving a Precision Grip

Capuchins achieved a precision grip by placing the dorsal aspect of the thumb tip against the volar aspect of the index tip. Thus, the objects made contact with the thumbnail or close to it (Fig. 1d), at the ulnar rather than at the volar surfaces. We observed the thumb was flexed and slightly abducted in the MCP joint and/or flexed in the IP joint, opposing the index or the dorsal aspect of other fingers.

Effect of Task on Interest and Endurance

The monkeys were interested in taking all the pieces of food from each board, but they did so in multiple short bouts (cycles of 1–3 reaches). That is, they had limited endurance to perform repetitive actions. The type of board affected both interest and endurance. When they had to retrieve the food from the narrowly angled grooves, four of the five subjects stopped reaching after a few trials. Each subject performed more trials at shallows and on sticks than in grooves (mean reaches per board: 32 ±11 vs. 8 ±1, $z\ (5) = -2.6, p < .01$). The monkeys performed more consecutive reaches towards shallows and sticks than towards grooves (mean reaches per bout = 2.1 ±1 vs. 1.4 ±1, respectively; $z\ (5) = -3.00$, $p < .01$). Apparently, prehending food from grooves required more effort than prehending it from the other boards.

Hand Preferences

All five subjects used the left hand more frequently than the right when reaching to grasp food from shallows (mean preference index, HP = −26 ±19) (Table I). The preference for the left hand is significant for 3 of the 5 subjects (binomial two-tailed, $p < .05$). At flat boards, 3 of 4 subjects preferred the left hand (mean HP −26 ±9, $p < .05$). In reaching to grasp food from grooves, 3 of 5 subjects switched to the right hand, and they showed a stronger hand preference for grooves than for shallows (mean HP 46 ±13 vs. 11 ±2, $p < .05$). Moreover, the same three subjects initiated each action at a new board exclusively with the right hand. The direction of preference varied more strongly across subjects when the monkeys were reaching towards sticks than towards other boards (for those preferring the left hand, mean HP = −34 ±21; for the right, mean HP = 51 ±5; Fig. 2). Thus, several directional preferences reached significance, but no clear pattern is evident within or among subjects in the direction of preference. Moreover, the monkeys used left and right hands equivalently often to begin a new bout of reaching towards the board (bout-hand range = −60% to +55%), regardless of differential use of one hand or the other among all reaches (Table I).

Movement Cycle Duration and Regularity

The monkeys took significantly longer to complete a movement cycle for the grooves than with the two easy tasks (mean cycle duration = 2.509

Table I. Hand preferences during different tasks, based on binomial two-tailed test for each subject ($p < .05$)[a]

Subjects/Tasks	Test 1	Test 2		Test 1,2	Initial hand (%)	Bout hand (%)
Easy tasks	(a)	(b)	(c)	a–c		
Chris	LH	LH	RH	RH	−100	±50
Jobe	LH	LH	LH	LH	−66	−55
Nick	—	*LH	LH	LH	+100	±50
Xaxier	LH	*LH	RH	LH	−67	−55
Xenon	non	LH	LH	LH	−100	−64
Grooves						
Chris	RH	RH		RH	+100	+60
Jobe	RH	RH		RH	+100	+63
Nick	—	RH		RH	+100	±50
Xavier	RH	LH		non	+67	−57
Xenon	LH	LH		LH	±50	−53

*$p = .06$.

[a] Two test series (1 and 2). In test series 1, flat surfaces (a) for easy tasks were provided. In test series 2, the flat surfaces were replaced by (b) shallows and (c) sticks. (RH, right hand; LH, left hand).

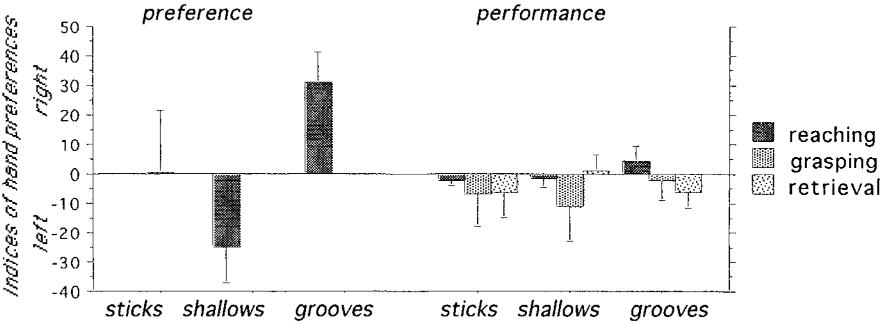

Fig. 2. Data from test series 2. Hand preferences (for reaching) across different tasks were more strongly expressed than asymmetries in performances (movement time) for reaching, grasping and hand retrieval. Negative values indicate a left side deviation. Standard error of five subjects.

msec, grooves, vs. 1.429 msec, shallows and 1.449 sticks; each Wilcoxon z (5) = $-2.1, p = .04$). Submovement time and regularity varied. Reaching typically lasted less than half a second (489 msec), and hand retrieval somewhat longer (761 msec; Wilcoxon z (5) = $-5.6, p < 000$). Generally, reaching was more regular than retrieval (Quotient of regularity = .41, reaching, vs. .21, retrieval, z (5) = -2.5, $p = .04$). Average reaches were quicker for grooves than for both other tasks (grooves 468 msec vs. shallows 492 msec and sticks 512 msec, each Wilcoxon z (5) = -2.0, $p = .05$) and more regular (*Qreg* = .62 vs. .56 and .45, each z (5) = $-2.0, p = .05$) (Fig. 3a).

However, object grasping required > 1 sec more with grooves than with easy tasks (1280 vs. 195 msec, z (5) = $-6.4, p < .001$). Thus, significantly longer movement cycles at grooves were due to time-consuming grasping actions. However, movements were much more regular with grooves than in both other tasks (Kruskal–Wallis H (2) = 7.6, $p = .02$) (Fig. 3b).

Lateral Asymmetries in Performance

Asymmetries were more strongly expressed in preferences than performance time (preference index, 42 ±38 vs. performance index, 12 ±8; z (5) = $-6.8, p < .001$) (Fig. 2, Table II). Overall, the right hand at grooves performed a whole cycle with higher regularity than the left (Qreg = .55 vs. .33; z (5) = -2.0, $p = .05$). The regularity of movement time was equivalent in the two hands with easy tasks. The right hand reached to grooves more quickly than the left did (mean differences = 49 msec, z (5) = 2.1, $p = .05$) and with a slightly higher regularity (z (5) = -1.8,

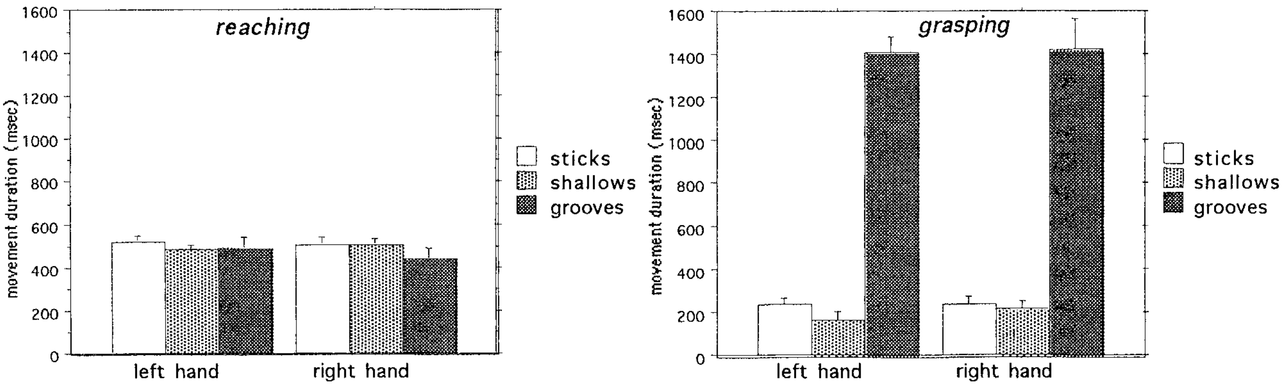

Fig. 3. (a) *Reaching* durations were *homogeneous* across tasks. (b) *Grasping* durations were *longest* for the grooves. Standard error of five subjects.

Table II. Asymmetries in choice of hand (indices for counts, c.IHP) were stronger than asymmetries in performance (indices for time, t.IHP)[a]

	Sticks				Shallows				Grooves			
	c.IHP	t.IHP			c.IHP	t.IHP			c.IHP	t.IHP		
	reach	reach	grasp	retrieve	reach	reach	grasp	retrieve	reach	reach	grasp	retrieve
Chris	**+56	+3	−5	+5	**−12	−11	**−37	+5	*+32	**+13	−1	**+23
Jobe	*−33	−6	*+20	+12	*−8	−7	**−16	−6	*+53	*+13	2	−11
Nick	**−14	+2	**−31	−5	−12	−11	*−36	0	+53	−6	**−20	−9
Xavier	*+46	−2	−24	−9	−39	−3	+21	5	*−31	+18	+7	−15
Xenon	−65	+2	−4	**−52	*−56	+7	**−18	6	**−15	*−8	+5	*−18
Averages	−1	−2	−7	−6	*−25	−1	−11	+1	*+28	*+5	−2	−6

Binomial two-tailed for subjects *) ≤ .01; **) $p \leq .05$.

[a] The right hand (+) was preferred by 3 subjects and overall for grooves, the left hand (−) by all 5 subjects for shallows. No consistent preference was evident among subjects with sticks.

$p = .07$) (Fig. 3a). Two of the three subjects that preferred the right hand for grooves demonstrated quicker right-handed reaches than left-handed reaches (mean differences 270 ±60 msec), whereas those preferring the left hand for the groove presented smaller intermanual differences (64 ±41 msec) (Table II).

The left hand grasped objects from shallows more quickly than the right hand did (−66 msec, z (5) = −2.2, $p = .03$) (Fig. 3b). Grasping from sticks shows no intermanual difference, but grasping times with the left hand were much more irregular (Qreg = −.08 vs. .02, z (5) = −2.0, $p = .05$) (Fig. 4). The right hand moved with greater regularity when grasping from grooves than the left hand did (Qreg = .5 vs. .3, z (5) = 2.1, $p = .05$). Forelimb retrieval from either task is not associated with significant intermanual differences.

DISCUSSION

Capuchins prehended small pieces of food quickly and with minimal shaping of the hands from shallows and from the tops of sticks, shaping the hands into "flexed undifferentiated or stretched undifferentiated postures.

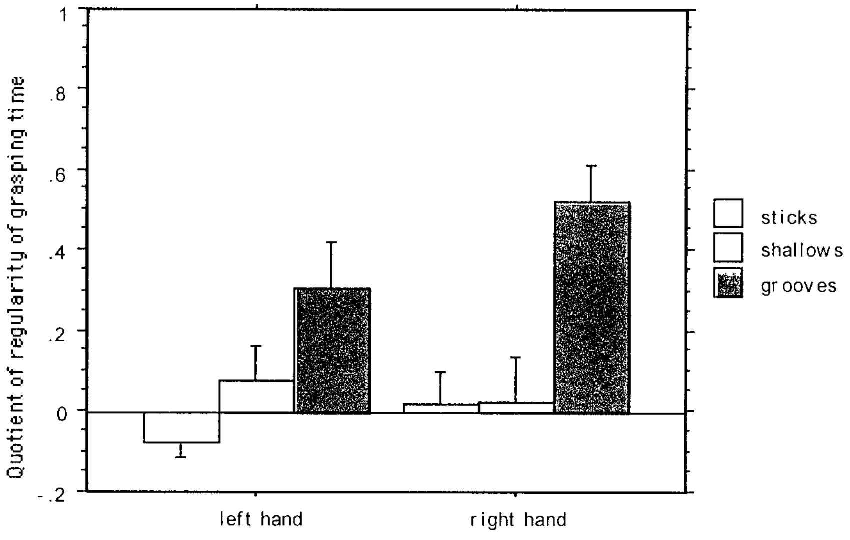

Fig. 4. Movement durations while grasping at grooves were more regular for the right hand than for the left hand. Quotient of 1 indicates highest regularity, a negative value indicates that SD was greater than the average. Standard error of five subjects.

They are undifferentiated because all the fingers moved in synchrony and with the same joints flexed or extended. Nevertheless they were able to grasp the food items with the fingertips, in precision grips. This type of hand shaping resulted in fast and uniform reaching times across the two hands; grasping occurred quickly; and, the monkeys repeated many action cycles.

The monkeys prehended objects more slowly from angled grooves, and under these circumstances, displayed slightly differentiated postures during reaching. Grasping movements were more variable between the hands, and the monkeys performed fewer consecutive action cycles. When reaching toward food in grooves, the preshaping resulted in the index finger leading the reach, and contacting the surface first. The net effect of this posture was that the index finger entered the groove by itself, as was necessary because the groove was too narrow for more than one finger. Thus, as we anticipated, the extent of preshaping correlated positively with demands for dexterity, and negatively with endurance and speed: our indices of routinization. Precision grips achieved in this situation involved opposition of the thumb to index finger, as the index finger drew the food item toward the thumb.

Grasping food from the grooves appeared more effortful than grasping food from shallows or sticks. Grasping from grooves took longer to complete, and the ulnar digits usually moved asynchronously with the radial digits during grasping. Time-consuming adjustments of the fingers at grooves reflect that capuchins did not develop a consistent or efficient manual strategy to deal with the objects. However, they demonstrated a capacity to move single digits independently when the fingers were resting on the surface of the board. This is in contrast to a relatively uniform preshaping pattern in which fingers had to be coordinated in space. The passive support at the substrate evidently supports coordination of single digits for diverse grips. Perhaps tactile stimuli in this context enhance perception of limb movements—(kinesthesia)—thereby enhancing the control of single fingers. Capuchins evidently reach elaborated exploratory procedures (Klatzky *et al.,* 1987) in a haptic search task similar to that of humans (Lacreuse and Fragaszy, 1997), suggesting that they can use haptic information to organize movement.

Comparisons with Old World Monkeys

Our observations confirm that capuchins prefer to use thumb and finger tips synchronously for picking up small objects from a grooved surface, and systematically oppose these digits when they do so. However, the opposition between thumb and index finger differed from that seen in catarrhines (Darian-Smith *et al.,* 1996; Christel, 1993b). The thumb adducted rather than opposed the index finger, and flexed at the IP rather than in the MCP joint. The objects made contact with the thumbnail or proximately to it, at the ulnar rather than at the volar surface, as characteristic of catarrhines. Thus, the term pseudo-opposability coined by Costello and Fragaszy (1988) to describe grip function of *Cebus apella* seems to be too conservative. Instead, we propose the term lateral opposability for this prehensive pattern.

A second characteristic distinguishes the hand function of *Cebus apella* from that of Old World monkeys. Occasionally we observed a cleft between digits II and III or between digits III and IV, formed by abduction of these fingers, while the others remained adducted. We observed this cleft most clearly when subjects extended forelimb in order to grasp objects placed at greater distances. A cleft during prehension in capuchins has not been described before. Haines (1958) classified a schizodactylous type of hand, in which category he included other genera in the Cebidae, such as *Cacajao* (uacari). Uacaris frequently align together the first and second digit for purposes of prehension, ‘‘to compensate for a somewhat ineffective thumb’’ (Napier, 1961), as the trapezium in uacaris is not markedly in-turned. This explanation for the functional significance of a cleft seems inappropriate for capuchins. Other genera in the Cebidae often place the digits over a narrow branch in this manner during locomotion, with digits I and II together on one side and digits III–V on the other, e.g., *Alouatta* and *Callicebus* (personal observation). We do not have a principled explanation why this pattern appears in capuchins when they reach for objects. Perhaps the musculotendinous division of the *M. flexor digitorum profundus* into radial and ulnar paths underlies this behavior.

Variations in mechanisms supporting dexterous finger control might produce differences among species in manual skills. Schieber (1990, 1991) proposed that individuation of single fingers in macaques could rely on an inhibitory mechanism, which prevents the muscle activation of other fingers, so that isolated finger movements can be extracted from a coarser synergy. The relatively uniform preshaping pattern in *cebus* suggests that this mechanism possibly is less elaborated in this genus. We propose recognition of two forms of hand movements: (a) digital individuation (as defined by Schieber, 1991) and (b) digital coordination. The term coordination refers to the fact that the central nervous system engages the muscles in a definite order so that their combined activities result in orderly movements (Weiss, 1941, Jeannerod, 1997). The first term defines the capacity to move fingers separately; the second defines the capacity to coordinate and to preshape single fingers for diverse grips. All capuchins were able to individuate their fingers. A differentiated preshaping between thumb and index finger mirrors the size of the object to be grasped. As the objects were small in our study, the aperture should have been small also. During less differentiated preshapings the fingers acted in concert, without a thumb-forefinger shaping. During differentiated preshapings, the thumb and index finger synchronized, with the index finger extended, while the digits III–V acted as a separate unit.

Hand Asymmetries

Our findings support the prediction of MacNeilage et al. (1987) that a right-hand preference should be evident in tasks requiring fine motor control, though our small N precludes a strong conclusion on this point. As others have found, more demanding tasks elicit stronger lateral bias (Anderson et al., 1996; Westergaard and Suomi, 1993). We found minimal evidence of performance asymmetries in speed of reaching. The most notable finding in this domain was that reaching with the right hand towards grooves was faster for subjects that had a right-hand preference for it. In this task, preshaping was slightly differentiated as the index was leading the reaching action, which indicates differentiated distal muscle coordination. Our finding supports the prediction that performance asymmetries occur in finely-controlled (contralateral) movements. We also have slight evidence that a left-hand preference appeared in tasks that allowed a uniform grip pattern during preshaping, i.e., where time-consuming fine-tuned muscle movements in space were absent, and reaching and grasping were quick. These findings underline the ballistic component of these actions, which, in humans, documents a right-hemispheric advantage for visuospatial functions (Geschwind and Galaburda, 1985).

Error and movement regularity of grasping are fine-grained measures for success of performance and asymmetry. Rigamonti and colleagues (1998) tested the success of grasping actions when *Macaca nemestrina* used their fingertips with a certain pressure to grasp pellets out of an opening in a horizontal wall. They found the following asymmetries in hand performances. Subjects with a right-hand preference consistently retained this preference across several tests. Subjects made fewer errors in dropping pellets when they used the preferred hand. The left hand, however, acted more quickly in picking up the objects. These findings show similarities to our results. However, we focused on other criteria of success. To gain insights into utmost routinized finger movements of *Cebus apella,* we scored movement durations after a number of trials when the subjects were practiced in using both hands in these conditions. Consequently, we focused on mean action duration and its movement regularity when reaching, grasping and hand retrieval occurred without errors, i.e. successful grasps. Nevertheless, our subjects often failed to achieve prehension on the first attempt to grasp the object. A preliminary examination of 10 actions with such errors showed that when grasping failed on the first attempt, in 8 of 10 cases the preceding reaches were distinctly slower than normally seen in successful attempts. This indicates that attention for success in grasping with either hand starts with reaching, as in humans (Jeannerod, 1997). Mean action time, however, does not provide full information about smooth and routinized performances. Movement regularity of subjects, measured as the variability of movement time within subjects, is a good criterion for fluctuation in performances. In our study, quick mean grasping time in easy tasks was associated with a high irregularity of movement times. In contrast, a relatively high regularity of grasping at difficult to handle grooves documents relatively stable, though long and effortful, performance. A higher regularity of the right than the left hand confirms the overall tendency for a right-hand advantage at difficult task.

CONCLUSION

Two differences with prehension in catarrhine primates stand out: capuchin thumbs achieve lateral opposability, rather than volar (tip-to-tip) opposability, and they sometimes exhibit a cleft during reaching and grasping, with the thumb and index finger placed on one side of an object and the other three fingers on the other side. Although capuchins have less differentiated control of the digits than those of humans and macaques, they display a small degree of manual preshaping during reaching. Capuchins can achieve coordinated movements of the digits in the course of reaching to grasp, but it appears more effortful and less lateralized than in Old World monkeys and humans. Moreover, although a slight dichotomy in hand preferences was detectable for tasks with different manipulative demands, overall small and inconsistent intermanual differences suggest that capuchins have greater symmetry of neural organization supporting prehensile activity than that of catarrhine primates.

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