

Contrast of hand preferences between communicative gestures and non-communicative actions in baboons: Implications for the origins of hemispheric specialization for language

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ABSTRACT

Gestural communication is a modality considered in the literature as a candidate for determining the ancestral prerequisites of the emergence of human language. As reported in captive chimpanzees and human children, a study in captive baboons revealed that a communicative gesture elicits stronger degree of right-hand bias than non-communicative actions. It remains unclear if it is the communicative nature of this manual behavior which induces such patterns of handedness. In the present study, we have measured hand use for two uninvestigated behaviors in a group of captive olive baboons: (1) a non-communicative self-touching behavior (“muzzle wipe” serving as a control behavior), (2) another communicative gesture (a ritualized “food beg”) different from the one previously studied in the literature (a species-specific threat gesture, namely “hand slap”) in the same population of baboons. The hand preferences for the “food beg” gestures revealed a trend toward right-handedness and significantly correlated with the hand preferences previously reported in the hand slap gesture within the same baboons. By contrast, the hand preferences for the self-touching behaviors did not reveal any trend of manual bias at a group-level nor correlation with the hand preferences of any communicative gestures. These findings provide additional support to the hypothesized existence in baboons of a specific communicative system involved in the production of communicative gestures that may tend to a left-hemispheric dominance and that may differ from the system involved in purely motor functions. The hypothetical implications of these collective results are discussed within the theoretical framework about the origins of hemispheric specialization for human language.

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1. Introduction

Nonhuman primates, particularly great apes, communicate frequently by gestures with conspecifics in many social contexts (e.g., Goodall, 1986; Pika, Liebal, Call, & Tomasello, 2005, for reviews). The investigation of this communicative system in our cousins provides some evidence that support the gestural origin of language hypothesis (reviewed in: Meguerditchian & Vauclair, 2008; Vauclair, 2004) which contrasts with the vocal hypothesis (e.g., Hauser, 1996; Snowdon, 2001; Zuberbühler, 2005). In effect, for a growing number of researchers, speech could have its first phylogenetic roots in gestural communication of our distant ancestors rather than in vocalizations (e.g., Arbib, 2005; Corballis, 2002; Hewes, 1973; Kendon, 1991; Kimura, 1993; Vauclair, 2004). This

theory rests also on evidence of strong links between speech and gestures in humans (see McNeill, 1992). For example, gestural and vocal modalities for language are synchronized and seem to share the same communicative system (Bernardis & Gentilucci, 2006; Goldin-Meadow & McNeill, 1999). In addition, most language functions are under the control of the left cerebral hemisphere (e.g., Knecht et al., 2000) and such a hemispheric asymmetry has been historically linked to right-handedness for manipulative actions. However, Knecht et al. (2000) reported that 70% of left-handed humans show also a dominance of the left-hemisphere for language, indicating that the direction of handedness for manipulation is a poor marker of hemispheric lateralization for language. Whether handedness for gestural communication constitutes a better landmark is still unclear. In fact, humans are mostly right-handed not only for manipulations (almost 90% are right-handed: Annett, 1985), a predominance of the use of the right-hand has been reported for (1) manual movements when people are talking (Kimura, 1973a, 1973b) and (2) signing in deaf people (Vaid, Bellugi, & Poizner, 1989; see also Grossi, Semenza, Corazza, & Volterra, 1996). Interestingly, a right-hand bias for

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pointing gestures in infant tends to increase during speech development (Blake, O'Rourke, & Borzellino, 1994). In addition, signing or symbolic actions in young children revealed stronger degree of right-handedness than other manual actions, indicating a stronger involvement of the left-hemisphere for sign language or symbolic signaling (Bates, O'Connel, Vaid, Sledge, & Oakes, 1986; Bonvillian, Richards, & Dooley, 1997). More recently, functional brain imaging studies (Positron emission tomography, PET) showed a "speech-like" activation of Broca's area particularly in the left-hemisphere for the production of signs in deaf people (e.g., Corina, San Jose-Robertson, Guillemin, High, & Braun, 2003; Emmorey, Mehta, & Grabowski, 2007). These collective findings suggest that the left-lateralized language areas may underlie the production of "language-related" gestures (see Kimura, 1993).

As nonhuman primates are our closest relative compared to other animal species, studying behavioral asymmetries in apes and monkeys may be a relevant way to investigate the phylogenetic precursors of human cerebral specialization (e.g., Vauclair & Meguerditchian, 2007). The first studies in this research area have concerned handedness for manipulative motor behaviors in non-human primates particularly for simple behaviors such as unimanual reaching in both wild and captive subjects (see McGrew & Marchant, 1997; Papademetriou, Sheu, & Michel, 2005 for reviews). Such measures of hand use have usually led to contradictory or nonsignificant results, supporting the historical view that hemispheric specialization and right-handedness represent a landmark of human evolution (e.g., Crow, 2004; Ettliger, 1988; Warren, 1980). This latter view has been challenged by a large body of evidence of population-level handedness in the primate literature (reviewed in Hopkins, 2007). Basically these studies conducted particularly in captive populations are distinguished from the rest of the literature by using both a large sample of subjects and more complex motor tasks than simple reaching (e.g., bimanual feeding, a bimanual coordinated tube task, throwing, tool use, etc.) and revealed in both monkeys and apes some continuities with humans (Hopkins, 2007) even if the degree of predominance of right-handedness reported in humans remains much more pronounced (Annett, 1985). Therefore, the conflict in the literature may be easily reconciled on the basis of both task complexity and sample-size rather than the contrast drawn between wild *versus* captive subjects.

More recently, whether the left-lateralization for language in humans may find precursors in the communicatory gestural system of nonhuman primates has been addressed in a novel way, namely by studying manual asymmetries of gestural behaviors. The authors investigated whether the gestural communication of our closest relatives elicit predominance of right-handedness (left-hemispheric dominance) and stronger bias than non-communicative actions.

Results from studies including large samples of captive chimpanzees (*Pan troglodytes*) and olive baboons (*Papio anubis*) showed a significant predominance of the use of the right-hand at the group-level not only for bimanual manipulative actions (e.g., "the tube task" in 110 chimpanzees: Hopkins, 1995; in 104 baboons: Vauclair, Meguerditchian, & Hopkins, 2005) but also, in a much higher degree, for communicative gestures. In fact, baboons and chimpanzees showed identical patterns of results for a given manual action, *i.e.*, bimanual manipulative actions *versus* communicative gestures (see Meguerditchian & Vauclair, 2006; Vauclair & Meguerditchian, 2008).

Concerning gestures, a right-hand dominance was demonstrated in chimpanzees by recording hand use for human-directed "food begs" in a sample of 227 captive subjects (Hopkins et al., 2005; see also Hopkins & Cantero, 2003; Hopkins & Leavens, 1998; Hopkins & Wesley, 2002). According to the hypothesis put forward by Tomasello (1996) for explaining the development of

most of gestures in apes (see also Pika et al., 2005), "food beg" behaviors in captive individuals may result from the progressive ritualization of simple reaching actions to a communicative signal in order to get out-of-reach food from a human. The ritualization of these atypical behaviors might be thus especially associated to the particular environmental conditions of the primates, *i.e.*, restrictive captivity and direct interactions with humans in an out-of-reach food context (Leavens, Hopkins, & Bard, 2005). In baboons, a species-specific gesture has been studied in a sample of 60 captive subjects (Meguerditchian & Vauclair, 2006). This latter gesture involves the repetitive slapping or rubbing of the hand on the ground exclusively toward a focused subject (a conspecific or human observer) in order to threaten or intimidate them (see Kummer, 1968, for the first description of this gesture). It is still unknown whether the emergence of "hand slap" gestures in baboons is genetically determined or results from the same ritualization process than that of "food beg" behaviors. In this latter case, threatening "hand slap" gestures toward a conspecific might be ritualized from the start of an aggressive chase.

Interestingly, baboons and chimpanzees revealed the same degree of group-level right-handedness for communicative gestures. Such biases appear stronger than for bimanual manipulative actions in both species, indicating that the left-hemisphere may be more activated for gestural communication. In addition, within the same subjects in both species, individual hand preferences for gestures showed no correlation with those for bimanual manipulative actions (*i.e.*, "the tube task" which consisted in removing food with fingers of one hand from inside a PVC tube while holding it with the opposite hand).

Such findings raise the interesting hypothesis that the production of gestures in baboons and chimpanzees involves a specific left-lateralized communicative cerebral system that may differ from the one involved in non-communicative bimanual manipulative actions. These investigations led us to hypothesize that lateralized gestural behaviors could serve as an ideal prerequisite from the common ancestor of baboons, chimpanzees and humans for the emergence of language and its typical left-lateralization (Meguerditchian & Vauclair, 2006, 2008). However, it is still unclear whether such a specific communicative system exists and involves especially stronger degree of right-handedness than non-communicative actions. If so, it might be fully or partially activated for any other gestural behavior directed to an audience for a desired behavioral feedback. By contrast, any other non-communicative actions that do not require an audience might not activate this cortical system and thus induce none or less pronounced manual bias. One way to test these points is to compare the respective patterns of hand preferences of additional non-communicative and communicative actions.

Thus, in the current study, we measured manual preferences in captive baboons for two unstudied categories of manual behaviors: (1) a "food beg" gesture used exclusively to request food from a human (this gesture has been ritualized using explicit training); (2) a non-communicative self-touching action (serving as a "control" behavior) referred to as "muzzle wipe" (Wallis, 2000, 2004). In addition, within part of the sample that performed "food beg" gestures, we assessed manual asymmetries for simple reaching through the cage. This latter non-communicative behavior corresponds to the initial motor action from which the "food beg" gesture is ritualized. Then it might be interesting to measure the correlation of individual hand preferences between these two behaviors in order to evaluate the potential effect of the functional evolution of the extended arm action (*i.e.*, motor reaching into communicative signaling) on hand preferences. Furthermore, the potential effect of sex and age-class on hand preferences for "food begs" and "muzzle wipe" will be assessed. No effect of sex

on hand preferences has been previously reported for “food begs” in chimpanzees (Hopkins et al., 2005) and for “hand slap” gestures in baboons (Meguerditchian & Vauclair, 2006) while the effect of age classes has been only studied for “hand slap” gestures in baboons. A significant predominance of right-handedness has been demonstrated only in adults subjects (Meguerditchian & Vauclair, 2006). We could thus test the hypothesis that “food beg” behaviors might not reveal an effect of sex but possibly an effect of age-class on hand preferences. To our knowledge, none of these analyses has been provided so far for “muzzle wipe” in nonhuman primates.

As the functional definition provided in the literature in apes (e.g., Pika, Liebal, & Tomasello, 2005), we consider “communicative manual gesture” in baboons as an expressive movement of limbs that is directed to another individual in order to influence its behavior and that appears to transfer a communicative message, e.g., a request and/or a desired action/event (Pika et al., 2005). The “threatening hand slap” in baboons (Kummer, 1968; Meguerditchian & Vauclair, 2006) and the “food beg” gestures in both captive baboons and chimpanzees (Hopkins et al., 2005) fulfill these criteria. These behaviors have exclusively been observed when directed to a recipient and when used for getting its behavioral feedback for a desired goal (i.e., escape or submission of the recipient for the “hand slap” gestures and receiving the food from a human for the “food begs”).

By contrast, when questioning the potential communicative nature of the self-directed “muzzle wipe” in baboons, Wallis (2000, 2004) has observed this behavior when the producers were alone with no specific desired goal. The author finally supports the common view that “muzzle wipe” is produced regardless of an audience when a baboon is nervous or hesitant about something in its environment. Moreover, there is a large body of evidence in the literature that such types of self-directed-behaviors are external signals of edginess, motivational ambivalence or frustration in primates including baboons (Castles, Whiten, & Aureli, 1999), chimpanzees (Aureli & de Waal, 1997; Leavens, Aureli, & Hopkins, 2004) and humans (e.g., Fairbanks, McGuire, & Harris, 1982; Troisi, 2002). Thus, in contrast to “food beg” gestures, “muzzle wipe” appears to not express a specific desired goal from an audience and to be rather emotional than communicative.

If the investigated hypothesis is valid, namely that a specific communicative system is involved for gestural communication in baboons, we might expect that: (1) “food begs” should involve fully or partially the same cortical system than “hand slap” gestures and thus induce a similar pattern of hand preferences; (2) by contrast, the self-directed “muzzle wiping” and unimanual reaching through the cage, being non-communicative, should not invoke this specific communicative system and therefore should reveal a different pattern of hand preferences compared to the communicative gestures.

2. Method

2.1. Subjects

We conducted the study at the Station de Primatologie of the C.N.R.S., Rousset (France) on captive olive baboons living in social groups in parks or in large cages. The data have been collected on 72 subjects for the “muzzle wipe” actions (25 males and 47 females). The sample was composed of 32 young (age range: 1–4 years) and 40 adults (age range: 5–35 years). Concerning the “food beg” gesture, 33 subjects participated in this study (20 males and 13 females); 14 were young and 19 were adults. Among these 33 subjects, hand preferences have been recorded in 19 subjects for reaching food through the wire mesh of the cage (12 males, 7 females; 16 adults, 3 young).

2.2. Procedure

2.2.1. The self-directed “muzzle wiping”

The “muzzle wipe” is a self-directed manual action performed spontaneously by baboons (Fig. 1b). It consists of a quick passage of the hand across the bridge of the nose. This action has been described in both monkeys and apes (e.g., Marchant & McGrew, 1996; Wallis, 2000, 2004). For comparative purposes with data on communicative gestures, the “muzzle wipe” was the ideal candidate for constituting the “control” measure of hand preference insofar as (1) this behavior is performed toward the middle of the face, avoiding positional biases of one hand over the other, (2) this action is part of the repertoire of non-communicative self-directed behaviors expressed when an individual is nervous (Wallis, 2000,

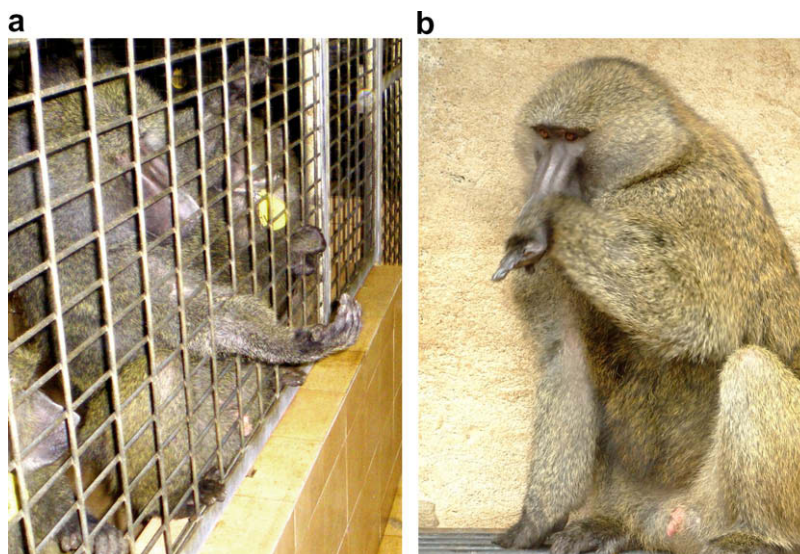


Fig. 1. (a) The communicative “food beg” gesture: a male adult baboon extends the right-hand through the cage in front of an experimenter for begging food. (b) The non-communicative self-directed “muzzle wipe”: a male adult baboon does a quick passage of the left-hand across the bridge of his nose.

2004). The data have been collected by observation of social groups of baboons using focal subject sampling. In total, 2067 actions have been recorded from 189 subjects and 1697 were included in the final analysis from the 72 baboons which performed a minimum of 10 responses to assess individual hand preferences (the number of observations per subject varied from 10 to 66 responses, $M = 23.57$, $SE = 1.50$).

2.2.2. The “food beg” gesture

The “food beg” gesture is a visual gesture which consists of extending one arm out of the cage in the presence of an experimenter in order to beg for food (Fig. 1a). It has been observed in only a limited number of baboons at the Station de Primatologie of the C.N.R.S. in Rousset (France) and does not belong to the species-typical gestural repertoire of olive baboons in the wild (Kummer, 1968). As described in captive chimpanzees (see introduction and Leavens et al., 2005) this behavior may thus result from the progressive ritualization of simple reaching actions to a communicative signal in captivity. In contrast to the large sample of captive chimpanzees that have not been explicitly trained for producing “food begs” gestures (Hopkins et al., 2005), the limitation of the number of baboons that performed this gesture might be explained by the fact that the type of feeding at the Station de Primatologie does not provide a favorable context for such a ritualization. While captive chimpanzees have daily individual interactions with humans in various contexts involving out-of-reach food (feeding-time, enrichment or behavioral studies), most of the baboons live in large social groups and the direct interaction of the human with single individuals during feeding time are unlikely and even avoided. In order to investigate in a much larger sample of baboons the hand preferences of this captivity-typical communicative gesture, we simulated this ritualization process by simple conditioning.

The training consisted in laying down repetitively a piece of banana in front of the cage of a focal subject. First, the food was laid down at an accessible distance for the animal in order to reach it. Second, between each trial, the food was laid down progressively further away from the cage until an ambiguous distance for the animal, *i.e.*, at the limit of being out-of-reach (but not so far as to discourage the subject to attempt to reach it). Third, for the following trials at this ambiguous distance, each time the subject initiated an arm extension, the experimenter had to anticipate the reaching of the food from the baboon by giving it back immediately the piece of banana. Finally, in order to check if the subject understood that the production of the “extended arm” gesture allowed it to get the food from the experimenter, the piece of banana was put at an out-of-reach distance from the animal. If the baboon did not extend the arm, the training was restarted from the third step until the subject produced the gesture in the “out-of-reach” context. If the baboon did extend the arm, then the experimenter gave the food to it. During the training phase, the use of both hands was equally rewarded in order to avoid reinforcing a particular hand during the ritualization process. Additionally, in order to remove any potential bias induced by human right-handedness, the experimenter symmetrically used both hands to give the food to the subject during the training. Thirty-three baboons were able to produce the “food beg” gesture.

In order to collect data on hand preferences for the “food beg” gesture, the experimenter elicited this behavior from a focal baboon by standing in front of the animal with visible food in his hand at approximately 1 m from the cage. The experimenter recorded the hand used for each gestural response from the animal until the subject stopped. Then, the baboon received the food. For a given subject, trials were repeated until the baboon produced more than 10 responses. In order to avoid postural biases in the

choice of the hand, a response was considered as valid when: (1) the experimenter and the food were positioned in front of a focal subject and equidistant to each of the baboon’s hands; (2) the gesture was produced either toward the experimenter or to the food; (3) the animal was sitting in a symmetrical posture with both hands initially free; (4) the hands were returned to their initial posture if the response observed was preceded by another gesture. In total, 1025 gestures were collected on 33 baboons (the number of observations per subject varied from 14 to 76 responses, $M = 31.06$, $SE = 2.77$).

2.2.3. Additional control measures

Hand preference for simple reaching (using mixtures of small seeds dispersed inside the enclosure of the subjects) has already been investigated in a previous study in a sample of 94 captive baboons (Vauclair et al., 2005) and did not reveal population-level handedness (see Fig. 3). Here, in order to assess the potential effect of reaching hand preferences on hand preferences for “food beg” gestures, we replicated these simple unimanual measures in 19 of the 33 subjects who were able to produce “food beg” gestures. In this case, hand preferences were recorded for reaching through the wire mesh to a piece of food outside of the subject’s enclosure (equivalent to the initial motor action from which the “food beg” gesture is ritualized). A piece of banana was repetitively laid down in front of the cage of a focal subject but at an accessible distance from the animal. The hand used when reaching the food was recorded on 25 trials per subject. A response was considered as valid when: (1) the animal was sitting in a symmetrical posture with both hands initially free; (2) the food was positioned in front of a focal subject and equidistant to each of the baboon’s hands; (3) the hands were returned to their initial posture between each trial.

2.3. Data analysis

In accordance with the literature on nonhuman primates’ handedness (see Hopkins, 1999), we used the following statistical tools for data analysis.

First, the direction of hand preference for each subject was determined by calculating an individual z -score on the basis of the total left and right-hand responses. This score was used to classify baboons as left-handed ($z \leq -1.96$), right-handed ($z \geq 1.96$) or ambiguously handed ($-1.96 < z < 1.96$) for each investigated manual action.

Second, the degree of hand asymmetries for a given subject was evaluated by calculating an individual handedness index score (HI) using the formula $(R - L)/(R + L)$, where R and L represent the total right and left-hand responses, respectively. The HI values varied on a continuum from -1.0 to 1.0 and the sign indicates the direction of hand preferences: positive, right-hand preference; negative, left-hand preference. The absolute values (ABS-HI) reflect the strength of individual hand preferences.

Finally, for each manual action, the degree of asymmetry at a group-level was evaluated by calculating the Mean of all the individual HI (M.HI). The M.HI values varied on a continuum from -1.0 to 1.0 and the sign indicates the direction of group-level hand preferences: positive, right-hand preference; negative, left-hand preference. The absolute values reflect the degree of group-level hand preference.

3. Results

3.1. Direction of hand preference

Distribution of handedness patterns for the self-directed muzzling and the food beg gestures are presented in Fig. 2.

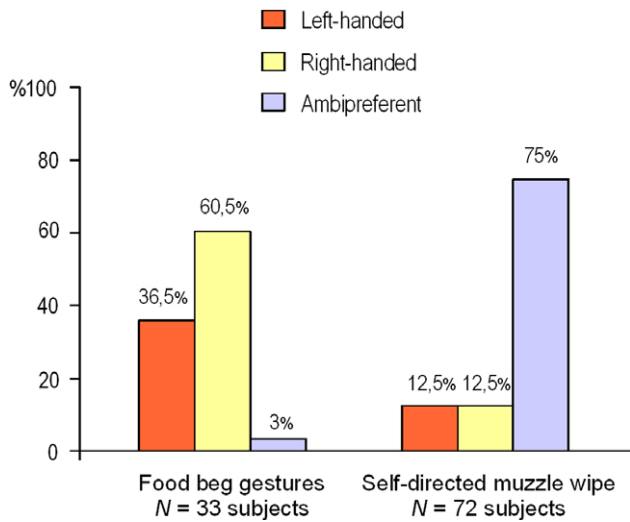


Fig. 2. Comparative distribution of percentages of right-, left- and ambiguously handed baboons between “Food beg” gestures and “muzzle wipe”.

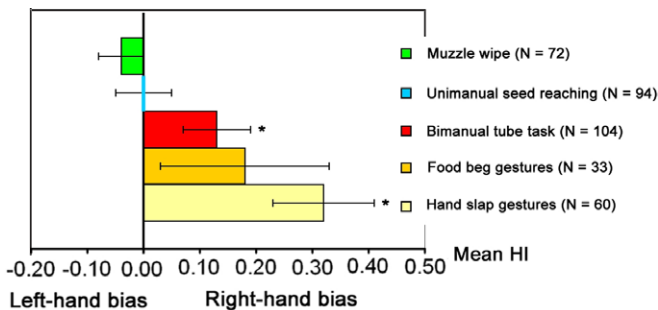


Fig. 3. Degrees of group-level handedness for self-directed (“muzzle wipe”), manipulative (unimanual and bimanual) and communicative behaviors (“food beg” and “hand slap” gestures). Mean handedness index scores (MHI) \pm SE. The error bar represents the standard error around the MHI score. Asterisk indicates that the MHI score differed significantly from zero. * $p < .05$.

3.1.1. The self-directed “muzzle wiping”

Among the 72 subjects which performed a minimum of 10 responses, 9 were classified as right-handed, 9 as left-handed, and 54 as ambiguously handed on the basis of the individual z-scores. Based on a chi-square goodness-of-fit test, the number of ambiguously handed baboons ($N = 54$) was significantly higher than the number of lateralized subjects ($N = 18$), $\chi^2(1, N = 72) = 18.00$, $p < .001$. Moreover, there was no difference between the number of right-handed and the number of left-handed subjects, $p = 1.00$, indicating no group-level asymmetries in the sample of baboons for these measures.

The mean handedness index score (MHI) of the 72 subjects confirms this absence of bias, $MHI = -0.04$ ($SE = 0.04$), a bias which is not significant according to a t -test, $t(72) = 0.95$, $p = .34$.

3.1.2. The “food beg” gesture

Among the 33 subjects which performed a minimum of 10 gestures, 20 were classified as right-handed, 12 as left-handed, and 1 as ambiguously handed on the basis of the individual z-scores. Compared to the number of left-handed baboons ($N = 12$), the predominance of the number of right-handed baboons ($N = 20$) was not significant, $\chi^2(1, N = 32) = 2.00$, $p = .15$.

The mean handedness index score (MHI) of the 33 subjects reveals a right-hand bias at the group-level, $MHI = 0.18$ ($SE = 0.15$), but this bias was not significant according to a t -test, $t(33) = 1.20$, $p = .24$.

3.2. Potential effects of age and sex

The effects of age and sex were assessed using an analysis of variance (ANOVA) with the Handedness Index score serving as the dependent measure.

There was no significant difference of group-level handedness between age classes concerning either the self-directed “muzzle wipe”, $F(1,72) = 0.35$, $p > .05$ (Adults $MHI = -0.02$, $SE = 0.05$, $N = 40$; Juveniles $MHI = -0.07$, $SE = 0.07$, $N = 32$), or the “food beg” gestures, $F(1,33) = 0.02$, $p > .05$ (Adults $MHI = 0.20$, $SE = 0.21$, $N = 19$; Juveniles $MHI = 0.21$, $SE = 0.20$, $N = 14$).

Concerning sex differences of group-level handedness, there was no significant difference between males and females for the “food beg” gesture, $F(1,33) = 0.07$, $p > .05$ (Females $MHI = 0.13$, $SE = 0.23$, $N = 13$; Males $MHI = 0.21$, $SE = 0.20$, $N = 20$), or for the self-directed “muzzle wipe”, $F(1,72) = 1.05$, $p > .05$ (Males $MHI = -0.10$, $SE = 0.06$, $N = 25$; Females $MHI = -0.01$, $SE = 0.05$, $N = 47$).

3.3. Potential effects of the experimenter on asymmetries of “food beg” gestures

Following the methodological precautions used to avoid a human bias (see Section 2.2.2), the potential influence of the experimenter (a right-handed human) on the manual asymmetries exhibited by a subject when food begging was evaluated by comparing the strength of manual biases (i.e., mean of absolute values of handedness index scores, M.ABS-HI) between the left-handed subjects and the right-handed subjects. In fact, if the right-handedness of the experimenter induced a bias during training by inadvertently reinforcing the exhibition of right-hand use for baboon food begging, we might expect that the strength of handedness may be more pronounced in the right-handed subjects than the left-handed subjects. However, strength of hand preferences did not differ between these two groups: $M.ABS-HI = 0.82$, $SE = 0.04$ in the 20 right-handed subjects versus $M.ABS-HI = 0.88$, $SE = .07$ for the 12 left-handed subjects, indicating that the risk of bias induced by the experimenter is minimized.

3.4. Potential influence of the hand preferences for reaching on asymmetries of “food beg” gestures

Using a Pearson product-moment correlation with handedness index scores (HI), individual hand preference for “food beg” gestures were not significantly correlated with hand preferences for simple food reaching through the cage in the same 19 subjects, $r(19) = 0.37$, $p > .10$. In addition, the strength of individual manual bias was much stronger for “food beg” gestures ($M.ABS-HI = 0.82$, $SE = 0.04$ in the 33 subjects) than for simple reaching through the cage ($M.ABS-HI = 0.29$, $SE = 0.06$ in the 19 subjects). This difference between the degree of lateralization for food begging and simple reaching through the cage was statistically significant, $t(52) = 7.61$, $p < .0001$. These collective results indicate that the pattern of handedness for unimanual reaching has only a weak influence on the asymmetries of the ritualized “food beg”.

3.5. Comparison of handedness indexes between different behaviors (see Fig. 3)

Using a Pearson product-moment correlation with handedness index scores (HI), individual hand preference results were compared to data obtained from other behaviors investigated previously in the same subjects (see Meguerditchian & Vauclair, 2006; Vauclair et al., 2005).

Handedness index scores for the non-communicative “muzzle wipe” did not correlate with the results for the species-typical “hand slap” gestures in the 28 individuals which were common to the two studies, $r(28) = -0.22$, $p > .10$, nor for the human-directed “food beg” gestures within the 9 common subjects, $r(9) = 0.00$, $p > .10$.

By contrast, handedness index scores for communicative “food beg” gestures significantly correlated with the results of the other communicative gestures investigated (*i.e.*, “hand slap” gesture) within the 15 common individuals to the two studies, $r(15) = 0.58$, $p < .05$. Additionally, as it has been reported for the “hand slap” gestures in baboons (Meguerditchian & Vauclair, 2006), hand preferences for “food begs” did not correlate with the results of any manipulative motor action: neither for unimanual seed reaching within the 20 common individuals concerned, $r(20) = -0.20$, $p > .10$, nor for the bimanual manipulative tube task within the 23 common subjects, $r(23) = 0.02$, $p > .10$.

The degree of group-level right-handedness for “food beg” gesture in baboons ($M.HI = 0.18$) is less pronounced than the biases previously reported for “hand slap” gestures ($M.HI = 0.32$) and for “food begs” in chimpanzees ($M.HI = 0.31$, see Hopkins et al., 2005). The bias for baboons’ “food begs” is however more pronounced than the biases reported for manipulative motor actions in baboons ($M.HI = 0.13$ for the bimanual tube task, $M.HI = 0.00$ for unimanual seed reaching, see Vauclair et al., 2005).

4. Discussion

Our findings in 33 olive baboons show that a novel unstudied communicative gesture, namely a ritualized “food beg” directed to a human, reveal a trend toward right-handedness at the group-level (60.5% right-handed *versus* 36.5% left-handed subjects, see Fig. 2). Even if this bias is statistically non significant, this pattern might be compared to the significant bias reported for another communicative gesture, *i.e.*, “hand slap”, in 60 baboons (58.5% right-handed *versus* 16.5% left-handed subjects, Meguerditchian & Vauclair, 2006). More interestingly, individual hand preferences (HI) for “food beg” gestures significantly correlate only with the hand preferences for the “hand slap” gestures in the same baboons and not with the hand preferences of any non-communicative manipulative motor actions previously studied, *i.e.* bimanual coordinated tube task and unimanual seed reaching (Vauclair et al., 2005). Moreover, although the degree of group-level right-handedness for baboons’ “food beg” gestures is less pronounced than the one reported for “hand slap” gesture, this bias is stronger than those reported for any manipulative motor actions (Fig. 3). By contrast, as it is usually reported in the literature for face-touching behaviors in monkeys and apes (Aruguete, Ely, & King; 1992; Diamond & Harries, 1984; Marchant & McGrew, 1996; but see Hopkins et al., 2006), the non-communicative self-touching action (“muzzle wipe”) did not elicit any trend of manual bias at a group-level in the 72 baboons studied (12.5% right-handed *versus* 12.5% left-handed subjects) that strongly contrasts with the patterns revealed in “hand slap” and “food beg” gestures (see Fig. 2). Moreover, in the same subjects, individual hand preferences for “muzzle wipe” did not correlate with the hand preferences of any communicative gesture (neither “food beg” nor “hand slap” gestures).

In other words, different communicative gestures in baboons show a similar pattern of hand preferences with each other and may thus share partially the same cerebral system, whereas non-communicative actions exhibit different patterns of handedness when compared with manual communication (either “hand slap” or “food beg” gestures). Moreover, although a certain degree of correlation has been found between the hand preferences for “food beg” and those for reaching food through the cage, this correlation

is poor, not significant and less pronounced than the significant correlation revealed between the “food beg” gesture and the communicative “hand slap” gesture. This evidence indicates that the “food beg” pattern of handedness might be better explained by its supposed communicative property (shared with the “hand slap” behavior) rather than the motor continuum resulting initially from reaching actions.

However, whereas for the “hand slap” gestures, it has been reported that the right-handedness predominance at a group-level is significant only in adults and not in young baboons, neither age-class effect nor sex effect on hand preference have been observed in the present study for both “food beg” gestures and “muzzle wipe”.

Such a difference of age effect between “hand slap” and “food begs” gestures, the absence of statistical significance for “food begs”, the limited sample-size as well as the explicit training used for the ritualization of this behavior constitute some limitations that do not allow us to propose firm conclusions. Nevertheless, the trend toward right-handedness for “food begs” and the contrasts between non-communicative and communicative actions remain quite congruent with the previous reports in chimpanzees and baboons (Hopkins et al., 2005; Meguerditchian & Vauclair, 2006) as well as the reports in children of a stronger degree of right-hand bias for signing or symbolic actions in comparison to other manual actions (Bates, O’Connell, Vaid, Sledge, & Oakes, 1986; Bonvillian et al., 1997). Our present study provide thus additional supports to the hypothesized existence of a specific system involved in the production of communicative gestures that may differ from the system involved in purely motor functions. Whether such a communicative system is left-lateralized remains unclear in baboons. Whereas the right-hand bias reported for “hand slap” gestures was significant, the “food begs” elicited only a non significant trend toward right-handedness. However, the direction and the degree of this trend are still congruent with the hypothesis that the specific system involved for gestural communication in baboons may tend to a left-hemispheric dominance. If so, regarding these collective findings, we suggest with caution that a phylogenetic continuity may exist between language lateralization in humans and asymmetries of communicative gestures in chimpanzees and baboons (Meguerditchian & Vauclair, 2006). Even if it is not excluded that such hypothetical convergent lateralization in baboons, chimpanzees and humans might have evolved independently, an alternative hypothesis may be that a communicative system that may tend to a left-hemispheric dominance involved in gesturing may have existed in their common ancestor at least 30 million years ago.

The cerebral localization of this specific communicative system and the hypothetical continuity with the cerebral language areas in humans remains unclear, and no data are available so far for baboons. However some MRI (magnetic resonance imaging) investigations of the chimpanzee’s brain shed some light on this question and are consistent with our hypothesis. Indeed, whereas asymmetries of homologous language areas are not associated with handedness for non-communicative manipulative motor actions (Hopkins & Cantalupo, 2004), left-asymmetries in the inferior frontal gyrus (a homologue of Broca’s area) were associated with right-handedness for food beg gestures (Tagliabata, Cantalupo, & Hopkins, 2006).

To our knowledge, this pattern of association between communicative signals and the localization in the left cerebral hemisphere of the nonhuman primate brain has no equivalent in vocal *production*. In effect, the nonhuman primates’ vocal *production* system seems to involve exclusively subcortical areas and the limbic system (cerebral regions usually related to the control of emotions in the human brain) but not homologous language areas (see Jürgen, 2002; Ploog, 1981, for reviews). In addition, with the excep-

tion of a report in marmosets of an oro-facial asymmetry toward the right-side of the mouth in producing social contact calls (Hook-Costigan & Rogers, 1998), there is no evidence that vocal production elicits a dominance in the left-hemisphere. In contrast to vocal production, there are some reports of left-lateralization only for vocal perception in both behavioral studies (Hauser & Andersson, 1994; Petersen, Beecher, Zoloth, Moody, & Stebbins, 1978) and neurobiological studies (Dewson, 1977; Heffner & Heffner, 1984; Poremba et al., 2004). However, we cannot ignore the contradictory results concerning the direction of asymmetries for vocal processing reported in both behavioral studies (Gil-da-Costa & Hauser, 2006; Teufel, Hammerschmidt, & Fischer, 2007) and a neurobiological study (Gil-da-Costa et al., 2006; for a review see Tagliatalata, 2007). Since such a cortical lateralization for processing meaningful vocalizations may be the precursor of the representational processes involved in the comprehension of language in humans (Gil-da-Costa et al., 2004), these abilities in nonhuman primates might be better related to their understanding of the external world rather than to their specific vocal production system, and could not be thus particularly regarded as a direct precursor of human speech production system (Meguerditchian & Vauclair, 2008).

However, a recent report has shown that chimpanzees voluntarily produce two novel “learned” sounds (an extended grunt involving the vocal tract and a splutter called “raspberry” involving only the lips with the air of the mouth) exclusively in the presence of both a human and out-of-reach food (Hopkins, Tagliatalata, & Leavens, 2007). It appears that these signals not only share the same communicative intent as the “food beg” gestures but also, when produced simultaneously with these gestures, induce a stronger right-hand preference than when the gesture is produced alone (Hopkins & Cantero, 2003), indicating that the left-hemisphere may be more activated when producing both gestures and these atypical vocalizations simultaneously. Moreover, in contrast to the left-sided oro-facial asymmetries (i.e. right-hemispheric dominance), detected for the species-typical vocal repertoire of chimpanzees, the use of the atypical attention-getting sounds involved an asymmetry toward the right-side of the mouth (Reynolds Losin, Russell, Freeman, Meguerditchian, & Hopkins, 2008). Thus, these findings may suggest that the specific communicative system used only for gestures in baboons (i.e., neither the intentional use of vocalizations nor any association between vocal and gestural signaling for transmitting the same intends have been observed in baboons) may be involved for both gestures and “learned” attention-getting sounds in chimpanzees. The existence of such a bimodal intentional communicative system in chimpanzees has been recently illustrated in a study using functional brain imaging (PET). Communicative signaling for begging food from a human in using either gestures, atypical attention-getting sounds, or both of them simultaneously, activated the inferior frontal gyrus (an homologous region of Broca’s area) predominantly in the left-hemisphere (Tagliatalata, Russell, Schaeffer, & Hopkins, 2008).

Within a general speculative framework about the origin of language, these collective findings in chimpanzees might support the hypothesis that speech has resulted from the evolution of a bimodal system in our ancestors rather than only a gestural system. Our global results in baboons (the present paper and Meguerditchian & Vauclair, 2006) might suggest that precursors of left-hemispheric dominance for language production have emerged first with the use of communicative gestures. Then this communicative system may have further turned bimodal with the progressive insertion of intentional vocalizations into the gestural system in the course of evolution to finally become, as it is currently, under the dominance of the vocal modality (speech) in humans (see Corballis, 2002). Additional behavioral and neurobiological studies in baboons as well as comparative investigations in other nonhuman

primate species are needed to evaluate such a hypothetical scenario and the potential continuity of hemispheric specialization for communication between humans and nonhuman primates.

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