

Right-Handedness Predominance in 162 Baboons (*Papio anubis*) for Gestural Communication: Consistency Across Time and Groups

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Whether nonhuman primates exhibit population level right manual bias remains a controversial topic. In captive baboons, population-level right-handedness has been reported for both coordinated bimanual actions and communicative gestures. However, some authors remain skeptical of these findings on both methodological and theoretical grounds. Here, we demonstrated the robustness and the consistency across time of the pattern of right-handedness for a species-specific communicative gesture in olive baboons (*Papio anubis*). First, we showed significant correlations in the 26 retested baboons for the measures of hand preferences between the first and the second session conducted 4 years later (2005–2009) by an observer blind to the previous handedness data. Second, the replication of the study in 96 novel individuals revealed a similar degree of population-level right-handedness than the one expressed in the first group of 66 subjects investigated in 2005. The implications of the findings are discussed within a theoretical framework about the origin of hemispheric specialization for language.

Keywords: handedness, gestural communication, hemispheric specialization, origins of language, primates

In humans, since the first evidence reported by Broca and Wernicke (Broca, 1865; Wernicke, 1874), it has been well documented that most of the language functions show a greater activation of the left-hemisphere of the brain especially for production (Cooper, 2006; Lieberman, 2003). Such a left-hemispheric asymmetry has been historically related to right-handedness for manipulative actions given that 96% of right-handed people show left-hemisphere dominance for language. However, it turns out that 70% of left-handers also exhibit left-hemisphere dominance for language (Knecht et al., 2000). This indicates that the direction of manual preference for manipulation is a poor marker of hemispheric lateralization for language, whereas some reports suggest that the direction of manual preference for communicative gestures

might constitute a better marker. Indeed, it has been shown that the degree of predominance of right-handedness for pointing in humans tends to increase during speech development (Blake, O'Rourke, & Borzellino, 1994). In addition, symbolic actions (e.g., pretend play), signing and pointing gestures in young children appeared to be much more lateralized toward the right-hand than non communicative motor manipulations (Bates, O'Connell, Vaid, Sledge, & Oakes, 1986; Bellugi et al., 1986; Blake et al., 1994; Bonvillian, Richards, & Dooley, 1997; Cochet & Vauclair, 2010; Vauclair & Imbault, 2009). Such specific patterns of right-handedness exhibited for symbolic activities and for gestural communication in humans might be thus related with the lateralization for language. Moreover, humans are mostly right-handed for manual movements when people are talking (Kimura, 1973) and for the production of signs in deaf people (Vaid, Bellugi, & Poizner, 1989). Interestingly, deaf people showed a "speech-like" activation of Broca's area particularly in the left-hemisphere according to functional brain imaging studies using positron emission tomography (e.g., Corina, San Jose-Robertson, Guillemin, High, & Braun, 2003; Emmorey, Mehta, & Grabowski, 2007). These collective reports suggest that the production of communicative gestures might involve the left-lateralized language areas (Bellugi, 1991; Kimura, 1993).

As nonhuman primates are our phylogenetically closest relatives compared to other animal species, studying manual preferences for communicative gestures in apes and monkeys may be a relevant way to investigate the phylogenetic precursors of left-lateralization for language (e.g., Meguerditchian & Vauclair, 2008). The first investigations of handedness in nonhuman primates have focused on manipulative motor behaviors in both wild and captive subjects

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and showed divergent patterns of population-level handedness according to the species, the sample size and the complexity of the manual tasks (see Hopkins, 2007; McGrew & Marchant, 1997; Papademetriou, Sheu, & Michel, 2005, for reviews). The reports of significant predominance of right-handedness in large samples of nonhuman primates have been demonstrated in captive chimpanzees (*Pan troglodytes*) and were related to complex manual tasks such as bimanual feeding, coordinated bimanual actions, bipedal reaching, throwing, and so forth (for review, see Hopkins, 2006, 2007). These findings also concerned captive baboons (*Papio anubis*) (Vauclair, Meguerditchian, & Hopkins, 2005) and captive gorillas (*Gorilla gorilla*) (Byrne & Byrne, 1991; Meguerditchian, Calcutt, Lonsdorf, Ross, & Hopkins, 2010a) for bimanual coordinated activities.

Concerning gestural communication, there are few available studies on manual preferences with large sample of subjects. Nevertheless, this literature is very consistent insofar as the studies have all revealed a significant predominance of the use of the right hand for different categories of gestures directed to humans (such as pointing) or to conspecifics in different primates species such as captive chimpanzees (e.g., Hopkins et al., 2005; Meguerditchian, Vauclair, & Hopkins, 2010b), olive baboons (Meguerditchian & Vauclair, 2006, 2009), bonobos (see Hopkins & Vauclair, in press, for a review), and gorillas (Shafer, 1993). Interestingly, the degree of predominance of right-handedness appeared to be much more pronounced than the one expressed in non communicative behaviors (see Hopkins & Vauclair, in press, for a review). In addition, in both chimpanzees and baboons, within an individual, hand preferences between different categories of gestures significantly correlated with each other. However, measures of hand preferences for each of category of gestures did not correlate with hand preferences for any noncommunicative manipulative motor actions (Meguerditchian & Vauclair, 2006, 2009; Meguerditchian et al., 2010b). Such findings led the authors to suggest that the production of gestures in nonhuman primates might involve a specific left-lateralized communicative cerebral system that may differ from the one involved in noncommunicative manipulative actions. Thus, the lateralized gestural communicative system might constitute 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, one might question the validity of these findings regarding the historical view that population-level behavioral and hemispheric lateralizations are hallmarks of human evolution (Crow, 2004; Ettlinger, 1988; Warren, 1980). This view has been challenged by a growing body of evidence of population-level behavioral and brain asymmetries in a host of vertebrates (Rogers & Andrew, 2002; Vallortigara & Rogers, 2005) including nonhuman primates (Hopkins, 2007). In fact, some authors have then expressed their skepticism on both methodological and theoretical grounds about the data that reported predominance of right-handedness for manipulative motor actions in nonhuman primates by arguing that the overall results on handedness in nonhuman primates are inconsistent across the literature (Crow, 2004; McGrew & Marchant, 1997; Palmer, 2002, 2003). In all human populations, predominance of right-handedness is consistent and remains stable over time although some variation has been re-

ported between different cultures (e.g., Annett, 1985; Perelle & Ehrman, 1994; Raymond & Pontier, 2004).

In the present study, we addressed the consistency issue by testing the robustness of our findings in captive olive baboons for the species-specific hand slap gesture used to intimidate or threaten another individual (Meguerditchian & Vauclair, 2006). First, we investigated whether the manual preferences for gestures remain stable over time: a sample of subjects studied in 2005 (Meguerditchian & Vauclair, 2006) has been retested by an experimenter who was blind to the previous set of data. Second, we replicated the measures of manual preferences in an additional and larger sample of subjects that had not previously been investigated in 2005. This procedure allowed us to not only significantly increase the sample size for evaluating population-level handedness for gestural communication in baboons but also to compare the patterns of hand preferences between the two different samples (the one investigated in 2005 and the one of the present study).

Method

Subjects

The study was conducted at the Station de Primatologie of the C.N.R.S. (Rousset, France) on captive olive baboons living in social groups in large cages or parks from 15 to 650 m². The data on manual preferences were collected on 216 subjects of whom 122 individuals have been included in the final analysis since they have produced the minimum of 6 responses required for evaluating individual handedness for the hand slap gesture. Among these 122 subjects, 96 corresponds to a novel sample including 72 females, 21 males, and 3 of which the sex was undetermined (38 young from 11 months to 4 years of age and 58 adults from 5 to 26 years of age). In addition, 26 subjects had already been tested in a previous study in 2005 (see Meguerditchian & Vauclair, 2006) that included 17 females and 9 males (all were adults at the time of the present study).

Procedure

The communicative gesture investigated in 2005 (Meguerditchian & Vauclair, 2006) and in the present study consists in a quick and repetitive rubbing or slapping of the hand on the ground. The baboons produce this gesture toward another individual (a conspecific or a human) to threaten or intimidate him or her (see Figure 1; Kummer, 1968, for a first description of the gesture). We consider that the hand slapping behavior is probably intentional, because this gesture is exclusively directed to a recipient and since the producer repeats the behavior until its final goal is reached (submission or escape from the recipient).

The data on hand use for hand slap gestures were collected from February to June 2009 by an experimenter (S. Molesti) who was blind to the previous set of data (see Meguerditchian & Vauclair, 2006). Data collection consisted of opportunistically recording hand use by daily observations of the social groups of baboons when this behavior occurred either directed toward a conspecific or toward a human. In this latter case, the experimenter would trigger agonistic hand slapping responses from a baboon, for example, by abruptly shaking of the head and glancing at the focused animal. Because the number of responses per subject is a

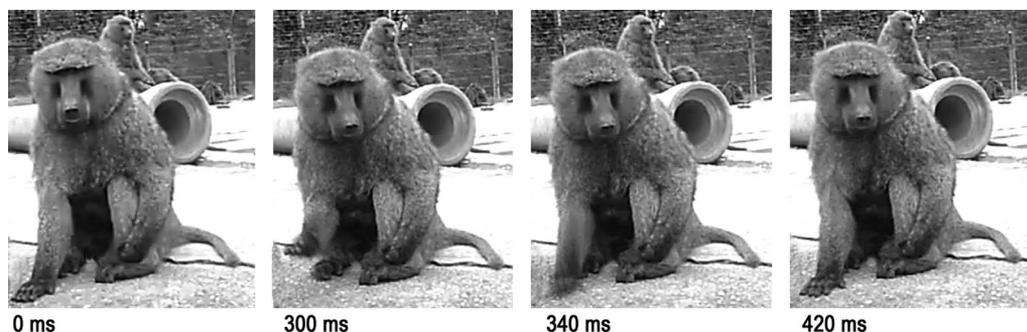


Figure 1. Picture of an adult male baboon threatening a human observer in slapping his right hand on the ground. Time is indicated in milliseconds. (Extracted from a video clip made by Sandra Molesti.)

critical point to determinate individual hand preferences, a minimum of 6 responses was required to include a subject in the handedness analysis. Given that some baboons produced gestures more frequently than others and that a large sample of subjects is needed for evaluating population-level handedness, we increased our overall sample size by making a concerted effort to focus on subjects that had the fewest observations whenever possible. To avoid postural biases in the choice of the hand from a baboon, we did not record data on hand use (1) when a subject used one hand to produce hand slap gesture while the other hand was not fully free and (2) when the recipient was not precisely in front of the producer.

In total, 3,243 hand slapping gestures were recorded on 216 baboons, 1,266 gestures were directed toward conspecifics (39%), and 1,977 were directed toward a human observer (61%). The minimum of 6 responses was reached by 122 subjects (the number of gestures per subject varied from 6 to 99 responses, $Mean = 24.79$, $SE = 1.87$).

Data Analysis

First, the direction of hand preference for each subject was determined by calculating an individual z -score on the basis of their total left and right hand responses. Then, based on their z -score, the individual baboons were classified as left-handed ($z \leq -1.96$), right-handed ($z \geq 1.96$), or ambiguously handed ($-1.96 < z < 1.96$). Second, the degree of manual 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 preference. Finally, the degree of asymmetry at a population-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 population-level hand preferences: positive, right-hand preference; negative, left-hand preference. The absolute values reflect the degree of population-level handedness.

Results

Details of the distribution of handedness patterns for the communicative hand slap gesture are presented in Table 1.

Consistency Across Time: Retested Population of Baboons

Since the measures of hand preferences for hand slap gestures has been replicated by a second observer 4 years after the first collection of the data by Meguerditchian and Vauclair (2006), it provided an opportunity to assess consistency in hand use across time of this behavior. Among the 30 retested subjects, 26 baboons had performed the minimum of 6 responses required to evaluate individual hand preferences. Using a Pearson product-moment correlation with HI, there is a significant correlation of hand preferences between the first session in 2005 and the second session in 2009, $r(26) = .44$, $p < .02$. Moreover, a paired-samples t test among the 26 retested individuals confirms that there is no

Table 1
Distribution of Hand Preferences and Degree of Population-Level Manual Biases

Hand slap gestures	# L	# R	# A	N	M.HI	SE	t	p
Total 2005 + 2009	24	79	59	162	0.26	0.05	5.35	<0.001, s
Population 2005	11	35	20	66	0.28	0.09	3.25	<0.002, s
Population 2009	13	44	39	96	0.25	0.06	4.16	<0.001, s

Notes. # L = number of left-handed subjects; # R = number of right-handed subjects; # A = number of ambiguously handed subjects; N = sample of subjects; M.HI = Mean Handedness Index score of N individuals that corresponds to the degree of population-level handedness; the sign indicates the direction of the manual bias (negative value: left-hand bias, positive value: right-hand bias); t = value of the t resulting from a t-test; p = significance of p; ns = nonsignificant; s = significant.

significant differences in the HI values between the two sessions, $t(25) = .11, p > .91$.

Consistency Across Groups: Direction of Hand Preferences in a Second Sample of Baboons

In comparison to the first group of 66 individuals investigated in 2005 (Meguerditchian & Vauclair, 2006), 96 new additional baboons were studied and included in the present analyses since they had performed a minimum of 6 responses. First, according to the individual z scores, 44 were classified as right-handed, 13 as left-handed, and 39 as ambiguously handed. Based on a chi-square goodness-of-fit test, the number of right-handed subjects is significantly higher than the number of left-handed subjects, $\chi^2(1, N = 57) = 16.86, p < .001$, indicating a significant population-level right-handedness. The $M.HI$ of the 96 subjects confirms this right-hand bias, $M.HI = .25, SE = .06$, a bias that is significant according to a one-sample t test, $t(95) = 4.16, p < .001$. This degree of right-hand bias at a population-level is similar to the one reported in the first group of 66 subjects ($M.HI = .28, SE = .09$). There is indeed no significant differences of the measures of hand preferences between these two independent samples of subjects according to a t test, $t(160) = .25, p > .80$ (see Table 1 and Figure 2 for comparison of the two set of results).

Potential Effect of the Experimenter

In the next analysis, as we did for the first sample in 2005 (Meguerditchian & Vauclair, 2006), we evaluated the potential effect of the experimenter on population-level right-handedness reported for the second and independent group of 96 subjects. Both gestures produced among conspecifics (734 gestures performed by 62 individuals) and those induced by the experimenter (1,262 gestures performed by 82 individuals) elicited identical degrees of population-level right-handedness ($M.HI = .27, SE = .09$ and $M.HI = .28, SE = .07$, respectively), which were both statistically

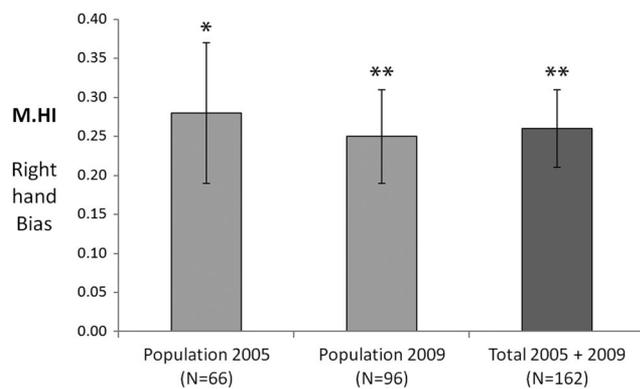


Figure 2. Degrees of population-level right-handedness ($M.HI$) in two different and independent samples of olive baboons assessed in separated sessions of observation (2005 and 2009). $M.HI$ scores $\pm SE$. The error bar represents the SE around the mean of HI scores ($M.HI$). Asterisk indicates that the $M.HI$ score differed significantly from zero. * $p < .002$, ** $p < .001$. All the $M.HI$ values are positive, indicating that the directions of the population-level handedness are toward the right-hand. The values of the $M.HI$ scores reflect the strength of population-level manual bias.

significant as revealed by one-sample t test, $t(61) = 3.02, p < .004$, $t(81) = 3.93, p < .001$, respectively. In addition, there was a significant correlation of hand preferences (HI) between intra- and interspecific gestures within the 48 subjects that performed gestures in these two contexts, $r(48) = .40, p < .005$. A paired sample t test confirmed that the difference of HI between gestures directed to humans and gestures directed to conspecifics was not significant among these 48 subjects, $t(47) = .61, p > .50$. Thus, the emergence of this right-handedness pattern did not result from biases because of the experimenter.

Hand Preferences in the Two Combined Samples (N = 162 subjects)

When combining the independent samples of the two sessions in 2005 and 2009, we obtained the hand preferences of 162 individuals that had performed a minimum of 6 responses (from 6 to 111 responses, $M = 22.98, SE = 1.54$). Then, 79 were classified as right-handed, 24 as left-handed, and 59 as ambiguously handed based on the z -score. The number of right-handed subjects is significantly higher than the number of left-handed subjects, $\chi^2(1, N = 103) = 16.86, p < .001$, indicating a significant population-level right-handedness. Among the 103 lateralized subjects, 77% were right-handed and 23% left-handed. The $M.HI$ of the 162 subjects, $M.HI = .26, SE = .05$, also shows a significant right-hand bias according to a one-sample t test, $t(161) = 5.35, p < .001$ (see Figure 2).

Potential Effects of Age and sex

Concerning the novel additional sample of 96 subjects investigated in the present study, there is no significant difference between males and females in population-level of HI, $t(91) = .16, p > 0.80$ (72 females: $M.HI = .25, SE = .07$; 21 males: $M.HI = .23, SE = .14$; 3 young subjects were undetermined) and in strength of handedness, $t(91) = 1.25, p > 0.20$ (females: $M.ABS-HI = .51, SE = .04$; males: $M.ABS-HI = .62, SE = .06$). In addition, there is no effect of age class in population-level handedness, $t(94) = .48, p > 0.60$ (38 young: $M.HI = .22, SE = .10$; 58 adults: $M.HI = .28, SE = .08$) or strength of hand preferences, $t(94) = .04, p > .90$ (young: $M.ABS-HI = .54, SE = .05$; adults: $M.ABS-HI = .54, SE = .04$).

When combining the present sample with the previous set of individuals studied in 2005 ($N = 162$), there is still no effect of sex in the manual biases, $t(157) = .44, p > .60$ (107 females: $M.HI = .28, SE = .06$; 52 males: $M.HI = .23, SE = .10$). However, although both adults and young individuals exhibited significant predominance of right-handedness, $t(82) = 5.71, p < .001$; $t(78) = 2.21, p < .04$; respectively, the difference between age classes approaches conventional levels of significance, $t(160) = 1.91, p = .058$. The 83 adults ($M.HI = .36, SE = .06$) showed a more pronounced right-hand bias than the 79 young subjects ($M.HI = .17, SE = .08$, see Figure 3).

Potential Effects of the Number of Responses per Subject

Because the number of observations derives a given HI value, it has been suggested that the evidence of predominance of right-

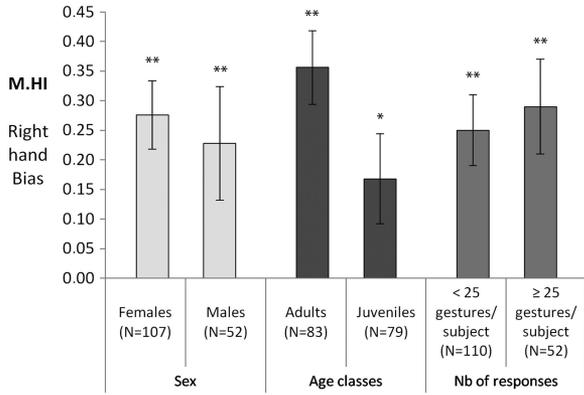


Figure 3. Comparison of the degrees of population-level right-handedness (*M.HI*) between (a) males and females; (b) adults and young individuals; (c) subjects that produced less than 25 hand slapping responses and subjects that produced 25 or more responses. *M.HI* scores \pm *SE*. The error bar represents the *SE* around the mean of *HI* scores (*M.HI*). Asterisks indicate that the *M.HI* score differed significantly from zero. * $p < .05$, ** $p < .001$.

handedness in some studies on chimpanzees might be an artifact because of the difference of the number of data among individuals, particularly for the subjects that have performed less than 25 responses (Palmer, 2002). As the number of responses per subject varied between 6 and 111 among the combined sample for the hand slap gesture, we addressed this issue by comparing the respective degrees of population-level handedness (*M.HI*) between the 110 baboons that produced less than 25 gestures (*M.HI* = .25,

SE = .06) and the 52 subjects that produced 25 or more gestures (*M.HI* = .29, *SE* = .08). In both groups, the *M.HI* scores were significantly different from 0, $t(109) = 4.03$, $p < .001$; $t(51) = 3.68$, $p < .001$, respectively. There was no significant difference in the degree of population-level right-handedness between the two groups, $t(160) = .32$, $p > .70$ (see Figure 3). In addition, we created a funnel plot in which the number of responses was plotted against the individual percentage of right-hand use. As can be seen in Figure 4, the number of ambiguously handed individuals (that could be seen in the center of the funnel between the two lines drawn by black lozenges and white circles) decreased when the number of responses per subject increased. This is in the opposite direction to the prediction made by Palmer (2002) about handedness in chimpanzees. Thus, these analyses indicate that our hand preference classification data and the report of the predominance of right-handedness were not biased because of differences in the number of responses among subjects.

Discussion

This paper provides several novel findings concerning handedness for gestural communication in baboons. First, the significant correlation between the first test and the retest of manual asymmetries shows that hand preferences for a communicative gesture is stable over time. This finding is consistent (1) with the significant correlation of hand preferences that has been reported in 58 retested captive chimpanzees for food-begging pointing gestures directed to humans 3 years after the first session of observation (Meguerditchian et al., 2010b) but also (2) with the reports of consistency over time of hand preferences for non communicative motor behaviors, particularly for bimanual coordinated activities,

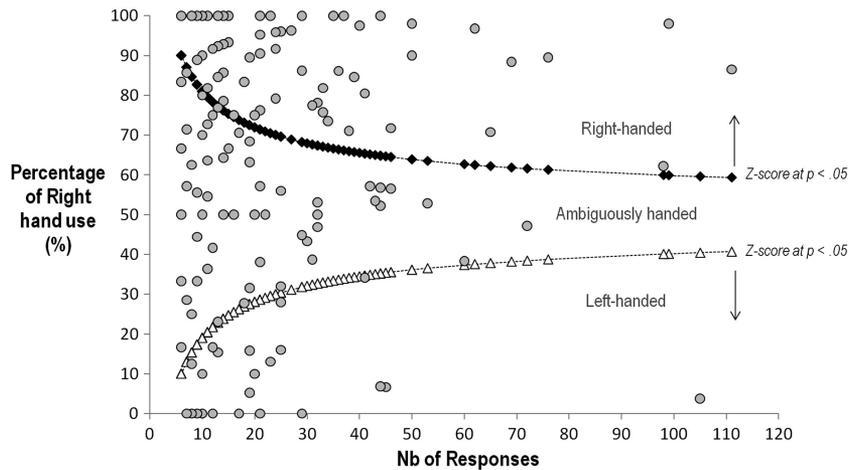


Figure 4. Funnel plot of the individual percentages of right hand plotted against the number of observations in hand use for gestures. The gray circles are the percentage of right-hand use for each subject based on the number of individual observations of hand use for hand slapping gestures (i.e., Nb of Responses). For each subject and its corresponding number of responses, there is a black lozenge and a white triangle that represent the critical percentages of right-hand use in which z-score values (+1.96 and -1.96, respectively) are at $p < .05$. Then, gray circles that lie above the black lozenges' line ($z = +1.96$) represent subjects with significant right-hand preferences ($p < .05$). Gray circles that lie below the white triangles' line ($z = -1.96$) represent subjects with significant left-hand preferences ($p < .05$). Gray circles that lie between the two lines represent those individuals who fail to show a significant hand preference. As can be seen, the majority of ambiguous subjects fall at the front of the funnel, indicating that these individuals had the fewest observations.

in several primate species (e.g., Meunier & Vauclair, 2007; Vauclair et al., 2005; Zhao, Gao, & Li, 2010), including humans (e.g., Annett, 1985). Second, the replication of the measures of handedness for the hand slap gesture in a novel and independent sample of 96 subjects showed a similar degree of predominance of right-handedness than the one assessed in a previous study in 66 baboons in 2005 (Meguerditchian & Vauclair, 2006). This result demonstrates consistency in the pattern of right-handedness across groups for this communicative gesture in baboons. Because these new additional measures have been collected by an experimenter who was blind to the previous set of data, these combined results are straightforward and demonstrate the robustness of the report of predominance of right-handedness for gestural communication in captive baboons. Third, when combining the new sample with the previous set of individuals studied in 2005, we have the largest sample of subjects ever investigated in a monkey species providing strong statistical power to demonstrate population-level right-hand bias. Such collective findings strongly support the view that gestural communication in baboons might involve the left-hemisphere. Interestingly, the degree of population-level right-hand bias for a species-specific gesture in the baboons ($M.HI = .26$ in 162 subjects including 48.77% of right-handed, 14.81% of left-handed, and 36.42 of ambiguously handed subjects) is similar to what has been previously reported in captive chimpanzees for species-specific gestures ($M.HI = .34$ in 70 subjects including 48.57% of right-handed, 4.29% of left-handed, and 47.14% of ambiguously handed subjects; Meguerditchian et al., 2010b) and for human-directed pointing gestures ($M.HI = .31$ in 227 subjects including 58.60% of right-handed, 15.85% of left-handed, and 25.55% of ambiguously handed subjects; Hopkins et al., 2005). These manual biases remain more pronounced than the one shown for bimanual coordinated manipulative activities in both baboons (Vauclair et al., 2005) and chimpanzees (Hopkins, Wesley, Izard, Hook, & Schapiro, 2004), while no correlation of hand preferences has been demonstrated in both species between communicative gestures and bimanual coordinated actions within the subjects that performed these two behaviors (Hopkins et al., 2005; Meguerditchian & Vauclair, 2006, 2009; Meguerditchian et al., 2010b). In comparison with humans (~90% of humans are right-handed, Annett, 1985), one can question the lower degree of predominance of right-handedness and the quite large proportion of ambiguously handed subjects in both baboons and chimpanzees. Unfortunately, it is difficult to compare such a distribution of hand preferences between humans and nonhuman primates because the criteria used to detect lateralized individuals are not congruent across studies. As mentioned by Uomini (2009), in contrast to observational data from nonhuman primates, the experimental data in humans usually come from laboratory tests or questionnaires (e.g., Bryden, 1977; Oldfield, 1971). In the present study, the criteria defined by the z -score for detecting lateralized individuals are very conservative in comparison to the criteria used in the studies on humans. For example, on the basis of the few responses of hand use generally recorded in the human literature to evaluate handedness, the z -score criteria we used in baboons and chimpanzees would automatically classify these human subjects as ambiguously handed regardless of the right- and left-hand ratio responses. We expect then that, if such ethological approach were used in humans, these criteria would increase the proportion of ambiguously handed individuals when producing communicative gestures. In fact, the

ethological approach requires the collection of many observational data points per subject to minimize potential situational or postural biases than may affect the use of the hand by a subject. Indeed, we have demonstrated with the funnel plot that the proportion of ambiguously handed subjects decreased when the number of responses per subject increased. Direct comparison of results between human and nonhuman primates would then require ethological observations of hand use for communicative gestures from human subjects. Moreover, the only study conducted on hand preferences in humans using ethological observations (Marchant, McGrew, & Eibl-Eibesfeldt, 1995) showed patterns of population-level right-handedness that may be similar to that of nonhuman primates. Fourth, the adults showed a tendency to be more right-handed at a group-level than the young individuals. This effect indicates that the predominance of right-handedness might be related to the ontogenesis of the individuals in terms of maturational processes of the involvement of the left-hemisphere for controlling intentional gestural communication (Meguerditchian & Vauclair, 2006). Such a tendency might be compared with the report of an increase of the degree of predominance of right-handedness for pointing in human infants from 4 to 12 months during speech development (Blake et al., 1994). This latter finding has been related to the maturation of the left-hemispheric specialization for the linguistic system.

This new set of data in baboons is congruent with the hypotheses suggested in our previous studies (Meguerditchian & Vauclair, 2006, 2009), namely: (1) a specific left-lateralized system might be involved in the production of gestures and might differ from the one involved in pure manipulative functions, (2) a continuity concerning left-hemispheric specialization for intentional communication might be drawn between baboons, chimpanzees, and humans, (3) lateralization for language may have evolved from a left-lateralized gestural system of communication in their common ancestor at least 30–40 million years ago. Such hypotheses are somewhat supported by brain imaging studies conducted in chimpanzees whereas no data are available so far about the cerebral substrate of gestural communication in baboons. Leftward asymmetries in the brain have been frequently documented in great apes concerning the homologous regions of language areas such as Broca's area (i.e., Inferior Frontal Gyrus [IFG]) and Wernicke's area (i.e., Planum Temporale [PT]) according to different assessment methods including analyses of neuronatomical asymmetries (Cantalupo & Hopkins, 2001; Cantalupo, Pilcher, & Hopkins, 2003; Cantalupo et al., 2009; Gannon et al., 1998; Hopkins et al., 2008) and cytoarchitectonic asymmetries only for the PT (Schenker et al., 2010; Spocter et al., 2010). Interestingly, chimpanzees who are right-handed for gesturing have been shown to exhibit a larger homologue of Broca's area in the left-hemisphere (Tagli-alatela, Cantalupo, & Hopkins, 2006) and greater leftward gray matter asymmetries in Wernicke's area compared to nonright-handed individuals (Hopkins & Nir, 2010). In contrast, it has been reported that handedness for bimanual coordinated actions are not related to neuroanatomical asymmetries of any of homologous regions of language areas but rather to hemispheric variations in the primary motor cortex (Hopkins & Cantalupo, 2004). Such neural correlates strengthen the hypothesis suggested above by the behavioral data that a specific left-lateralized communicative system exists and may constitute a precursor to language areas. To our knowledge, the first functional brain imaging study related to the

production of gestures in nonhuman primates has been conducted in captive chimpanzees using positron emission tomography (PET) by Tagliatalata, Russell, Schaeffer, and Hopkins (2008). The authors have reported an activation of the homologue of Broca's area in the left hemisphere for the production of pointing gestures but also for the use of learned atypical vocalizations that have been shown to be produced intentionally, as gestures, for getting the attention of a human to get out of reach food (Hopkins, Tagliatalata, & Leavens, 2007). In addition, a study has revealed an orofacial asymmetry toward the right side of the mouth during the production of these atypical vocal signals, whereas the species-typical vocal repertoire of the chimpanzees (that seems to be better related to an emotional control, e.g., Goodall, 1986) elicited a left-orofacial asymmetry (Losin et al., 2008). This latter finding supports the view that, in contrast to the species-typical vocal repertoire, atypical sounds might be under the control of the left-hemisphere as it has been suggested for gestural communication. Thus, we advocate that the specific left-lateralized communicative system involved exclusively for the production of gestures in baboons might be bimodal (gesture and vocal) in chimpanzees for the individuals that are able to produce these atypical vocalizations.

To conclude, regarding these combined findings, we can propose a rudimentary scenario for the origins of language. Prerequisites of left-hemispheric lateralization for language production may have emerged first with the use of communicative gestures in the common ancestors of baboons and humans at least 30–40 million years ago. 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 from at least 5–7 million years ago in the common ancestor of chimpanzees and humans. Finally, with the emergence of *Homo sapiens* at least 200,000 years ago, this bimodal communication may have evolved into a more and more complex system including an increasing sophistication of the control of the vocal-tract, the tongue and the oro-facial movements until becoming the modern articulated language associated with speech-related gestures in humans.

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