Communicative Signaling, Lateralization and Brain Substrate in Nonhuman Primates: Toward a Gestural or a Multimodal Origin of Language?

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ABSTRACT

Language is a complex intentional, syntactical and referential system involving a left-hemispheric specialization of the brain in which some cerebral regions such as Broca's and Wernicke's areas play a key-role. Because nonhuman primates are phylogenetically close to humans, research on our primate cousins might help providing clues for reconstructing the features of our ancestral communicative systems. In the present paper, after emphasising the tight relation between gestures and language in humans, we underlie the specific significance of communicative gestures and of the progressive control of the oro-facial system and the vocal tract in the course of the language evolution. For this purpose, we will then review the findings related to the features, the lateralization and brain correlates of both vocal and gestural systems in nonhuman primates.

Keywords: Communication, Gesture, Hemispheric specialization, Primate, Language

1. Introduction

Given the phylogenetical proximity between human and nonhuman primates, the researches on the communicative, motor and cognitive systems of our

primate cousins could help us determining the continuities/discontinuities between human language and animal communication. Such a comparative approach among primate species might thus have some significant implications for reconstructing the features of our ancestral communicative system that have been inherited from our common ancestor and for evaluating the evolutionary prerequisites of language. Most of the studies have focused naturally on the vocal modality and some researchers have suggested that language resulted from the evolution of the vocal system in our ancestors (e.g., Ghazanfar & Hauser, 1999; Snowdon, 2001; Zuberbühler, 2005; Lemasson, 2011). This theory is now challenged by a growing number of authors supporting the "gestural origins" view that gestural communication may be the first phylogenetic precursor of human language (e.g., Arbib et al., 2008; Corballis, 2002, 2003; Kendon, 1991; Kimura, 1993; Vauclair, 2004). Such an alternative gestural theory finds support in the considerable evidence of strong and tight links between gestures and language in humans including infants, adults and deaf people using sign language. It is well known that infants start using gestures for communication before being able to speak. Indeed, before about 12 months of age, gesture is the first mode of intentional and referential communication in infants (Bates, 1976). In other words, infants can not only voluntary express by gestures a wish or an intention (that they cannot yet be expressed verbally) to a specific social partner and expect a response from the recipient (i.e. intentional properties), but also to direct the adult's attention toward external objects or events (i.e., referential properties) by pointing gestures (Butterworth & Morissette, 1996). Such gestural productions have been shown to play an active role in the development of linguistic skills. For instance it has been shown that the size of gestures repertoire in infants predict vocabulary development (e.g., Iverson & Goldin-Meadow, 2005). Moreover, it is also very well described that we speak using systematically synchronized expressive manual gestures (co-speech gestures, see McNeill, 2005). Based on several reports showing how the two modalities interact with each other in both production (e.g., Bernardis & Gentilucci, 2006) and perception (Willems et al., 2007), it has been proposed that speech and gesture might share the same integrated communication system (Gentilucci & Dalla Volta, 2008). It has also been well documented that human signed languages share the same "phonological", morphological and syntactical properties than spoken languages (for reviews: Bellugi, 1991; Emmorey, 2002) as well as some similar left-cortical lateralization and key-

cerebral areas such as Broca's areas (Corina et al., 2003; Emmorey et al., 2007). Given the existence of such strong links between gestures and speech in humans, one can question the implication of the gestural system in the evolution of language.

In the present paper, after reviewing briefly the recent findings on the features of gestural and vocal communication in nonhuman primates and their potential relations to some language properties, we will present research on the behavioral lateralization of these communicative systems and their cortical correlates. We will thus discuss their continuities and discontinuities with the brain hemispheric specialization of language and their implications regarding the origins of language.

2. Human language and gestures in nonhuman primates

The gestural origin theory finds also supports with the recent investigation of the properties of the gestural communicative system in nonhuman primates. Indeed, it is well documented that great apes, particularly chimpanzees, and in a lower degree some monkey species, use manual gestures and body movements to communicate with conspecifics in various social contexts and with different goals such as play, threat (see Figure 1), aggression, greeting, invitation for grooming, in case of shared excitation, of reassurance-seeking after stress, and for food begging (e.g., Goodall, 1986; Pika et al., 2005; Call & Tomasello, 2007 for review; see also Cartmill & Byrne, 2010; Hobaiter & Byrne, 2014). Interestingly, this communicative system has revealed some potential continuities with several key properties of human language, such as flexibility of morphology, intentional and referential properties (see for reviews, Meguerditchian & Vauclair, 2008; Pika, 2008). Indeed, although some of species-specific gestures - such as chest-beat in gorillas - seem quite stereotyped and might likely be genetically determined (e.g., Genty et al., 2009), the gestural system has been shown to be very flexible, depending of the individual social experience, eliciting variations of the composition, the morphology and the size of the gestural repertoire between individuals and also between different populations (Pika et al., 2005; Call & Tomasello, 2007 for reviews). In fact, among individuals, different gestures may be produced for the same goal and, conversely, similar gestural signals may be used for divergent goals (Tomasello et al., 1985; Tomasello et al., 1989). Those findings are

consistent with the previous research projects aimed at trying to teach American sign language to apes (Gardner & Gardner, 1969; see also Terrace, 1979 ; Patterson, 1978; Miles, 1990), revealing the remarkable ability of apes to learn and to use novel manual signs (more than one hundred) to communicate with humans rather than novel vocalizations.

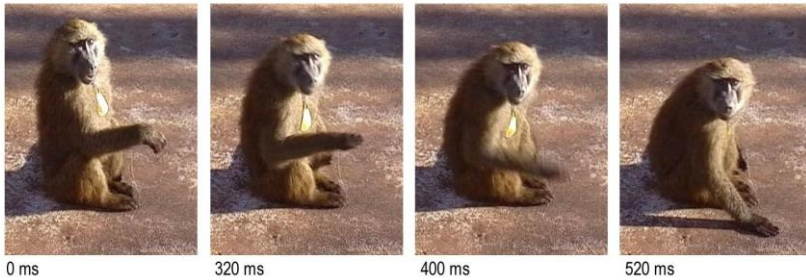0 ms   320 ms   400 ms   520 ms

Figure 1. Manual gesture performed by a male baboon. A young baboon intimidates a human observer by quickly slapping his right-hand on the ground. Time is indicated in milliseconds (ms). *Picture: © Adrien Meguerditchian*

In addition, it has been described that gestures can be referential by the use of imperative pointing for getting food from a human (Call & Tomasello, 1994; Leavens & Hopkins, 1999; Leavens et al., 2004) or to inform about the location of a tool (Zimmermann et al., 2009). Similar observations of referential gestures have also been made in chimpanzees and bonobos within intraspecific interactions for indicating to a conspecific a particular spatial location or an object in the environment (Inoue-Nakamura & Matsuzawa, 1997; Veà & Sabater-Pi, 1998; Hobaiter et al., 2014; Genty et al., 2014) or an area of the body in order to be groomed (Pika & Mitani, 2006). Finally, we know that the production of gestures in apes and monkeys is under intentional control (e.g., Bard, 1992; Leavens et al., 1996; Tomasello et al., 1994; Genty et al., 2009; Bourjade et al., 2014). Without a doubt, in contrast to vocalisations, the production of gestures involves systematically a social partner (a conspecific or a human), within a dyadic interaction or even triadic interaction when it is referring to external objects (reviewed in Leavens, 2004 and in Pika et al., 2005). Moreover, when the recipient is not responding or is not attending, gestures can persist or be adjusted to the attentional state of the recipient until the goal is reached (Leavens et al., 2005; Cartmill & Byrne,

2007; Tomasello, 2003). For instance, in this latter case, nonhuman primates can change their position to face the recipient before producing visual gestures (e.g., Liebal et al., 2004) or elaborate more auditory or tactical gestures in order to get the attention of the recipient (Tomasello et al., 1994; 1997; Leavens et al., 2010; Bourjade et al., 2014). In short, those collective findings offer solid evidence of intentional communication when involving the manual or body motor system.

3. Human language and vocalizations in nonhuman primates

Regarding those latter collective findings, there is some debate whether or not the properties of the vocal system in nonhuman primates is less convincing than the gestural system as the best prerequisite for the emergence of speech (Vilain et al., 2011; Liebal et al., 2013). Recent findings have shown relative flexibility of the vocal system. For instance, audience effects have been shown to affect differentially vocal production depending on the type of social partner in both chimpanzees and monkeys (e.g., Mitani & Nishida, 1993; Wich & de Vries, 2006; Schel et al., 2013a, 2013b; Zuberbuhler et al., 2011), thus questioning the potential existence of intentional properties in call productions. Some degree of plasticity in the acoustical structure of calls has also been described between or within social groups in relation to social, environmental and contextual changes in the group (reviewed in Lemasson, 2011), indicating a probable influence of a learning component during the individual's lifetime as well as some control of the production of vocal signals (e.g., for reviews: Roian-Egnor & Hauser, 2004; Meguerditchian & Vauclair, 2008). Nevertheless, although such a flexibility, in comparison to gestures' repertoire, there is very little variation of the content and the size of the vocal repertoire in a given species across individuals and different groups. There is poor evidence that monkeys and apes are able to generate new vocal signals, suggesting that the bases of the vocal features in the repertoire of nonhuman primates might be mostly genetically determined, although they can be influenced on top by a learning component from the social environment (see Roian-Egnor & Hauser, 2004). Moreover, the production of vocalizations is much context-dependent than gestures (Pollick & De Wall, 2007) in being systematically related to a specific reaction to events and likely to a specific internal emotional state (Goodall, 1986). This suggests rather poor intentional

properties. According to this hypothesis, it does not mean that nonhuman primates cannot have some degree of voluntary control on their vocal production in relation to other conspecifics. But the voluntary modulation, exaggeration or inhibition of their calls in relation to specific contexts and audience can still be interpreted as the results of an internal emotional state. From this point of view, this kind of production looks then very similar to the production of any human emotional vocalisations (e.g., cry, laugh, scream, etc.) which include also some degree of voluntary control and which can vary according to the type of the social partner (but also be expressed without any audience). Indeed, in contrast to human language and gestural communication, there is still no evidence that the production of those species-specific vocalizations could be dissociated from an emotional state and from their determined contexts of use. It is thus not excluded that this flexibility related to species-specific vocalisations does not involve intentional properties and does not require a specific goal in mind in order to motivate the production of vocalisations.

However, recent exceptional reports may provide some new clues to the evolution of the vocal system as well as an evolutionary scenario of the emergence of language (speech). Hopkins and colleagues (2007) have thus described the use of two atypical novel "learned" sounds produced by several chimpanzees among the captive groups from the Yerkes Primate Research Center: Some chimpanzees are not only able to produce non-voiced "raspberries" or "kiss" sounds (involving only the lips with the air of the mouth) but also "extended grunts" which clearly engage the vocal tract and laryngeal sound production mechanisms. The authors showed that the production of these atypical sounds and vocalizations is often produced with pointing gestures and is used exclusively in the presence of both a human and an out-of-reach food in order to beg for food, while typical species-specific 'food' calls were more frequent in the presence of food alone (Hopkins et al., 2007). Such atypical productions were interpreted as signals used intentionally to capture the attention of the human. Great apes have been shown to use those acoustic signals - vocal and lips sounds, cage banging or clapping gestures - especially when the recipient is not attentive, whereas visual pointing gestures are preferentially used when the recipient is attentive (e.g., Leavens et al., 2004, 2010; see also in orangutans: Cartmill & Byrne, 2007; for a review of the literature: Hopkins et al., 2011). In other words, some chimpanzees are able to extend to the vocal system this special feature of

social cognition and their ability to intentional signaling in adjusting relevantly the modality of the signal to the attentional state of the recipient. In addition, given the inter-individual variability among chimpanzees concerning the ability to produce or not those novel sounds, it has been interpreted that, as for human speech but in contrast to species-typical vocalizations, those atypical vocal and lips sounds might be socially learnt. In fact, it has been reported that chimpanzees raised by a biological mother who were able to produce those sounds, were more likely to also be able to do so than chimpanzees raised by humans in a nursery (Taglialatela et al., 2012). Moreover, a recent study showed that, among the chimpanzees that were not able to produce these atypical vocalizations, it was not only possible to explicitly train them to do it using operant conditioning, but also that those subjects would further use these novel vocalizations in a communicative context for getting the attention of a human (Russell et al., 2013). Similarly, it has been reported that the language-trained bonobo Kanzi was able to use four additional vocalizations in a context of human communicative exchanges only (Hopkins & Savage-Rumbaugh, 1991).

4. Lateralization of the production of signals

In humans, most of the language functions are under the control of the left hemisphere of the brain in both left-handed and right-handed individuals (Knecht et al., 2000) and involve complex neural networks in which Broca's and Wernicke's areas play a key role (Broca, 1865; Wernicke, 1874). Regarding the strong links between language and gesture as well as the relative independence between language lateralization and handedness (Mazoyer et al., 2014; Ocklenburg et al., 2014), it is possible that manual preferences for gestural communication may constitute a better predictor of hemispheric lateralization for language than hand preference for manipulative functions (Bellugi, 1991; Kimura, 1993). Indeed gestures including signing in deaf people, co-speech gestures or pointing gestures in children have been shown to elicit robust predominance of right-handedness (see the review of Cochet & Vauclair, 2010) that could be better related to left-hemispheric dominance for language. Does gestural communication in nonhuman primates involve a left-hemispheric dominance like human speech does? In other words, are nonhuman primates predominantly right-handed for gestural communication?

Interestingly, the only studies available on hand preference for gestures - conducted in large samples of nonhuman primates including captive chimpanzees, bonobos, gorillas and baboons - have all reported population-level right-handedness for different categories of gestures (for reviews: Hopkins et al., 2012; Meguerditchian et al., 2013), a degree that was much more pronounced that the ones reported in non-communicative motor tasks, such as bimanual manipulation (Figure 2). Those gestures included communicative clapping, intraspecific gestures (e.g., hand slap, see Figure 1) and human-directed food begging gestures in both captive chimpanzees and baboons (Hopkins & Cantero, 2003; Hopkins et al., 2005; Meguerditchian et al., 2010; Meguerditchian & Vauclair, 2006, 2009; Meguerditchian et al. 2011b). Similar, though less well documented, evidence of slighter rightward asymmetries in undistinguished types of gestures have also been reported in a sample of captive gorillas (Shafer, 1987), captive bonobos (Hopkins & Vauclair, 2012) and wild chimpanzees (Hobaiter & Byrne, 2013). Such gestural asymmetries in these two species are consistent over time, across different groups and across different categories of gestures whereas, in contrast, no correlation of individual hand preferences was found between bimanual actions and any type of communicative gestures (Meguerditchian & Vauclair, 2006, 2009; Meguerditchian et al., 2010, 2012). To sum up, in contrast to non-communicative actions, different communicative gestures in nonhuman primates showed a similar pattern of hand preferences with each other and may thus share partially the same cerebral system.

Collectively, within an evolutionary perspective, these findings support the hypothesis of a continuity between baboons, gorillas, bonobos, chimpanzees and humans concerning left hemispheric specialization for gestural communication. It might then be hypothesized that such a communicative lateralized system in nonhuman primates constitutes an ideal prerequisite of the cerebral substrate for human language in the common ancestor of these species at least 30-40 million years ago (Meguerditchian & Vauclair, 2008; Meguerditchian et al., 2011a).
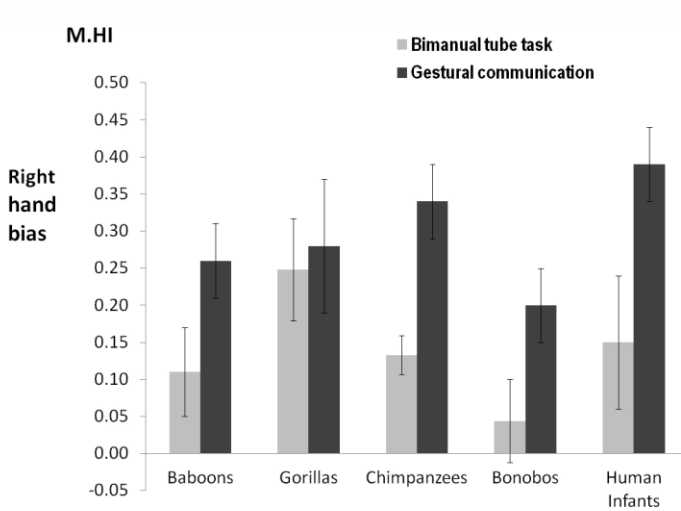
Figure 2. *(Adapted from Meguerditchian et al., 2013)* Degrees of population-level right-handedness (M.HI) for species-typical communicative gestures in 162 baboons (Meguerditchian et al., 2011b), in 18 gorillas (Shafer, 1987), in 70 chimpanzees (Meguerditchian et al., 2010), in 51 bonobos (Hopkins & Vauclair, 2012) and whole-hand pointing in 37 human infants (Cochet & Vauclair, 2010) compared with the bimanual coordinated task. M.HI scores ± S.E. On the basis of total left- and right-hand responses, an individual Handedness Index (HI) was calculated for each subject and varied on a continuum from -1.0 to 1.0. 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. The error bar represents the S.E. around the M.HI score. Asterisks indicate that the M.HI score differed significantly from zero. * $P < 0.05$. The positive M.HI values all indicates bias toward right-handedness at group level.

Concerning the vocal system, several studies have investigated hemispheric lateralization for vocal control in nonhuman primates via indirect studies of behavioural oro-facial asymmetries. In humans, the right side of the mouth opens first and wider than the left side, indicating the dominance of the left cerebral hemisphere for language control (Graves et al., 1982; Wolf & Goodale, 1987). Thus, Hook-Costigan and Rogers (1998) evaluated the asymmetries of mouth expressions during call production in marmoset monkeys and reported a larger right side of the mouth (i.e., left hemisphere

bias) in producing social contact calls (positive emotional signals) and a larger left side of the mouth (i.e., right hemisphere bias) in producing fear expressions (negative emotional signals). The authors hypothesized that the asymmetry of call production could be due to the emotional valence of the signal. However, similar studies on species-specific vocalizations in rhesus monkeys (Hauser & Akre, 2001), baboons (Wallez & Vauclair, 2011) and chimpanzees (Fernandez-Carriba et al., 2002) reported oro-facial asymmetries toward the left-side of the mouth, suggesting a right-hemispheric dominance related rather to emotional processing than to a human-like language processing.

Interestingly, in contrast to the species-typical vocal repertoire, the use of the atypical attention-getting sounds in some chimpanzees has been shown to involve an asymmetry toward the right-side of the mouth, i.e. left-hemispheric dominance (Losin et al., 2008; Wallez et al., 2012). Moreover, it turns out that these signals not only share the same communicative intent as the "food beg" gestures in captive chimpanzees 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 vocal and lips sounds simultaneously. Thus, we might support the view that the specific left-lateralized communicative system suggested above for gesture production in baboons and chimpanzees by the reports of specific patterns of right-handedness for gestures, may be involved for both gestures and "learned" attention-getting sounds in chimpanzees. To test such hypotheses, further researches are needed on neural correlates of communicative signalling in nonhuman primates.

5. Neural correlates of gestural and vocal communication

As for humans, leftward neuroanatomical asymmetries (i.e., asymmetries of the volume or surface of a given cortical region between the two hemispheres) have been frequently reported in great apes concerning the Inferior Frontal Gyrus (IFG) and the Planum Temporale, (PT), two cerebral regions that are known to overlap keys cerebral regions of language in humans (i.e., Broca and Wernicke areas respectively). This result has been found according to different assessment approaches such as *post-mortem* morphological analyses for the PT

(Gannon et al., 1998), *in vivo* and *post mortem* imaging studies using traditional tracing of specific areas of interest for the IFG (Cantalupo & Hopkins, 2001) and for the PT (Cantalupo, Pilcher, & Hopkins, 2003) and voxel-based morphometry for both PT and IFG (Hopkins et al., 2008).

Interestingly, morphometric analyses of MRI (Magnetic Resonance Imaging) anatomical brain images of chimpanzees have shown that the PT and IFG neuroanatomical asymmetries were driven by the direction of hand preference (i.e., left- or right-handed) for communicative gestures exclusively, including visual food begging gestures (Taglialatela et al., 2006; Hopkins & Nir, 2010) or auditory clapping gestures (Meguerditchian et al., 2012) but not by hand preferences for non-communicative bimanual coordinated actions (Hopkins & Cantalupo, 2004). Such neuroanatomical correlates strengthen the hypothesis suggested above by the hand preferences' data (1) of a possible neural dissociation between gestural communication and manipulative motor functions and (2) that the manual asymmetries for communicative gestures may reflect a left-lateralized specific communicative system involving, at least in chimpanzees and maybe baboons, cortical homologues of language areas and (3) may thus constitute an ideal precursor of hemispheric specialization for language.

To our knowledge, the only existing functional brain imaging studies conducted on communicative signaling in great apes are consistent with those hypotheses. Thus, the use of positron emission tomography (PET) in 3 captive chimpanzees has revealed that begging food from a human by using either gestures, atypical attention-getting sounds, or both of them simultaneously, activated a homologous region of Broca's area (IFG) predominantly in the left hemisphere (Taglialatela et al., 2008), a pattern of activation which is enhanced in subjects who used both gestural and vocal signals simultaneously (Taglialatela et al., 2011). Those unique neurofunctional data provide additional support to the potential existence in chimpanzees of a multimodal intentional system that not only includes gestures but can also integrate, in some individuals, oro-facial and atypical vocal sounds into the same left-lateralized lateralized system.

Further functional brain imaging studies related to the production of signals are needed but these researches are very limited. It is indeed difficult to put an awaked monkey or ape in a very noisy MRI machine and invite it to produce vocalizations or gestures on command in order to measure its brain activation... Thus, most of the functional brain imaging studies in nonhuman

primates investigate the passive *perception* of stimuli including acoustic signals. Those latter studies have used positron emission tomography (PET) and have showed that the passive listening of conspecifics' vocalizations involves cerebral areas within the superior temporal gyrus in rhesus monkeys (e.g., Gil-da-Costa et al., 2006; Petkov et al., 2008; Poremba et al., 2004) and in chimpanzees (Taglialatela et al., 2009), that might be related to the areas that are involved in the *comprehension* of language in humans. Those findings might be interpreted as evidence of the remarkable capacities of nonhuman primates to understand and categorize the external world (Cheney & Seyfarth, 1990; Seyfarth et al., 2005) – that are at work also in the *comprehension* of human language – without having anything to do with the features of their specific vocal *production* system, and could not be thus particularly regarded as a direct precursor of the human speech *production* system (Meguerditchian & Vauclair, 2008) but rather as the precursor of the representational processes involved in the *comprehension* of language in humans (Gil-da-Costa et al., 2004; Russ et al., 2007; Zuberbühler et al., 1999).

Concerning the production of vocalizations, contrary to human language and the production of gestures in chimpanzees and baboons, vocal control in nonhuman primates seems to imply non-lateralized subcortical structures (limbic or cingulate systems) but not homologous of language areas (Aitken, 1981; reviewed in Jürgens, 2002; Ploog, 1981). In rhesus monkeys, Aitken (1981) reported that ablation of the homologue of Wernicke's and Broca's areas did not affect vocal behaviours, whereas lesions of the anterior cingulate cortex did. In squirrel monkeys, only electrical stimulations performed in limbic and subcortical structures were able to induce vocalizations, but not the stimulation of homologous language areas or other cortical regions (see Ploog, 1981). These findings strengthen the argument for the emotional control of call productions. More recently, in electrophysiological studies conducted in Rhesus macaques, the authors were successful in training some subjects to increase the rate of their calls under the control of a visual stimulus and measured their patterns of neuronal discharge in comparison to *spontaneous* vocalizations. Those studies have confirmed that *spontaneous* production of species-specific vocalizations did not involve neither the motor cortex, or homologue regions of language areas, suggesting an absence of cortical control in vocal communication (and likely an underlying emotional control). In contrast, the *trained* vocal production under visual stimuli elicited neuronal discharges within the premotor cortex (Coudé et al., 2011) and within the

prefrontal cortex in a region known to include Broca's area in humans (Hage & Nieder, 2013), reporting the first evidence of cortical control in vocal productions in monkeys. However, in this latter study, it must be noted that the neurons discharged only when the visual command was presented but not when the trained vocalization was emitted afterward. As the Broca area in humans has been shown to be involved not only for speech production but also in motor planning for non-communicative actions (e.g., Nishitani et al., 2005; Koechlin & Jubault, 2006), these findings would suggest that this homologue region of Broca's area in macaques was involved in motor planning related to the vocal training but not to vocal communication *per se* which rather showed a lack of cortical control. It has not yet been demonstrated that these trained voluntary vocalizations could be used by macaques for intentional communication with social partners as it has been reported for attention-getting "learnt" atypical sounds in some chimpanzees (Hopkins et al., 2007).

6. Links between hand, mouth and Broca's area

These latter neurobiological studies in macaques as well as the use of attention-getting sounds in chimpanzees question the role of the oro-facial and vocal system in the origin of language and the tight motor connexions between the mouth, the hand and Broca's area. The control of the oro-facial motor system is essential in the production of articulated language. In fact, speech involves complex motor sequences in the mouth (e.g., tongues, lips), which could be considered as "internal fine gestures" of the oro-facial system (see Corballis, 2003) that have been shown to be tightly linked with co-speech manual gestures (Bernardis & Gentilucci, 2006). Interestingly, electrical stimulation of Brodmann's area 44 in rhesus monkeys induced hand and lip movements, suggesting the existence of a neural connexion between the manual and the oro-facial motor system in relation to Broca's area (Petrides et al., 2005). Studies of macaque monkeys have also demonstrated the existence of mirror-neurons in area F5 of the brain, i.e., the homologous to Broca's area (Rizzolati & Arbib, 1998), which have been considered as an ideal substrate for the emergence of imitation, theory of mind and language as well (e.g., Arbib, 2005; Rizzolati & Arbib, 1998). These neurons are activated not only when the monkey is performing a manual action, e.g., cracking nuts, but also during the observation of these actions (Gallese et al., 1996), their passive listening

(Kohler et al., 2002) as well as the observations of the use of tools (Ferrari et al., 2005) and of communicative facial actions ("lip-smacking" and lip protrusion) carried out by the experimenter standing in front of the monkey (Ferrari et al., 2003). It thus seems that, in the monkey brain, area F5 is predisposed to control and recognize visuo-gestural manual actions as well as oro-facial communication, confirming the strong links between the oro-facial motor system, the manual motor system and Broca's area.

These collective findings support thus the hypothesis that the oro-facial system might constitute a relevant mediator between the gestural communicatory system and speech in the evolution of language. On the assumption that the basic structure of syllables derives from the succession of constrictions and mouth openings involved in chewing, sucking, swallowing and visuo-facial communicative cyclicities, such as lipsmacks, MacNeilage (1998) proposed the "frame-content" theory of speech. According to this theory, the basic components of speech – an oscillatory one (frame) and a segmental one (content) – have their source in cyclic activities of ingestion in our ancestors. Thus, it might be hypothesised that ingestive behaviours- which involved sequentially the hand to the month - were progressively ritualized in oro-facial (lipsmacking) and gestural communication in monkeys (Arbib, 2005). Gentilucci and Corballis (2006) have speculated that facial elements were gradually introduced with vocal elements into the gestural system during language evolution.

7. Conclusion

The investigations of the communicative and motor systems in apes and monkeys have revealed some potential behavioural and neural continuities with some features of language in humans. We believe these collective researches support the view of the existence of a left-lateralized intentional communicative system in nonhuman primates that could be referential and multimodal in chimpanzees (including both gestures and atypical vocalizations) and only gestural in Old World monkeys such as baboons. Indeed contrary to chimpanzees, there is no observation that Old World monkeys can use intentional vocalizations for communication or associate vocal and gestural signalling for transmitting the same intents. Nevertheless, regarding the existence of mirror neurons in the prefrontal cortex of macaques, it is possible

that cortical connexions already exist between the hand and the oro-facial motor system in Old World Monkeys and seem to involve the cerebral homologue of Broca's area. As a conclusion, on the bases of those combined findings, we propose the following rudimentary scenario for the origin of the intentional and left-lateralized communicative system involved in human language:

1. Precursors of a left-hemispheric cerebral substrate for language production might have emerged first with the use of communicative gestures in the common ancestor of humans, great apes and Old World monkeys at least 30-40 million years ago. This system includes neuromotor connexions between hand and the oro-facial system.

2. Then, thanks to these pre-existing motor and cortical links between the hand and mouth, this communicative system may have further turned multimodal with the progressive insertion of intentional vocalizations and oro-facial expressions into the gestural system in the course of evolution in the common ancestor of chimpanzees and humans at least 5-7 million years ago.

3. Regarding the selective evolutionary advantages of controlling intentionally vocal communication (which allow intraspecific intentional communication at night, in the dark and at long distances, e.g., Snowdon, 2001), this multimodal system and its vocal component would keep increasing in complexity. With the emergence of *Homo sapiens* at least 170 000 years ago, this system would then turn into a syntactic and generative system to finally become, as it is currently, a complex articulated language associated with co-speech gestures (see Corballis, 2003). In this view, co-speech manual gestures during speech production in humans might constitute the inherited part of our ancestral gestural and bimodal intentional communicatory system (McNeill, 1992).

This theory is consistent with the researches on gestural communication in human adults (e.g., Gentilucci, & Dalla Volta, 2008), in infants and children (e.g., Bernardis et al., 2008) which argue strongly for the view that a single integrated communication system in the left cerebral hemisphere might be in charge of both vocal and gestural communication in human language.

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