



Hand preference in fast-moving versus slow-moving actions in capuchin, *Sapajus* spp., and squirrel monkeys, *Saimiri sciureus*



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Among the many hand preference studies on nonhuman primates, several have demonstrated the effect of diverse action demands on the direction and magnitude of hand preference. However, few studies have assessed hand preference in the natural repertoire of motor behaviours in nonhuman primates, especially in actions that differ in velocity. Nevertheless, velocity is involved in the coordination between the upper limb joints and could be related to cerebral hemispheric specialization. Indeed, depending on the velocity, some joints, and so some muscles, are used more than others. The purpose of this study was to quantify hand preference across various natural actions to evaluate how the nature of the action modifies hand preference in capuchin and squirrel monkeys. First, we observed seven female tufted capuchin monkeys during spontaneous foraging, performing fast actions (pounding and capturing fast-moving prey) and slow actions (picking fruit, carrying, tapping and catching slow-moving prey). Second, we observed seven squirrel monkeys performing fast actions (capturing fast-moving prey) and slow actions (picking fruit and catching slow-moving prey) in their enclosure. The results showed that (1) capturing fast-moving prey and pounding were associated with a left-hand preference and (2) slow actions were associated with variable hand preferences. Fast manual actions may elicit consistent hand preference. Given that many nonhuman primates use fast actions to capture prey, this possibility deserves further investigation. If this finding is confirmed, a novel link between motor control processes and hand preference can be pursued.

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Between 74% and 96% of humans exhibit a right-hand preference (Annett, 1985; Porac & Coren, 1981). This result is attributed to a left-hemispheric lateralization linked with manual control of dexterous actions and language. Among nonhuman primates, there is increasing evidence showing right-hand preference for fine manual movements at the population level during coordinated bimanual actions (e.g. *Cebus*: Spinozzi, Castorina, & Truppa, 1998; *Pan*: Hopkins, Stoinski, Lukas, Ross, & Wesley, 2003; *Macaca*: Westergaard & Suomi, 1996; *Papio*: Vauclair, Meguerditchian, & Hopkins, 2005) and left-hand preference for some unimanual tool-using tasks such as 'termite fishing' (*Pan*: Lonsdorf & Hopkins, 2005). The 'task complexity' theory (Fagot & Vauclair, 1991) suggests that hand preferences at the population level exist only for

'complex tasks' involving bimanual coordination or precise action. In the literature, more 'complex tasks' are associated with a stronger hand preference at the individual level than are simpler actions such as reaching (e.g. *Cebus*: Anderson, Degiorgio, Lamarque, & Fagot, 1996; Lilak & Phillips, 2008; Spinozzi et al., 1998; *Cercocebus*: Blois-Heulin, Guitton, Nedellec-Bienvenue, Ropars, & Vallet, 2006; *Gorilla*: Pouydebat, Reghem, Gorce, & Bels, 2010; *Pan*: Hopkins & Rabinowitz, 1997; *Papio*: Vauclair et al., 2005; for a review of earlier literature see Fagot & Vauclair, 1991), yet subjects do not consistently display reliable hand preferences across various complex actions (Fagot & Vauclair, 1991; sensu Anderson et al., 1996; Colell, Segarra, & Sabater-Pi, 1995; Spinozzi & Truppa, 1999). However, the actions used in these studies (e.g. grasping food on the ground or in a hole, reaching into a tube, inserting a probe, opening a box) do not correspond to all manual actions typically displayed by primates during foraging in natural conditions, such as prey capture. Some authors have found different results. For example, common marmosets, *Callithrix*

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jacchus, showed consistent hand preferences across tasks (Hook & Rogers, 2008), showing that task complexity is probably not the only factor involved. In addition, Rogers (2009) suggested that the nature of the task and its demands have more impact on hand preference than its apparent or inherent complexity. The relevant features of the task seem to be related to the type of object (animated or nonanimated) and to the constrained use of a specific hand/limb (e.g. Rogers, 2009). Indeed, there is now much evidence that these features affect manual preferences in both apes and human children (Forrester, Quaresmini, Leavens, Mareschal, & Thomas, 2013; Forrester, Quaresmini, Leavens, Spiezio, & Vallortigara, 2011; Forrester, Quaresmini, Leavens, & Vallortigara, 2012; Quaresmini, Forrester, Spiezio, & Vallortigara, 2014).

To capture small moving prey with the hand requires processing visuospatial information, such as velocity and trajectory of movement, to move the forelimb and grasp quickly (Hellner-Burris, Sobieski, Gilbert, & Phillips, 2010; Janson & Boinski, 1992; Nekaris, 2005; Niemitz, 1984). Given that capturing insects in the hand(s) is a primitive foraging strategy, in the sense of appearing as a distinguishing feature in early primates (Martin, 1990), it is possible that motor coordination supporting fast prey capture is a characteristic shared among primates. With rare exceptions in humans, fast reaching movements cannot be modified or adjusted by visual feedback during the motor performance (Keele & Posner, 1968; Woodworth, 1899). Slow movements induce a different type of motor control (concerning all the body parts, such as muscles, joints, bones and neural system, involved in the movement). Slow movements are visually guided and involve coordination of senses such as haptic (sense of touch), visual, kinaesthetic (sense of body and limb movement) or proprioceptive (sensibility of the nervous system to information arising from the muscles, joints and bones), allowing modulation in the course of the movement (Beaubaton, 1983; Jeannerod, 1983, 1984, 1990). Finally, in humans, some authors suggest that the hand preference depends on biomechanical factors and not on visual perception (Dounskaja, Wang, Sainburg, & Przybyla, 2014) as has also been suggested for foot preferences in birds (Tommasi & Vallortigara, 1999). In the course of evolution, hemispheric specialization emerged as motor complexity changed (Mutha, Haaland, & Sainburg, 2013). In particular, Mutha, Haaland, and Sainburg (2012) pointed out the importance of the left hemisphere during the learning of new sequences and skills related to predictive control (capacity of planning and coordinating motor actions). The right hemisphere is more important for encoding perceptual stimuli and 'for updating ongoing actions and stopping at a goal position, through modulation of sensorimotor stabilization mechanisms such as reflexes' (Mutha et al., 2012, p. 455).

The distinction in movement control between fast and slow prey capture movements appears to be phylogenetically widespread. King and Landau (1993), in a study with squirrel monkeys, suggested that catching moving objects may induce visually guided movements involving a motor system linked to the left hand. In contrast, grasping immobile objects may involve a motor system linked to the right hand. Data for other terrestrial tetrapods are relatively scarce, although it has been demonstrated that for rapid ballistic tongue projection in chameleons (Chamaeleonidae) and plethodontid salamanders (*Plethodontidae*), feed forward control, obtained from visual information preceding the movement, is required (Schaerlaeken, Meyers, & Herrel, 2007; see also Deban, 1997; Harkness, 1977). Visual information is the most important stimulus used for feeding behaviour (Anderson, 1993; Deban & Dicke, 2004; Valdez & Nishikawa, 1997). Finally, there is some evidence for specialization of the left hemisphere for planned manipulation actions and the right hemisphere for rapid responses, as in detection of novel stimuli (including moving prey) and escape

responses (MacNeilage, Rogers, & Vallortigara, 2009; Rogers, Vallortigara, & Andrew, 2013). In addition, the role of the left hemisphere in the control of feeding behaviour seems to be widespread among vertebrates (Vallortigara, 2000; Vallortigara, Chiandetti, & Sovrano, 2011). Thus, we can hypothesize that one part of the brain will be more specialized for fast actions dependent upon visual information, inducing manual laterality in order to be more efficient.

Pounding and tapping are two fast actions that capuchin monkeys (*Cebus* spp. and *Sapajus* spp.) commonly use in foraging. Pounding presents a different array of challenges for dexterous performance than capturing moving prey. It consists of striking an object (e.g. a nut) against a substrate in order to open it. The pounding action executed in our study required the use of the whole upper limb, bimanual coordination during repositioning the object in the hands (recognized to induce a hand preference, Fagot & Vauclair, 1988) and control of the pounding movement to produce enough force to break but not so much force as to crush the fruit or nut. The subject needs to stabilize its body posture and choose an appropriately rigid substrate (Pouydebat, Gorce, Bels, & Coppens, 2006). But pounding also involves a rapid visually guided movement. This action probably taps into the same action systems as prey capture. Finally, tapping involves rapidly striking the fingertips against a substrate, such as a branch or a hard fruit, apparently to determine the density of the material (Gunst, Boinski, & Frigaszy, 2010; Phillips, Goodchild, Haas, Ulyan, & Petro, 2004; Phillips, Grafton, & Haas, 2003; Visalberghi & Néel, 2003). This is a fast action but, unlike pounding and capturing moving prey, not necessarily visually guided. So, from the point of view of hand preference associated with fast action, it is also an interesting action to study.

Grasping fruit or other plant parts is a slow action in comparison to prey capture or pounding, and gorillas, *Gorilla gorilla*, and chimpanzees, *Pan troglodytes*, do not have a hand preference for grasping stationary food (Pouydebat, Reghem, Borel, & Gorce, 2011; Pouydebat et al., 2010). In contrast, in many primates and rats, *Rattus norvegicus*, grasping stationary food induces a strong use of the nearest hand to the location of the food (Ivanco, Pellis, & Whishaw, 1996; Lehman, 1993; Meunier, Blois-Heulin, & Vauclair, 2011; Warren, 1980). The subject does not have to anticipate motion of a stationary item and the forelimb movement is more stereotypical than for grasping a moving target (Christel & Billard, 2002; Reghem, Tia, Bels, & Pouydebat, 2011). However, a group bias, but not a population bias, favouring the use of the right paw for reaching in rats has been reported (Güven, Elalmis, Binokay, & Tan, 2003). Finally, carrying an object is also a slow action in the sense that the hand is not moving, or moving slowly in comparison to the whole body.

Tufted capuchin monkeys are ideal primates for investigating the relationship between 'natural' foraging actions and hand preference for several reasons. These monkeys are known for the flexibility of their foraging behaviour (Fragaszy, Visalberghi, & Fedigan, 2004), consuming a wide range of plant and animal foods, including moving insects, lizards, small rodents, coati and fish (Jack, 2007; Mendes, Martins, Pereira, & Marquezan, 2000; Rose, 1997). Although numerous primates catch and eat invertebrate prey, capuchins (*Sapajus* spp. and *Cebus* spp.) are one of the few species, along with chimpanzees, bonobos, *Pan paniscus*, and vervet monkeys, *Chlorocebus pygerythrus* (Fairbanks, 1984; Hohmann & Fruth, 2008; Wrangham & van Zinnicq Bergmann Riss, 1990) that catch and consume vertebrate prey (Fragaszy et al., 2004). Capuchins are also known for the multitude of manual actions performed during foraging such as pounding, ripping, tapping, carrying and probing (e.g. Fragaszy et al., 2004; Pouydebat et al., 2006).

Squirrel monkeys are also of interest. Indeed, previous studies with this species have documented unimanual behaviours including reaching (Aruguete, Ely, & King, 1992; Laska, 1996; McGonigle & Flook, 1978), grasping food items from a rotating tray (with and without vision, and from smooth and grooved surfaces: Costello & Frigaszy, 1988), a task necessitating skilled digit movement (Nudo, Jenkins, Merzenich, Prejean, & Grenda, 1992), and reaching for food in various body postures (Roney & King, 1993). King and Landau (1993) found that in squirrel monkeys the capture of moving objects was linked to the left hand whereas grasping immobile objects was linked to the right hand. We suggest that each of these actions presents different constraints (i.e. spatial organization, eye–hand coordination, movement anticipation and/or body posture) that could influence hand preference.

It is worth investigating whether fast foraging actions (i.e. prey capture and pounding) are associated in primates with a different degree or direction of hand preference than slower foraging actions or actions that do not require visual orientation. The purpose of this study was to collect hand preference data during spontaneous foraging to evaluate how the nature of the action influences the expression of hand preference. To meet this aim, we quantified the effect of the task on hand preference in capuchins and squirrel monkeys, housed in different environments (i.e. a naturalistic setting and more controlled conditions, respectively). They were expected to display a stronger hand preference for fast, visually guided actions (pounding and capturing fast-moving prey) than for slow actions (fruit grasping, carrying and slow-prey catching) or fast but nonvisually guided actions (tapping).

METHODS

Ethical Note

The research complied with protocols approved by the legal requirements of the European Union and adhered to the legal requirements of France, the country in which the research was conducted. It also adhered to the ASAB/ABS guidelines for the use of animals in research.

Subjects

Capuchins

Behavioural data were collected for seven adult female (8–24 years old, mean \pm SD = 15.8 \pm 4.9 years old) tufted capuchins housed at the Monkey Valley, in Romagne, France. (See Lynch Alfaro, Boubli, et al. (2012) and Lynch Alfaro, De Sousa e Silva, and Rylands (2012) for recent changes in taxonomy.) All individuals were mother-raised and all except the oldest female were born in captivity. Observations were collected under semifree conditions, as the monkeys resided in an outside area (about 5000 m²) that was surrounded by water and contained rich vegetation, a brook, many trees such as sweet chestnut, *Castanea sativa*, and hawthorn, *Crataegus monogyna*, numerous bushes, grass, earth and various indigenous animals (rodents, birds, invertebrates, frogs, fishes).

Squirrel Monkeys

Behavioural data were collected for seven squirrel monkeys (1–14 years old, mean \pm SD = 7.28 \pm 5.7 years old) housed at the Tropical Zoo of La Londe les Maures in France. All the subjects were living in their social group. They resided outdoors in a wire enclosure (11 \times 6 m and 3.50 m high) connected with a covered building in which they could circulate freely during the day. The enclosure contained a rich vegetation (bamboo, diverse bushes) and tree trunks and the ground was covered with bark allowing

naturalistic foraging. The individuals were given vegetables and a fruit three times a day, occasional mealworms and hard-boiled eggs three times a week. They also ate insects that they found in their enclosure and had access to pellets and water ad libitum.

Procedure

For all behaviours, we waited until individuals of both species had both hands free before recording a new behaviour. Also, for each action in both species, we considered bout and not frequency in order to avoid overestimation of hand preference. In statistical tests, we considered only individuals with more than 15 responses (Garber, Gomes, & Bicca-Marques, 2008; Meguerditchian, Calcutt, Lonsdorf, Ross, & Hopkins, 2010) for both species except for capuchins capturing fast-moving prey (a relatively rare action) for which we report all cases. As we made observations in real time, some actions may not have been recorded. Thus, our data represent a sampling of actions rather than true frequencies of actions.

Capuchins

A single observer recorded hand use for unimanual behaviours using ad libitum sampling techniques (Altmann, 1974) during feeding times and other daily activities, from 0800 to 1800 hours 5 days per week for 3 months. Several juveniles were in the same enclosure but were not observed during this study. The following behaviours were recorded: grasping fruit, tapping, carrying, catching slow-moving prey, capturing fast-moving prey and pounding (cracking walnuts against substrates). If multiple capuchins were performing these behaviours, we focused on the one that had the fewest number of recorded observations among the most visible subjects (because some capuchins foraged and manipulated more frequently than others) to obtain the highest number of observations for each subject (Meguerditchian, Calcutt, et al., 2010).

Grasping fruit was recorded when a subject grasped a hawthorn fruit (width: 0.6 cm; length: 1 cm) available in the enclosure trees. As the food was static, this unimanual action involved slow movements and was not very challenging for capuchins in terms of upper limb coordination (velocity, $v = 702 \pm 160$ mm/s). However, it was sometimes challenging in terms of body posture. Indeed, capuchins needed to stabilize their body on the branches, leaving both of their hands free before grasping the fruits. A single bout was coded when a subject grasped the fruit. The bout was considered finished when the subject ate the fruit or if the subject repositioned itself and moved to another location (Meguerditchian, Calcutt, et al., 2010). Tapping was recorded when a subject used the fingertips of one hand to tap against a branch. This action always involved a rhythmic series of rapid taps on one branch with the fingers of one hand ($v = 1452 \pm 174$ mm/s); therefore the tapping of one branch constituted a bout. The bout was considered finished when the subject stopped the sequence by changing location and/or branch. Carrying was coded when an individual transported an object (nut, branch, small prey or sweet chestnut) in one hand over more than 1 m. In terms of velocity it was the slowest movement since the object did not move during the transport. A single bout was considered finished when the subject deposited the object on any substrate. Catching occurred when capuchins grasped slow-moving prey (snails, worms or slugs). This action looked like grasping fruit in terms of upper limb coordination (the movements were always slow: $v = 740 \pm 142$ mm/s) but different in terms of detection (fruits are easy to detect from a distance whereas snails, worms or slugs were detected after searching on the ground). A single bout was recorded when a subject caught a prey item. The bout was considered finished when the subject ate the prey. Capturing

fast-moving prey (frog, mouse or flying insect) always involved fast movement ($v = 1604 \pm 204$ mm/s). A single bout was recorded when a subject captured the prey. The bout was considered finished when the subject ate the prey, abandoned it or began to play with it. Finally, pounding occurred when subjects used their hands to crack open a walnut against a substrate. Capuchins use one hand almost exclusively during this action and choose the hardest substrates to optimize opening the nut (Pouydebat et al., 2006). This movement must be fast and was always rapid in our study ($v = 1345 \pm 131$ mm/s), but was executed with control to open the nut without crushing the kernel. Walnuts were the only food distributed by humans each day in the present study. They were abundantly dispersed (16 per day) in the capuchins' enclosure to minimize competition between subjects. A bout was recorded when a subject began pounding a walnut. The bout was considered finished when the subject opened the walnut (the capuchins never changed hands during pounding).

Squirrel monkeys

Data were collected between 1000 and 1600 hours 6 days a week for 4 months. Data were collected through two sessions of 2 h each per day using all-occurrences sampling, as used by Meguerditchian, Vauclair, and Hopkins (2010, p. 42): 'the social groups were randomly observed during an observation session and an all occurrences sampling procedure was used in which responses of each individual were collected opportunistically when behaviour of interest occurred'. All the members of the group had access to the food. Two observers (observing the same events) recorded hand use for unimanual behaviours in real time. Each person coded the same behaviours as the other at the same time, for the same animal, but only one code per event was used in the analysis. Before the observation, it had been decided that when there was a discrepancy between the two coders the event would not be taken into account. However, no discrepancy was found between coding of observers during this study. A session was stopped when there was no more food on the ground or when the 2 h were over.

The observed behaviours included hand grasping of three types of food: pieces of apple grasped with slow movements, mealworms also grasped with slow movements and crickets grasped with fast movements ($v = 802 \pm 151$ mm/s, $v = 832 \pm 173$ mm/s and $v = 1711 \pm 207$ mm/s, respectively). We tried providing the monkeys with dead crickets in order to replace pieces of apple but they did not show any interest even after several presentations. All of the items were of nearly the same size in order to avoid an effect on hand preference (Hopkins et al., 2005; Hopkins, Cantalupo, Wesley, Hostetter, & Pilcher, 2002). The size of all the items provided favoured a power grip (a grasp with the whole hand, palm and fingers) and limited variability in manual postures which could also induce differences in hand preference (Pouydebat, n.d.). We gave 10 items of each category of food during each session. The food was dispersed widely in order to avoid competition between the subjects. During the experiment, the mealworms and the crickets moved freely until captured by the subjects.

Individual Hand Preference in Each Action

Two measures allowed us to evaluate the monkeys' hand preference during unimanual feeding behaviour. First, a two-tailed binomial test based on the total number of bouts of right- and left-hand responses gave a z score and the corresponding P value for each subject (Forsythe & Ward, 1988; Hopkins, 1999). Monkeys with z scores higher than 1.96 or lower than -1.96 (corresponding to an α level of 5%) were classified as having a right- or left-hand preference, respectively. Between these values, monkeys were

considered as ambipreferent. To remain comparable with most of the previously published studies on this topic we classified hand preference on the z score and unadjusted P value. However, adjusted P values with correction for multiple testing (e.g. McGrew & Marchant, 1997) by the Holm - Bonferroni method (Holm, 1979) are also presented in Table 1. The z score is very sensitive to the sample size (Hopkins, 1999) so we also used an individual handedness index (HI) which gives information about the degree of hand asymmetries. The HI is calculated for each subject using the formula $(RH - LH)/(RH + LH)$, in which RH and LH are the total number of right- and left-hand responses, respectively (Lonsdorf & Hopkins, 2005; Spinuzzi & Cacchiarelli, 2000). This measure varies from -1.0 (strong LH preference) to 1.0 (strong RH preference). The laterality package (Borel, Pouydebat, & Reghem, 2012) for R (R Core Team, 2013) was used for these data analyses and for plotting the graphs.

Group Hand Preference in Fast- and Slow-moving Actions

We examined our data for evidence of group response tendencies. To test our hypothesis about the different degree and direction of hand preference between actions involving fast-moving and visually guided actions (pounding and capturing fast-moving prey) and slow-moving and/or not visually guided actions (carrying, fruit grasping, catching slow-prey and tapping) in capuchins, the data of all subjects were fitted with a generalized linear mixed model (GLMM) following the recommendations of Bolker et al. (2009) and Moscatelli, Mezzetti, and Lacquaniti (2012). The full data set from squirrel monkeys involving the capture of fast-moving prey (crickets), slow-moving prey (mealworms) and static food grasping (piece of apple) was fitted with the same kind of model. These models separately account for random effects and fixed effects (Agresti, 2013) and are suitable for dealing with repeated measures on the same individuals and different numbers of observations (bouts) per subject. We fitted the model using the Laplace approximation and restricted maximum likelihood except for comparing models with different fixed effects where we used maximum likelihood. We used a binomial error distribution with a 'logit' link function as our response was the hand (left versus right) used by both species for each observation. We included one random effect (the random intercept) at the individual level to account for repeated measurements on several individuals and one fixed-effect parameter corresponding to the kind of action (with 'carrying' as the reference level for capuchins as this task involves no movement of the hand, as the object is already grasped, and with static food grasping as the reference level for squirrel monkeys) carried out by the monkeys. We noticed some overdispersion in our models and thus included a random effect at the observation level (see Bolker et al., 2009). However, this did not provide any improvement so we did not retain this parameter. To make inferences about random effects we compared the full model with reduced models using the corrected quasi-Akaike information criterion (QAICc) to account for overdispersion and small sample size and ran the likelihood ratio test via ANOVA and parametric bootstrap comparison with 1000 replicates (see Bolker et al., 2009).

Inferences about fixed effects were made comparing the full model with the reduced model using QAICc and parametric bootstrap comparison with 1000 replicates using the 'pbkrtest' from Halekoh and Højsgaard (2012). Finally, we performed multilevel bootstrapping with 1000 replicates to obtain simulated estimates and confidence intervals. GLMM was fitted using the R package 'lme4' (Bates, Maechler, & Bolker, 2012) and the functions of Bolker et al. (2009).

Table 1
Individual frequencies of left- and right-hand use and hand preference for each action among capuchins

	Subjects	Age	LH	RH	No. of observations	HI	z	P	adj. P	Hand
Fruit grasping (mean=22.14, SD=2.61)	Sarah	24	8	13	21	0.24	1.09	0.275	1.000	A
	Sandra	18	10	12	22	0.09	0.43	0.670	1.000	A
	Pia	17	12	12	24	0.00	0.00	1.000	1.000	A
	Silke	17	11	14	25	0.12	0.60	0.549	1.000	A
	Francisca	14	5	18	23	0.57	2.71	0.007	0.215	RH*
	Paula	13	5	12	17	0.41	1.70	0.090	1.000	A
	Sunny	8	6	17	23	0.48	2.29	0.022	0.545	RH*
Tapping (mean=19.43, SD=1.81)	Sarah	24	10	10	20	0.00	0.00	1.000	1.000	A
	Sandra	18	6	15	21	0.43	1.96	0.050	1.000	RH*
	Pia	17	9	12	21	0.14	0.65	0.513	1.000	A
	Silke	17	10	7	17	-0.18	-0.73	0.467	1.000	A
	Francisca	14	6	15	21	0.43	1.96	0.050	1.000	RH*
	Paula	13	10	7	17	-0.18	-0.73	0.467	1.000	A
	Sunny	8	7	12	19	0.26	1.15	0.251	1.000	A
Carrying (mean=14.14, SD=6.49)	Sarah	24	6	9	15	0.20	0.77	0.439	1.000	A
	Sandra	18	9	7	16	-0.13	-0.50	0.617	1.000	A
	Pia	17	6	15	21	0.43	1.96	0.050	1.000	RH*
	Silke	17	—	—	—	—	—	—	—	—
	Francisca	14	6	15	21	0.43	1.96	0.050	1.000	RH*
	Paula	13	—	—	—	—	—	—	—	—
	Sunny	8	7	8	15	0.07	0.26	0.796	1.000	A
Catching slow-moving prey (mean=13.29, SD=4.50)	Sarah	24	6	9	15	0.20	0.77	0.439	1.000	A
	Sandra	18	9	7	16	-0.13	-0.50	0.617	1.000	A
	Pia	17	4	13	17	0.53	2.18	0.029	0.697	RH*
	Silke	17	—	—	—	—	—	—	—	—
	Francisca	14	3	13	16	0.63	2.50	0.012	0.348	RH*
	Paula	13	—	—	—	—	—	—	—	—
	Sunny	8	7	8	15	0.07	0.26	0.797	1.000	A
Capturing fast-moving prey (mean=5.86, SD=4.88)	Sarah	24	8	1	9	-0.78	-2.33	0.020	0.530	LH*
	Sandra	18	7	0	7	-1.00	-2.65	0.008	0.253	LH*
	Pia	17	10	2	12	-0.67	-2.31	0.021	0.544	LH*
	Silke	17	2	1	3	-0.33	-0.58	0.564	1.000	A
	Francisca	14	9	1	10	-0.80	-2.53	0.011	0.342	LH*
	Paula	13	—	—	—	—	—	—	—	—
	Sunny	8	—	—	—	—	—	—	—	—
Pounding (mean=59.29, SD=21.22)	Sarah	24	46	21	67	-0.37	-3.05	0.002	0.077	LH*
	Sandra	18	38	19	57	-0.33	-2.52	0.012	0.344	LH*
	Pia	17	51	24	75	-0.36	-3.12	0.002	0.064	LH*
	Silke	17	52	39	91	-0.14	-1.36	0.173	1.000	A
	Francisca	14	41	15	56	-0.46	-3.47	0.001	0.018	LH*
	Paula	13	14	12	26	-0.08	-0.39	0.695	1.000	A
	Sunny	8	31	12	43	-0.44	-2.90	0.004	0.124	LH*

Mean: mean of individual responses; SD: standard deviation of individual responses; age in years; LH: frequency of left-hand use; RH: frequency of right-hand use; no. of observations: total number of observations; HI, Handedness Index score that corresponds to the degree of manual asymmetry, the sign indicates the direction of the manual bias (negative value: left-hand bias; positive value: right-hand bias); z: individual z score; hand: hand preference based on the result of the z score (RH: subject with right-hand preference; LH: subject with left-hand preference; A: ambipreferent subject). P: P value of the two-tailed binomial test that gave the z score. adj. P: P value corrected for multiple tests with the Holm - Bonferroni method. Italicized data indicate that we did not obtain a minimum of 15 responses (preliminary result).

* $P < 0.05$.

Finally, the effect of the number of observations on the hand preference was visualized with funnel plots (Palmer, 2002). No particular effect was noticed (see 'No. of observations' and 'Hand' in Tables 1 and 2).

RESULTS

Descriptive Information

We coded 939 bouts from the seven capuchins and 1065 bouts from the seven squirrel monkeys. The number of bouts per subject varied from 73 to 170 for all actions (mean \pm SD = 134.14 \pm 31.46) for capuchins and from 110 to 304 (mean \pm SD = 152.14 \pm 68.25) for squirrel monkeys. Tables 1 and 2 present the data on hand preference for each action in

capuchins and squirrel monkeys, respectively. The details of the bouts of left- and right-hand use, associated HI, z scores and P values are also included.

Direction of Individual Hand Preferences in Each Action

Capuchins

The number of bouts per subject for fruit grasping varied from 17 to 25 among the seven capuchins (155 total bouts recorded). Two individuals showed a right-hand preference (two-tailed binomial test: $P < 0.05$; see Table 1 for all exact P values) whereas all others were ambipreferent ($P > 0.05$).

Bouts per individual varied from 17 to 21 for tapping (136 total bouts recorded). Two individuals showed a right-hand preference ($P < 0.05$) whereas all others were ambipreferent ($P > 0.05$).

Table 2
Individual frequencies of left- and right-hand use and hand preference for each action among squirrel monkeys

	Subjects	Age	LH	RH	No. of observations	HI	z	P	adj. P	Hand
Fruit grasping (mean=54.43, SD=12.31)	Crapiti	1	14	38	52	0.46	3.33	0.001	0.014	RH*
	Crapoto	1	40	34	74	-0.08	-0.70	0.486	1.000	A
	Line	10	18	40	58	0.38	2.89	0.004	0.053	RH*
	Maxou	14	14	23	37	0.24	1.48	0.139	0.973	A
	West	11	32	31	63	-0.02	-0.13	0.900	1.000	A
	Xena	11	31	12	43	-0.44	-2.90	0.004	0.053	LH*
	Yoda	3	41	13	54	-0.52	-3.81	0.000	0.002	LH*
Catching slow-moving prey (mean=57.71, SD=56.31)	Crapiti	1	17	18	35	0.03	0.17	0.866	1.000	A
	Crapoto	1	24	11	35	-0.37	-2.20	0.028	0.280	LH*
	Line	10	15	15	30	0.00	0.00	1.000	1.000	A
	Maxou	14	28	14	42	-0.33	-2.16	0.031	0.280	LH*
	West	11	23	11	34	-0.35	-2.06	0.040	0.317	LH*
	Xena	11	164	21	185	-0.77	-10.51	<0.001	<0.001	LH*
	Yoda	3	41	2	43	-0.91	-5.95	<0.001	<0.001	LH*
Capturing fast-moving prey (mean=40, SD=17.47)	Crapiti	1	11	19	30	0.27	1.46	0.144	0.973	A
	Crapoto	1	18	11	29	-0.24	-1.30	0.194	0.973	A
	Line	10	20	8	28	-0.43	-2.27	0.023	0.257	LH*
	Maxou	14	24	7	31	-0.55	-3.05	0.002	0.034	LH*
	West	11	26	11	37	-0.41	-2.47	0.014	0.164	LH*
	Xena	11	67	9	76	-0.76	-6.65	<0.001	<0.001	LH*
	Yoda	3	42	7	49	-0.71	-5.00	<0.001	<0.001	LH*

Mean: mean of individual responses; SD: standard deviation of individual responses; age in years; LH: frequency of left-hand use; RH: frequency of right-hand use; no. of observations: total number of observations; HI, Handedness Index score that corresponds to the degree of manual asymmetry, the sign indicates the direction of the manual bias (negative value: left-hand bias; positive value: right-hand bias); z: individual z score; hand: hand preference based on the result of the z score (RH: subject with right-hand preference; LH: subject with left-hand preference; A: ambipreferent subject). P: P value of the two-tailed binomial test that gave the z score. adj. P: P value corrected for multiple tests with the Holm - Bonferroni method.

* $P < 0.05$.

The number of bouts for carrying varied from four to 21 (99 total bouts recorded). In carrying, two subjects showed a right-hand preference ($P < 0.05$) and the five others were ambipreferent ($P > 0.05$). Two subjects had only four and seven bouts, respectively.

Bouts per subject for catching slow-moving prey varied from five to 17 (93 total bouts recorded). Two subjects showed a right-hand preference ($P < 0.05$). One subject caught only five slow-moving prey and another only nine. For fast-moving prey capture, the number of bouts per subject varied from 0 to 12 (41 total bouts recorded). Four individuals showed a left-hand preference ($P < 0.05$) whereas one was ambipreferent ($P > 0.05$).

The number of bouts per subject varied from 26 to 91 for pounding behaviours (415 total bouts recorded). Five of the subjects showed a left-hand preference ($P < 0.05$) whereas two were ambipreferent ($P > 0.05$).

At the individual level, we clearly saw an effect of the actions on hand preference (Fig. 1, Table 1). Four of five capuchins used their left hands significantly more often to capture fast-moving prey and five of seven to pound. Two individuals did not show any hand preference regardless of the action ($P > 0.05$). One was lateralized for all the actions, towards the right hand for fruit grasping, catching slow prey, tapping and carrying and towards the left hand for capturing fast prey and pounding.

Squirrel monkeys

The number of bouts per subject for fruit grasping varied from 37 to 74 among the seven individuals (381 total bouts recorded). Two individuals showed a right-hand preference and two a left-hand preference (two-tailed binomial test: $P < 0.05$; see Table 2 for all exact P values). The others were ambipreferent ($P > 0.05$).

For catching slow-moving prey, bouts per subject varied from 30 to 185 (404 total bouts recorded). Five subjects showed a left-hand preference ($P < 0.05$) and two were ambipreferent.

We recorded 28 to 76 bouts per subject for fast-moving prey capture (280 total bouts recorded). As for the mealworms, five subjects showed a left-hand preference ($P < 0.05$). The other two subjects, the two youngest males, demonstrated no hand preference.

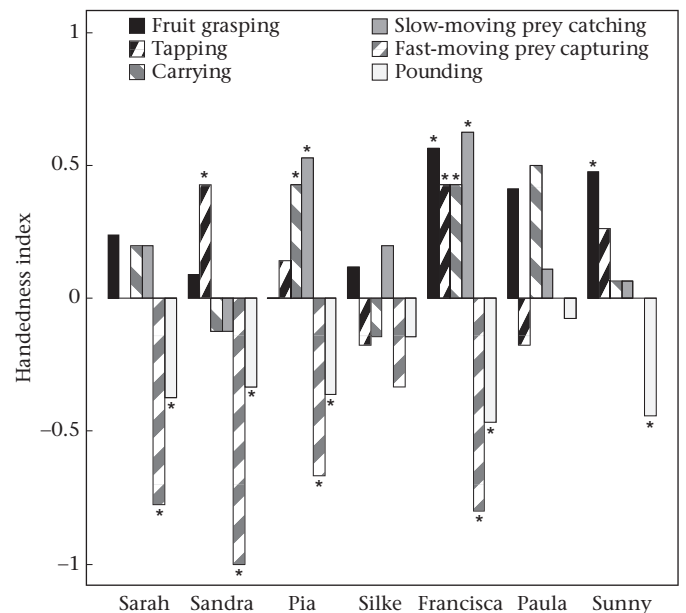


Figure 1. Degrees of individual hand preference (handedness index, HI) for actions among capuchins. Asterisks refer to the result of the two-tailed binomial test and indicate that the observed proportion of right- and left-hand use differs significantly from a proportion that could be obtained by chance ($P < 0.05$). The sign of the HI values indicates the direction of the individual hand preference: positive = individual right-hand preference, negative = individual left-hand preference.

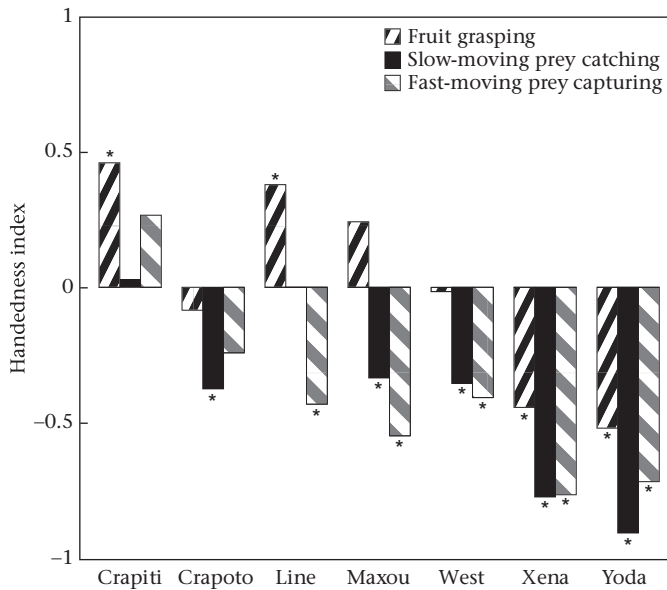


Figure 2. Degrees of individual hand preference (handedness index, HI) for actions among squirrel monkeys. Asterisks refer to the result of the two-tailed binomial test and indicate that the observed proportion of right- and left-hand use differs significantly from a proportion that could be obtained by chance ($P < 0.05$). The sign of the HI values indicates the direction of the individual hand preference: positive = individual right-hand preference, negative = individual left-hand preference.

At the individual level, we clearly saw an effect of the actions on hand preference (Fig. 2, Table 2). Five of seven squirrel monkeys used their left hand significantly more often to capture moving prey, either fast or slow. Two individuals (Xena and Yoda) used the left hand significantly more often than the right hand independent of the action. However, when the individuals had a hand preference for catching prey it was always a left-hand preference whereas it could be either left or right when grasping static food items.

Group Hand Preference in Fast- and Slow-moving Actions

Capuchins

Handedness is a function of the individual and 'group' level or 'population' level hand preference exists only when a majority of individuals exhibit that preference (Ward, Milliken, & Stafford, 1993). Therefore, our results, while providing a reliable measure of individual preferences, should be considered with more caution at the group level, given our small sample size. Comparisons between the full model (see Data analysis in Methods section) and the reduced model (i.e. with no random effect at the individual level) showed that the effect of the individuals was not significant (QAICc of the full model = QAICc of the reduced model = 1223.187; likelihood ratio test via ANOVA: $\chi^2_1 = 0$, $P = 0.5$; parametric bootstrap comparison test: $P = 1$). However, this random effect is part of the experimental design so we kept it in the model. Comparisons between the model including versus not including the fixed effect showed a strong effect of the type of action in which the capuchins were involved (QAICc of the full model = 1223.187 < QAICc of the reduced model = 1302.281; parametric bootstrap comparison test: $P < 0.01$). The estimates of the fixed effects of the full model (Table 3) showed that two modalities were significant: for pounding ($P < 0.05$), a one unit increase is associated with a 1.085 unit decrease in the expected logit of the hand used; for catching fast-moving prey ($P < 0.05$), a one unit increase is associated with a 2.405 unit decrease in the expected logit of the hand used. In other words, capuchins involved in pounding and catching

Table 3
Fixed-effects parameters of the GLMM for capuchins

Variables	Estimate	SE	z	P	Bootstrap with 1000 replicates		
					Mean	0.025	0.975
(Intercept)	0.431	0.206	2.094	0.036	0.440	-0.096	0.993
Fruit grasping	0.111	0.265	0.420	0.675	0.133	-0.580	0.806
Catching	0.074	0.297	0.250	0.802	0.097	-0.506	0.746
slow-moving prey							
Tapping	-0.135	0.269	-0.500	0.617	-0.137	-0.913	0.691
Pounding	-1.085	0.230	-4.710	<0.001	-1.113	-1.769	-0.454
Capturing	-2.405	0.520	-4.628	<0.001	-2.948	-4.583	-1.352
fast-moving prey							

No. of observations = 939. Estimates and SE as well as z and P values were computed with the 'glmer' function of the package 'lme4' for R. Multilevel bootstrap results (mean and 95% confidence interval) obtained from 1000 replicates are also given. Statistically significant results are in bold. The variance and SD of the random effects (i.e. the seven individuals) are <0.001.

fast-moving prey are expected to have, respectively, 1.085 and 2.405 higher log odds of using the left hand than capuchins involved in carrying (as carrying was used as the reference level). The results of the multilevel bootstrapping with 1000 replicates confirmed this tendency (Table 3). The results also showed that the hand preference for fruit grasping, slow-moving prey catching and tapping did not differ significantly from what could be expected for carrying.

Squirrel monkeys

As for capuchins, group responses were estimated using GLMM. Comparisons between the full model (see Data analysis in Methods section) and the reduced model (i.e. with no random effect at the individual level) showed that the random effect of the individuals was significant (QAICc of the full model = 1190.245 < QAICc of the reduced model = 1288.94; likelihood ratio test via ANOVA: $\chi^2_1 = 98.695$, $P < 0.01$; parametric bootstrap comparison test: $P < 0.01$). Comparisons between the model including versus not including the fixed effect showed a strong effect of the type of action in which the squirrel monkeys were involved (QAICc for the full model = 1190.245 < QAICc for the reduced model = 1226.975; parametric bootstrap comparison test: $P < 0.01$). The estimates of the fixed effects of the full model (Table 4) showed that the effects of both slow- and fast-moving prey catching were significant: for mealworm captures ($P < 0.01$), a one unit increase is associated with a 0.951 unit decrease in the expected logit of the hand used; for cricket captures ($P < 0.01$), a one unit increase is associated with a 0.938 unit decrease in the expected logit of the hand used. In other words, squirrel monkeys catching mealworms and crickets are expected to have, respectively, 0.951 and 0.938 higher log odds

Table 4
Fixed-effects parameters of the GLMM for squirrel monkeys

Variables	Estimate	SE	z	P	Bootstrap with 1000 replicates		
					Mean	0.025	0.975
(Intercept)	-0.028	0.309	-0.090	0.928	-0.029	-0.541	0.509
Catching	-0.951	0.172	-5.525	<0.001	-0.954	-1.328	-0.586
slow-moving prey							
Capturing	-0.938	0.182	-5.148	<0.001	-0.955	-1.513	-0.430
fast-moving prey							

No. of observations = 1065. Estimates and SE as well as z and P values were computed with the 'glmer' function of the package 'lme4' for R. Multilevel bootstrap results (mean and 95% confidence interval) obtained from 1000 replicates are also given. Statistically significant results are in bold. The variance and SD of the random effects (i.e. the seven individuals) are, respectively, 0.586 and 0.765.

of using the left hand than squirrel monkeys grasping fruit. The results of the multilevel bootstrapping with 1000 replicates confirmed this similar tendency for both actions of moving prey catching (Table 4).

DISCUSSION

This study supplies new data on hand preference during spontaneous natural foraging actions in tufted capuchin and squirrel monkeys even if our small sample size (seven individuals per species) limits the power and generalizability of our arguments. The most important findings of the study are that fast capture actions induced a left-hand preference in the majority of our seven posturally unconstrained monkeys for each species, and suggested a tendency to favour the left hand at the group level for this kind of activity. These findings open new questions about the relation between actions and hand preference.

In squirrel monkeys, only the two juveniles lacked a left-hand preference for fast-moving prey capture, which may be due to their limited experience. Indeed, grasping crickets requires good coordination in time and space, a capacity that the juvenile squirrel monkeys may not yet have developed. In many cases, we observed the juveniles trying and failing, compared with adults who more often succeeded. Some studies have shown that hand preference can be related to the age of nonhuman primates and varies among species (e.g. chimpanzees: Bard, Hopkins, & Fort, 1990; capuchin monkeys: Westergaard & Suomi, 1993; marmosets: Hook & Rogers, 2000; for more examples on New World primates see also the review from Hook-Costigan & Rogers, 1996). Bard et al. (1990) found significant right-hand bias among infant chimpanzees (i.e. less than 3 months old) in hand-to-mouth behaviours. Hook and Rogers (2000) reported that hand preference reaches adult form between 5 and 12 months in marmosets. Westergaard and Suomi (1993) showed that immature individuals (i.e. less than 4 years old) exhibit a weaker lateral bias than do adults with a lower proportion of right-handed sponging actions.

Contrary to our findings of left-hand preference for four of five female capuchins in capturing crickets, a previous study in which tufted capuchin monkeys captured freely swimming small fish reported a significant left-hand preference for male capuchins ($N = 3$) whereas females ($N = 4$) showed no significant hand preference (Hellner-Burris et al., 2010). Sex may not be a parameter influencing the hand preference in capuchins. However, a left-hand bias for capturing moving prey with rapid actions is in accord with findings from several previous studies with humans, strepsirrhines, monkeys and cats, *Felis silvestris catus*. Several studies have pointed to a left-hand preference for food and insect grasping in lemurs (*Lemur macaco*: Forsythe & Ward, 1988; male *Propithecus verreauxi coquereli*: Mason, Wolfe, & Johnson, 1995; lemur spp.: Ward, Milliken, Dodson, Stafford, & Wallace, 1990; prosimians: Ward et al., 1993). Others documented left-hand preference in platyrrhines for prey capture (squirrel monkeys: King & Landau, 1993). Cats, use predominantly the left paw to grasp small moving targets (Fabre-Thorpe, Fagot, Lorincz, Levesque, & Vauclair, 1993).

In capuchins, pounding to crack walnuts involved a left-hand preference for five subjects and no hand preference for two subjects. We found a tendency towards the use of the left hand at the group level, with due caution because of our small sample. This result is very different from those obtained by Panger (1998) who found that three wild white-faced capuchins, *Cebus capucinus*, showed right-hand preference and two showed left-hand preference for similar pounding actions (called 'object-substrate use' in Panger's study). However, for all the actions studied by Panger (carrying, tapping, fruit grasping and pounding), the pounding

actions showed the most extreme individual deviations from symmetrical hand use.

What is special about pounding and fast prey capture compared with other foraging actions? Prey capture in primates probably involves special coordination of the upper limb with visual perception. This is suggested by the finding that mouse lemurs, *Microcebus murinus*, grab stationary food with the mouth but moving prey with the hands (Toussaint et al., 2013). In primates, catching fast-moving prey involves the integration of visuospatial information about the trajectory and speed of the prey with aimed rapid movement of the forelimb (Hellner-Burris et al., 2010). The right hemisphere is known to be used for spatial processing in many species (rats: Cowell, Waters, & Denenberg, 1997; chickens, *Gallus gallus domesticus*: Tommasi & Vallortigara, 2004; humans: Wendt & Risberg, 1994; De Renzi, 1982; other species: Vallortigara & Rogers, 2005). Bryden (1982) showed that the right hemisphere in humans is specialized in the visuospatial domain and it is well known for its spatial function in humans (De Renzi, 1982) and other species (Vallortigara & Rogers, 2005). Guiard, Diaz, and Beaubaton (1983) found a left-hand preference for 'ballistic' movement in humans. More generally, a left-visual field/right-hemisphere advantage for left-hand movements to targets moving along perceived trajectories exists in humans (Boulinguez, Ferrois, & Graumer, 2003).

Carson, Goodman, Kelso, and Elliott (1995) demonstrated that when humans do not have the time to prepare and anticipate their pointing movement (movement executed in the direction of a target), they show a left-hand preference. Our results suggest that a similar process may also exist in nonhuman primates, as we found a left-hand preference for most individuals when capturing fast-moving prey, as have others (see above). MacNeilage, Studdert-Kennedy, and Lindblom (1987) have suggested that a precursor to this right-hemisphere spatial specialization in humans may be evident in the left-hand preference for unimanual prey capture in strepsirrhines. However, right-hemisphere specialization has been demonstrated in various vertebrate species and it contradicts the hypothesis suggesting that left-hemisphere specialization for prey capture in monkeys is a precursor to right-hemisphere spatial ability in humans (MacNeilage et al., 2009; Vallortigara, 2000; Vallortigara et al., 2011).

We found far less evidence in capuchins for hand preferences in other actions than capturing moving prey or pounding nuts. For example, only two of seven capuchins exhibited a right-hand preference for carrying. Previous studies on nonhuman primates have suggested, at the population level, that actions that require maintenance of balance were associated with hand preferences (King & Landau, 1993; Lacreuse & Frigaszy, 1996). Diamond and McGrew (1994) demonstrated a right-hand preference for carrying in cottontop tamarins, *Saguinus oedipus*. Panger (1998) found a right-hand preference for carrying at the group level for capuchins. However, these previous studies described tripod locomotion during carrying whereas we almost always observed bipedal locomotion during carrying. Tripedal locomotion may constrain the subject to choose one hand to stabilize the body and one hand to carry whereas bipedal locomotion leaves this individual free to choose one hand or the other (or both) to hold the object.

The tapping data (in capuchins) showed two subjects with right-hand preference and no significant hand preference at the group level. These data are similar to those obtained by Panger (1998), who reported no significant preference at the group level for tapping. Similarly, for grasping fruit, we observed no hand preference for most of the individuals and at the group level for both species. As previously shown, these actions are not typically associated with a hand use preference at the individual level

(Fagot & Vauclair, 1991; McGrew & Marchant, 1996) or at the group level (Panger, 1998) in primates.

Concerning catching slow-moving prey, two subjects showed a right-hand preference and five were ambipreferent in capuchin monkeys, whereas squirrel monkeys showed a preference towards the left hand. This finding might reflect a difference between the species but we suggest that it is more likely to be due to the contexts in which the two species were observed (e.g. Meunier & Vauclair, 2007; Panger, 1998): semifree conditions for capuchins versus more controlled conditions for squirrel monkeys. In our study, capuchins grasped fruit in trees using several body postures which may favour the nearest hand associated with the different positions of the fruits. Animals moving freely in a three-dimensional space probably adopt variable body postures that induce ambipreferent choices. Indeed, the demand for balance and use of one hand for support varied across these foraging contexts and it has been shown that posture influences hand preference in capuchin monkeys (Westergaard, Kuhn, Lundquist, & Suomi, 1997). Primates demonstrate higher individual and group level hand preferences in captivity than in the wild (Hopkins, 1993, 1996, 2006; Hopkins et al., 2005; Lonsdorf & Hopkins, 2005). For example, white-faced capuchins exhibited a significant left-hand preference when grasping food in captivity (Meunier & Vauclair, 2007), but not in the wild (Panger, 1998). Perhaps many captive environments provide less variation in substrates (and therefore postures in the monkeys) and therefore allow hand preferences to develop that are not evident in natural environments.

In conclusion, we found that hand use patterns in a group of semifree-ranging tufted capuchins and a group of squirrel monkeys in more controlled conditions were influenced by the foraging action used to obtain a food item and the properties of the food item. Most of the subjects showed no hand preference during grasping, collecting immobile prey, tapping and carrying actions, despite the fact that these actions required different postural regulation and manual movements. In contrast, actions involving powerful rapid movement that is visually guided at least at its initiation towards a moving external element, such as pounding nuts and capturing fast-moving prey, induced a left-hand preference in most monkeys. Hellner-Burris et al. (2010) suggested a relationship among prey capture, the degree of lateralization and the morphology of the corpus callosum in capuchin monkeys, and our findings suggest that this set of related asymmetries may have an adaptive explanation. However, the neurobiological bases of hand preference remain unresolved (Phillips & Hopkins, 2007), even though manual laterality in capuchins and chimpanzees seem to be linked to brain asymmetries (Dunham & Hopkins, 2006; Hopkins & Cantalupo, 2004; Hopkins, Cantalupo, & Tagliatela, 2007; Phillips & Hopkins, 2007; Phillips & Sherwood, 2005; Phillips, Sherwood, & Lilak, 2007).

This study, like many studies of hand preference in primates, is limited by the size of our sample. Therefore, it should be replicated, first with capuchin monkeys and squirrel monkeys, ideally in natural environments, and second, in other species of platyrrhines and other families (strepsirrhines, tarsiers and catarrhines). We predict that slower grasping actions, such as collecting fruit with a slow movement and actions that are not strongly visually guided, such as tapping, are not associated with hand preference, but that fast visually guided actions or actions involving moving elements separate from the body itself, such as capturing moving prey and pounding objects against a substrate, are associated with a preference to use the left hand.

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