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# Patterns of Hemispheric Specialization for a Communicative Gesture in Different Primate Species

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**ABSTRACT:** We review four studies investigating hand preferences for grasping versus pointing to objects at several spatial positions in human infants and three species of nonhuman primates using the same experimental setup. We expected that human infants and nonhuman primates present a comparable difference in their pattern of laterality according to tasks. We tested 6 capuchins, 6 macaques, 12 baboons, and 10 human infants. Those studies are the first of their kind to examine both human infants and nonhuman primate species with the same communicative task. Our results show remarkable convergence in the distribution of hand biases of human infants, baboons and macaques on the two kinds of tasks and an interesting divergence between capuchins' and other species' hand preferences in the pointing task. They support the hypothesis that left-lateralized language may be derived from a gestural communication system that was present in the common ancestor of macaques, baboons and humans.  
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**Keywords:** communicative gestures; handedness; hemispheric specialization; human infants; language origins; olive baboons; grasping; pointing; Tonkean macaques; tufted capuchins

## INTRODUCTION

Our language is one of the most obvious expressions of hemispheric specialization and has often been linked to the fact that 90% of humans are right-handed for many actions (Annett, 1985). Nevertheless, the possible relationship between the emergence of these two asymmetries opened many discussions and is still largely debated (Corballis, 2003, 2009). Are we predominantly right-handed because of our left-hemisphere specialization for language? Is our left-hemisphere specialized for language because we are right-

handed? Or did manual and language lateralization evolve independently?

In nonhuman primates, hemispheric specialization for manual actions is less evident than for humans. Left-handers and right-handers are generally equally represented in their population regarding simple reaching tasks, whereas biases at the population-level can appear in more complex tasks such as for bimanual coordinated tasks (Hopkins, 1995, see also Chapelain & Hogervorst, 2009 for a review) and even more consistently regarding communicative gestures (chimpanzees: Hopkins & Cantero, 2003; Hopkins & Wesley, 2002; olive baboons: Meguerditchian & Vauclair, 2006). One can thus assume that the study of hand preferences for communicative gestures (vs. noncommunicative gestures such as grasping) constitutes a highly relevant approach to considering language origin and lateralization (Meguerditchian & Vauclair, 2009; Vauclair, 2004) as already suggested by Kimura (1993). This view is supported by the existence of strong links between speech and gestures in humans

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(Goldin-Meadow & McNeill, 1999). It has been shown, for example, that we predominantly use our right hand for manual movements when we are talking (Kimura, 1973) and that the degree of right-hand asymmetry for manual communication (e.g., pointing) increases during the development of speech in young children (e.g., Blake, O'Rourke, & Borzellino, 1994; Vauclair & Imbault, 2009). The facts (1) that nonhuman primates' gestures (e.g., pointing in the chimpanzee), as human infants' pointing gesture, convey intentional, and relational content (Leavens, Hopkins, & Thomas, 2004), and (2) that great apes (Hopkins & Leavens, 1998), monkeys (Meguerditchian & Vauclair, 2009), as well as human infants (Esseily, Jacquet, & Fagard, 2011; Vauclair & Imbault, 2009) show preferential use of the right hand when pointing, indicate that nonhuman primates and humans who have not yet acquired language are ideal models to investigate some precursors of speech.

However, systematic and comprehensive studies comparing handedness in communicative gestures and in noncommunicative manual actions (e.g., grasping) are still scarce and many methodological problems appear when comparing findings on hand preferences between humans and nonhuman primates (Uomini, 2009). Even between studies on a same species, postural (subject's posture, e.g., MacNeilage, Studdert-Kennedy, & Lindblom, 1987) and situational (object position, see Lehman, 1993 for a review) factors as well as task complexity (Fagot & Vauclair, 1991) or type of data (observational vs. experimental, e.g., Hopkins et al., 2012) have been often neglected despite of their crucial influence on hand preferences. We thus crucially lack comparable methods based on observations while subjects (human and/or nonhuman) perform the same manual tasks (see McGrew & Marchant, 1997 for a review). A consistency in data analyses could also help to compare reliably studies and species, especially humans with nonhumans (Hopkins et al., 2012; Hopkins, Gardner, Mingle, Reamer, & Schapiro, 2013). Our study aims to overcome this deficit by testing human infants and nonhuman primates using a similar experimental setup and the same statistical analyses. For that purpose, we used a test initially designed to quantify hand preference in humans (the QHP task) by Bishop, Ross, Daniels, and Bright (1996). These authors were the first to propose a standard method for quantifying laterality in humans using a behavioral measure to ensure uniformity in a field where data consistency is a major problem. This task requires subjects to reach objects that are placed on varying spatial positions on a half-circle in front of them (see Bishop et al., 1996 for details). The idea is to assess the flexibility of hand preferences by determining where in the preferred hand's contralateral space the subject shifts to using his/her nonpreferred ipsilateral hand. The stronger a subject

preference for his/her right hand, the further in the contralateral space from his/her body midline he/she is likely to switch to using his/her left hand and vice versa. We adapted this task in such a way that it could be used to investigate both human infants and nonhuman primates. Moreover, our adaptation of the QHP task included the design of two experiments to compare both hand preferences while subjects grasped an object and hand preferences while subjects displayed a communicative gesture (see also Bourjade, Meunier, Blois-Heulin, & Vauclair, 2013). One can remark that nonhuman primates do usually not point spontaneously for each other (but see in apes Inoue-Nakamura & Matsuzawa, 1997 and Veà & Sabater-Pi, 1998) and that pointing is a gesture more specific for nonhuman primate-human interactions (e.g., Call & Tomasello, 1994; Leavens & Hopkins, 1998; Mitchell & Anderson, 1997). However, this pointing can emerge spontaneously, without any explicit training (Call & Tomasello, 1994) or can be learnt by monkeys (e.g., Hattori, Kuroshima, & Fujita, 2007; Meunier, Fizet, & Vauclair, 2013; Meunier, Prieur, & Vauclair, 2013) without losing its communicative function.

Thus, our experimental paradigm allowed us to assess hand preferences in several species both in a communication task and a simple (manipulative) grasping task, while controlling spatial and postural factors, two factors considered to affect hand preferences (Bishop et al., 1996; Calvert & Bishop, 1998; Leconte & Fagard, 2004). Even though these positional factors may have a crucial influence on hand preferences, they have almost never been quantified in nonhuman primates (but see Bourjade et al., 2013; Chapelain et al., 2012; Meunier, Blois-Heulin, & Vauclair, 2011). The present report grouped results issued from several studies taking into consideration all of these critical methodological points. The same experimental setup was proposed to four species (human infants: Jacquet, Esseily, Rider, & Fagard, 2012; baboons: Meunier, Vauclair, & Fagard, 2012; macaques: Meunier, Fizet, et al., 2013; capuchins: Meunier, unpublished data). Those studies are the first ones quantifying the effect of situational factors in both a grasping task and a communicative task and in both human and nonhuman primates.

The aims of our study was (1) to look for possible convergences and divergences in hand use between a motor action and a communicative gesture, (2) to look for possible convergences and divergences between different species of nonhuman primates and human infants with respect to the laterality of their motor actions and gestural communication. We expected that human infants and nonhuman primates would present a comparable difference in the pattern of laterality according to the task: all the tested species should be

more right-hand/left-hemisphere specialized when communicating by pointing than when simply grasping objects. We also predicted that the position of laterally presented objects would influence hand choice for pointing to a lesser extent than for object grasping.

## METHODS

This experiment included only behavioral investigations, routine training, and noninvasive contact with both the infants and the nonhuman primates. The infant experiment was conducted in accordance with the ethical standards specified in the 1964 declaration of Helsinki, and written formal parental consent was granted before observation. Our institutional review boards approved this study for both infants and nonhuman primates (authorization numbers for experimentation on baboons: C 13-087.7, on macaques and capuchins: B 67-273). All the experiments were carried out in accordance with the Principles of Laboratory Animal Care, and with the CNRS guidelines on animal care.

### Subjects

The subjects were 12 captive Olive baboons (*Papio anubis*) including 2 adult females, 9 adult males, and 1 subadult male. All the subjects lived in social groups, and were housed at the Rousset Center of Primatology, France, either in parks or large cages, both with free access to an indoor shelter in which water was available ad libitum. All groups were fed with monkey chows, fodder seeds and fresh vegetables several times a day. Individuals participated spontaneously in the experiments, so our subjects are mainly dominant individuals from each group.

Six captive Tonkean macaques (*Macaca tonkeana*) and six captive tufted capuchins (*Cebus apella*) were also tested at the Primatology Center of Strasbourg University, France. Macaques included three adult males, one adult female and two subadult males. All the subjects lived in the same social group of 22 individuals and were housed in a one-acre wooded area. Capuchins included two adult males, three adult females, and one subadult male, all living in the same social group of 12 individuals. They were housed in a multi-cage complex of 94 m<sup>2</sup>, with indoor and outdoor enclosures. Both species had free access to an indoor shelter in which monkey chows and water were available ad libitum and were fed with commercial primate pellets twice a day, fresh fruits and vegetables once a day, and seeds three times a week.

Finally, we tested 10 infants, including three girls and seven boys, on three occasions, that is, at 14, 17, and 20 months of age. This age range was chosen because it has been shown that infants start to point around the end of the first year (Liszkowski, Carpenter, Henning, Striano, & Tomasello, 2004) and that about two-thirds of infants point at 14 months (Murphy, 1978). We stopped at 20 months since we did not want to test pointing gestures accompanying language and since many infants undergo a language spurt at the end of the second year (Goldfield & Reznick, 1990).

### Training

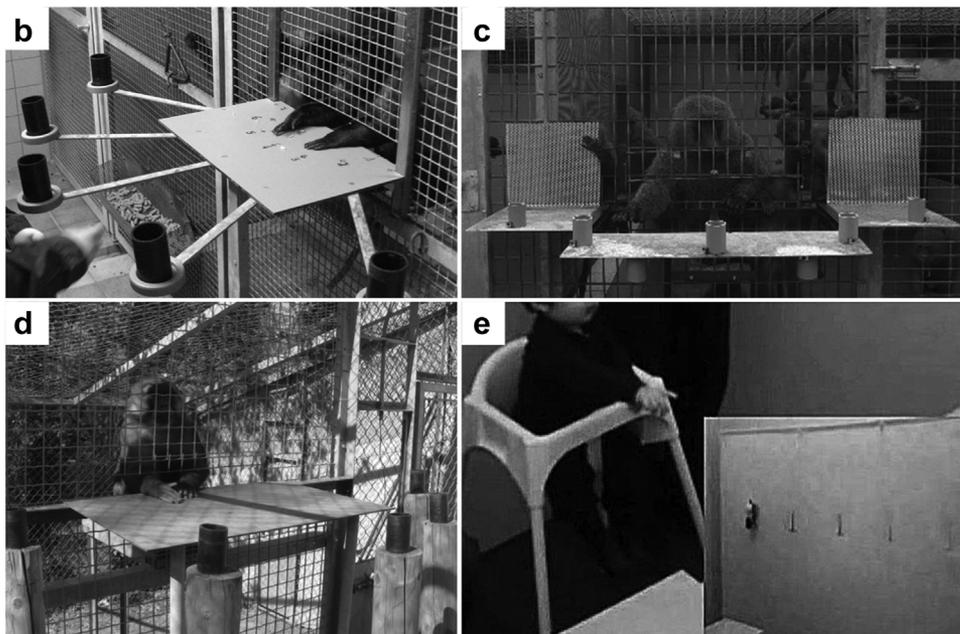
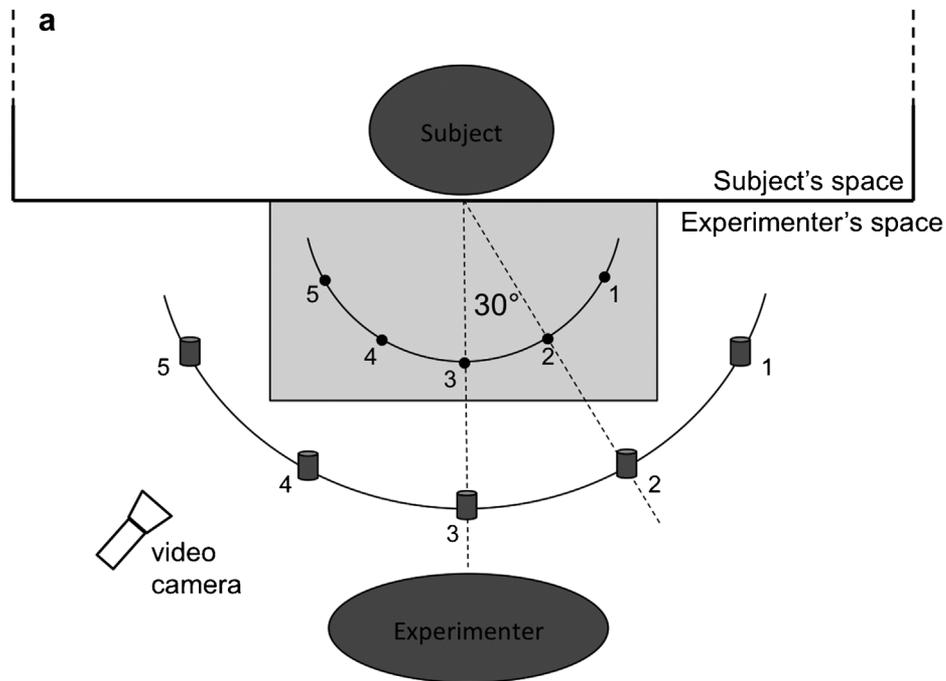
For the nonhuman primates, a training phase was necessary until each subject was able to point at one baited container with its whole hand. Initially, a reachable raisin was presented to the subject on the experimental table so that the subject was able to grasp it. Next, the raisin was progressively moved further away up to an ambiguous distance (the raisin was almost reachable) so that when the subject attempted to grasp the raisin, the experimenter gave it directly to the animal. Finally, the raisin was placed at 70 cm from the subject, that is, beyond the subject's reach. Training was terminated when the subject was able to point at the out-of-reach raisin with one hand (left or right) and without trying to grasp it.

### Previous Experience of the Subjects

Four of our adult males baboons had already participated in experiments in which they were trained to point toward unreachable food using the same methodology (see Meguerditchian & Vauclair, 2009) as the one described above. Capuchins and macaques had previously participated to others studies in relation to the investigation of their cognitive skills. Human infants were previously tested at 8 months old for grasping and at 11 months old for both grasping and pointing but the number of pointing collected were not sufficient for analyzing hand preferences.

### Experimental Procedure

For the grasping task, an attractive item (a toy for infants and a raisin for nonhuman primates) was placed in a randomized order at one of five positions, each separated from the adjacent position(s) by 30° on a half-circle, at a distance reachable by each subject's hand (Fig. 1, see also Meunier et al., 2011). For the pointing task with infants, we presented puppets through holes made in a white sheet lining the wall facing the infant, with an angle of 20° between adjacent holes. Infants were seated at a distance of 2 m from the screen, between a parent and an observer who encouraged them to indicate the puppet when they did not point spontaneously. For pointing in nonhuman primates, an opaque container in which raisins were hidden was placed at each of the five positions. Only one of the five containers was baited at a time. Two experimenters performed the task. The first experimenter hid the raisin in one of the five containers, in the view of the subject. The second experimenter was present, but could not see where the raisin was hidden. Then the second experimenter faced the subject, who then had to point toward the correct container so the experimenter would retrieve the raisin for the animal. Two experimenters were used for the nonhuman primates in order to avoid any ambiguity concerning the production and the interpretation of the gesture performed by the monkey, given that Experimenter 2 had no knowledge of the baited position and had to rely solely on the cues provided by the animal. Above all, the use of two experimenters allowed us to impose a delay in the production of the pointing gesture, and consequently it facilitated discrimination between a response that could be considered as a "frustrated reaching response" from an



**FIGURE 1** Schema of the experimental setup (a). Points on the smaller semicircle represent the five positions used for the simple reaching task and points on the larger semicircle represent the five positions used for the communicative task. Pictures of the pointing task setup for capuchins (b), baboons (c), macaques (d), and human infants (e).

intentional communicative gesture. If the subject pointed to the correct container, it was rewarded with the food placed under the container. In the rare cases when the subject pointed to another container, the food was removed, the trial was cancelled, and a new trial started. We noted the hand used for

grasping and pointing in both infants and nonhuman primates. We recorded five trials per position and per subject for grasping and three trials per position and per subject for pointing. We then compared hand-biases for each species and task.

## Data Analysis

We calculated an individual handedness index (HI) for each individual and each position using the formula  $(R - L) / (R + L) = (\text{Number of Right Hand} - \text{Left Hand choices}) / (\text{Number of Right Hand} + \text{Left Hand choices})$ . This index ranges from  $-1.0$  to  $1.0$  and estimates the strength of hand preference along a continuum, with negative values indicating a left-hand preference and positive values indicating a right-hand bias.

We performed an ANOVA calculated on the handedness index HI as a function of species, with position ( $\times 5$ ) and task ( $\times 2$ ) as repeated measures.

Results were considered to be significant when  $p$  was less than .05.

## RESULTS

Our data reveal a main effect of task ( $F(1,30) = 18.07$ ,  $p < .001$ ), a main effect of position ( $F(4,120) = 67.25$ ,  $p < .001$ ), a task  $\times$  position interaction ( $F(4,120) = 27.34$ ,  $p < .00001$ ), a position  $\times$  species interaction ( $F(12,120) = 6.95$ ,  $p < .00001$ ), and a task  $\times$  position  $\times$  species interaction ( $F(12,120) = 3.08$ ,  $p < .001$ ) but no task  $\times$  species interaction ( $p = .99$ ) (Fig. 2). There was also no species effect ( $p = .39$ ). A LSD post hoc test on the task  $\times$  position  $\times$  species interaction indicates that in human infants the HI differed between the two tasks on position 1 and 2 (left targets), but not on the other positions. For the baboons and the macaques, the HI differed between the two tasks on position 1, 2, and 3, but not on the right positions. For the capuchins the HI differed between the two tasks independently of the position.

Interestingly, if one removes the capuchins data, the task  $\times$  position  $\times$  species interaction disappears ( $p = .14$ ) whereas all other effects remain. Removing another species from the analysis did not change the results.

When grasping, hand preferences of all the species were shown to depend on item's position. Subjects reached for spatial positions located to the left (positions 1 and 2) predominantly with their left hand, and positions situated to the right of their body's midline (positions 4 and 5) predominantly with their right hand. In the pointing task, the position of the object to point is still influent but elicited a rather different pattern of bias. Hand preferences for the communicative task significantly favored the use of the right hand in human infants, baboons and macaques. Capuchins' hand preferences differed from those of human infants, baboons and macaques. As human infants, baboons and macaques, capuchins are affected by positional factors and this effect is dependent on the task, but, contrary to the other tested species, capuchins mainly produced manu-

al gestures directed toward laterally placed raisins by using the contralateral hand.

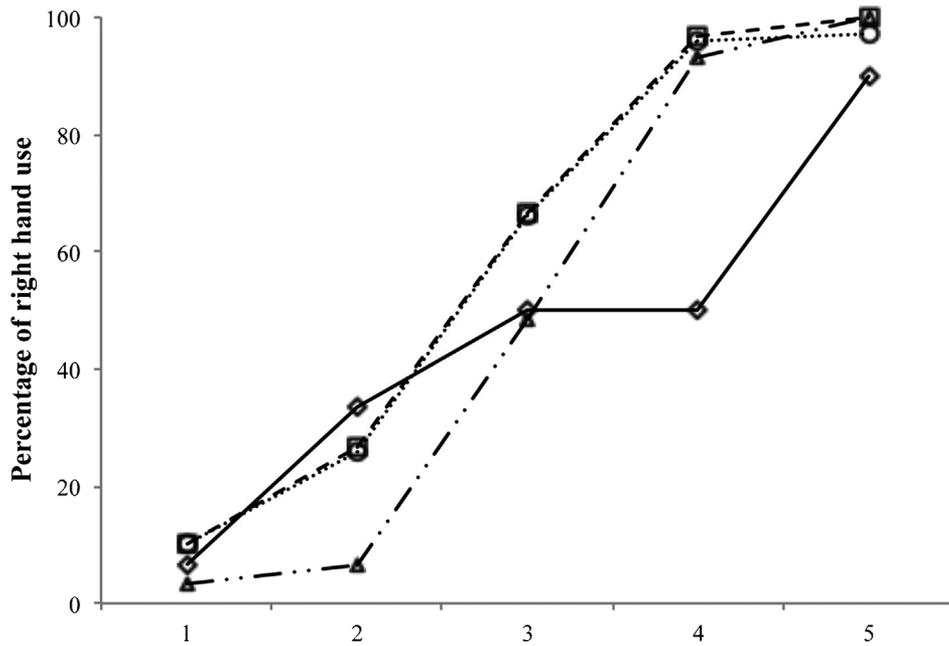
## DISCUSSION

Those studies highlighted several original results. Using a same setup for several species including both human and nonhuman primates, they quantified the effect of the position of items to grasp or point to on handedness expression for each species, and confirmed the crucial effect of the nature of the task. Moreover, results show a remarkable convergence in the distribution of the human infants, baboons and macaques hand biases on the two kinds of tasks and an interesting divergence between capuchins' and other species' hand preferences in the pointing task. More particularly, our results highlighted an important positional effect, an important task effect and an interaction between the position and the task, meaning that position of the object did not influence handedness in the same way according to task's nature, that is, communicative or not.

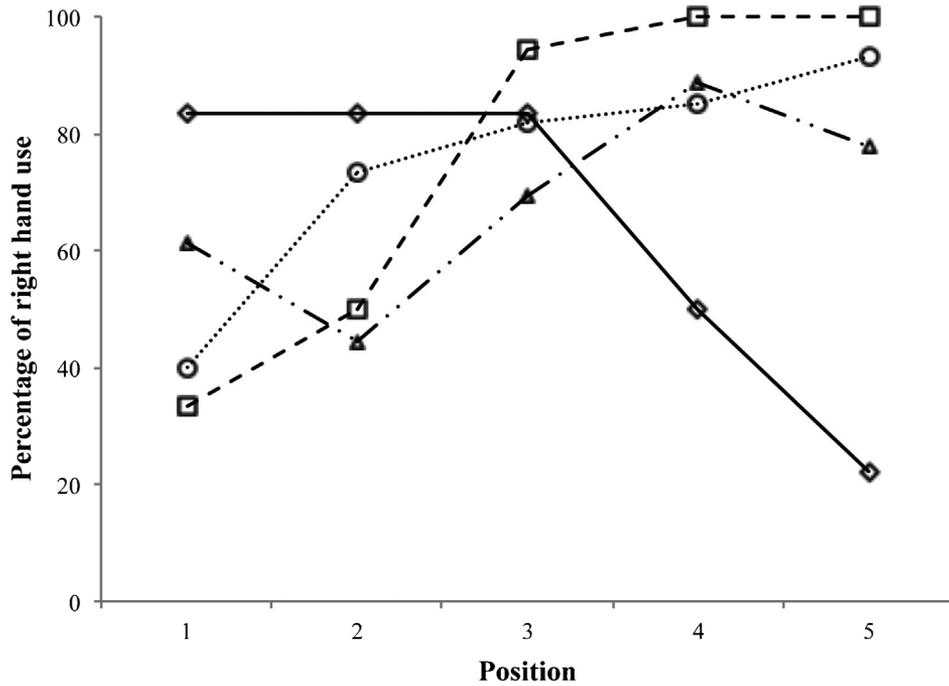
### Positional Effects, Task Nature, and Hand Preferences

When grasping, hand preferences of all the species were shown to depend on item's position, which is in accordance with several studies in monkeys, apes, and humans (Bourjade et al., 2013; Carlson & Harris, 1985; Chapelain et al., 2012; Cronholm, Grodsky, & Behar, 1963; Doyen, Dufour, Caroff, Cherfouh, & Carlier, 2008; Fagard, 1998; Lehman, 1980; Meunier et al., 2011), agreeing that reaching is strongly influenced by situational factors. In other words, humans (infants, children, and adults, e.g., Calvert & Bishop, 1998; Leconte & Fagard, 2006), as well as nonhuman primates, strongly prefer to use the hand that is closest to the item to be reached for in a simple reaching task. By contrast, concerning the pointing task, the position of the object to point elicited a rather different pattern of bias. Human infants, baboons and macaques significantly favored the use of the right hand for the communicative task (Esseily et al., 2011; Meunier et al., 2012, Meunier, Fizet, et al., 2013). The fact that these three species follow the same pattern is even more noteworthy that children and monkeys may have used pointing for different functions. Indeed, in spite of our effort of standardization, the type of pointing (declarative vs. imperative) was not controlled in our experiment. The human infants needed to point to inform the experimenter whenever a puppet appeared, while the monkeys pointed to request the food from the experimenter. However, both children

**a Grasping task**



**b Pointing task**



···○··· Human Infants    -▲- Baboons    -□- Macaques    -◇- Capuchins

**FIGURE 2** Percentage of right hand use for each position and each species in the grasping task (a) and in the pointing task (b).

and monkeys were not able to obtain the toys/food by themselves, and thus needed to communicate its location to the experimenter. Capuchins behave differently by mainly producing manual gestures directed toward laterally placed raisins by using the contralateral hand (see Fig. 2). Although in contradiction with our other tested species and also with chimpanzees (Hopkins & Wesley, 2002), this kind of hand preference's pattern had already been described in galagos (Ward, Milliken, & Stafford, 1993), mangabeys and guenons (Maille, Chapelain, Déruiti, Bec, & Blois-Heulin, 2013), while pointing or grasping to objects placed at far distances. We suggest that this difference of behavior could be due to differences between species in terms of ecological habits and more particularly to the fact that capuchins, galagos, and guenons are arboreal, mangabeys are both arboreal and terrestrial, whereas Tonkean macaques, olive baboons, chimpanzees, and human infants are terrestrial (Schmitt, 2010). Arboreal locomotion should confer easier and higher amplitude in shoulders and arms movements, allowing them to use more easily their contralateral arm/hand in communicative gestures. Another explanation could be that capuchins did not understand that pointing gestures influence the internal mental state of the recipient, that is, they did not point to distal objects but exhibited a kind of "extending reach" for unreachable food, as suggested also for great apes' pointing (e.g., Povinelli & Davis, 1994). However, (i) our results highlighted that the nature of the task induced changes in capuchins hand use and (ii) intentional aspects of capuchins' pointing have been highlighted, that is, they flexibly used pointing to adapt to the attentional state of their human partner (Defolie, Malassis, Serre, & Meunier, in preparation; Mitchell & Anderson, 1997). Both arguments suggest that capuchins produced their pointing gesture as an intentional communication and not as an "extending reach."

Our results confirm the interest of using a standardized protocol, the crucial impact of positional factors but also the critical role of task's nature and thus the importance of considering simultaneously those factors to investigate hand preference and to make reliable comparison between both tasks and species.

### **Hand Preferences in a Communicative Gesture—Implication for Theories of Language Origins**

Human infants, olive baboons, and Tonkean macaques are more right-handed when communicating than when grasping (Esseily et al., 2011; Meunier et al., 2012; Meunier, Fizet, et al., 2013), which leads us to postulate that the left hemisphere plays a specific role in controlling communicative gestures such as pointing.

This greater right hand preference for communicative gestures compared with object manipulation concurs with previous reports concerning pointing gestures, symbolic gestures, and ASL signs in human infants and toddlers (Bates, O'Connell, Vaid, Sledge, & Oakes, 1986; Bonvillian, Richards, & Dooley, 1997; Vauclair & Imbault, 2009) but also with reports concerning gestural communication in nonhuman primates (Hopkins et al., 2005; Meguerditchian, Vauclair, & Hopkins, 2010). Moreover, chimpanzees' right-handedness for food-begging gestures (Tagliatalata, Cantalupo, & Hopkins, 2006) and for clapping, that is, a communicative signal (Meguerditchian, Gardner, Schapiro, & Hopkins, 2012) is associated with morphological left asymmetries in the homologue of Broca's area (inferior frontal gyrus). Taken together, these findings support the hypothesis that left lateralization for language may be derived from a gestural communication system that was present in the common ancestor of macaques, baboons, chimpanzees, and humans.

In conclusion, despite of the low number of subjects for each species, all the reviewed studies converge and provide additional evidence toward the need of using standardized tasks to investigate hand preference and compare efficiently and reliably findings within and between species. Human infants, baboons, macaques, and capuchins were indeed tested successfully, independently of their differences in terms of size, morphology, and main habitat. By controlling both the subjects' posture and the position of the item they had to reach for or point to, we provided findings that corroborate the notion that both the position of the object and the nature of the task, that is, communicative or not, crucially influence hand preference patterns.

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