



Right hemisphere dominance for emotion processing in baboons

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ABSTRACT

Asymmetries of emotional facial expressions in humans offer reliable indexes to infer brain lateralization and mostly revealed right hemisphere dominance. Studies concerned with oro-facial asymmetries in nonhuman primates largely showed a left-sided asymmetry in chimpanzees, marmosets and macaques. The presence of asymmetrical oro-facial productions was assessed in Olive baboons in order to determine the functional cerebral asymmetries. Two affiliative behaviors (lipsmack, copulation call) and two agonistic ones (screeching, eyebrow-raising) were recorded. For screeching, a strong and significant left hemi-mouth bias was found, but no significant bias was observed for the other behaviors. These results are discussed in the light of the available literature concerning asymmetrical oro-facial productions in non-human primates. In addition, these findings suggest that human hemispheric specialization for emotions has precursors in primate evolution.

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1. Introduction

Cerebral and behavioral asymmetries have long been regarded as exclusive features of human beings. However, studies of fish, reptiles, amphibians, nonprimate mammals and nonhuman primates have revealed evidence of behavioral asymmetries, such as handedness and whole-body turning (Andrews & Rogers, 2002; Bisazza, Rogers, & Vallortigara, 1998; Hook, 2004). Because of their anatomical, physiological and motor action likeness to humans, many investigations have been conducted on nonhuman primates in order to investigate the possible existence of hemispheric specialization for cognitive processing and motor patterns, and thus elucidate the phylogenesis of human cerebral asymmetries (for reviews, see Hopkins, 2007; Vauclair, Fagot, & Dépy, 1999).

In human and nonhuman primates, faces and voices are the primary means of transmitting social signals. Authors interested in nonhuman primates' communication have claimed that the vocal system of nonhuman primates conveys mostly emotional information (e.g., Meguerditchian, Cochet, & Vauclair, in press; Seyfarth & Cheney, 2003; Vauclair, 2003). This idea has been reinforced by the demonstration that nonhuman primates' vocalizations are

controlled by subcortical and limbic structures that also regulate emotions in humans (for a review, see Jürgens (2002)).

It is commonly accepted, and has been since Darwin (1872), that animals and humans share basic emotions and have common motor patterns. For example, facial expressions are regarded as an index of emotional behavior. Brain laterality in the production and perception of emotional facial expressions in humans has been a subject of discussion since the 1970s (e.g., Borod & Koff, 1984; Campbell, 1978; Rinn, 1984; Sackeim, Gur, & Saucy, 1978), whereas the study of other behavioral asymmetries in nonhuman primate species is relatively recent (for reviews, see Hauser, 1997; Hiscock & Kinsbourne, 1995). Studies of hemispheric specialization for emotion have led authors to develop two distinct conceptual models. According to the most widely held view, the perception and expression of emotions would appear to be controlled by the right hemisphere, whether the emotional valence is negative or positive. Although research on the cerebral lateralization of emotion has highlighted a greater involvement of the right hemisphere in negative emotions (Borod, 1993; Borod, Haywood, & Koff, 1997; Campbell, 1982). Davidson, Saron, Senulis, Ekman, and Friesen (1990), on the other hand, champion an emotional valence theory based on EEG measures, indicating a differential involvement of the two hemispheres in emotion processing. The right hemisphere would appear to be involved in negative/withdrawal emotions (e.g., fear) and the left in positive/approach ones (e.g., happiness).

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To infer whether functional cerebral asymmetries do exist in humans, some studies have used mouth asymmetry measurements. In adult humans, Graves and Landis (1990) observed the mouth movements of participants during laughing and speaking. Results indicated an asymmetrical bias correlated with the participants' activity. During smiling, a left hemimouth bias appeared (i.e., right hemisphere), while during speaking, a right bias was noticed (i.e., left hemisphere). These findings were replicated by Holowka and Petitto (2002) in babies (age range: 5–12 months). A left bias was found during smiling and a right one during babbling. Given the noninvasive nature of this reliable technique, it appears to be a suitable index for surmising the hemispheric lateralization of vocal and facial emotion production in nonhuman primates.

The handful of studies that have investigated oro-facial asymmetries in nonhuman primates during the production of vocal and facial expressions have highlighted a left hemiface bias, suggesting the involvement of the right hemisphere in emotion processing (for reviews, see Hook, 2004; Hopkins & Vauclair, *in press*; Tagliatalata, 2007). These findings are consistent with the view that these expressions represent emotional signals, rather than a form of linguistic information. Hauser (1993) found that the left side of a rhesus macaque's face begins to move first and is more expressive (as reflected in the number of skin folds and the height of the corner of the mouth) than the right side. This author observed four different facial expressions: the fear grimace, the copulation grimace, the open-mouth threat and the ear flap, in 4–19 rhesus macaques. Hook-Costigan and Rogers (1998) found slightly different results when they assessed oro-facial asymmetries in a sample of 11 marmosets. The authors videotaped two facial expressions accompanied by vocalizations, which were referred to as the tsik (characterized as fearful, induced by the experimenter) and the twitter (defined as a social contact call). A third expression was described as a silent fear expression. Hook-Costigan and Rogers (1998) noticed a larger left hemimouth during the production of fear expressions, whether or not they were produced with vocalizations, and a right-sided asymmetry for the twitter expression. Hauser and Akre (2001) studied the onset of mouth opening asymmetries in rhesus macaques during the production of several types of expression, classified as either vocal or facial. Results revealed a general bias toward the left side of the face, without any difference between vocal and facial productions. Chimpanzees manifest significant left-sided oro-facial asymmetry for several vocal and facial expressions, including hooting, play, silent-bared-teeth and scream face (Fernández-Carriba, Loeches, Morcillo, & Hopkins, 2002a, 2002b). Losin, Freeman, Russel, Meguerditchian, and Hopkins (2008) based their assessment on a comparison of two oro-facial production categories: species-typical sounds tallying with food-barks and pant-hoots, and learned sounds corresponding to “raspberry” and “extended food grunts”. The latter have been shown in previous studies to be learned vocal signals directed toward humans (Hopkins, Tagliatalata, & Leavens, 2007; Leavens, Hostetter, Wesley, & Hopkins, 2004). The authors found that food-barks and pant-hoots (species-typical sounds) were expressed more intensely on the left side of the face, whereas extended food grunts and raspberries (atypical-species sounds) showed a rightward asymmetry.

A review of the available literature on oro-facial asymmetry in nonhuman primates led us to examine spontaneous instances of this phenomenon in the production of vocal and facial expressions in order to address the issue of emotional cortical lateralization in baboons. Facial asymmetries had never been explored in this species before, although there is a relatively large body of literature on behavioral asymmetries in baboons, providing strong evidence of hemispheric lateralization of motor action patterns. Many investigations have demonstrated a significant group-level hand prefer-

ence for different manipulation tasks and manual gestural communication, as well as perceptual asymmetries (Fagot & Vauclair, 1988; Meguerditchian & Vauclair, 2006; Vauclair & Meguerditchian, 2006; Vauclair, Meguerditchian, & Hopkins, 2005; for a review, see Vauclair & Meguerditchian, 2007). Moreover, Casper and Dunbar (1996) analyzed the orientational asymmetries of male gelada baboons during agonistic interactions. These authors discovered that both opponents used their left visual field significantly more frequently than their right. Furthermore, left visual field preferences increased with the level of negative emotion, pointing to the strong involvement of the right hemisphere in negative emotions. In the light of these studies, baboons appeared to present an interesting and promising model for understanding the evolution of human hemispheric lateralization of emotion. Based on previous findings in human and nonhuman primates, and in accordance with the hemispheric dominance theory, we expected the left side of the baboon's face and hence the right hemisphere - to be more involved in the production of vocal and facial expressions, whatever their emotional valence. However, in line with the valence theory, we also expected to observe different patterns of hemispheric specialization, depending on the emotional valence of the expressions. According to this theory, the right hemisphere is involved in negative emotion production, whereas the production of positive emotions is controlled by the left hemisphere.

2. Method

2.1. Subjects and housing

The study was conducted from May 2009 to January 2010 at the primate field station of the CNRS Primatology Center in Rousset sur Arc (France), with a sample of 69 captive olive baboons (*Papio anubis*) living in social groups in parks or large cages. We recorded the facial expressions of 55 adults aged more than 5 years (46 females and 9 males) and 14 adolescents aged less than 4 years (10 females and 4 males). The age range of the sample was 3–22 years ($M = 10$, $SE = 1$). The baboons were housed in outdoor compounds (15–650 m²) connected to indoor quarters. They could move freely between the two structures, except during the observation periods, when they were locked in their outdoor compounds. The baboons had access to water *ad libitum*, vegetables and fruits were distributed twice a day, after the observation periods. Observations were made in accordance with CNRS guidelines on animal care.

2.2. Procedure

The first part of the study consisted in defining and recognizing facial expressions and vocal productions when subjects expressed emotions. After performing scan sampling behaviors on individuals, we decided to observe frequent salient social interactions considered to be essential for the coordination of social activities. We selected three behaviors based on the ethogram devised by Estes (1991): screeching, eyebrow-raising and lip-smacking. We also included the copulation calling described by Dixson (1998). Screeching is an agonistic/negative behavior, characterized by repeated high-pitched scream calls. Often accompanied by a fear grimace, it is produced in response to aggression, especially from a dominant individual, and serves to inhibit this aggression. Eyebrow-raising is another agonistic/negative behavior, during which the gaze is fixed on a subordinate. The eyebrows are raised and the scalp is retracted. The facial skin is also stretched by moving the ears back. This display is used as a threat display. Lip-smacking is an affiliative/positive behavior, defined as the

rapid, repetitive opening and closing of the lips. It is a greeting gesture that conveys reassurance and affiliative intent, and serves to facilitate positive social relationships between individuals. Sometimes, it may also serve as an appeasement or submissive display. Finally, copulation calling is also an affiliative/positive behavior, characterized by low-pitched rhythmic vocalizations during and following copulation. The lips are usually pursed. The function of copulation calling is not entirely clear, but the most accepted interpretation is that it allows the female to indicate her postcopulatory choice and stimulate mating with multiple males, thus increasing sperm competition, confusing paternity and reducing the risk of infanticide (Maestriperi, Leoni, Raza, Hirsh, & Whithman, 2005).

Most of the data were collected from two multimale-multifemale social groups living in parks housing around 50 individuals, allowing us to maximize the number of observations of social interactions. Sample sizes varied across selected behaviors, as we could not control when and which individual would produce a behavior of interest, or whether it would be looking straight at the observer's camera. Moreover, the video data were recorded in a naturalistic and opportunistic way. Altogether, we collected 288 images of 69 baboons: 116 pictures of 39 individuals for screeching, 70 of 19 subjects for lip-smacking, 24 of 11 females for copulation calling and 78 of 27 individuals for eyebrow-raising (see Fig. 1). In order to increase the number of individuals per expression category, we decided to take into account the individuals' still images of which we only had one (12%) or two (6%) pictures for each expression.

Videos were recorded on a SANYO Xacti VPC-FH1 dual camera (60fps, HD). The still images of full expressions from the videos were captured using the Avidemux 2.5.1 video editor. The methodology applied to scoring the lateralization of vocal and facial emotional productions was borrowed from Hook-Costigan and Rogers (1998). This procedure has been widely used in the literature on oro-facial asymmetries (e.g., Fernández-Carriba et al., 2002a, 2002b; Losin et al., 2008). Adobe Photoshop CS2 was used to analyze still pictures: a line was drawn between the inner corners of the eyes and compared with the horizontal lines on a fixed grid in order to rotate the face into a vertical position. Measurements were then made with Scion Image software (Scion Corporation, Frederick, MD, USA). We drew a perpendicular vertical line passing through the midpoint of the line between the inner corners of the eyes to split the face into two halves. To measure the hemimouth area, we traced around the inner side of each hemimouth freehand and calculated the surface (in pixels) for both hemimouths. Lines were also drawn between the outer corners of the mouth to the midline for each half of the face, to measure hemimouth length. For each image, a separate facial asymmetry index (FAI) was calculated for area and length, based on the method used in studies of lateralization (e.g., handedness) in nonhuman primates (Hopkins, 1999). Thus, the FAI was computed by subtracting the left hemimouth measure from the right hemimouth measure, then dividing the result by the sum of the right and left measures ($FAI = (right - left)/(right + left)$). Next, a line was drawn between the

outer corners of the eyes and the distance from these to the midpoint was measured in order to compute an index for the eyes (eFAI). Finally, the eFAI obtained for each picture of each individual in the four emotions categories was subtracted from the area and length FAIs in order to adjust for possible asymmetries due to the rotation of the face in relation to the camera. If more than one picture of an individual was digitized for a given category, we averaged the FAIs.

In accordance with the literature on oro-facial asymmetries (Fernández-Carriba et al., 2002a; Hook-Costigan & Rogers, 1998; Losin et al., 2008), we decided to calculate an interrater agreement. To that purpose, two different procedures have been used: one for classifying the behaviors at the beginning of the study and another one for oro-facial measures when the experimenter had completed the measures of the whole data set. Firstly, a rater, naïve to baboons' behaviors, was asked to identify and classify the behaviors. For this reliability test, video sequences were randomly selected, representing 20% of the data sets for each expression category. A Pearson product-moment correlation coefficient calculated for the behavior classifications by the two raters was positive and significant, $r(92) = 0.84, p < .01$, indicating a high level of agreement between them. Secondly, a rater who was blind to the topic of asymmetrical vocal and facial productions in baboons and to our hypotheses was trained to use the software and analyze the still images. We randomly selected 15% of the data sets for each expression category, and flipped half the pictures horizontally. A Pearson correlation coefficient was then calculated for the two raters, yielding scores of 0.70 ($df = 47, p < .01$) for area FAI and 0.73 ($df = 35, p < .01$) for length FAI. These values indicate a high consistency between the two raters' measures.

3. Results

A one-sample *t*-test was performed on the eFAIs to check that there was no influence of the orientation of the baboons' faces toward the camera (greater exposure of one side of the face or the other) which might compromise the measures. Results showed that there was no main effect of orientation, indicating that the baboons' faces were filmed head-on, $t(96) = -0.23, p = .81$. The eFAIs were nonetheless taken into consideration when analyzing hemimouth asymmetries and interpreting the data sets. Mean area FAIs for each vocal and facial expression showed a strong and significant left asymmetry at the group level during screeching, $t(39) = -4.56, p < .001$, but not during lip-smacking, $t(19) = 0.05, p = .95$, copulation calling, $t(11) = -0.66, p = .52$ or eyebrow-raising, $t(27) = -0.90, p = .38$ (see Table 1). Regarding mean length FAIs, results were similar to those for area FAIs, in that a left bias was found for screeching, $t(39) = -2.2, p = .03$, but there was no bias at the group level for the other two behaviors ($t(19) = 0.69, p = .5$ for lip-smacking and $t(11) = -0.39, p = .71$ for copulation calling; see Table 1). The correlation between the two hemimouth measures (length and area) computed for each image was positive



Fig. 1. Examples of FAI-areas' measures during baboons' expressions. From left to right: screeching, eyebrow-raising, lipsmack and copulation call.

Table 1
Mean area and length FAIs for each oro-facial expression.

	<i>n</i>	Mean FAI	SE	<i>t</i>
<i>Mean area FAIs</i>				
Screeching	39	−0.1109	0.0242	−4.5652**
Eyebrow-raising	27	−0.0153	0.0153	−0.9023
Lip-smacking	19	0.0037	0.0646	0.0578
Copulation calling	11	−0.0515	0.0777	−0.6634
<i>Mean length FAIs</i>				
Screeching	39	−0.0437	0.0199	−2.1957*
Lip-smacking	19	0.0316	0.0455	0.6946
Copulation calling	11	−0.0323	0.0830	−0.3894

* $p < .05$.** $p < .01$.

and significant ($r(70) = 0.88, p < .01$). This result indicates that both hemimouth measures are reliable indices for inferring hemispheric lateralization in vocal and facial productions.

An ANOVA was performed in order to assess the influence of expression category on absolute values (ABS.FAIs) for oro-facial asymmetry. There was a significant main effect of expression on area ABS.FAIs, $F(3, 92) = 8.56, p < .001$, and length ABS.FAIs, $F(2, 66) = 9.92, p < .001$. These positive results led us to conduct a Post hoc comparison using Tukey's HSD test to compare expressions by pairs in order to understand more precisely the effect of each emotion on ABS.FAIs. The results revealed that there was no difference between area ABS.FAIs for screeching ($M = 0.14, SD = 0.13$), lip-smacking ($M = 0.21, SD = 0.18$) and copulation calling ($M = 0.23, SD = 0.12$). However, these three behaviors all had a greater effect on the strength of laterality than eyebrow-raising ($M = 0.05, SD = 0.06$). As for differences in the effect of expression category on length ABS.FAIs, results indicated that lip-smacking ($M = 0.15, SD = 0.13$) and screeching ($M = 0.1, SD = 0.09$) had similar effects, but that copulation calling ($M = 0.25, SD = 0.09$) had a greater effect.

Whenever we obtained several images of an individual for the same expression category, we applied repeated-measures ANOVA on the facial asymmetry indices in order to assess consistency of bias. Subjects displayed high consistency in all four asymmetrical facial and vocal expressions, both in the different data sets and in area and length FAIs (see Table 2 for details).

Finally, we analyzed the influence of social hierarchy, sex and age on our results. We evaluated hierarchy by recording agonistic behaviors in dyadic interactions (biting, hitting, slapping, chasing and threatening) and designed a linear matrix to identify the rank of each individual within the sample (Furuichi, 1997; Kano, 1996). The effects of hierarchy and sex were assessed using an ANOVA, with the FAIs and their absolute values serving as the dependent variable. There was no significant difference in group-level vocal and facial asymmetry between hierarchy and sex on any measure. Age was taken as a continuous variable. A Pearson correlation coefficient revealed only a positive and significant influence of age on length FAIs, $r(19) = 0.50, p = .02$ for lip-smacking, and a negative

one for copulation calling, $r(11) = -0.61, p = .04$. These results could be due to the high age variability between subjects, small amount of data collected and small sample size for these two behaviors (lip-smacking: mean age = 8 years; $SE = 1.18$, 70 pictures of 19 individuals; copulation calling: mean age = 11.27; $SE = 1.74$, 24 pictures of 11 females).

4. Discussion

The aim of this study was to assess whether baboons display evidence of directional asymmetries in the production of vocal and facial emotional expressions. According to our results, a strong and significant left hemimouth asymmetry was observed during screeching, highlighting a functional right hemisphere lateralization in the production of this behavior. No bias, however, was detected for either copulation calling, lip-smacking or eyebrow-raising (based on both area and length measures). This result is in line with the right dominance theory (Borod, 1993; Borod et al., 1997; Campbell, 1982). Given that we performed our measures in relation to the distance between the outer corners of the eyes and the facial midline, these findings cannot be attributed to greater exposure of one or other side of the baboons' faces in the still images we recorded. The observation of a left bias in screeching behavior therefore indicates the predominant involvement of the right hemisphere in the production of this vocal and facial emotion. This result is in agreement with a number of studies reporting the involvement of the right hemisphere in negative/agonistic behaviors. It has been widely reported not only in humans (Borod, 1993; Borod et al., 1997; Campbell, 1992) but also in nonhuman primates, notably in rhesus macaques (Hauser, 1993), marmosets (Hook-Costigan & Rogers, 1998) and chimpanzees (Fernández-Carriba, Loeches, Morcillo, & Hopkins, 2002a, 2002b). Furthermore, similar results have been found in species other than primates, such as lizards (Deckel, 1995), toads (Robins, Lippolis, Bisazza, Vallortigara, & Rogers, 1998), rats (Garbonati et al., 1983) and chicks (Bullock & Rogers, 1986). The right hemisphere specialization for vocal and facial emotional expressions in baboons, an Old World monkey species, attests to the existence of a homologous cortical area among primates which appeared very early in evolution, at least 30–40 million years ago (see, for example, Boyed & Silk, 2000), and was retained in species that evolved later.

The absence of oro-facial asymmetry in eyebrow-raising, the second negative/agonistic behavior, could be explained by a lower intensity of negative emotion compared with the screeching behavior, as reported by Casper and Dunbar (1996) for agonistic behaviors in gelada baboons. Other studies have demonstrated a visual preference for the eye region in baboons (Kyes & Candland, 1987) and rhesus macaques (Ghazanfar, Nielsen, & Logothetis, 2006; Guo, Robertson, Mahmoodi, Tadmor, & Young, 2003). The authors found that this preference existed even when they presented facial stimuli with a frozen open mouth or a video that featured vocalizations. The strong role of this species-typical

Table 2
Repeated-measures ANOVA on area and length FAIs per expression.

Behaviors	FAIs	MS	<i>df</i> 1	<i>df</i> 2	<i>F</i>	<i>p</i>	η^2
Screeching	Area FAI	0.0204	9	68	0.4115	0.9248	0.0517
	Length FAI	0.0116	9	68	0.3313	0.9616	0.0420
Lip-smacking	Area FAI	0.0620	9	42	0.7617	0.6515	0.1403
	Length FAI	0.0412	9	42	1.1651	0.3416	0.1998
Copulation calling	Area FAI	0.1445	4	8	1.1604	0.3959	0.3672
	Length FAI	0.0926	4	8	1.6873	0.2450	0.4576
Eyebrow-raising	Area FAI	0.0067	10	38	0.9740	0.4813	0.2040

expression as an emotional communicative signal has led researchers to put forward a second hypothesis to explain the lack of asymmetry in eyebrow-raising. Morecraft, Louie, Herrick, and Stilwell-Morecraft (2001) studied cortical innervation of the facial nucleus in nonhuman primates and reported neurological differences in motor cortex specialization for the upper and lower parts of the face. The lower part of the face is predominantly innervated by the contralateral hemisphere, while the upper part is bilaterally innervated. Similar findings have been described for humans (Borod & Koff, 1984; Dejong, 1979, cited in Borod, 1993; Rinn, 1984). However, recent research has revealed ipsilateral innervation of the upper part of the face (*i.e.*, right hemisphere control; Asthana & Mandal, 1997; Richardson, Bowers, Bauer, Heilman, & Leonard, 2000; Ross, Prodan, & Monnot, 2007). With regard to our results, we can make the assumption that the eyebrow-raising movement in baboons is bilaterally innervated. Thus, while this communicative signal is still emotionally controlled, in contrast to linguistic information, the measurement of the upper part of baboons' faces would appear not to be a reliable index for inferring hemispheric specialization for emotion processing.

Furthermore, we failed to find a significant hemiface bias for the two positive/affiliative behaviors, namely lip-smacking and copulation calling. These results appear at first sight to invalidate the valence theory (Davidson *et al.*, 1990), as no left hemisphere specialization was found for the control of positive emotions. However, the limited number of samples for both copulation calling ($n = 11$) and lip-smacking ($n = 19$) probably accounts for the lack of significance for each of these two categories. One consequence of this relatively limited sample was a major disparity in measures within the population. The standard errors for lip-smacking and copulation calling were relatively high (see Table 1 for details). While the repeated-measures ANOVA indicated a high consistency of asymmetrical facial and vocal expressions across the different data sets, coherent with the significant asymmetries observed at an individual level, the fact that there was a directional asymmetry at the individual level does not imply that there was a similar degree of asymmetry each time. Facial expressions rarely last for more than 5 s, and form part of the complex dynamics of interaction, in which the magnitude of the facial asymmetry varies throughout the whole sequence, whether it is observed in humans (Richardson *et al.*, 2000) or in nonhuman primates (Hook-Costigan & Rogers, 1998). Thus, in the still images we collected, the intensity of the emotion peak varied hugely from one picture to another within the same expression category, depending on the emotional intensity of the behavior, whether or not the emotional peak had been reached and which image was extracted from the sequence.

A marginally nonsignificant right asymmetry in length FAI was found for lip-smacking. We consider that this behavior deserves particular attention and should be taken into account in further investigations. Many studies have demonstrated the usefulness of focusing on lip-smacking because of the complexity of this communicative signal in different social interactions and the neurophysiological control of this oro-facial movement. However, researchers attempting to clarify its meaning and function have so far failed to reach a consensus. Lip-smacking is widely performed by many Old World monkey species (Van Hoof, 1967). In baboons, it is thought to convey reassurance and affiliative intent, and may also serve as an appeasement or submissive display (Pelaez, 1982; Redican, 1975; Van Hoof, 1967). An early study of olive baboons in captivity indicated that lip-smacking is displayed more often by dominant individuals toward their subordinates (Rowell, 1966). By contrast, Easley and Coelho (1991) found that lip-smacking was independent of social status, but positively associated with affiliative behaviors. To our knowledge, authors interested in the study of communicative signaling in nonhuman

primates have never reported lip-smacking toward humans, even though it is routinely performed by baboons. Most primate vocalizations are directed toward the whole population rather than to one specific individual (Arbib, 2005), whereas lip-smacking is essentially directed toward individuals, making it an interesting communicative signal because of its singularity. Furthermore, a study of rhesus macaques highlighted the bilateral activation of mirror neurons in Area F5 of the ventral premotor cortex (homologous to Broca's area) during observation of lip-smacking by an experimenter (Ferrari, Gallese, Rizzolatti, & Fogassi, 2003). The authors named these neurons "communicative mirror neurons", regarding them as an evolutionary precursor of social communication mediated by facial gestures. The firing of mirror neurons in Area F5 during the observation of ingestive gestures and communicative signals in monkeys (*e.g.*, lip-smacking) may well have supported the emergence of human abilities such as language (*e.g.*, Arbib, 2005; Rizzolatti & Arbib, 1998). Thus, this finding raises questions about the function of lip-smacking and its potential phylogenetic consequences for the evolution of speech. Given the variety of social interactions in which lip-smacking occurs, we believe that future investigations should identify the context of production and take it into account when examining the lateralization of this communicative signal.

The asymmetrical facial and vocal productions we observed in this study do not seem to have been influenced by sociodemographic factors. The interaction of the hierarchy and sex variables had no influence on the results, but the limited number of older subjects prevented us from interpreting the greater facial asymmetry for the lip-smacking and copulation calling categories among older subjects. These conclusions are in agreement with the results of several studies in humans showing that age (Moreno, Borod, Welkowitz, & Alpert, 1990) and sex (Borod, Koff, Yecker, Santschi, & Schimdt, 1998) do not affect the lateralization of motor patterns in the control of emotions.

In conclusion, this study provides some evidence of right hemisphere specialization in the production of vocal and facial expressions in nonhuman primates. Our findings point to neurophysiological and neuroanatomical homologies between baboons and humans in the cortical control of emotional vocal and facial expressions. The growing interest in emotion in the animal literature has increased our understanding of the continuities and discontinuities in the mechanisms behind emotional communicative signals in human and nonhuman primates. However, further investigations are needed to elucidate the phylogenetic paths leading to human hemispheric specialization for emotion.

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