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ORIGINAL PAPER

Hand preference and its flexibility according to the position of the object: a study in cercopithecines examining spontaneous behaviour and an experimental task (the Bishop QHP task)

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Abstract The extant literature on manual laterality in non-human primates is inconclusive, plagued by inconsistent or contradictory findings and by disturbing methodological issues (e.g. uncontrolled influential factors, comparability issues). The present study examined hand preference and its flexibility in 15 red-capped mangabeys (*C. t. torquatus*) and 13 Campbell's monkeys (*C. c. campbelli*), two species that differ in their degree of arboreality. We investigated the influence of the spatial position of the object on hand preference for reaching. We considered spontaneous behaviour (reaching for food during daily feeding) and an experimental task: the QHP task. The QHP is a task that is used in humans. This is a simple reaching task that involves high spatial constraints on hand use. In our study, the subject had to reach for items that were placed on a semi-circle in front of it on five positions, including in the centre position, in the ipsilateral space and in the contralateral space. We assessed hand preference for reaching in front (baseline condition), and we examined how this preference changed when reaching in lateral positions. For reaching in front, about half of the subjects were lateralized and no group-level bias occurred, for both spontaneous and experimental conditions. When considering reaching in the lateral positions, we observed that the position of the object influenced hand use: individuals used the hand that was closest to the object. The results are discussed in relation to previous findings in humans and in non-human primates and regarding theories on handedness and flexibility of hand preference.

Keywords Handedness · Manual preference · Monkeys · Spatial constraints on hand use · Reaching

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Introduction

In humans, most individuals exhibit a hand preference, with very few individuals being unlateralized (3 %) (Annett 1985; Fagard 2004; Faurie and Raymond 2004; Vuoksimaa et al. 2009). The majority of humans usually or always use the same hand for most unimanual activities and for the most active component in bimanual activities. This hand preference is thought to be related to brain lateralization, although the hand chosen can also be influenced by spatial (Leconte and Fagard 2004) and cultural (Dahmen and Fagard 2005) constraints. Around 80–90 % percent of the individuals are right handed (Annett 1985; Fagard 2004; Faurie and Raymond 2004; review in McManus 2002). This extreme group-level bias is present in all cultures around the world (Coren and Porac 1977; Fagard 2004; Marchant et al. 1995; Marchant and McGrew 1998; Raymond and Pontier 2004), and archaeological evidence indicates that it would be an ancient trait in the evolution of man (reviews in Cashmore et al. 2008; Uomini 2009). Therefore, human right-handedness is thought to be a universal trait that has always existed in human-beings (Coren and Porac 1977; Fagard 2004; Faurie and Raymond 2004).

This fascinating feature has given rise to intensive research that strives to elucidate its origins and functions. Research concerns mainly humans and their closest living relatives: non-human primates (reviews in Chapelain 2010; McGrew and Marchant 1997; Hopkins 2006). The extant literature on manual laterality in non-human primates is inconclusive, plagued by inconsistent or contradictory findings and by disturbing methodological issues. Thus, the issue remains largely unclear and is matter of important scientific debate and inquiry (Chapelain 2010; Hopkins 2006; Hopkins and Cantalupo 2005; Llaurens et al. 2009; McGrew and Marchant 1997; Palmer 2002; Papademetriou et al. 2005). To summarize, the results showed that non-human primates exhibit significant manual laterality (data reviewed in Cashmore et al. 2008; Chapelain 2010; Chapelain and Hogervorst 2009; Hopkins 2006; Hopkins and Cantalupo 2005; McGrew and Marchant 1997; Papademetriou et al. 2005). Studies have found evidence of manual preferences for a variety of actions, such as feeding, reaching, carrying, manipulating, throwing, using tools and gesturing. However, the proportion of non-lateralized subjects was generally high, and the lateralized individuals displayed non-exclusive preferences; although certain complex tasks, like manipulative bimanual coordination (Byrne and Byrne 1991; Byrne and Corp 2003; Corp and Byrne 2004) and tool-use (review in Marchant and McGrew 2007) were shown to elicit a marked laterality. In laterality research, we observe two levels of laterality: individual-level laterality when an individual exhibits a significant preference for one hand and group-level laterality when the majority of individuals display the same preference, i.e. when the numbers of right handers and left handers are significantly different. In non-human primates, the numbers of right handers and left handers are generally similar. There is some evidence of group-level biases for certain behaviours, including bimanual coordination on the "tube task" (review in Chapelain and Hogervorst 2009), bipedal reaching (Hopkins 1993; Olson et al. 1990), bimanual feeding (Hopkins 1994), throwing (Hopkins et al. 2005a) and gesturing (e.g. Hopkins et al. 2005b; Meguerditchian et al. 2010, 2011), but the biases observed in non-human primates are generally small, around 65 % of individuals of one kind, which is weaker than the 90 % bias reported in humans.

One should note that there are problems that make it difficult to compare the findings between humans and non-human primates. Indeed, there are important differences between the methods that are used to assess hand preferences in humans and in non-human primates (Faurie 2004; Uomini 2009). In non-human primates, hand preferences are assessed by observing the subjects while they perform manual tasks. In humans, hand preferences are assessed with questionnaires, in the majority of studies on adult participants. Questionnaires usually consist of 5–20 items that are daily activities (e.g. writing, throwing, using a spoon, using a toothbrush, using a hammer) (Annett 1970; Oldfield 1971). The extent to which self-reported handedness is reliable may be disputable, but most researchers say that there is a good correlation between the answers at the questionnaire and the scores when the subject actually performs the action (Raczkowski et al. 1974). However, to evaluate hand preference, the ideal method is to observe the behaviour of the individual when he performs a task.

Behavioural studies are used in human infants, but they are scarce in adults. There are only a few experimental tasks, such as peg-moving, tapping and dotting that assess the hand performance (e.g. Annett 1985; Bishop 1984; Bishop et al. 1996; Bryden et al. 1994; Connolly and Bishop 1992; Tapley and Bryden 1985). Bishop et al. (1996) has designed a very interesting behavioural task that measures hand preference and its flexibility: the QHP (Quantification of Hand Preference) task. The QHP task is a simple reaching task that requires participants to take items that are placed on a semi-circle in front of them.

The purpose of the task is to assess the flexibility of hand preference as a function of the position of the item. Here, we used this task to evaluate the effect of the position of the object on hand preference. Indeed, hand preference has been shown or suggested to be influenced by a number of factors, including intrinsic factors that are related to the individual (age, sex) and extrinsic factors that are related to the environment, such as the task (Fagot and Vauclair 1991) and the position of the object (Bishop et al. 1996; Calvert and Bishop 1998; Carlson 1985; Cronholm et al. 1963; Doyen et al. 2008; Fagard 1998; Leconte and Fagard 2004). The position of the object relative to the hands is intuitively and obviously important. It is assumed to be able to strongly affect hand preference, and researchers generally strive to limit and control for this factor when assessing laterality (e.g. Chapelain et al. 2006; Fagot et al. 1991; Marchant and Steklis 1986; Vauclair and Fagot 1987). However, the effect of this factor has almost never been quantified in non-human primates. In humans, the QHP task has demonstrated that the position of the object significantly influences hand use: the hand that is used is usually the hand that is closest to the item: the left hand when the item is located on the left of the individual and the right hand when the item is located on the right of the individual (e.g. Bishop et al. 1996; Calvert and Bishop

1998). The QHP task has only been used once in non-human primates before. The results indicate that baboons perform similarly to adult humans on the QHP task: they reached with the hand that was closest to the item (Meunier et al. 2011).

The present study aimed to investigate hand preference for simple reaching and to assess the effect of the position of the object on this preference. Specifically, we wanted to determine whether the effect of the position of the object was significant and the extent to which it can affect hand preference. Can it reduce an existing preference? Can it cancel an existing preference? Can it create a preference? We examined hand preference in two conditions: a spontaneous condition and an experimental condition using an adaptation of the QHP task (Bishop et al. 1996). We studied two species of old-world monkeys: red-capped mangabeys which are semi-terrestrial (Gautier-Hion et al. 1999) and Campbell's monkeys which are arboreal (Oates 1988). We chose species that exhibit different degrees of arboreality to test the hypothesis of Marchant and McGrew (2007). This hypothesis proposes that arboreality may be a constraint against the development of laterality, because in the trees, the animals must keep both hands equally able to perform the crucial task of preventing the animal from falling on the ground. It predicts that arboreal monkeys should be less strongly lateralized and more flexible in hand use, compared to more terrestrial monkeys. We aimed to compare red-capped mangabeys and Campbell's monkeys and to compare our data with the previous QHP data in terrestrial baboons (Meunier et al. 2011).

We also considered the "postural origins theory" (McNeilage et al. 1987), which proposes the following evolutionary story. First, the left hand may have been specialized for visually guided reaches, the right hand being specialized for postural support (McNeilage 1993). This evolved as an adaptation to unimanual predation in prosimians, along with the prehensile hand. Later, the right hand may have become specialized for manipulations and bimanual coordination. This emerged along with the opposable thumb and the decrease of postural demands in monkeys. Finally, the right hand may have become dominant for all activities in humans. This theory predicts that monkeys should still exhibit a left-hand preference for reaching.

We examined both spontaneous conditions and experimental conditions, which allows for investigating Warren's hypothesis (1980). This hypothesis proposes that the laterality observed in non-human primates would be an artificial phenomenon, a non-natural preference that would be created or reinforced by the experiment. It predicts that the preferences should be stronger and less flexible in experimental compared to spontaneous condition.

The following questions were considered: Is there laterality for reaching on object located on the midline of the subject (with no spatial constraint on hand use)? Is hand preference flexible according to the position of the object: do the subjects preferentially use the hand that is closest to the item to take it? How does the position of the object affect the preference of each individual? Are there behavioural differences between right-handers and left-handers: are right-handers more resistant to changing hands to reach into the contralateral space compared to left-handers? Do we find similar results in the experimental condition and in the spontaneous condition? Do non-human primates exhibit a pattern that is similar to that observed in humans on the QHP task? Does the species biology (e.g. locomotion, diet, degree of arboreality) influence the results? And do sex or age (maturation) influence the results?

Materials and methods

Subjects

All subjects were born in captivity at la station biologique de Paimpont (France). Thirteen Campbell's monkeys (*Cercopithecus campbelli campbelli*) (10 females and 3 males) and 15 red-capped mangabeys (*Cercocebus torquatus torquatus*) (7 females and 8 males) were studied (Tables 1, 2). Two age classes were distinguished: adults and juveniles (*C. c. campbelli*: Hunkeler et al. 1972; *C. t. torquatus*, based on *C. albigena*: Danjou 1972). There were 8 adults and 5 juveniles in Campbell's monkeys and 11 adults and 4 juveniles in mangabeys (Tables 1, 2). The guenons lived in two social groups and the mangabeys lived in four social groups. The monkeys were housed in heated (22 °C) indoor cages (around 20 m^2) connected to outdoor wire-net cages (around 50 m^2). Both indoor and outdoor cages were provided with vertical and horizontal perches. The observations were conducted indoors and outdoors. The monkeys were given fresh fruit and vegetables in the morning meal and food pellets in the evening. Water was provided ad libitum.

Methods

We assessed hand preference for reaching in front (baseline condition) and for reaching in lateral positions. Manual laterality was studied in two conditions: in the spontaneous condition, when we observed the daily spontaneous behaviour of the subjects, and in the experimental condition, when we used an experimental design to investigate hand preference.

Table 1 Spontaneous condition: raw data for each individual for reaching in each zone: mangabeys

	Sex	Age (years)	Age class	ZLL				ZL				ZC				ZR				ZRR			
				LH	RH	B test	HI	LH	RH	B test	HI	LH	RH	B test	HI	LH	RH	B test	HI	LH	RH	B test	HI
Rapide	M	20.7	A	**17**	1	0.0001	−0.89	**96**	8	0.0001	−0.84	**225**	48	0.0001	−0.64	**35**	15	0.007	−0.40	1	2	–	–
Bandit	M	17.9	A	**11**	0	0.001	−1.00	**81**	26	0.0001	−0.51	160	166	0.782	0.01	12	**53**	0.0001	0.63	0	**11**	0.001	1.00
Pirate	M	16.6	A	2	0	–	–	**32**	2	0.0001	−0.88	**119**	63	0.0001	−0.30	17	17	1.136	0.01	2	0	–	–
Filou	M	14.7	A	**30**	14	0.023	−0.36	49	59	0.387	0.09	143	**214**	0.0001	0.19	48	**78**	0.010	0.23	8	**22**	0.016	0.46
Marti	M	10.6	A	**39**	10	0.0001	−0.59	**98**	42	0.0001	−0.40	130	140	0.584	0.03	24	**68**	0.0001	0.47	6	**31**	0.0001	0.67
Isba	M	5.1	J	**8**	0	0.008	−1.00	**24**	8	0.007	−0.50	68	**107**	0.004	0.22	2	**24**	0.0001	0.84	1	2	–	–
George	M	2.9	J	5	0	–	–	**57**	1	0.0001	−0.96	**140**	27	0.0001	−0.67	6	**25**	0.001	0.61	1	1	–	–
Lenni	M	2.6	J	3	1	–	–	**41**	1	0.0001	−0.95	88	87	1.000	−0.01	1	**35**	0.0001	0.94	1	4	–	–
Zunie	F	21.9	A	0	0	–	–	**15**	3	0.008	−0.66	67	**137**	0.0001	0.34	1	**28**	0.0001	0.93	0	4	–	–
Chipie	F	16.9	A	5	0	–	–	**42**	2	0.0001	−0.90	50	**84**	0.004	0.25	7	**31**	0.0001	0.63	0	2	–	–
Gofrette	F	12.5	A	2	0	–	–	**43**	4	0.0001	−0.83	**92**	42	0.0001	−0.37	4	**26**	0.0001	0.73	0	2	–	–
Joly	F	8.2	A	3	0	–	–	**52**	0	0.0001	−1.00	**118**	64	0.0001	−0.29	1	**52**	0.0001	0.96	0	11	0.001	1.00
Bell	F	7.1	A	**6**	0	0.031	−1.00	**55**	1	0.0001	−0.96	**119**	50	0.0001	−0.40	2	**35**	0.0001	0.89	0	3	–	–
Julie	F	5.0	A	**9**	0	0.004	−1.00	**55**	5	0.0001	−0.83	51	**88**	0.002	0.26	5	**23**	0.001	0.64	0	**6**	0.031	1.00
Chipse	F	3.4	J	2	0	–	–	**38**	1	0.0001	−0.94	**103**	45	0.0001	−0.39	4	**25**	0.0001	0.72	0	3	–	–
Mean HI				−0.834 (s.e. 0.257)				−0.74 (s.e. 0.08)				−0.118 (s.e. 0.089)				0.59 (s.e. 0.10)				0.83 (s.e. 0.06)			
t test				$T = -8.575$, $\boldsymbol{P = 0.0001}$				$T = -9.58$, $\boldsymbol{P = 0.0001}$				$T = -1.33$, $P = 0.206$				$T = 5.99$, $\boldsymbol{P = 0.0001}$				$T = 7.52$, $\boldsymbol{P = 0.002}$			
L versus R				$\boldsymbol{P = 0.016}$				$\boldsymbol{P = 0.0001}$				$P = 0.774$				$\boldsymbol{P = 0.001}$				$P = 0.063$			
Lat versus NL				$\boldsymbol{P = 0.016}$				$\boldsymbol{P = 0.001}$				$\boldsymbol{P = 0.035}$				$\boldsymbol{P = 0.0001}$				$P = 0.063$			

Sex: *M* male, *F* female. *Age class*: *A* adult. *J* juvenile, *LH* number of left-hand reaches, *RH* number of right-hand reaches, *B test P* value of the Binomial test performed on the number of right-hand versus left-hand reaches (when the test is significant, the higher value is in bold), *HI* laterality index.–: insufficient data for testing. *t test*: *t* value and *P* value of the *t* test performed on the mean HI value for the group. *L versus R*: *P* value of the Binomial test performed on the number of right handers and left handers. *Lat versus NL*: *P* value of the Binomial test performed on the number of lateralized and non-lateralized subjects. Bold indicates significant *P* values ($P \leq 0.05$) for these tests

Table 2 Spontaneous condition: raw data for each individual for reaching in each zone: Campbell's monkeys

	Sex	Age (years)	Age class	ZLL				ZL				ZC				ZR				ZRR			
				LH	RH	B test	HI	LH	RH	B test	HI	LH	RH	B test	HI	LH	RH	B test	HI	LH	RH	B test	HI
Arbok	M	6	A	1	1	–	–	15	6	0.078	−0.42	84	**176**	0.0001	0.35	1	**75**	0.0001	0.97	0	1	–	–
Lombric	M	2.4	J	2	0	–	–	**18**	3	0.001	−0.71	33	**63**	0.003	0.31	1	**28**	0.0001	0.93	0	1	–	–
Lowi	M	3.7	J	0	0	–	–	**9**	1	0.021	−0.80	52	64	0.307	0.10	3	**13**	0.021	0.63	0	3	–	–
Plume	F	16.8	A	1	0	–	–	**20**	0	0.0001	−1.00	48	55	0.555	0.07	3	**18**	0.001	0.71	0	3	–	–
Lowina	F	15.6	A	1	0	–	–	**18**	1	0.0001	−0.89	55	54	1.000	−0.01	5	**15**	0.041	0.50	1	0	–	–
Shawnee	F	15.5	A	1	0	–	–	**17**	2	0.001	−0.79	45	60	0.172	0.14	2	**11**	0.022	0.69	0	1	–	–
Maricopa	F	14.3	A	0	1	–	–	**18**	3	0.001	−0.71	38	**94**	0.0001	0.42	0	**26**	0.0001	1.00	6	6	1.226	0
Tilamook	F	13.3	A	4	0	–	–	**32**	0	0.0001	−1.00	**70**	26	0.0001	−0.46	4	11	0.118	0.47	0	1	–	–
Chilula	F	13.1	A	2	1	–	–	**23**	2	0.0001	−0.84	41	51	0.348	0.11	4	**21**	0.001	0.68	0	0	–	–
Amande	F	4.7	A	1	0	–	–	**10**	0	0.002	−1.000	31	**66**	0.0001	0.36	3	**33**	0.0001	0.83	0	1	–	–
Chili	F	3.6	J	4	0	–	–	**16**	2	0.001	−0.78	59	56	0.852	−0.03	3	5	0.727	0.25	0	2	–	–
Pincette	F	2.7	J	2	0	–	–	13	5	0.096	−0.44	26	**72**	0.0001	0.47	1	**23**	0.0001	0.92	0	3	–	–
Ecureuille	F	2	J	2	0	–	–	**26**	2	0.0001	−0.86	**66**	37	0.006	−0.28	1	**16**	0.0001	0.88	0	0	–	–
Mean HI								−0.79 (s.e. 0.05)				0.12 (s.e. 0.08)				0.73 (s.e. 0.06)							
t test				–				$T = -15.36$, $\boldsymbol{P = 0.0001}$				$T = 1.59$, $P = 0.14$				$T = 11.65$, $\boldsymbol{P = 0.0001}$				–			
L versus R				–				$\boldsymbol{P = 0.001}$				$P = 0.453$				$\boldsymbol{P = 0.001}$				–			
Lat versus NL				—				$\boldsymbol{P = 0.022}$				$P = 0.549$				$\boldsymbol{P = 0.022}$				–			

See legend of Table 1

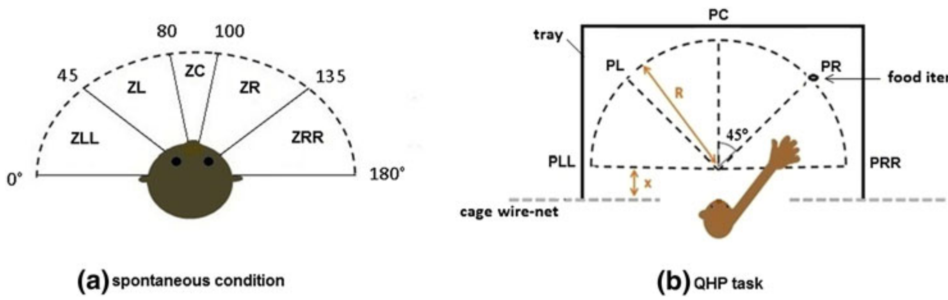

Fig. 1 Reaching zones for the spontaneous condition and positions for the QHP task. **a** Spontaneous condition: ZLL to ZRR are the five zones where we recorded the reaches of the subject. **b** QHP task apparatus. PLL to PRR are the five positions where the item could be placed on the semi-circle. R: diameter of the semi-circle. R was 10 cm for juveniles and 14 cm for adult Campbell's monkeys; 14 cm for juveniles, 20 cm for adult females and 24 cm for adult male mangabeys. x: distance between the wire-net and the semi-circle. x was 3 cm for Campbell's monkeys and 5 cm for mangabeys

Spontaneous condition

The subjects were observed during their daily meal. The food consisted of fruits and vegetables. The food items were cut into small pieces (6–12 cm^3) so that they could be manipulated with one hand by all the individuals. The items were spread on the floor of the cage.

Each individual was observed for 1.5 h in total, using Focal animal sampling (Altmann 1974) (5 or 10 or 15 min per day for 7–19 days, depending on the subject housing). The order in which the subjects were observed was changed each day to minimize possible effects of satiety or food availability.

For each data point, we recorded the hand that did the reaching action, the activity of the other hand (i.e. inactive, holding another food item, helping the other hand, postural support), the posture of the subject (i.e. seated, tripedal, bipedal), the type of fruit and the position of the item taken relative to the subject (Fig. 1a). The area of potential reaching was divided into five zones based on the subjects' shoulders axis: ZLL, ZL, ZC, ZR, ZRR, from the left to the right of the subject (Fig. 1a).

These observations were conducted by the authors MV and AM.

Experimental condition: the QHP task

In humans, the participant is standing or seated in front of the apparatus (a table) and has to take an object amongst 5 or 7 objects (playing cards in the original version of the task (Bishop et al. 1996)) that are placed on a semi-circle in front of him or her. The experimenter tells the participant which object to take. This task has been adapted to non-human primates (baboons: Meunier et al. 2011). The object was replaced by a food item that was randomly and successively placed at one of the seven positions that were marked on a semi-circle drawn on the apparatus. In the present study, we used five positions for the object: PLL, PL, PC, PR, PRR, from the left to the right of the subject (Fig. 1b). Five positions were used to allow for comparisons with the spontaneous condition, in which five but not seven positions could be reliably scored. Only one item was placed at a time. The experimenter randomly used her left hand and right hand to place it. The apparatus was a tray fixed onto the wire-net, outside the cage. There was a large hole (40–45 cm) in the wire-net that allowed the subject to pass its arms through. The object positions were located on a semi-circle, at a reaching distance adapted to the subject's arm length (according to its sex and age class) (Fig. 1b). The posture of the subject was standardized so that the individual was seated, with its body midline aligned with the midline of the apparatus. We chose the food items according to the preferences of the species: a small piece of apple for the red-capped mangabeys and a sunflower seed for the Campbell's monkeys.

Each subject was tested once a day, and did 15 trials per day, 3 for each position. Thus, each individual did 60 trials in total, 12 for each position. For each trial, the position of the item was randomly chosen. The sequence of presentations was set up in advance and was the same for all the subjects. A trial was considered valid and recorded only when the subject was seated, aligned with the midline of the apparatus, with both hands free when starting. For each trial, we recorded the hand that did the reaching action.

To ensure data independence, a seed was thrown into the back of the cage after each trial. The subject had to move off and pick up the seed, before coming back and repositioning itself in front of the apparatus for another trial. This requirement was to ensure that the next action was not influenced by the hand that has been used previously (Marchant and McGrew 1991; McGrew and Marchant 1996, 1997).

The subjects were isolated for the test, to avoid the presence of competitive congeners influencing hand use (except for Lowi, who was the dominant male of the

Campbell's monkeys group and did not need to be isolated from others). A period of habituation was necessary to allow the subjects to become accustomed to the apparatus. Most mangabeys only needed one day of habituation. The Campbell's monkeys needed several days to accustom to sit to perform the task.

These observations were conducted by the author AL.

Statistical analyses

We used the Binomial test (Siegel and Castellan 1988) to compare the number of responses performed with the left and right hands so as to categorize each subject as lateralized or non-lateralized. The individual exhibited a right-hand preference if the number of right-hand responses was significantly greater than the number of left-hand responses, based on the Binomial test. We also used the commonly used handedness index (HI) to quantify laterality on a continuum. HI was calculated for each individual, using the formula HI = (right − left)/(right + left), where right and left are the numbers of responses performed with the right and left hands. HI gives the direction of laterality, from −1 to +1, with positive values indicating a bias toward the right hand and negative values indicating a bias toward the left hand. The absolute value of HI (absHI) gives the strength of laterality, from 0 to 1. To assess group-level biases, we performed a Binomial test (Siegel and Castellan 1988) on the numbers of right-handers and left-handers in the group, when at least six subjects were lateralized. We also evaluated the bias in hand use by performing a one-sample *t* test (Siegel and Castellan 1988) on the mean HI value for the group. For the QHP task, we calculated an index to characterize flexibility of hand use. For each subject, we calculated the index as follows: we gave five points to each right-hand reach made on the extreme left position (PLL), four points to each right-hand reach made on the left position (PL), three points to each right-hand reach made on the central position (PC), two points to each right-hand reach made on the right position (PR) and one point to each right-hand reach made on the extreme right position (PRR); then the sum of these numbers was divided by the total number of trials (60). This index varies from 0 for an exclusive left-hander that never changes hand, to 3 for an exclusive right-hander that never changes hand. This index could not be calculated for the spontaneous condition because the number of trials varied

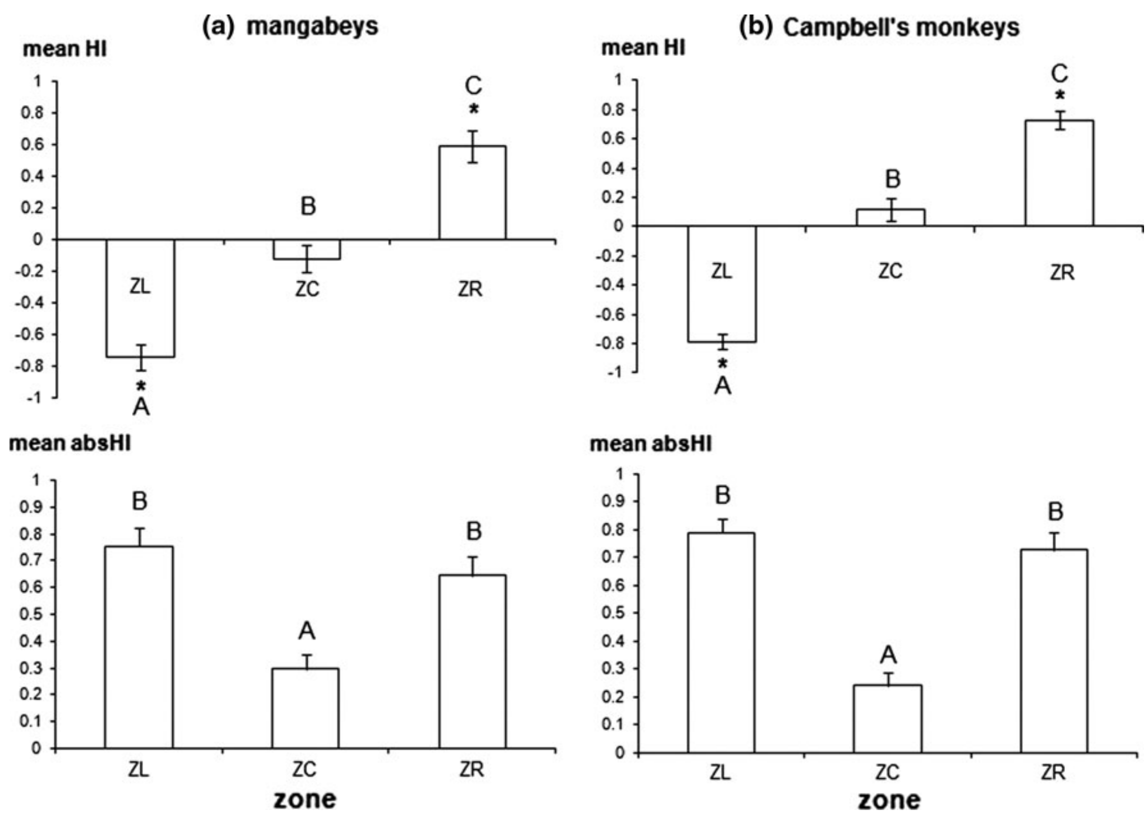

Fig. 2 Spontaneous condition: variation of the direction (HI) and strength (AbsHI) of laterality according to the reaching zone, for red-capped mangabeys (**a**) and for Campbell's monkeys (**b**). Letters (*A*, *B*, *C*) give the results of the Wilcoxon tests: *same letters*: no significant difference, *different letters*: significant difference ($P < 0.008$). *Asterixes* (*) indicate significant biases in hand-use, based on *t* tests ($P < 0.0001$)

between positions and subjects, and there were too few trials for the extreme positions.

We investigated the effects of several possible influential factors, including sex, age, species and the position of the item by examining the direction of laterality (HI values), the strength of laterality (absHI values), the numbers of lateralized versus non-lateralized subjects and the numbers of right handers versus left-handers. These analyses were performed using Friedman test, Wilcoxon test, Mann–Whitney test, Fisher test and Spearman correlation test (Siegel and Castellan 1988). Excel, R, Statistica and Minitab were used to analyse the data. The statistical tests were considered significant when $P \leq 0.05$, two-tailed. The Bonferroni correction was applied whenever multiple comparisons were done.

Results

Spontaneous condition

We collected data on 4,972 reaches in mangabeys and 2,163 reaches in Campbell's monkeys. The majority of reaches occurred in the central zone: ZC (mangabey: 61 %, Campbell's monkeys: 70.4 %). There were so few reaches (below 2.5 %) in the extreme zones ZLL and ZRR that these were excluded from the analyses. We found no effect of the posture of the subject or of the type of fruit on laterality (Wilcoxon tests $P > 0.05$).

The strength of laterality was influenced by the position of the item. In both species, laterality (absHI values) was stronger in zones ZL and ZR that involve spatial constraints, compared with the central zone ZC that involves no spatial constraint (Friedman test mangabeys: $N = 15$ $H = 13.7$ $P = 0.001$, Campbell's monkeys: $N = 13$ $H = 14.3$ $P = 0.0008$; Wilcoxon tests $P \leq 0.02$) (Fig. 2).

The direction of laterality was strongly affected by the position of the item. When considering the central zone ZC, no group-level bias occurred in the number of left-handed versus right-handed subjects (Tables 1, 2, 3). However, for the zones ZL and ZR, almost all the subjects were lateralized, and the direction of laterality depended on the zone. There was a group-level left bias for ZL (Binomial test $P \leq 0.001$) and a group-level right bias for ZR in both species (Binomial test $P \leq 0.002$) (Tables 1, 2, 3). Analysis of the mean HI value also shows significant biases: a bias toward left-hand use for ZL and a bias toward right-hand use for ZR, in both species (t test $P < 0.008$) (Fig. 2). The mean HI varied significantly as a function of the reaching zone (Friedman test mangabeys: $N = 15$ $H = 30$ $P < 0.0001$, Campbell's monkeys: $N = 13$ $H = 22$ $P = 0.0002$) with lower values (greater left-hand use) in ZL compared with the other zones, and higher

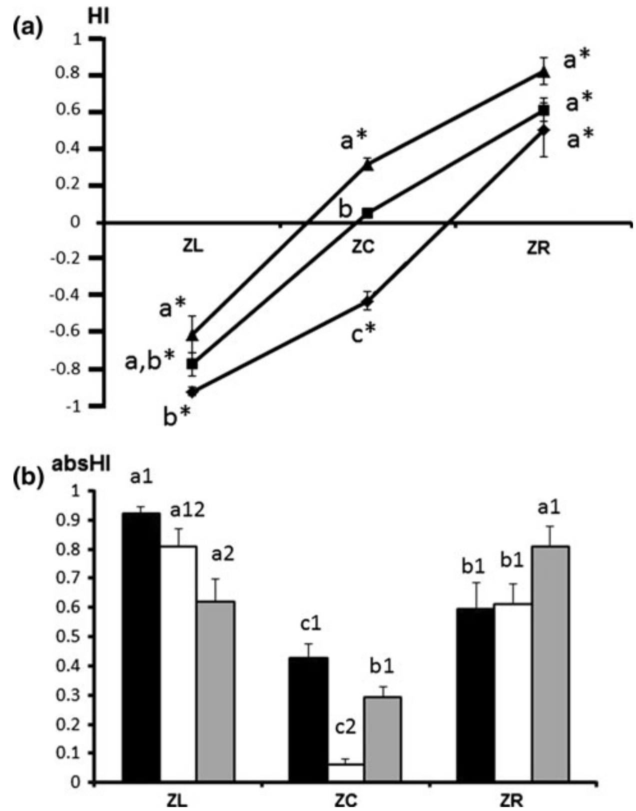

Fig. 3 Spontaneous condition: Variation of the direction (HI) and strength (AbsHI) of laterality according to the reaching zone, according to the subject categorization based on reaching in ZC. **a** Direction of laterality: *symbols*: Lozenge: subjects that are left-handed in ZC, *triangle*: subjects that are right-handed in ZC, *square*: subjects that are non-lateralized in ZC. *Letters* give the results of the Mann–Whitney tests: *same letters*: no significant difference between the two categories of subjects ($P > 0.05$), *different letters*: significant difference ($P \leq 0.05$). *Asterixes* (*) indicate significant biases in hand-use, based on t tests ($P < 0.05$). **b** Strength of laterality: *black*: subjects that are left-handed in ZC, *grey*: subjects that are right-handed in ZC, *white*: subjects that are non-lateralized in ZC. *Letters* give the results of the comparisons intra-category between different zones; numbers give the results of comparisons inter-category for each zone, based on Wilcoxon tests and Mann–Whitney tests, respectively. *Same letters* or *same numbers*: no significant difference, *different letters* or numbers: significant difference ($P < 0.008$)

values (greater right-hand use) in ZR (Wilcoxon tests $P < 0.004$) (Fig. 2). This shows that the individuals used the left hand to reach for items that were located on their left, and used the right hand to reach for items that were located on their right.

Based on the laterality observed in the central zone ZC, we classified the subjects into three categories: right-handers (36 % of the subjects), left-handers (32 %) and non-lateralized (32 %) (taking both species together) (Tables 1, 2, 3). Whatever their category based on ZC, almost all the individuals "became right-handed" in ZR: they used the right hand significantly more than the left hand to reach for items located on their right, and they

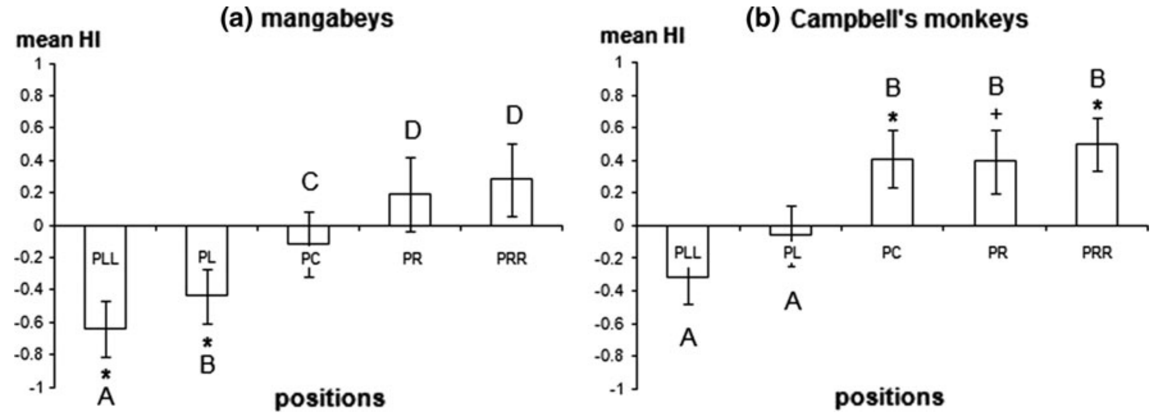

Fig. 4 Experimental condition: variation of the direction (HI) and strength (AbsHI) of laterality according to the position, for red-capped mangabeys (**a**) and Campbell's monkeys (**b**). Letters (*A*, *B*, *C*, *D*) give the results of the Wilcoxon tests: *same letters*: no significant difference, *different letters*: significant difference ($P < 0.01$). *Asterixes* (*) indicate significant biases in hand-use, based on *t* tests ($P < 0.0001$) and cross (+) indicate trends ($P < 0.10$)

Table 3 Summary of the results

Spontaneous condition	ZLL	ZL	ZC	ZR	ZRR
Mangabeys					
Right handed	0	0	5	13*	5
Left handed	7*	14*	7	1	0
Non-lateralized	0	1	3	1	0
Campbell's monkeys					
Right-handed	–	0	5	11*	0
Left-handed	–	11*	2	0	0
Non-lateralized	–	2	6	2	1
Experimental condition (QHP)	**PLL**	**PL**	**PC**	**PR**	**PRR**
Mangabeys					
Right-handed	1	1	3	5	6
Left-handed	9*	6	4	4	3
Non-lateralized	3	6	6	4	4
Campbell's monkeys					
Right-handed	0	1	4	5	7
Left-handed	4	3	1	1	1
Non-lateralized	7	7	6	5	3

Numbers of right-handed, left-handed and non-lateralized individuals for each condition and each zone or position. Asterixes indicate significant group-level biases based on the Binomial test

"became left-handed" in ZL: they preferentially used the left hand to reach for items located on their left. This effect also appears when analysing the mean HI value of each category (Fig. 3).

We compared the different categories of subjects and found some behavioural differences. When we compared the subjects that were right-handers and left-handers (based on laterality in ZC), right-handers used the left hand less than left-handers in ZL (Mann–Whitney test $P < 0.05$) (Fig. 3) and left-handers displayed a stronger laterality than right-handers in ZL (Mann–Whitney test $P \leq 0.05$) (Fig. 3).

Experimental condition: QHP task

The strength of laterality (absHI) was not influenced by the position of the item (Friedman tests mangabeys: $N = 13$ $H = 4.18$ $P \geq 0.140$, Campbell's monkeys: $N = 11$ $H = 6.18$ $P \geq 0.140$).

The direction of laterality was strongly affected by the position of the item. When considering the central position PC, no group-level bias occurred in the number of left-handed versus right-handed subjects (Tables 3, 4, 5). For the extreme lateral positions, PLL and PRR, the majority of the subjects were lateralized, and the direction of laterality depended on the position. However, a significant group-level bias occurred in only one case: a left bias in PLL in mangabeys (Binomial test $P = 0.021$) (Tables 3, 4, 5). For the positions PL and PR, there was no group-level bias in either species (Binomial test $P \geq 0.125$). However, the small number of lateralized subjects often prevented testing. When analyzing the mean HI value, several biases in hand use occurred: in Campbell's monkeys, there was a bias toward right-hand use in PC (*t* test $P = 0.04$) and in PRR (*t* test $P = 0.01$); and in mangabeys, there was a bias toward left-hand use for PLL and PL (*t* test PLL: $P = 0.003$, PL: $P = 0.024$) (Fig. 4). The mean HI varied significantly as a function of the position (Friedman test mangabeys: $N = 13$ $H = 12.41$ $P < 0.02$, Campbell's monkeys: $N = 11$ $H = 17.70$ $P < 0.01$); with lower HI values (greater left-hand use) in PLL and PL compared with the other positions, and higher HI values (greater right-hand use) in PR and PRR (Wilcoxon tests, mangabeys: $P \leq 0.036$) (Fig. 4). This shows that the individuals

Table 4 Experimental condition (QHP): raw data for each individual for reaching in each position: mangabeys

	PLL				PL				PC				PR				PRR				Index of flexibility
	LH	RH	B test	HI	LH	RH	B test	HI	LH	RH	B test	HI	LH	RH	B test	HI	LH	RH	B test	HI	
Rapide	**12**	0	0.0005	−1	**12**	0	0.0005	−1	**12**	0	0.0005	−1	**11**	1	0.006	−0.83	**12**	0	0.0005	−1	0.03
Bandit	0	**12**	0.0005	1	0	**12**	0.0005	1	1	**11**	0.006	0.83	0	**12**	0.0005	1	0	**12**	0.0005	1	2.95
Pirate	**12**	0	0.0005	−1	**12**	0	0.0005	−1	**12**	0	0.0005	−1	**11**	1	0.006	−0.83	**12**	0	0.0005	−1	0.03
Filou	**12**	0	0.0005	−1	9	3	0.15	−0.5	5	7	0.77	0.17	5	7	0.77	0.17	4	8	0.39	0.33	0.92
Marti	**11**	1	0.0063	−0.83	**11**	1	0.0063	−0.83	**12**	0	0.0005	−1	**12**	0	0.0005	−1	6	6	1	0	0.25
Isba	9	3	0.15	−0.5	6	6	1	0	5	7	0.77	0.17	0	**12**	0.0005	1	1	**11**	0.006	0.83	1.58
George	**12**	0	0.0005	−1	**12**	0	0.0005	−1	**12**	0	0.0005	−1	**12**	0	0.0005	−1	**12**	0	0.0005	−1	0.00
Zunie	7	5	0.77	−0.17	5	7	0.77	0.17	0	**12**	0.0005	1	0	**12**	0.0005	1	0	**12**	0.0005	1	2.08
Chipie	5	7	0.77	0.17	5	7	0.77	0.17	2	**10**	0.0386	0.67	0	**12**	0.0005	1	1	**11**	0.006	0.83	2.13
Gofrette	**12**	0	0.0005	−1	**12**	0	0.0005	−1	6	6	1	0	3	9	0.15	0.5	0	**12**	0.0005	1	0.80
Bell	**12**	0	0.0005	−1	**10**	2	0.0386	−0.67	6	6	1	0	0	**12**	0.0005	1	0	**12**	0.0005	1	1.03
Julie	**12**	0	0.0005	−1	9	3	0.15	−0.5	8	4	0.39	−0.33	6	6	1	0	5	7	0.77	0.17	0.72
Chipse	**12**	0	0.0005	−1	9	3	0.15	−0.5	6	6	1	0	3	9	0.15	0.5	3	9	0.15	0.5	0.95
Mean HI	−0.64 (s.e. 0.17)				−0.40 (s.e. 0.17)				−0.10 (s.e. 0.20)				0.19 (s.e. 0.23)				0.19 (s.e. 0.23)				
t test	$T = -3.7$, $\mathbf{P = 0.003}$				$T = -2.57$, $\mathbf{P = 0.024}$				$T = -0.58$, $P = 0.571$				$T = 0.83$, $P = 0.424$				$T = 1.27$, $P = 0.23$				
L versus R	$\mathbf{P = 0.02}$				$P = 0.125$				$P = 1$				$P = 1$				$P = 0.51$				
Lat versus NL	$P = 0.09$				$P = 1$				$P = 1$				$P = 0.27$				$P = 0.27$				

LH number of left-hand reaches, *RH* number of right-hand reaches, *B test P* value of the Binomial test performed on the number of right-hand versus left-hand reaches (when the test is significant, the higher value is in bold) *HI* laterality index.–: insufficient data for testing. *t test*: *t* value and *P* value of the *t* test performed on the mean HI value for the group. *L versus R*: *P* value of the Binomial test performed on the number of right-handers and left-handers. *Lat versus NL*: *P* value of the Binomial test performed on the number of lateralized and non-lateralized subjects. Bold indicate significant *P* values ($P \leq 0.05$) for these tests. Index of flexibility: value of the index of flexibility of hand-use

Table 5 Experimental condition (QHP): Raw data for each individual for reaching in each position: Campbell's monkeys

	PLL				PL				PC				PR				PRR				Index of flexibility
	LH	RH	B test	HI	LH	RH	B test	HI	LH	RH	B test	HI	LH	RH	B test	HI	LH	RH	B test	HI	
Lombric	6	6	1.00	0.00	6	6	1.00	0.00	3	9	0.15	0.50	7	5	0.77	−0.17	2	**10**	0.04	0.67	1.68
Lowi	4	8	0.39	0.33	6	6	1.00	0.00	1	**11**	0.006	0.83	3	9	0.15	0.50	1	**11**	0.006	0.83	2.10
Plume	**10**	2	0.04	−0.67	8	4	0.39	−0.33	3	9	0.15	0.50	1	**11**	0.006	0.83	1	**11**	0.006	0.83	1.43
Lowina	**12**	0	0.0005	−1.00	**11**	1	0.006	−0.83	6	6	1.00	0.00	3	9	0.15	0.50	4	8	0.39	0.33	0.80
Shawnee	**12**	0	0.0005	−1.00	**12**	0	0.0005	−1.00	**12**	0	0.0005	−1.00	**12**	0	0.0005	−1.00	**11**	1	0.006	−0.83	0.02
Maricopa	5	7	0.77	0.17	0	**12**	0.0005	1.00	0	**12**	0.0005	1.00	0	**12**	0.0005	1.00	0	**12**	0.0005	1.00	2.58
Tilamook	9	3	0.15	−0.50	3	9	0.15	0.50	0	**12**	0.0005	1.00	0	**12**	0.0005	1.00	1	**11**	0.006	0.83	2.03
Chilula	**12**	0	0.0005	−1.00	**10**	2	0.04	−0.67	6	6	1.00	0.00	8	4	0.388	−0.33	7	5	0.39	−0.17	0.65
Amande	4	8	0.39	0.33	3	9	0.15	0.50	4	8	0.39	0.33	1	**11**	0.006	0.83	2	**10**	0.04	0.67	2.20
Chili	7	5	0.77	−0.17	7	5	0.77	−0.17	3	9	0.15	0.50	2	**10**	0.04	0.67	1	**11**	0.006	0.83	1.72
Pincette	6	6	1.00	0.00	4	8	0.39	0.33	1	**11**	0.006	0.83	3	9	0.15	0.50	3	9	0.15	0.50	2.03
Mean HI	−0.32 (s.e. 0.16)				−0.06 (s.e. 0.19)				0.41 (s.e. 0.18)				0.39 (s.e. 0.19)				0.50 (s.e. 0.16)				
t test	$T = -1.97$, $P = 0.77$				$T = -0.32$, $P = 0.75$				$T = 2.32$, $\mathbf{P = 0.04}$				$T = 2.06$, $P = 0.07$				$T = 3.03$, $\mathbf{P = 0.01}$				
L versus R	–				–				–				$P = 0.22$				$P = 0.07$				
Lat versus NL	$P = 0.55$				$P = 0.55$				$P = 1$				$P = 1$				$P = 0.23$				

See legend of Table 4

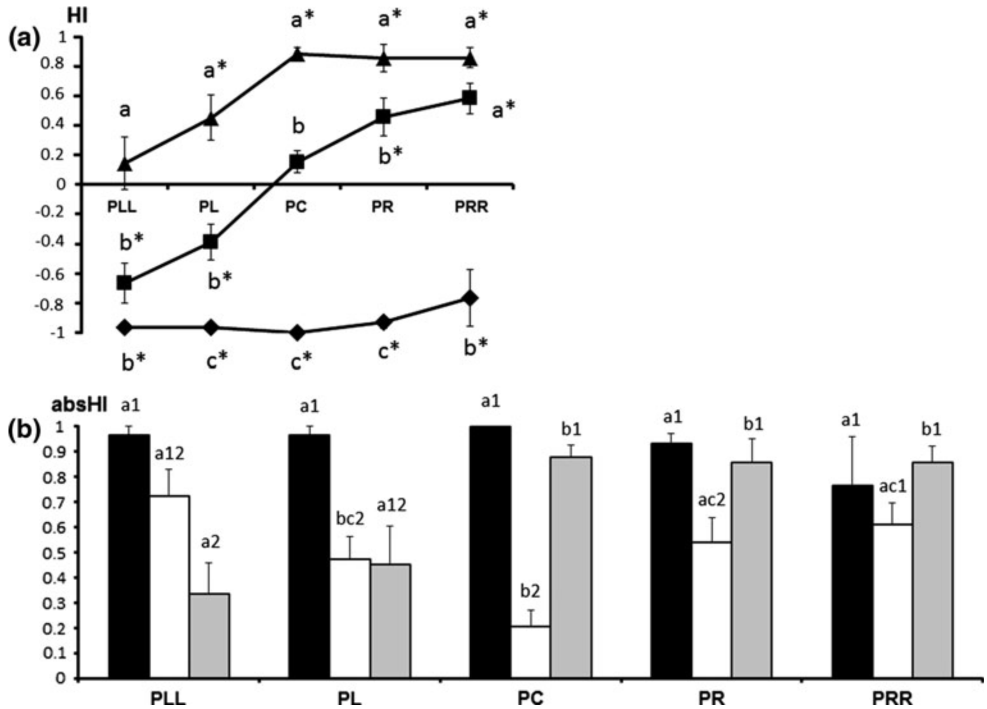

Fig. 5 Experimental condition: variation of the direction (HI) and strength (AbsHI) of laterality according to the reaching zone, according to the subject categorization based on reaching in PC. **a** Direction of laterality: *symbols*: *Lozenge*: subjects that are left handed in PC, *triangle*: subjects that are right-handed in PC, *square*: subjects that are non-lateralized in PC. *Letters* give the results of the Mann–Whitney tests: *same letters*: no significant difference between the two categories of subjects ($P > 0.05$), *different letters*: significant difference ($P \leq 0.05$). *Asterixes* (*) indicate significant biases in hand-use, based on *t* tests ($P < 0.05$). **b** Strength of laterality: *black*: subjects that are left-handed in PC, *grey*: subjects that are right handed in PC, *white*: subjects that are non-lateralized in PC. *Letters* give the results of the comparisons intra-category between different positions; *numbers* give the results of comparisons inter-category for each position, based on Wilcoxon tests and Mann–Whitney tests, respectively. *Same letters* or *same numbers*: no significant difference, different letters or numbers: significant difference ($P < 0.008$)

tended to use rather the left hand to reach for items located on their left, and the right hand to reach for items located on their right. One should note that five individuals (4 mangabeys and 1 Campbell's monkey) were not influenced by the position of the item, keeping their hand preference over the five positions (Tables 3, 4, 5).

We examined the concordance between the position of the item and the hand preferentially used. The majority of the subjects preferentially used the hand that was appropriate to the position of the object, i.e. the hand that was on the same side as the item to reach. The proportions of concordant versus non-concordant subjects were 9/1 in PLL, 6/1 in PL, 5/4 in PR and 6/3 in PRR in mangabeys and 4/0 in PLL, 3/1 in PL, 5/1 in PR and 7/3 in PRR in Campbell's monkeys (Table 3). This shows that the subjects that were lateralized used the hand that was on the same side as the object (with a few exceptions).

Based on the laterality observed in the central position PC, we classified the subjects into three categories: right-handers (29 % of the subjects), left-handers (21 %) and non-lateralized (50 %) (taking both species together) (Tables 3, 4, 5). The subjects that were left-handers in PC ($N = 5$) remained left-handed for the other positions (except one subject in PRR) (Tables 4, 5). The subjects that were right handers in PC ($N = 7$) tended to remain right-handed for the other positions, although they were often not right-handed on PLL or/and PL (Tables 4, 5). The subjects that were non-lateralized in PC often "became right-handed" to reach for items located on their right (especially on the extreme position PRR) and "became left-handed" to reach for items located on their left (especially on the extreme position PLL) (Tables 4, 5).

We compared the different categories of subjects and found some behavioural differences. When we compared the subjects that were right-handers and left-handers (based on laterality in PC): right-handers used the right hand significantly more than left-handers in PR and PRR (Mann–Whitney tests $P < 0.05$) (Fig. 5) and left-handers used the left hand significantly more than right-handers in PL and PLL (Mann–Whitney tests $P < 0.05$) (Fig. 5). In right-handers, the mean asbHI varied according to the position (Friedman test $N = 7$ $X2 = 14.37$ $P = 0.005$), with higher values in positions C, R and RR, compared with LL and L (Fig. 5) (Wilcoxon tests $P < 0.05$). In left-handers, the mean asbHI was not influenced by the position (Friedman test $N = 5$ $X2 = 4.00$ $P = 0.41$) (Fig. 5). Left-handers showed a stronger laterality than right-handers in PLL (Mann–Whitney test $P \leq 0.05$) (Fig. 5).

We calculated an index that reflects flexibility of hand use, from 0 for an exclusive left-hander that never changes hand, to 3 for an exclusive right-hander that never changes hand. The mangabeys showed indexes that ranged from 0 to 2.95, with a mean of 1.037 (Table 4). This shows that there were several individuals (Georges, Rapide, Pirate and Bandit) that were exclusive or almost exclusive in hand use, never changing hand whatever the position of the object. Most mangabeys exhibited indexes that were below or close to 1, with only four subjects having high values. This indicates that few subjects used the right hand a lot. This suggests that right-hand use was relatively unfrequent, and mostly restricted to right-sided positions. The Campbell's monkeys showed indexes that ranged from 0.017 to 2.583, with a mean of 2.033 (Table 5). Only one individual (Shawnee) was almost exclusive in hand use, never changing hand whatever the position of the object. Most Campbell's monkeys had indexes that were above or close to 1.5, with only three subjects having low values. This indicates that many subjects used the right hand a lot. This suggests that right-hand use was relatively frequent, and not restricted to right-sided positions.

Comparison of the laterality in spontaneous and experimental conditions

For the central position/zone C, the seven individuals that were lateralized exhibited the same preference in the two conditions (only one subject changed preference) (Tables 1, 2, 4, 5). With regard to the lateral positions that we could compare, the lateralized subjects generally kept the same preference in the spontaneous and experimental conditions (with a few cases of opposite preference for one position) (Tables 1, 2, 4, 5).

In mangabeys, there was no difference between the spontaneous and the experimental condition regarding HI and absHI values (Wilcoxon test $P > 0.09$). Campbell's monkeys were more lateralized (higher absHI values) in the experimental than spontaneous condition in position C/zone C (Wilcoxon $P = 0.02$) (but there were many more data points in the spontaneous condition). In position L/zone L, Campbell's monkeys were less lateralized in the experimental than spontaneous condition (Wilcoxon $P = 0.03$) and the HI values were lower (greater left-hand use) in spontaneous than experimental condition (Wilcoxon $P = 0.001$).

Effect of age

Spontaneous condition There was no difference between adults and juveniles regarding the direction and strength of laterality (Mann–Whitney tests $P \geq 0.22$). There was no correlation between age and the direction or strength of laterality (Spearman correlations $-0.44 < \text{rho} < 0.34$, $P > 0.11$).

QHP task In most cases, there was no difference between adults and juveniles regarding the direction and strength of laterality (Mann–Whitney tests $P \geq 0.18$). There was an age difference in Campbell's monkeys in some cases: in PLL, the adults were more left handed than the juveniles (Mann–Whitney test $P = 0.03$), and in PLL and PL, the adults were more lateralized than the juveniles (Mann–Whitney tests PLL: $P = 0.02$, PL: $P = 0.02$). There was no correlation between age and the direction or strength of laterality (Spearman correlations $-0.44 < \text{rho} < 0.34$, $P > 0.11$), except in Campbell's monkeys in PLL and PL, for which the strength of laterality increased with age (Spearman correlations PLL: $\text{rho} = 0.77$, $P = 0.005$, PL: $\text{rho} = 0.67$, $P = 0.02$). There was no effect of age on the index of flexibility of hand use (Mann–Whitney test mangabeys: $P = 0.735$, Campbell's monkeys: $P = 0.507$).

Effect of sex

Spontaneous condition In mangabeys, females showed higher HI and absHI values than males in ZR (Mann–Whitney test $P = 0.04$).

QHP task There was no effect of sex on laterality and on the index of flexibility of hand use (Mann–Whitney tests $P > 0.05$). However, one can note that the mangabeys that were exclusive or almost exclusive in hand use (never changing hand whatever the position of the object) were all males (Georges, Rapide, Pirate and Bandit).

Effect of species

Spontaneous condition There was no difference between the two species regarding the direction of laterality (Mann–Whitney test $P \geq 0.14$), the strength of laterality (Mann–Whitney test $P > 0.62$), and the distribution of lateralized versus non-lateralized subjects and right-handed versus left-handed subjects (Fisher tests $P > 0.05$).

QHP task We found three cases of significant between-species differences. In positions PLL and PL, the mangabeys were significantly more left handed than the Campbell's monkeys (Mann–Whitney test PLL: $P = 0.006$, PL: $P = 0.046$). In position PLL, the mangabeys were more lateralized than the Campbell's monkeys (Mann–Whitney test $P = 0.03$). There was no difference between the two species regarding the distribution of lateralized versus non-lateralized subjects, right-handed versus left-handed subjects (Fisher tests $P > 0.05$) and also regarding the index of flexibility of hand use (Mann–Whitney test $P = 0.182$).

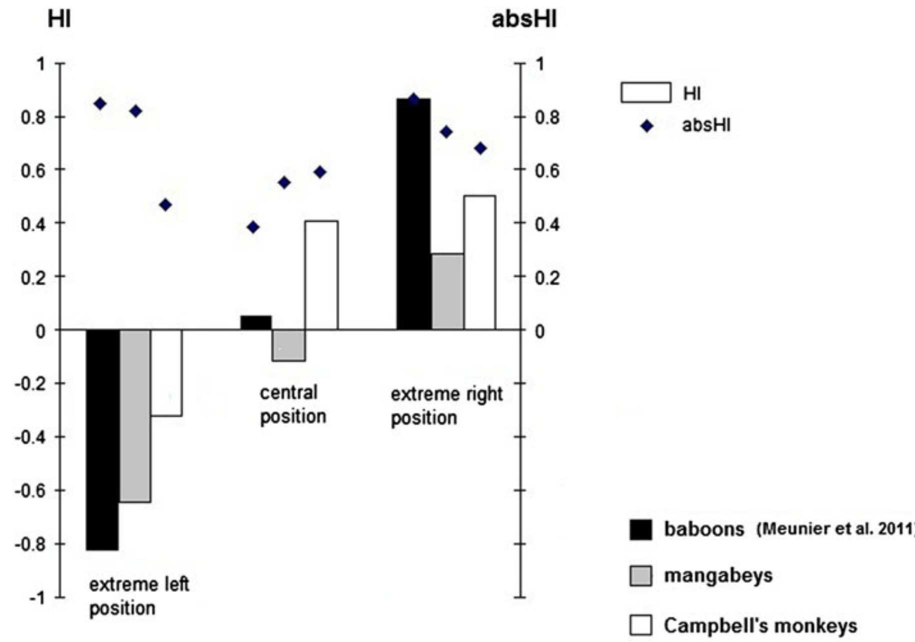

Fig. 6 Comparison between species: mean HI and absHI for each species and position

We compared our data with the data in baboons on the three positions that were comparable (centre, extreme left, extreme right) (Meunier et al. 2011) (Fig. 6). Based on HI values, baboons were more right handed than mangabeys and Campbell's monkeys on the extreme right position (Mann–Whitney tests $P \leq 0.0134$), and they were more left handed than Campbell's monkeys on the extreme left position (Mann–Whitney test $P = 0.0065$). For reaching in the central position, Campbell's monkeys were significantly more right-handed than baboons (Mann–Whitney test $P = 0.0195$). Regarding the strength of laterality (absHI values), baboons were similarly lateralized as the other species in the central position (Mann–Whitney tests $P > 0.05$), but they exhibited a stronger laterality than Campbell's monkeys in the extreme positions (Mann–Whitney tests $P \leq 0.007$).

Discussion

Laterality is known to be influenced by many intrinsic and extrinsic factors, whose precise effects remain unclear. The present study investigated hand preference for simple reaching and the effect of the position of the object on this preference, in two species of cercopithecines. We found significant individual-level laterality for reaching in front with no spatial constraint. We demonstrated a strong influence of the position of the object on hand use for reaching in the lateral positions.

First, we asked whether there was a laterality for reaching an object located in the midline of the subject, with no spatial constraint on hand use (ZC and PC). We found individual-level hand preferences, with about half of the subjects exhibiting a significant preference. No group-level bias occurred in the number of right-handed versus left-handed subjects, in either species. This result might be related to the small size of the samples tested, as significant biases may be difficult to reveal in small samples (Hopkins 2006). However, if a strong group-level bias existed (e.g. a human-like 90 % bias), it would appear even with a small sample. When considering the mean HI value, a group-level right bias in hand use appeared in Campbell's monkeys on the QHP task. Many studies have examined hand preference for simple reaching, but the results are inconsistent and contradictory. A review and meta-analysis suggested that a left-hand bias would exist in prosimians and in old-world monkeys (Papademetriou et al. 2005). Our results do not match this view, but the review article also stated that the left bias observed in old-world monkeys was due especially to the data in macaques. When considering the previous data in cercopithecines (Chapelain et al. 2006; Laurence et al. 2011; Blois-Heulin pers. comm.), there is no evidence of group-level bias for reaching. Thus, our data add to the current results indicating that non-human primates exhibit laterality for simple reaching but providing no support for the existence of group-level biases. This suggests that non-human primates are less lateralized than humans (Fagard 2004). However, the tasks used with humans and non-human primates are never identical, and there may also be uncontrolled influential factors in non-human primate studies, which may bias the results.

In the present study, we were interested in the effect of the position of the object. The effect of the position of the object on hand preference has rarely been studied and quantified. We asked whether hand preference is flexible according to the position of the object: do the subjects use the hand that is closest to the item to take it? We demonstrated a strong influence of the position of the object on hand use. We showed that the monkeys preferentially used the hand that was closest to the item to take it: the left hand to reach items located on their left and the right hand to take items located on their right. In the spontaneous condition, there was a group-level left bias for reaching on the left side and a group-level right bias for reaching on the right side, in both species. The results in the experimental condition also go in this direction, although the effect was less marked.

We were particularly interested in the individual level. We asked how the position of the object can affect hand use in each individual. We wanted to determine the extent to which it can affect hand preference: can it reduce an existing preference? Can it cancel an existing preference? Or, can it create a preference? We found that most of the subjects displayed a preference for the hand that was on the same side as the object. In other words, when the subjects exhibited a significant preference, this was toward the hand that was closest to the item. Very few subjects used the hand that was opposite to the object, and these were subjects that always used their preferred hand, whatever the position of the item. Second, we demonstrated that the effect of the position of the object could create significant preferences in non-lateralized subjects, because many subjects were not lateralized in the central position PC, but were lateralized in the lateral positions (especially on the extreme positions PLL and PRR). Third, we showed that the effect of the position of the object could induce a loss of preference in lateralized individuals. Indeed, several subjects were lateralized in the central position PC and on the two positions corresponding to their preferred hand, but lost their preference on the opposite side. Generally, even the subjects that were very strongly lateralized lost their preference due to spatial constraints (at least on the extreme positions PLL or PRR). Therefore, our findings demonstrate that the position of the object had a marked effect on hand use and laterality: laterality varied according to spatial constraints. This is one of the first times that this effect has been shown and quantified. Our results are consistent with the limited previous data in other non-human primate species (macaques: Cronholm et al. 1963, Lehman 1970, 1978, 1980, baboons: Meunier et al. 2011) and with the data in humans (Bishop et al. 1996; Calvert and Bishop 1998; Carlson 1985; Doyen et al. 2008; Fagard 1998; Jacquet et al. 2012).

Together, our results and previous findings in non-human primates clearly demonstrate an effect of the position of the object on laterality, showing how an individual can change its preference according to spatial constraints. It is difficult to know whether and how this factor was controlled in previous non-human primate studies, and whether an effect of the position of the object might account for the negative results reported. We emphasize the importance of controlling this factor when assessing manual preferences in future studies.

We compared an experimental condition and a spontaneous condition to assess possible differences. We found similar results in the experimental condition and in the spontaneous condition. This shows that the QHP task is a biologically valid measure of hand preference and of hand preference flexibility. Moreover, this is important regarding Warren's hypothesis (Warren 1980), which predicts that the preferences should be stronger and less flexible in experimental condition compared to spontaneous condition, if laterality was an artificial phenomenon created by experimental biases. Our results do not support this hypothesis.

We investigated the effect of the species tested to determine whether the biology (e.g. locomotion, diet, degree of arboreality) could influence laterality and flexibility in hand use. With regard to the direction of laterality, there was no effect of species in the spontaneous condition. The results in the experimental condition may suggest a slightly stronger right-hand use in Campbell's monkeys compared to mangabeys. With regard to the strength of laterality, Marchant and McGrew's hypothesis (Marchant and McGrew 2007) predicts that arboreal monkeys should be less strongly lateralized and more flexible in hand use compared to more terrestrial monkeys. We compared semi-terrestrial red-capped mangabeys (Gautier-Hion et al. 1999) to arboreal Campbell's monkeys (Oates 1988). The hypothesis predicts a stronger laterality in mangabeys compared to Campbell's monkeys on position 3 and a greater flexibility in hand use in Campbell's monkeys compared to mangabeys on positions 1, 2, 4, 5. We found no between-species difference in the strength of laterality (except in PLL on the QHP).

We compared our data with the data in baboons (Meunier et al. 2011). The study in baboons showed similar results to ours, in that the mean HI varied according to the position of the item, indicating greater right-hand use to reach on the right side, and greater left-hand use to reach on the left side. However, the baboons showed significant biases in HI values in all lateral positions, which was not the case here. With regard to the strength of laterality, it increased from the central position to the extreme positions in baboons, while we found no effect of the position on the strength of laterality in our study. These differences might be accounted for by a smaller sample size of data per subject in our study (12 trials per subject per position here versus 20–60 (mean 45) trials per subject per position in Meunier et al. 2011), which could make significant effects more difficult to reveal in our study. Marchant and McGrew's hypothesis (Marchant and McGrew 2007) predicts a gradient from baboons (terrestrial) to mangabeys (semi-terrestrial) to Campbells (arboreal). We expected a decrease of absHI in the central position, but an increase of absHI in the lateral positions, reflecting a weaker laterality and a higher flexibility according to spatial constraints, from baboons to Campbell's monkeys. The results do not support this hypothesis, in the central position (similar laterality in the three species) or in the lateral extreme positions (higher laterality in baboons compared to Campbell's monkeys). As for the postural origins theory (McNeilage et al. 1987), it predicts a left-hand preference for reaching in monkeys. We found no group-level left bias for reaching in the central position in either species.

In conclusion, we studied hand use to reach for an item that was placed in front of the subject or on its side to assess hand preference and its flexibility according to spatial constraints. We found significant individual-level laterality in the central position, and we demonstrated that laterality was strongly influenced by the position of the item. Thus, the position of the object was demonstrated to be an important influential factor on laterality. We emphasize the need to systematically and strictly control for this effect when assessing laterality. We encourage future work using the QHP in other species and in larger samples.

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