



Sex difference in squirrel monkeys' handedness for unimanual and bimanual coordinated tasks

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Whether nonhuman primates exhibit population-level manual bias remains controversial. There is a growing body of evidence showing consistent individual lateralization and population-level handedness particularly for complex manual behaviours such as bimanual coordinated actions in both monkeys and apes. Whereas the few published studies on hand preferences in squirrel monkeys, *Saimiri sciureus*, have focused only on unimanual behaviours and generally failed to elicit population-level handedness, we report in this paper the first set of data on hand use for a bimanual coordinated behaviour elicited by the manipulation of an opaque tube with one hand and removing the food inside the tube with the other hand. For comparison, hand use data were collected from 38 subjects for unimanual reaching for food from an experimenter when the squirrel monkeys were clinging vertically on the door of the cage. For bimanual coordinated actions, we found a nonsignificant trend towards left-handedness at a population level, especially in males, whereas unimanual reaching when clinging elicited a significant predominance of right-handedness, especially in females. These results are discussed within comparative approaches across primate species and within different theoretical frameworks about the determining factors of handedness in nonhuman primates.

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Behavioural and hemispheric lateralization at a population level has been historically considered as one of the hallmarks of human evolution (e.g. Warren 1980; Ettlinger 1988; Crow 2004). Almost 90% of humans are right-handed but the proportion of right-handedness for object manipulation varies across cultures (Porac & Coren 1981; Annett 1985; Marchant et al. 1995; Raymond & Pontier 2004). Whether population-level asymmetries in limb use may be found in other animals remains a topic of debate. In fact, there is a growing body of evidence of manual and neuroanatomical population-level asymmetries in a host of vertebrates (Rogers & Andrew 2002; Vallortigara & Rogers 2005; MacNeilage et al. 2009; Vallortigara et al. 2011) including nonhuman primates (reviewed in Hopkins 2007). For example, population-level limb preferences for motor actions have been found in some species of toads, *Bufo* spp., rats, *Rattus* spp., and dogs, *Canis familiaris* (e.g. Bisazza et al. 1996;

reviewed in Hook 2004). In nonhuman primates specifically, the studies revealed divergent patterns of handedness within and between the species but showed also a large variability concerning the method of data collection, the environment of the subjects (e.g. captive versus wild subjects), the manual behaviours observed or the experimental manual tasks used for assessing hand preferences (reviewed in McGrew & Marchant 1997; Papademetriou et al. 2005; Hopkins 2007). It remains then difficult to interpret these inconsistent results with respect to evolutionary models of handedness (e.g. MacNeilage et al. 1987; Crow 2004; Hopkins 2004). Predominance of right-handedness has been reported particularly in captive chimpanzees, *Pan troglodytes*, for complex manual tasks such as coordinated bimanual actions, bipedal reaching, throwing, gestural communication, etc. (reviewed in Hopkins 2006a, 2007; Hopkins et al. 2010). However, some authors remain sceptical of the claims of population-level handedness in nonhuman primates on both methodological and theoretical grounds (McGrew & Marchant 1997; Palmer 2002, 2003; Crow 2004; Cashmore et al. 2008; Uomini 2009). For instance, some authors have suggested that population-level right-handedness is evident only in captive chimpanzees and not in wild apes, suggesting that right-handedness in captive chimpanzees is an artefact of being raised

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in a human right-handed environment rather than a species-typical trait (e.g. McGrew & Marchant 1997). Looking at the data more closely shows that most of the available studies in wild populations of chimpanzees that have failed to report population-level manual bias have largely focused on simple measures of hand use, such as unimanual reaching for food (Marchant & McGrew 1996; McGrew & Marchant 1997, 2001), a task that poorly elicits handedness (reviewed in Papademetriou et al. 2005), even in captive chimpanzees (e.g. Hopkins 1993; Llorente et al. 2009). In fact, according to 'the task complexity' model proposed by Fagot & Vauclair (1991), low-level tasks such as simple unimanual reaching are less sensitive for detecting individual handedness and thus are poor measures for evaluating manual bias at a population level whereas high-level tasks such as bimanual coordination would be better predictors of hemispheric specialization of the brain (see Rogers 2009).

Indeed, there is a large set of data showing that variations in the demands and complexity of the tasks have an effect on the direction, strength or consistency of hand preferences in various primates including: (1) New World monkeys such as captive squirrel monkeys, *Saimiri sciureus* (King & Landau 1993; Laska 1996), captive tufted capuchin monkeys, *Cebus apella* (Fragaszy & Mitchell 1990; Westergaard & Suomi 1993; Anderson et al. 1996; Spinozzi et al. 1998; Lilak & Phillips 2008), white-faced capuchin monkeys, *Cebus capucinus* (Meunier & Vauclair 2007); (2) Old World monkeys such as captive Guinean baboons, *Papio papio* (Fagot & Vauclair 1988b), free-ranging Japanese macaques, *Macaca fuscata* (Leca et al. 2010), wild vervet monkeys, *Cercopithecus aethiops* (Harrison & Byrne 2000), captive red-capped mangabeys, *Cercocebus torquatus* (Blois-Heulin et al. 2006), grey-cheeked mangabeys, *Cercocebus albigena* (Blois-Heulin et al. 2007), De Brazza's monkeys, *Cercopithecus neglectus* (Trouillard & Blois-Heulin 2005), Campbell's monkeys, *Cercopithecus campbelli* (Chapelain et al. 2006); (3) great apes such as captive orang-utans, *Pongo pygmaeus* (Rogers & Kaplan 1996; O'Malley & McGrew 2006); wild and captive chimpanzees (e.g. Boesch 1991; Colell et al. 1995; McGrew et al. 1999), captive western lowland gorillas, *Gorilla g. gorilla* (Fagot & Vauclair 1988a); (4) and even humans (e.g. Steenhuis & Bryden 1989; Perelle & Ehrman 1994; Marchant et al. 1995).

In most of these studies, the distinction between unimanual and bimanual coordinated behaviours has been critical for underlying the task complexity's effects on individual hand preferences and for revealing population-level handedness. It has frequently been shown within a given sample of subjects that, whereas unimanual behaviours did not induce manual biases at a population level, bimanual coordinated behaviours elicited significant population-level handedness in captive olive baboons, *Papio anubis* (Vauclair et al. 2005), captive De Brazza's monkeys (Schweitzer et al. 2007), wild Sichuan snub-nosed monkeys, *Rhinopithecus roxellana* (Zhao et al. 2010), wild mountain gorillas, *Gorilla g. beringei* (Byrne & Byrne 1991), captive western lowland gorillas (Meguerditchian et al. 2010) and captive chimpanzees (Hopkins & Rabinowitz 1997; Wesley et al. 2002; Hopkins et al. 2007; Llorente et al. 2009). These collective findings suggest that bimanual coordinated behaviours are more appropriate than unimanual behaviours for investigating manual asymmetries. Bimanual coordination consists of engaging the two hands in an asymmetrical and coordinated action: while one hand holds or maintains an item, the other hand (dominant) is used to manipulate the item. Hopkins (1995) designed the tube task for chimpanzees to measure hand preference for coordinated bimanual actions. This task consists of holding a PVC tube with one hand and removing the food inside the tube (e.g. peanut butter) with the fingers of the other hand. Within a comparative approach

between primate species, standardization of the methodology and the manual tasks used for assessing hand preferences has been pursued, especially with respect to the distinction between unimanual (e.g. Meunier et al. 2011) and bimanual tasks (e.g. Hopkins et al. 2011). For instance, the bimanual tube task has been successfully replicated in many captive primate species such as capuchin monkeys, baboons, De Brazza's monkeys, mangabeys, rhesus macaques, *Macaca mulatta*, bonobos, *Pan paniscus*, gorillas, orang-utans and chimpanzees (Westergaard & Suomi 1996; Westergaard et al. 1997; Spinozzi et al. 1998; Hopkins et al. 2003, 2004, 2011; Vauclair et al. 2005; Blois-Heulin et al. 2006, 2007; Meunier & Vauclair 2007; Schweitzer et al. 2007; Bennett et al. 2008; Lilak & Phillips 2008; Chapelain & Hogervorst 2009; Llorente et al. 2009, 2011). In contrast to simple unimanual reaching, such a bimanual coordinated tube task has been shown to elicit hand preferences that are related to neuroanatomical asymmetries within the primary motor cortex in both captive chimpanzees (Hopkins & Cantalupo 2004) and capuchin monkeys (Phillips & Sherwood 2005). In six adult squirrel monkeys, a study has also demonstrated such neuroanatomical correlates of individual hand preferences in the primary motor cortex for a high-level unimanual motor task requiring skilled digit use, which consisted of inserting a finger in a hole to remove food (Nudo et al. 1992).

However, to our knowledge, no study has investigated hand preferences for bimanual coordinated behaviours in squirrel monkeys. Squirrel monkeys are arboreal New World monkeys; their diet is omnivorous including mostly fruits but they are frequently seen to capture stationary insects on plant surfaces (Kinzey 1997). Among the few studies available, all of them have exclusively assessed hand preferences in different unimanual tasks. The published first studies on squirrel monkeys involved too few subjects (i.e. from six to 13 individuals) for evaluating population-level handedness but reported individual hand preferences for unimanual behaviours including reaching (McGonigle & Flook 1978; Aruguete et al. 1992; Laska 1996), precision grip (Costello & Fragaszy 1988) and a motor task requiring skilled digit use (Nudo et al. 1992). In another study, Roney & King (1993) assessed hand preferences in 30 subjects for unimanual food reaches from either a horizontal, quadrupedal posture or a vertical, clinging posture. Although no manual bias at the population level was reported for these tasks, the authors showed that the degree of individual manual preferences was more pronounced for reaching in the vertical cling posture than from the quadrupedal posture. The first demonstration of population-level handedness in squirrel monkeys was reported by King & Landau (1993) in a study of 37 subjects that contradicts the previous report of an absence of manual bias for unimanual reaching in a vertical clinging posture (see Roney & King 1993). These authors demonstrated not only a significant right-hand bias in a vertical cling reaching context but also a significant left-hand bias at the population level for catching moving goldfishes and no manual bias in a static reach. Such results provide additional evidence of a task effect on the direction of the population-level handedness depending on the unimanual reaching context.

In the present study, we measured hand preferences for a bimanual coordinated tube task with a relatively large sample of captive squirrel monkeys to enlarge the data sets on hand preferences for the tube task within a comparative approach between primate species. For comparative purposes, we also measured hand preferences for unimanual reaching in a vertical clinging posture to provide an additional set of data on this behaviour (King & Landau 1993; Roney & King 1993) and to compare them with the patterns of handedness elicited by the bimanual coordinated task.

METHODS

Subjects

We studied 39 captive-born squirrel monkeys (21 females and 18 males) at the Station de Primatologie, CNRS (Rousset, France). The subjects were 1–20 years old (mean \pm SE = 7.59 ± 0.59 years). Considering that squirrel monkeys are adult at the age of 3 years, 33 were adults and six were young monkeys. The treatment of our animal sample met with CNRS ethical standards. The procedure we used consisted of observing the social groups of squirrel monkeys after introducing several experimental tubes in their cages. The monkeys were born at the Station de Primatologie of Rousset and were raised by their conspecific mothers. The squirrel monkeys were housed in different indoor compounds (2.40 or 2.20 m high, surface range from 1.70×1.60 m to 5.45×2.75 m) in two separate buildings. In one of these buildings, each compound was connected to an outdoor enclosure (3.10 m high, surface range from 4.0×3.1 m to 4.9×3.9 m). The squirrel monkeys were living in large, relaxed, social groups with minimal interactions with humans. The groups were unimale, unifemale or mixed. Each indoor compound contained woodchip litter on the ground, large nets and PVC climbing structures while the outdoor compound contained bark litter on the ground, a wooden climbing structure with a sliding ramp and tyres to swing on. The squirrel monkeys could pass freely between the indoor building and outdoor compound. Water was available ad libitum and monkey chow, fresh fruits (apples, oranges, etc.) were given every day. The males were tested in three large cages (2.40 m high, surfaces: 3.10×1.85 m, 2.90×2.20 m and 5.45×2.75 m) while females and young individuals were tested in five large cages (2.2 m high, surface of four cages: 1.7×1.6 m; of one cage: 2.5×1.6 m).

Procedure

Unimanual reaching when clinging

Most of the unimanual reaching behaviours measured in the primate handedness literature consist of reaching for an item when the animal is seated on the ground or in a quadrupedal posture (e.g. Papademetriou et al. 2005). However, it is difficult to get squirrel monkeys to adopt these postures when reaching for food. With raisins placed on the cage's floor, squirrel monkeys furtively jumped across the cage picking up raisins on their way out. Squirrel

monkeys are arboreal species and are thus better adapted to climb in the trees when feeding. We therefore focused on reaching behaviour when clinging vertically on the door of the cage. To solicit unimanual reaching, the experimenter had to offer a raisin in front of a monkey that was clinging to the door of the cage. Then, the experimenter recorded the hand use when the monkey grabbed the raisin with one hand and put it in its mouth while the other hand was used to hang vertically from the door of the cage. To avoid potential biases in hand use, such as postural effects or repetitions of reaching actions, (1) the monkey was not tested twice in the same session, (2) before each trial, the animal had to hang from the cage with both hands at the same height, (3) the experimenter alternated the hand used to offer the raisin to the monkeys, and (4) the hand of the experimenter had to be directed at the midline body of the animal.

Bimanual coordinated actions

Adapting the bimanual tube task to squirrel monkeys was a real challenge. First, the monkeys could hold with one hand a tube with a diameter of 11 mm filled with peanut butter but were not able to insert a single finger inside the tube to remove the food and they kept trying, unsuccessfully, to insert the whole hand. We tried a larger tube (30 mm diameter) to allow the monkeys to insert the whole hand into it. However, they were not able to hold the larger tube with the other hand and instead used their feet to keep it on the ground. Finally, the solution we found was to make a specific tube divided into two parts: (1) a large opaque tube (length 40 mm and diameter 30 mm) at one extremity to allow the monkey to insert a whole hand inside it fixed into (2) a metal rod (length 50 mm, diameter 4 mm) at the opposite extremity to be held with the other hand. This tube successfully initiated bimanual coordination for removing the food in the squirrel monkeys (see Fig. 1). Before each trial, eight tubes were introduced into each cage to minimize competition between animals and to test subordinate monkeys. Data collection consisted of opportunistically recording the maximum number of hand use responses per subject by daily observations of the social groups when the bimanual behaviour occurred after introducing the tube into the cages. An observation was considered as valid when the monkey did not hold the tube with the feet and when both hands were free before taking the tube. As all the monkeys performed the task simultaneously, the experimenter recorded a maximum of five occurrences in an experimental session for a given animal before switching to another.



Figure 1. Bimanual coordinated tube task. An adult male squirrel monkey holds the tube with one hand and removes the food inside the tube by inserting the other hand.

Data Analysis

We used two different methods to evaluate individual hand preferences on the basis of the total left and total right responses for a given manual behaviour. First, a *z* score was calculated to classify squirrel monkeys as left-handed ($z \leq -1.96$), right-handed ($z \geq 1.96$) or ambiguously handed ($-1.96 < z < 1.96$). Second, we used a handedness index score (HI) for each animal following the formula $HI = [(number\ of\ right-hand\ responses - number\ of\ left-hand\ responses) / (number\ of\ total\ responses)]$. Values of HI range from -1 to 1 . The sign indicates the direction of hand preference (negative: left-hand preference; positive: right-hand preference) while the absolute values of HI indicate the strength of manual asymmetries.

RESULTS

Direction of Handedness

In total, 2112 occurrences of unimanual food reaching when clinging were recorded on 38 monkeys. The number of occurrences per animal ranged from 19 to 88 (mean \pm SE = 55.58 ± 2.77).

According to *z* scores, 25 monkeys were right-handed, eight were left-handed and five were ambiguously handed (see Tables 1, 2). This distribution was significantly different from chance (chi-square test: $\chi^2_2 = 18.37$, $P = 0.0001$). Among the 33 lateralized animals, the distribution of right-handed (76%) versus left-handed individuals (24%) differed significantly from chance (chi-square test: $\chi^2_1 = 8.76$, $P = 0.003$). Consequently, we noted for the unimanual reaching task a significant right-hand bias at population level. This right-hand bias is confirmed by the analysis of the handedness index (Fig. 2). The mean HI of the population (mean \pm SE = 0.37 ± 0.11) is significantly different from 0 (*t* test: $t_{37} = 3.47$, $P = 0.001$).

Thirty-seven animals were observed with the tube task and 3128 occurrences were collected. The number of occurrences per animal ranged from 28 to 256 (mean number of occurrences = 84.54 ± 7.01). According to *z* scores, 14 monkeys were right-handed, 21 were left-handed and two were ambiguously handed (Tables 1, 2). This distribution was significantly different from chance ($\chi^2_2 = 14.97$, $P = 0.0006$). Among the 35 lateralized subjects, the distribution of right-handed (40%) versus left-handed subjects (60%) was not significantly different from chance ($\chi^2_1 = 1.4$, $P = 0.24$). Analysis of the means of all the individual HI scores

Table 1
Individual hand preferences and frequencies of left- and right-hand responses for the bimanual coordinated tube task and unimanual reaching when clinging

Subject	Age	Sex	Bimanual tube task						Unimanual reaching when clinging					
			L	R	N	HI	<i>z</i>	Hand	L	R	N	HI	<i>z</i>	Hand
D106C	9	F	18	17	35	-0.03	-0.17	A	3	21	24	0.75	3.67	R
E033C	2	F	41	0	41	-1.00	-6.40	L	20	46	66	0.39	3.20	R
6-29C	8	F	0	42	42	1.00	6.48	R	14	57	71	0.61	5.10	R
E130C	2	F	41	14	55	-0.49	-3.64	L	/	/	/	/	/	/
D019C	14	F	60	10	70	-0.71	-5.98	L	1	62	63	0.97	7.69	R
D(0)64C	8	F	3	70	73	0.92	7.84	R	8	36	44	0.64	4.22	R
06-17C	9	F	6	75	81	0.85	7.67	R	4	55	59	0.86	6.64	R
D046C	8	F	82	0	82	-1.00	-9.06	L	39	20	59	-0.32	-2.47	L
juil-23	2	F	95	0	95	-1.00	-9.75	L	7	61	68	0.79	6.55	R
E029C	2	F	62	34	96	-0.29	-2.86	L	3	58	61	0.90	7.04	R
D008C	9	F	15	81	96	0.69	6.74	R	4	64	68	0.88	7.28	R
D027C	1	F	97	0	97	-1.00	-9.85	L	6	56	62	0.81	6.35	R
E108C	8	F	1	109	110	0.98	10.30	R	2	56	58	0.93	7.09	R
89-14	9	F	0	110	110	1.00	10.49	R	2	60	62	0.94	7.37	R
06-15C	9	F	40	86	126	0.37	4.10	R	3	62	65	0.91	7.32	R
6-28C	8	F	128	3	131	-0.95	-10.92	L	4	81	85	0.91	8.35	R
AE87C	20	F	0	136	136	1.00	11.66	R	4	51	55	0.85	6.34	R
6-09C	3	F	100	37	137	-0.46	-5.38	L	0	81	81	1.00	9.00	R
C020C	3	F	42	214	256	0.67	10.75	R	1	58	59	0.97	7.42	R
95003	14	F	/	/	/	/	/	/	3	19	22	0.73	3.41	R
C067C	10	F	/	/	/	/	/	/	1	31	32	0.94	5.30	R
sans	8	M	41	0	41	-1.00	-6.40	L	5	54	59	0.83	6.38	R
94-10	2	M	45	0	45	-1.00	-6.71	L	39	49	88	0.11	1.07	A
07-(00)1	10	M	75	0	75	-1.00	-8.66	L	68	1	69	-0.97	-8.07	L
1003	8	M	62	14	76	-0.63	-5.51	L	20	56	76	0.47	4.13	R
1004	8	M	4	82	86	0.91	8.41	R	8	11	19	0.16	0.69	A
1005	8	M	57	8	65	-0.75	-6.08	L	13	31	44	0.41	2.71	R
3001	6	M	96	41	137	-0.40	-4.70	L	38	6	44	-0.73	-4.82	L
3002	6	M	46	1	47	-0.96	-6.56	L	34	34	68	0.00	0.00	A
3003	6	M	11	71	82	0.73	6.63	R	68	12	80	-0.70	-6.26	L
AE75C	8	M	9	59	68	0.74	6.06	R	37	2	39	-0.90	-5.60	L
D002C	9	M	28	6	34	-0.65	-3.77	L	11	27	38	0.42	2.60	R
D060C	9	M	1	80	81	0.98	8.78	R	42	3	45	-0.87	-5.81	L
D065C	9	M	67	0	67	-1.00	-8.19	L	19	22	41	0.07	0.47	A
D085C	9	M	57	9	66	-0.73	-5.91	L	3	52	55	0.89	6.61	R
D104C	9	M	76	0	76	-1.00	-8.72	L	3	38	41	0.85	5.47	R
E013C	8	M	19	9	28	-0.36	-1.89	A	22	16	38	-0.16	-0.97	A
E036C	8	M	49	8	57	-0.72	-5.43	L	36	12	48	-0.50	-3.46	L
F004C	7	M	29	99	128	0.55	6.19	R	52	4	56	-0.86	-6.41	L

F: female; M: male; L: number of left-hand responses; R: number of right-hand responses; HI: handedness index score which corresponds to 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; R: right-handed subject; L: left-handed subject; A: ambiguously handed subject.

Table 2
Distribution of hand preferences and degree of population-level manual bias

Manual behaviours	L	R	A	N	Mean HI	SE
Unimanual reaching task	8	25	5	38	0.37	0.11
Females	1	19	0	20	0.77	0.07
Males	7	6	5	18	-0.08	0.15
Bimanual tube task	21	14	2	37	-0.16	0.13
Females	9	9	1	19	0.03	0.19
Males	12	5	1	18	-0.35	0.18

L: number of left-handed subjects; R: number of right-handed subjects; A: number of ambiguously handed subjects; N: sample of subjects; Mean HI: mean handedness index score of *N* individuals which corresponds to degree of population-level handedness, the sign indicates the direction of the manual bias (negative value: left-hand bias; positive value: right-hand bias).

(see Fig. 2) showed a trend towards left-handedness at the population level (mean \pm SE = -0.16 ± 0.13), but this manual bias did not differ significantly from 0 ($t_{36} = 1.17$, $P = 0.25$).

Age and Sex Effects

We ran an ANOVA to evaluate the effect of sex and age on HI (cf. Fig. 2). For the unimanual task, no significant age class effect was observed (mean \pm SE = 0.52 ± 0.30 in the six young monkeys and 0.34 ± 0.11 in the 32 adults; $F_{1,34} = 0.63$, $P = 0.43$). By contrast, we observed a significant sex effect on HI ($F_{1,34} = 25.86$, $P < 0.0001$; Table 2), but no effect of the interaction age class*sex ($F_{1,34} = 0.007$, $P = 0.94$). The mean HI of females differed significantly from 0 ($t_{19} = 11.63$, $P < 0.0001$), whereas the mean HI of males did not ($t_{17} = 0.53$, $P = 0.60$). Female squirrel monkeys therefore showed a stronger right-hand preference than males for the unimanual reaching task.

In the bimanual tube task, the analysis of variance failed to show an age effect on the HI (mean \pm SE = -0.27 ± 0.39 in the six young monkeys and -0.13 ± 0.14 in the 31 adults; $F_{1,33} = 0.14$, $P = 0.71$). No significant sex effect was observed for the bimanual task ($F_{1,33} = 2.25$, $P = 0.14$; Table 2), as well as no effect of the interaction age class*sex ($F_{1,33} = 1.19$, $P = 0.28$). However, in males, the degree of population-level left-handedness approaches conventional levels of statistical significance (one-sample *t* test: $t_{17} = 1.94$, $P = 0.068$), whereas the females did not show any population-level asymmetry ($t_{18} = 0.15$, $P = 0.88$).

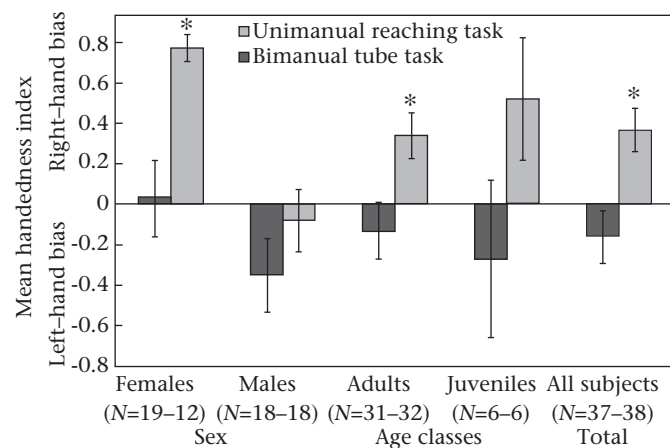


Figure 2. Degrees of population-level right-handedness (mean handedness index, HI) for unimanual and bimanual tasks in males/females, adults/young individuals and the overall sample. Mean HI scores are given \pm SE. Asterisks indicate that the HI score differed significantly from zero. * $P < 0.05$. The positive HI values indicate a bias towards right-handedness, the negative HI values towards left-handedness.

Task Effect

We compared HI of the 36 animals who performed both unimanual and bimanual tasks. No correlation of HI was observed between unimanual and bimanual tasks (Pearson correlation: $r_{34} = -0.0005$, $P = 0.997$). In fact, 22 of the 36 monkeys showed opposite hand preferences between the unimanual and the bimanual tasks. Moreover, the comparison between the mean HI of the unimanual task (mean \pm SE = 0.34 ± 0.11) and the mean HI of the bimanual task (mean \pm SE = -0.15 ± 0.14) showed a significant difference (paired-sample *t* test: $t_{35} = 2.78$, $P = 0.009$).

Potential Effects of Number of Responses per Subject

According to Palmer (2002), the evidence of population level of right-handedness that has been reported in captive chimpanzees for the bimanual tube task (e.g. Hopkins 1995) might be biased by the variation in number of responses across subjects. In other words, the number of ambiguously handed subjects would increase when collecting more responses of hand use per subject. As the number of responses per subject varied from 19 to 88 for the unimanual task and from 28 to 256 for the bimanual task in our sample of subjects, we evaluated the potential variations in the patterns of results according to the number of responses per subject in both tasks. For this purpose, we created a funnel plot for each manual task in which the number of hand use responses was plotted against the individual percentage of right-hand use. As can be seen in Fig. 3a, b, the number of ambiguously handed individuals (those in the centre of the funnel between the two lines drawn by black lozenges) decreased when the number of responses per subject increased. As can be seen with the discontinuous grey lines at the top of the graphs, additional analyses showed that there is no correlation between the number of responses per subject and the strength of hand preferences (regardless of the direction of hand preferences) for both the bimanual task ($r_{35} = -0.03$, $P > 0.10$) and the unimanual task ($r_{36} = 0.14$, $P > 0.10$). Thus, contrary to the predictions made by Palmer (2002), these analyses indicate that our hand preference classification data were not biased because of differences in the number of responses between subjects.

DISCUSSION

To our knowledge, this is the first study investigating hand preferences for bimanual coordinated actions in squirrel monkeys. No population-level handedness was found in our sample of 37 subjects in the bimanual tube task. This finding is thus congruent with the absence of population-level handedness generally reported for unimanual simple reaching in nonhuman primates (reviewed in Papademetriou et al. 2005) and for the bimanual coordinated tube task used in other New World monkey species such as capuchin monkeys (Westergaard & Suomi 1996; Phillips & Sherwood 2005; Meunier & Vauclair 2007; Phillips & Sherwood 2007; Lilak & Phillips 2008; but see Spinozzi et al. 1998 for a report of a predominance of right-handedness). Unimanual reaching when clinging elicited a significant predominance of right-handedness, as demonstrated in a previous study on this species (King & Landau 1993; but see Roney & King 1993). This contrast of findings between bimanual and unimanual tasks is in the opposite direction to the patterns of handedness reported in humans (Fagard & Marks 2000), captive chimpanzees (Hopkins & Rabinowitz 1997; Wesley et al. 2002; Hopkins et al. 2007; Llorente et al. 2009), captive and wild gorillas (Byrne & Byrne 1991; Meguerditchian et al. 2010) and captive baboons (Vauclair et al. 2005; see also in capuchin monkeys: Spinozzi et al. 1998). Indeed, in these latter species, unimanual reaching elicited a lower

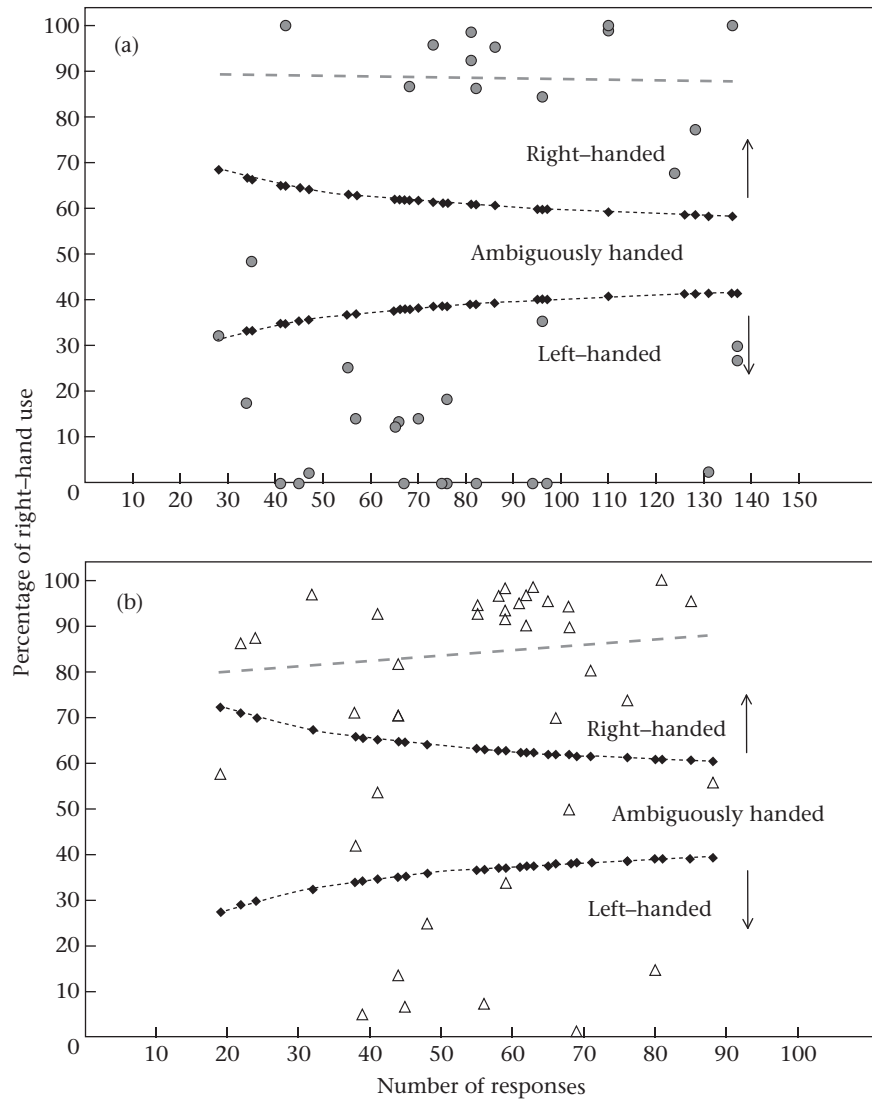


Figure 3. Funnel plot of the individual percentages of right-hand use plotted against the number of observations in hand use for (a) the bimanual tube task and (b) the unimanual task. Based on the number of individual observations of hand use (i.e. number of responses), the grey circles (a) and the white triangles (b) are the percentage of right-hand use in each subject for the bimanual and the unimanual task, respectively. For each number of responses performed by the subjects in the manual tasks, there are two corresponding black lozenges (top and bottom) that represent the critical percentages of right-hand use in which z score values ($+1.96$ and -1.96 , respectively) are at $P < 0.05$. Then, grey circles (a) and white triangles (b) that lie above the top black lozenges' line ($z = +1.96$) represent subjects with significant right-hand preferences ($P < 0.05$). Grey circles (a) and white triangles (b) that lie below the bottom black lozenges' line ($z = -1.96$) represent subjects with significant left-hand preferences ($P < 0.05$). Grey circles and white triangles that lie between the two lines represent those individuals who failed to show a significant hand preference. In addition, the discontinuous grey lines at the top of both graphs represent the linear regression between the number of responses of hand use per subject and its corresponding value of strength of hand preference which varies from 50% (no hand preference) to 100% (exclusive hand preference) in all subjects regardless of the direction (left or right) of their hand preference. To make a legible funnel plot for the bimanual tube task (a), we excluded an outlier right-handed subject 'C020C' ($z = 10.75$) from this graph since its number of responses (i.e. 256 responses) was very different from the number of responses of the rest of the sample (i.e. from 28 to 137 responses).

degree or an absence of predominance of right-handedness in comparison to bimanual coordinated behaviours within the same sample of subjects. One can question why the task effect on hand preference (bimanual task versus unimanual task) was opposed to our prediction in squirrel monkeys. First, we might suggest that the task's demands and the patterns of manual skills elicited by the bimanual tube task used in the present study is not totally similar to those generally involved in the tube tasks used with other species. Namely, even if the squirrel monkeys were able to perform bimanual coordinated motor actions within our experimental task, they inserted the whole hand inside the tube rather than a single digit, a feature that contrasts with the other tube task studies conducted in monkeys and apes. Second, one might question the ecological validity of such measures of handedness since

squirrel monkeys are not particularly known to perform bimanual coordinated actions in their natural environment, in contrast to gorillas for example (Byrne & Byrne 1993). Squirrel monkeys are arboreal species and thus better adapted to climb in the trees when feeding. Unimanual reaching with one hand involved in supporting the body in the tree/cage might constitute a better ecological measure of hand preference than bimanual coordinated action. The feeding ecology of the species might be related to manual specialization at a population level in nonhuman primates as suggested in gorillas for bimanual coordinated actions (Meguerditchian et al. 2010).

When we look more closely at the effect of sex, the patterns of results between the bimanual task (absence of manual bias at the group level) and the unimanual reaching task (predominance of

right-handedness) are not so straightforward. It was not only the nature of the tasks but also the sex of the individuals that affected hand preferences in squirrel monkeys. Only females were right-handed for the unimanual task and not the males, whereas the bimanual task elicited a population-level left-hand bias approaching conventional levels of statistical significance only in males. Similar sex effects on the direction of population-level handedness have also been demonstrated not only for unimanual behaviours (e.g. in baboons, Meunier et al. 2011) but also for bimanual coordinated feeding in wild chimpanzees (Corp & Byrne 2004), in rehabilitated orang-utans (Rogers & Kaplan 1996) and somewhat in captive gorillas (i.e. borderline significance for the sex effect, Meguerditchian et al. 2010) and for the bimanual tube task in De Brazza's monkeys (Schweitzer et al. 2007) and capuchin monkeys (Spinuzzi et al. 1998; Meunier & Vauclair 2007; Phillips & Sherwood 2007). In all these studies, females were more right-handed than males or males were more left-handed than females at a group level. However, the role of sex remains unclear in the rest of the literature. A large set of data in various primate species failed to show any sex effect on the patterns of handedness (reviewed in McGrew & Marchant 1997).

It has been argued that bimanual coordinated activities in our ancestors may have played a major role in the evolution of human handedness (e.g. Hopkins 2006a, b; Meguerditchian et al. 2010). Specifically, right-lateralization of hand use may have been selected in our ancestors for such bimanual actions rather than tool use exclusively (Bradshaw & Rogers 1993) and may constitute an ideal prerequisite for human hemispheric specialization. This view is supported by reports of significant population-level right-handedness for bimanual coordinated activities in captive baboons (Vauclair et al. 2005), in different large groups of captive chimpanzees (Hopkins 1995; Hopkins et al. 2004, 2011; Llorente et al. 2011) and in both wild and captive gorillas (Byrne & Byrne 1991; Hopkins et al. 2003, 2011; Meguerditchian et al. 2010). However, a predominance of left-handedness has also been reported for

bimanual coordinated behaviours in a great ape species, the orang-utan (tube task in 19 and in 44 captive subjects: Hopkins et al. 2003, 2011) and in Old World monkey species such as De Brazza's monkeys (tube task in 12 captive subjects: Schweitzer et al. 2007) and Sichuan snub-nosed monkeys (bimanual grooming in 26 wild subjects: Zhao et al. 2010). Such divergent findings across primate species might be reconciled if we consider the variations in the postural and biomechanical factors related to the ecology of the species (i.e. arboreal versus terrestrial species). Indeed, according to the postural origins theory of handedness proposed by MacNeilage et al. (1987; reviewed in MacNeilage 2007), whether primate species are arboreal or terrestrial may constitute another major factor in addition to the complexity of the manual behaviours for explaining the phylogenetic distribution of population-level handedness among primate lineages. Then, according to this theory, arboreal species (such as orang-utans, De Brazza's and Sichuan snub-nosed monkeys) preferentially developed right-handedness for supporting the body in trees while the left hand has been favoured for manipulative actions. By contrast, because of the liberation of the hands from the biomechanical constraints of living in the trees, more terrestrial primates such as chimpanzees, baboons and gorillas would have developed a predominant right-handedness for manipulative tasks. Although nonsignificant, the tendency towards left-handedness found in our squirrel monkeys (an arboreal species), especially in males but not in females, for the bimanual tube task might provide additional support to the postural origins theory of handedness within a comparative approach. When compared to the other arboreal primate species, the degree of predominance of left-handedness in male squirrel monkeys is similar to that reported in captive orang-utans, captive De Brazza's monkeys and wild Sichuan snub-nosed monkeys for bimanual coordinated behaviours, whereas more terrestrial primate species such as gorillas, chimpanzees and baboons showed fairly similar degrees of population-level right-handedness for the bimanual tube task (see Fig. 4 for comparison of handedness data for the bimanual

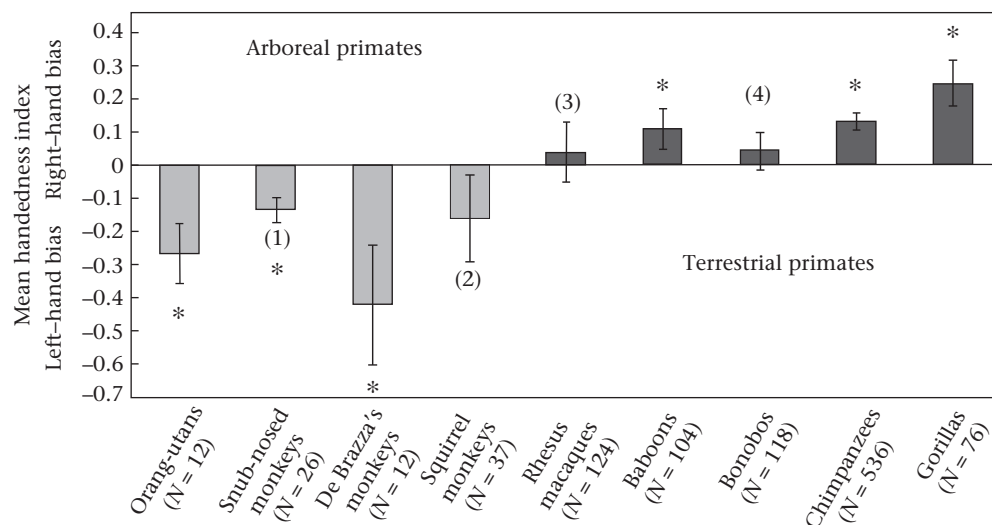


Figure 4. Comparison of the degrees of population-level handedness (mean handedness index, HI) for the bimanual coordinated tube task between arboreal and terrestrial primates. Arboreal primates: orang-utans (Hopkins et al. 2011); snub-nosed monkeys (Zhao et al. 2010); De Brazza's monkeys (Schweitzer et al. 2007); squirrel monkeys (the present study); Terrestrial primates: rhesus macaques (Bennett et al. 2008); baboons (Vauclair et al. 2005); bonobos (Chapelain et al. 2011; Hopkins et al. 2011); chimpanzees (Hopkins et al. 2011); gorillas (Hopkins et al. 2011). Mean HI scores are given \pm SE. Asterisks indicate that the mean HI score differed significantly from zero. * $P < 0.05$. (1) Snub-nosed monkeys were not tested with the bimanual tube task but for bimanual grooming; (2) male squirrel monkeys showed population-level left-handedness that approaches conventional level of significance ($P = 0.068$); (3) mother-reared females rhesus macaques and (4) adults bonobos showed significant predominance of right-handedness ($P = 0.05$; see Bennett et al. 2008; Chapelain et al., 2011). Note that capuchin monkeys, *Cebus* (arboreal New World primates) showed generally no population-level handedness in the literature for the tube task. This species is not represented in this figure since its results are dispersed in different studies and are difficult to combine and represent into a single mean HI of the overall sample without having the raw data.

tube task exclusively). However, some studies that investigated hand preferences for bimanual coordinated tasks in other primate species revealed no manual bias at a population level and are therefore not strictly consistent with this theory (wild vervet monkeys: Harrison & Byrne 2000; bonobos: Chapelain & Hogervorst 2009; Chapelain et al. 2011; Hopkins et al. 2011; rhesus macaques: Bennett et al. 2008). Nevertheless, these studies have revealed the involvement of complementary or contradictory factors (e.g. sample size, sex, rearing history effects, age effect) other than the posture and the task complexity for reconciling the divergent findings in the primate handedness literature. For instance, only a large sample of adult bonobos (Chapelain et al. 2011) and female mother-reared rhesus macaques (Bennett et al. 2008) showed a significant degree of right-hand bias for the bimanual tube task and thus consistency with the postural origin theory of handedness. We might hypothesize that our nonsignificant left-hand bias for the bimanual tube task in squirrel monkeys might be related to variations in the results between males and females that led to a large standard error (the males being more left-handed than females). Further investigations should be conducted to increase the sample of subjects and evaluate these hypotheses.

In conclusion, these joint findings indicate that it remains difficult to determine the factors that would explain the phylogeny of the distribution of hand preferences among primate lineages. Whether the effects of sex, rearing history and age on manual bias are not entirely consistent across the studies in nonhuman primates and might depend on the species, the contrasts of hand preferences between terrestrial versus arboreal primates, and between unimanual versus bimanual coordinated behaviours, seem to represent the most critical factors for explaining the divergent patterns of handedness reported in the literature between and within nonhuman primate species. Within a large comparative approach, this kind of investigation including large samples of monkeys and apes is still needed for better detecting which factors drive the expression and the variations in the direction of handedness not only at individual and population levels but also at a species or cross-species level among primates.

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