Short communication

Baboons communicate with their right hand

Adrien Meguerditchian [a,b], Jacques Vauclair [a,*]

[a] *Department of Psychology, Research Center in Psychology of Cognition, Language and Emotion, University of Provence,*
29, Av. Robert Schuman, 13621 Aix-en-Provence, France
[b] *Center of Primatology-CNRS, 13790 Rousset-sur-Arc, France*

Abstract

Humans are mainly right-handed for many actions including gestures. This bias is strongly linked to a left cerebral hemispheric dominance for language functions. Whether similar lateralized systems for communicative behaviors are present in other animals is unclear. Here we report the first evidence of strong population-level right-handedness in 60 captive baboons for a species-specific communicative manual gesture. Our findings support the view that lateralization for language may have evolved from a gestural system of communication controlled by the left hemisphere.
© 2006 Elsevier B.V. All rights reserved.

Keywords: Gestural communication; Handedness; Brain lateralisation; Monkeys; Baboons

1. Introduction

Comparative studies of non-human and human primates concerning communicative gestures show a renewed interest regarding the evolution of communicatory systems, in particular language. Although gestures are efficient means of communication among groups of non-human primates (e.g., [8,30]), they have been relatively little studied compared to vocalizations and facial expressions. The available studies have shown that Pongidae use their arm and their hand to communicate intentions to other individuals [5,7,19,24]. Whether these communicative behaviors involve lateralized systems is still unclear. Humans are mainly right-handed for many actions [1] including manual gesturing and such asymmetries are linked to a left cerebral hemispheric dominance for the perception and the production of language [21]. Thus, in a broad approach on the origin of speech and its lateralization, the study of manual communicative gestures and their asymmetries in non-human primates constitutes an ideal framework to clarify the hypothesis of the gestural origin of language and its lateralization [6,31].

Some investigations of manual gestural communications by humans reveal links between handedness and hemispheric specialization for language. Firstly, it has been shown that the activity of the right hand is predominant for manual movements when people are talking [20] and for signing by deaf humans with left-hemispheric dominance for the control of sign language functions [2,9]. Secondly, the degree of right-hand asymmetries for manual communication such as "pointing" increases during the development of speech in young children [3]. Additionally, the use of the right hand is more pronounced for signing than for non-communicative manual actions among children of deaf parents [4].

Concerning non-human primates, research on handedness has mainly focused on non-communicative motor actions (see Ref. [28] for a review) and some studies have reported a significant population-level handedness in particular those using a coordinated bimanual manipulative tube task (a task designed by Hopkins [11]) which consisted in removing food with fingers of one hand from inside a PVC tube while holding it with the opposite hand (in capuchin monkeys [29], in Olive baboons [32] and in great apes [11,17,18]). Concerning the lateralization of communicative behaviors, if strong left-hemispheric advantages have already been reported for the perception of vocalizations in rhesus monkeys (e.g., [10]), research on gestural communication has only concerned captive chimpanzees (*Pan troglodytes*). These studies have shown a population-level
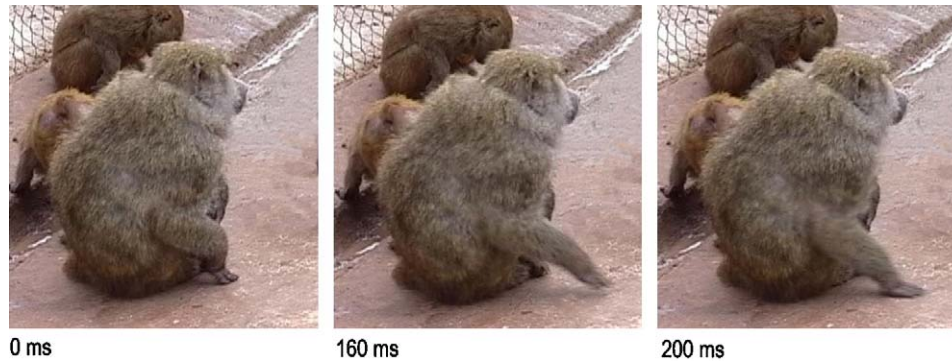
Fig. 1. Communicative gesture in a baboon. An adult female intimidates another individual by quickly rubbing her right hand on the ground. Time is indicated in milliseconds (ms).

right-handedness for communicative gestures [14,15], a bias which is stronger than the bias exhibited in manipulative tasks [16]. Thus, the continuity between humans and chimpanzees has been interpreted as supporting the hypothesis [6] that lateralization for language may have evolved from a gestural system of communication lateralized in the left hemisphere in the common ancestor as recently as 5 or 6 million years ago [16].

To our knowledge, no investigation has been undertaken in monkeys. Our research aims thus at detecting communicative gestures and their lateralization in Olive baboons (*Papio anubis*).

2. Method

2.1. Subjects

At the Center of Primatology of Rousset (France), a sample of 60 captive Olive baboons (*Papio anubis*) living in social groups in parks or in large cages was selected. The sample was composed of 30 males and 30 females; 37 were young (age range: 1–4 years, mean = 2.38, S.E. = 0.17) and 23 were adults (age range: 5–28 years, $M = 11.48$, S.E. = 1.20).

2.2. Procedure

Baboons produce a species-specific manual gesture that is clearly communicative. It consists in a quick and repetitive rubbing or slapping of the hand on the ground; this gesture is used to threat or intimidate other individuals [22] (see Fig. 1 and the video-clip available online). Hand slapping is probably intentional, insofar as it was most of the time repetitive and as 100% of the observed gestures were performed toward a social partner (human or conspecific). Thus, this behavior seems to fulfill the criteria usually retained to define intentional communication [23], namely (a) it is only performed when an audience is present, (b) the visual orienting behavior of the signaler is in phase with the social partner, and (c) the signaler persists when the social partner is not attending or is not responding.

Data were collected in two contexts: (a) spontaneous agonistic interactions between conspecifics and (b) between baboons and the human experimenter. In this latter case, the experimenter would trigger agonistic responses (hand slapping) from a baboon, for example by abruptly shaking of the head and glancing at the focused animal. In total, 1828 communicative gestures were observed on 115 baboons. Sixty subjects performed the minimum of 10 responses fixed to assess individual hand preference (the number of gestures per subject varied from 10 to 111 responses, $M = 28.13$, S.E. = 3.02). Among the 1688 hand slapping gestures retained, 1246 (74%) came from interactions between baboons and the experimenter, the 442 others (26%) provided from 92 interactions observed between baboons.

2.3. Data analysis

First, a *z*-score was calculated for each baboon on the basis of the total left- and right-hand responses for threat gestures; this score was used to classify baboons as left-handed ($z \leq -1.96$), right-handed ($z \geq 1.96$) or ambiguously-handed ($1.96 < z < 1.96$).

Second, an individual handedness index score (HI) was calculated for each subject 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 reflect the strength of hand preference.

3. Results

3.1. Direction of hand preference

Thirty-five animals were classified as right-handed, 10 as left-handed and 15 as ambiguously-handed. Thus, among the 45 lateralized subjects, 78% were right-handed (see Fig. 2). The number of right-handed baboons (35 subjects) was significantly higher than the number of left-handed subjects (10 subjects), $\chi^2 (1, N = 45) = 13.89$, $p < 0.0002$, indicating a significant population-level right-handedness.
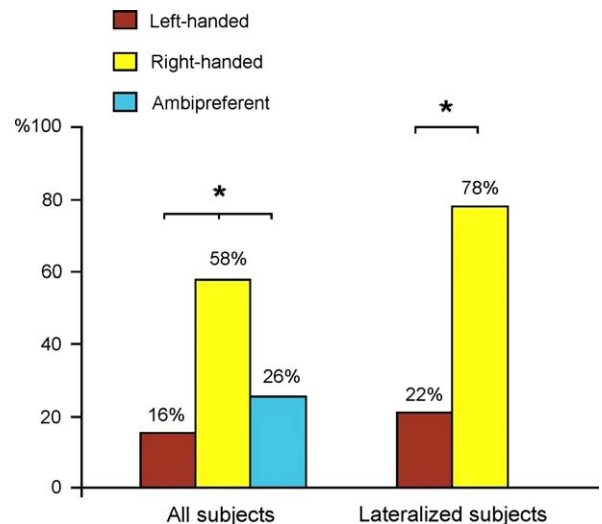

Fig. 2. Asymmetries of manual gestures in baboons' population. Percentages of right-, left- and ambiguously-handed baboons for gestures ($N = 60$). $^*p < 0.0002$.
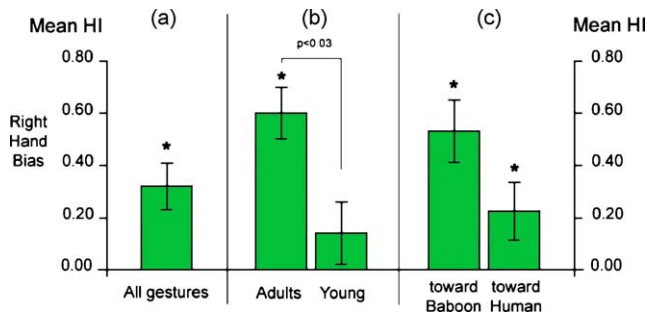
Fig. 3. Degrees of population-level right-handedness. Mean handedness index scores (MHI) ± S.E. The error bar represents the standard error around the MHI score. Asterisk indicates that the MHI score differed significantly from zero. $^*p < 0.05$. (a) MHI for total communicative hand slapping gestures ($N = 60$); (b) MHI scores for age classes: young baboons ($N = 37$) and adults ($N = 23$); (c) MHI scores for baboons who produced gestures toward a conspecific ($N = 27$) and for subjects who produced gestures toward the experimenter ($N = 48$).

The mean handedness index score (MHI) of the 60 individuals for threat gestures was equal to 0.32 (S.E. = 0.09), and this result confirms the clear right-hand bias in the population, as revealed by one sample t-test, $t(60) = 3.58$, $p < 0.0008$ (see Fig. 3a).

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. A non-significant difference in population-level handedness was found between sexes ($F(1,60) = 1.39$, $p > 0.05$, MHI = 0.42, S.E. = 0.11 for the 30 females; MHI = 0.21, S.E. = 0.14 for the 30 males), but a significant difference was found between age classes, $F(1,60) = 6.67$, $p < 0.03$ (MHI = 0.14, S.E. = 0.12 for the 37 young baboons; MHI = 0.60, S.E. = 0.10 for the 23 adults). The degree of population-level right-handedness was stronger for adults than for young baboons, indicating that age classes could have an effect on the development of the population-level right-hand bias (see Fig. 3b). Only adults' MHI value differed significantly from 0, $t(23) = 6.00$, $p < 0.0001$.

3.3. Potential effect of the experimenter

In the next analysis, the potential effect of the experimenter on population-level right-handedness was evaluated. Both gestures produced among conspecifics (442 gestures performed by 27 individuals, MHI = 0.53, S.E. = 0.12) and those induced by the experimenter (1246 gestures performed by 48 individuals, MHI = 0.23, S.E. = 0.11) led to a significant population-level right-handedness as revealed by one sample t-test, $t(27) = 4.50$, $p < 0.0002$, $t(48) = 2.18$, $p < 0.04$, respectively (see Fig. 3c). Thus, the emergence of this right-handedness pattern did not result from biases due to the experimenter. Although right-handedness was stronger for intra-specific gestures compared to inter-specific gestures (see MHI), this difference is not significant ($F(1,75) = 3.26$, $p > 0.05$, using an analysis of variance with the HI score serving as the dependent measure.

3.4. Comparison of handedness indexes between threat gestures and non-communicative motor actions

Additionally, results for gestures were compared with results obtained previously in the tube task and in a unimanual reaching task (see Ref. [32]) with some of the baboons also involved in the present study. Handedness index scores did not significantly correlate within the 16 same individuals which produced the threat gestures and performed the tube task (Pearson product–moment correlation: $r(16) = 0.214$, $p > 0.10$), as 10 subjects out of the 16 exhibited dissimilar hand preferences. In addition, handedness index scores did not significantly correlate within the 18 same individuals which produced the threat gestures and performed the unimanual task (Pearson product–moment correlation: $r(18) = 0.245$, $p > 0.10$), as 12 subjects out of the 18 exhibited dissimilar hand preferences. It must be noted that the degree of right-handedness in baboons' populations was the strongest for communicative gestures (MHI = 0.32, S.E. = 0.09 versus MHI = 0.13, S.E. = 0.06 for the tube task and MHI = 0.00, S.E. = 0.05 for the unimanual task).

Finally, 10 subjects performed the three tasks (gesture: MHI = 0.69, tube: MHI = −0.01, reaching: MHI = 0.21). A repeated ANOVA showed a strong significant task effect on HI scores, $F(1,10) = 10.22$, $p < 0.006$.

3.5. Potential effect of the number of responses per subject

The potential effect of the sample size (the number of responses per subject) on reported handedness is a topic of recent debate [18,27,32]. In fact, some researchers are not convinced by the handedness data collected on captive primates [25–27]. For example, Palmer [27] is particularly suspicious of the reliability of handedness indices calculated on fewer than about 25 observations. This author called into question chimpanzees' right-handedness in showing an effect of the sample size on manual laterality data. In fact, right-handedness reported in chimpanzees seems to be less pronounced among individuals who performed more than 25 responses [27]. To test the reliability of our results, the MHI scores were calculated for the 24 baboons whose number of responses was 25 gestures and above (from 25 to 111 responses, $M = 49$, S.E. = 5.05): MHI = 0.45, S.E. = 0.12, a score which is significantly different from 0 ($t(24) = 3.88$, $p < 0.0009$). We calculated also the MHI scores for the 36 baboons whose number of responses was under 25 gestures (from 10 to 23 gestures, $M = 14.25$, S.E. = 0.77): MHI = 0.23, S.E. = 0.12, a score which is not significantly different from 0, ($t(36) = 1.81$, $p = 0.07$). The observed difference in the degree of population-level right-handedness (see MHI) is not significant using an analysis of variance with the HI score serving as the dependent measure ($F(1,60) = 1.59$, $p > 0.05$). This analysis supports the view that our right-handedness data did not result from a sample-size effect.

4. Discussion

To our knowledge, this is the first study reporting manual asymmetries for gestures in monkeys which suggests a left cere-

bral dominance for the control of communicative functions of the hands.

Previous studies showing population-level right-handedness for communicative manual behaviors in apes have concerned inter-specific gestures only produced to communicate with humans [14–16]. The present study is the first of its kind realized with non-human primates on the lateralization of intra-specific gestures and confirms the results obtained for inter-specific gestures in chimpanzees [14–16]. Additionally, it must be noted that the relationships between the captive baboons and humans (staff and experimenters) are not easy to engage and are avoided at the field station where the study was carried out. Thus, the gestures we recorded being spontaneous, species-specific and realized in social groups, our study strongly supports the view that hand preference did not result from biases induced by humans, as it has been proposed by some researchers [25–27]. In effect, our results have showed that both intra- and inter-specific gestures are significantly right-handed and that the degree of population-level right-asymmetries is the most pronounced for intra-specific gestures.

We also showed that the number of responses per individual did not significantly bias our right-handedness data. And we observed that the degree of right-handedness (see MHI) was the strongest when the data collected per individual were above 25 responses. This is in the opposite direction to the prediction made by Palmer [27] about handedness in chimpanzees.

We showed in a previous study that baboons also presented a population-level right-handedness (61% were right-handed, see Ref. [32]) for the tube task. We could think that an individual would rather communicate with the hand used preferentially for manipulations. Thus, according to this view, we could expect that the same bias would appear for gestures and for the manipulative task. However, we showed that patterns of laterality were different, with non-significant correlations of manual preferences within the same individuals who performed both types of actions and we showed that the population-level right-handedness was the strongest for communicative gestures. Such a difference of degree between communicative and non-communicative actions has also been reported in chimpanzees [16] and in children raised by deaf parents [4]. It turns out that the MHI scores reported for hand slapping gestures (MHI = 0.32) and the tube task (MHI = 0.13) in baboons are very closed to those reported in chimpanzees by Hopkins et al. [16] (MHI = 0.31 for gestures and MHI = 0.14 for the tube task). Moreover, whereas an effect of age classes on the development of population-level right-handedness was shown for communicative gestures, this was not the case for the tube task [32]. We note that these findings were contrary to what has been shown in chimpanzees [11,16]: a significant main effect for age has been reported in the strength of right-handedness for the tube task [11], but not for asymmetries of communicative gestures [16].

We thus suggest that the communicative functions of the hand could imply a different cerebral substrate than that involved in their manipulative functions: a communicatory left-hemisphere system may be involved for the production of gestures. This system would more strongly favor the use of the right hand than bimanual coordinations for object manipulations. More-over, results from recent studies in chimpanzees that used RMI (magnetic resonance imaging) to investigate the neurobiological basis of handedness are convergent with this argument. In effect, it was found that asymmetries of homologous language areas did not correlate with handedness for non-communicative motor actions [13], but a significant correlation was shown between asymmetries in Brodmann's area 44 (homologous of Broca's area) and hand preferences for communicative gestures [12].

From a comparative viewpoint, regarding our results and the literature, we suggest the existence of a continuity between asymmetries of speech related gestures and asymmetries of communicative gestures in chimpanzees and now in baboons, even though the degree of population-level right-handedness is lower in non-human primates than in humans. From an evolutionary viewpoint, we suggest that the neuroanatomical substrate of manual communication controlled by the left cerebral hemisphere may have existed in their common ancestor at least 30 million years ago and may be considered as the precursor of the human language area. Our results hence bring additional support to the view that lateralization for language in humans may have evolved from a gestural system of communication lateralized in the left hemisphere (e.g., [6,16]).

Acknowledgments

Appendix A. Supplementary video

Supplementary video associated with this article can be found, in the online version, at doi:10.1016/j.bbr.2006.03.018.

References

[1] Annett M. Left, right, hand and brain: the right shift theory. Hillsdale, NJ: Erlbaum; 1985.

[2] Bellugi U. The link between hand and brain: implications from a visual language. In: Martin DS, editor. Advances in cognition, education, and deafness. Washington, DC: Gallaudet University Press; 1991. p. 11–35.

[3] Blake J, O'Rourke P, Borzellino G. Form and function in the development of pointing and reaching gestures. Infant Behav Dev 1994;17:195–203.

[4] Bonvillian JD, Richards HC, Dooley TT. Early sign language acquisition and the development of hand preferences in young children. Brain Language 1997;58:1–22.

[5] Call J, Tomasello M. Production and comprehension of referential pointing by orangutans (*Pongo pygmaeus*). J Comp Psychol 1994;108:307–17.

[6] Corballis MC. From hand to mouth. In: The origins of language. Princeton, NJ: Princeton University Press; 2002.

[7] Gomez JC. The emergence of intentional communication as a problem-solving strategy in the gorilla. In: Parker ST, Gibson KR, editors. "Language" and intelligence in monkeys and apes: comparative developmental perspectives. Cambridge, England: Cambridge University Press; 1990. p. 333–55.

[8] Goodall J. The chimpanzees of Gombe. Cambridge, MA: Harvard University Press; 1986.

[9] Grossi G, Semenza C, Corazza S, Volterra V. Hemispheric specialization for sign language. Neuropsychologia 1996;34:737–40.

[10] Hauser MD, Andersson K. Left hemisphere dominance for processing vocalizations in adult, but not infant, rhesus monkeys: field experiments. PNAS 1994;91:3946–8.

[11] Hopkins WD. Hand preferences for a coordinated bimanual task in 110 chimpanzees: cross-sectional analysis. J Comp Psychol 1995;109:291–7.

[12] Hopkins WD, Cantalupo C. Brodmann's area 44, gestural communication, and the emergence of right handedness in chimpanzees. Behav Brain Sci 2003;26:224–5.

[13] Hopkins WD, Cantalupo C. Handedness in chimpanzees is associated with asymmetries in the primary motor but not with homologous language areas. Behav Neurosci 2004;118:1176–83.

[14] Hopkins WD, Cantero M. From hand to mouth in the evolution of language: the influence of vocal behavior on lateralized hand use in manual gestures by chimpanzees (*Pan troglodytes*). Dev Sci 2003;6:55–61.

[15] Hopkins WD, Leavens DA. Hand use and gestural communication in chimpanzees (*Pan troglodytes*). J Comp Psychol 1998;112:95–9.

[16] Hopkins WD, Russel J, Freeman H, Buehler N, Reynolds E, Schapiro SJ. The distribution and development of handedness for manual gestures in captive chimpanzees (*Pan troglodytes*). Psychol Sci 2005;6:487–93.

[17] Hopkins WD, Stoinski TS, Lukas KE, Ross SR, Wesley MJ. Comparative assessment of handedness for a coordinated bimanual task in chimpanzees (*Pan troglodytes*), gorillas (*Gorilla gorilla*), and orangutans (*Pongo pygmaeus*). J Comp Psychol 2003;117:302–8.

[18] Hopkins WD, Wesley MJ, Izard MK, Hook M, Schapiro SJ. Chimpanzees (*Pan troglodytes*) are predominantly right-handed: replication in three populations of apes. Behav Neurosci 2004;118:659–63.

[19] Hostetter AB, Cantero M, Hopkins WD. Differential use of vocal and gestural communication in response to the attentional status of a human. J Comp Psychol 2001;115:337–43.

[20] Kimura D. Manual activity during speaking. Part I: right-handers. Neuropsychologia 1973;11:45–50.

[21] Knecht S, Deppe M, Draeger B, Bobe L, Lohman H, Ringelstein EB, et al. Language lateralization in healthy right-handers. Brain 2000;123:74–81.

[22] Kummer H. Social organization of Hamadryas baboons: a field study. Chicago: The University of Chicago Press; 1968.

[23] Leavens DA. The evolution of manual deixis: interaction studies. Soc Behav Comm Biol Artif Syst 2004;5:363–84.

[24] Leavens DA, Hopkins WD, Thomas RK. Referential communication by chimpanzees (*Pan troglodytes*). J Comp Psychol 2004;118:48–57.

[25] Marchant LF, McGrew WC. Laterality of function in wild chimpanzees of Gombe National Park: comprehensive study of spontaneous activities. J Human Evol 1996;30:427–43.

[26] McGrew WC, Marchant LF. On the other hand: current issues in and meta-analysis of the behavioural laterality of hand function in nonhuman primates. Yearbook Phys Anthropol 1997;40:201–32.

[27] Palmer AR. Chimpanzee right-handedness reconsidered: evaluating the evidence with funnel plots. Am J Phys Anthropol 2002;118:191–9.

[28] Papademetriou E, Sheu CF, Michel GF. A meta-analysis of primate hand preferences, particularly for reaching. J Comp Psychol 2005;119:33–48.

[29] Spinozzi G, Castornina MG, Truppa V. Hand preferences in unimanual and coordinated-bimanual tasks by tufted capuchin monkeys (*Cebus apella*). J Comp Psychol 1998;112:183–91.

[30] Tomasello M, Camaioni L. A comparison of the gestural communication of apes and human infants. Hum Dev 1997;40:7–24.

[31] Vauclair J. Lateralization of communicative signals in nonhuman primates and the hypothesis of the gestural origin of language. Interaction studies. Soc Behav Comm Biol Artif Syst 2004;5:363–84.

[32] Vauclair J, Meguerditchian A, Hopkins WD. Hand preferences for unimanual and coordinated bimanual tasks in baboons (*Papio anubis*). Cog Brain Res 2005;25:210–6.