

Lateralization of communicative signals in nonhuman primates and the hypothesis of the gestural origin of language

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This article argues for the gestural origins of speech and language based on the available evidence gathered in humans and nonhuman primates and especially from ape studies. The strong link between motor functions (hand use and manual gestures) and speech in humans is reviewed. The presence of asymmetrical cerebral organization in nonhuman primates along with functional asymmetries in the perception and production of vocalizations and in intentional referential gestural communication is then emphasized. The nature of primate communicatory systems is presented, and the similarities and differences between these systems and human speech are discussed. It is argued that recent findings concerning neuroanatomical asymmetries in the chimpanzee brain and the existence of both mirror neurons and lateralized use of hands and vocalizations in communication necessitate a reconsideration of the phylogenetic emergence of the cerebral and behavioral prerequisites for human speech.

Keywords: evolution, communication, primates, gesture, language, vocalization, mirror neurons

The gestural hypothesis of speech origin and animal models

The idea that nonhuman primates are as efficient in producing gestures as in vocalizing was proposed long ago. In 1661, a British gentleman, Samuel Pepys, wrote in his diary about an animal he called a “babooe,” which was more likely a chimpanzee: “I do believe it already understands much English; and I am of the mind it might be taught to speak or make signs” (cited by Wallman,

1992, p. 11). In more recent times, Hewes (1973) championed the view that gestural communication played a crucial role in human language evolution. He suggested that very early in the history of the human species, gestures were under voluntary control and thus became an easy way to communicate long before the emergence of speech. Several researchers have since endorsed this view (e.g., Armstrong, Stokoe, & Wilcox, 1995; Kendon, 1991, 1993; Kimura, 1993). The thesis is also central to the propositions made by Corballis (1989, 1991, 2003), for whom manual gesturing was the mediating factor in the evolution of handedness and speech in humans. Corballis has emphasized that during the course of evolution, the left cerebral hemisphere acquired a general capacity for “generativity.” As this capacity is understood to be one of the hallmarks of language, it would serve as common substratum for image generation as well as an organizer of actions and pre-adaptations for speech production. A left hemispheric control for gestural acts would thus represent a feature much older than speech. Moreover, such control by the left hemisphere is viewed as the origin of the left cerebral lateralization for language in humans.

According to a slightly different view, vocal as well as gestural communication would imply a sequential and temporal organization of movements (Bradshaw, 1988). Evolutionary pressures could thus have favored both functions in relation to the control of gestures and speech within the same cerebral hemisphere (the left). Note that this latter view presents the advantage of tracing an evolutionary path from animal to human communication without referring to animal vocalizations.

This article aims to show that several features of the brain and of communicatory behaviors (gestural and vocal) of nonhuman primates, especially apes, can provide useful clues for discussing the issue of the origins of speech and language. Since the question of gestures and speech and their cerebral control is central for the debate concerning the origins of language, I will first summarize the current state of knowledge in humans in this area. I will then introduce the question of cerebral and functional asymmetries in nonhuman primates with an emphasis on the perception and production of vocal and gestural signals in cases of spontaneous and induced communication. I will then review other kinds of evidence which support the gestural origin hypothesis, namely the existence of mirror neurons in the monkey brain, and the characteristics of primate communication compared with those of human communication and language. Finally, I will pinpoint the implications and limitations of the primate model for discussing the question of the origin of speech, language and handedness.

Gestures, speech and hemispheric control in adults, children, infants and fetuses

Studies carried out with deaf people are useful to show the close relation between gestures and the left hemisphere. Firstly, it has been demonstrated that similar areas within the left hemisphere are involved in the comprehension and in the production of signs by deaf people (Corina, Vaid, & Bellugi, 1992; Grossi et al., 1996). Moreover, the acquisition of sign language and that of speech present strong similarities in human infants that can be exemplified by the presence of “silent babbling” among hearing infants born to profoundly deaf parents during the course of their acquisition of natural signed languages (Petitto et al., 2001). Furthermore, Holowka and Petitto (2002) discovered that babies babble with a greater mouth opening on the right side of their mouths, indicating left brain hemisphere control for this activity. The authors conclude that babbling engages the language processing centers in the left hemisphere of the brain. Other findings support the role of the left cerebral hemisphere in the simultaneous control of vocal and gestural communication in humans. Such a relation is clear in the preferential usage of the right hand in situations in which participants are asked to recall lists of words or narratives (Kimura, 1973). It has also been observed that the complexity and frequency of gestures made by adults and children are highly related to the complexity and frequency of their spontaneous language. Thus, it is not surprising to observe that stuttering people interrupt their gestures until speech goes on (Mayberry, Jacques, & DeDe, 1998). The relation between gestures and speech is very strong during human ontogeny, with an increasing involvement of the right hand for gestural communication (Blake, O’Rourke, & Borzellino, 1995). This association is reinforced when vocalizations and speech intervene simultaneously (Locke et al., 1995).

As far as human ontogeny is concerned, two sets of data favor the predominance of manual and gestural activities over oral activity. Firstly, in human infants, intentional control of the hands and arms is present at around three months of age (e.g., grasping an object placed in the hands and bringing it to the mouth: Rochat, 1989) and precedes the full coordination of vision and prehension by three to four weeks. By contrast, the development of infant intentional vocal control takes much longer (till the end of the first year: Iverson & Thelen, 1999), and remains imperfect for a much longer period of time (sounds substitutions, reversals and omissions are frequent in young children’s language).

Secondly and complementarily, the control of the forelimbs (arms and hands) seems to be lateralized long before vocal asymmetry. Thus, newborns have been reported to show predominant right side biases in head-turning and Moro responses (Michel, 1981; Rönqvist & Hopkins 1998). Motor asymmetries favoring the right side for arm activity (Hepper, MacCartney, & Shannon, 1998) and thumb sucking (Hepper, Shahidullah, & White, 1991) have even been reported in 10- to 15-week old fetuses. Altogether, these ontogenetic data suggest that asymmetries of the forelimbs develop before vocal asymmetry. Of course, this advance does not implicate this development occurred during the evolution from nonhuman primates to humans. However, the fact remains that these features highlight the early maturation of motor functions and their later cerebral control in our species. In particular, it is very likely that speech and gesture have their developmental origins in early hand-mouth linkages, such that as oral activities become gradually used for meaningful speech, these linkages are maintained and strengthened. For Iversen and Thelen (1999), hand and mouth are tightly coupled in the mutual cognitive activity of language, and these authors argue that these systems are initially linked together as these sensorimotor linkages form the bases for their later cognitive interdependence.

Evidence of structural and functional asymmetries in nonhuman primates

It appears that recent neuropsychological and behavioral findings in great apes are of significant interest because they pertain to basic theories on the origin of language and speech in humans. There is now a growing body of evidence that challenges the long-held view that brain asymmetries and handedness are exclusively human traits (e.g., Warren, 1980; Corballis, 1991). This section will thus be devoted to summarizing the major findings in support of the view that both at the cerebral and behavioral levels, nonhuman primates show clear patterns of asymmetric processing of information, some of which are of obvious importance for the theory of language and for its evolution (Vauclair, Fagot, & Dépy, 1999). I will examine, in turn, demonstrations of hemispheric asymmetries in great apes and functional lateralized processing of information in relation to audition and to the motor systems within the context of intentional communication.

Evidence for neuroanatomical asymmetries in the brain of apes

Two areas of the brain which are crucial for speech and language (namely Broca's area and Wernicke's area) have been studied in apes, in search of possible size differences between the left and the right cerebral hemispheres. Using magnetic resonance imaging, Gannon et al. (1998) found that the planum temporale of great apes (gorillas, chimpanzees and orangutans) was larger in the left than in the right cerebral hemisphere (this was true for 17 of 18 chimpanzee cadaver specimens studied). More recently, Cantalupo and Hopkins (2001) used an MRI technique to measure Broadman area 44 (roughly corresponding to Broca's area) in a sample of 27 great apes. These researchers found that 20 of the apes had a left hemisphere asymmetry, six had a right hemisphere asymmetry and one ape (a bonobo) had no bias. It remains to be shown that this strong similarity in asymmetrical organization of the brain between humans and apes is related to functional asymmetries. This issue will be touched upon below in the discussion of the production of intentional gestures and associated vocalizations in the chimpanzee. It can be observed that some asymmetries in the Sylvian region have also been found in non-ape species. For example, the length of the left Sylvian fissure has been found to be significantly longer than its right counterpart in the rhesus monkey (Falk et al., 1986).

Behavioral evidence of asymmetries in the perception and production of auditory communications

I will now review some of the main findings obtained in relation to the processing of communicatory information in nonhuman primates.

Asymmetries in the perception of auditory communication. A widely cited study by Petersen et al. (1978) used the dichotic technique to examine lateralized processing in the perception of species-specific vocalizations in macaques. Japanese macaque vocalizations were presented either to the left or the right ear of the subjects (Japanese macaques and other macaque species). The authors reported that all five Japanese macaques responded faster in the task when the stimuli were presented to the right ear, whereas only one of the remaining five monkeys showed the same right ear advantage. None of the subjects showed a significant left ear advantage. Since right ear information predominantly reaches the left hemisphere, the authors concluded that the left hemisphere of the Japanese macaque was specialized to process meaningful (i.e., species-specific) vocalizations. Using the same technique, Heffner and Heffner (1984)

further demonstrated that monkeys with a left hemisphere lesion of the posterior temporal lobe showed a greater decrement in post-operative performance and took longer to re-learn the discrimination task than did right hemisphere-lesioned monkeys. This set of studies suggests that vocalizations in monkeys are controlled by the left hemisphere.

In a more naturalistic context, Hauser and Andersson (1994) examined orienting asymmetries to different auditory stimuli in rhesus monkeys living as a social group on the island of Cayo Santiago. While feeding at a food dispenser, individual monkeys were presented with different types of vocalizations. The stimuli (played over a concealed loudspeaker 4 to 10 meters behind the monkey) were presented to the subject. The experimenters recorded which direction (left or right) the monkeys turned to orient toward the sound. Hauser and Andersson (1994) reported that significantly more monkeys oriented to the right compared to the left for conspecific calls but not for a heterospecific call (that of a songbird). These authors interpreted their findings as evidence that the left hemisphere is dominant in processing species-specific calls in rhesus monkeys. In a more recent study, Hauser, Agnetta, and Perez (1998) tested the same monkeys with an identical procedure and manipulated the interpulse interval for three different types of rhesus monkey vocalizations, such as grunts and alarm calls. Variations in the interpulse intervals were either longer or shorter than the population mean pulse interval for each of the call types. The main results indicate that manipulations of the interpulse intervals outside the range of natural variation either eliminated the orienting bias or caused a shift from right- to left-ear bias. Altogether, the above results show that a) temporal properties such as interpulse interval provide significant information to listeners about whether or not the signal is from a conspecific, and that b) the orienting bias is controlled by left hemispheric asymmetries. In a final experiment, Ghazanfar, Smith-Rohreberg, & Hauser (2001) studied orienting responses of rhesus monkeys to time-reversed vocalizations. The monkeys in the study oriented to the left, behaving as if these stimuli were novel to them. These results suggest that rhesus macaques use temporal cues to recognize conspecific vocal signals and that, at least for the kind of response used in this set of studies, it is the left hemisphere that is predominantly involved. Interestingly, the relation between the temporal features of the rhesus monkey vocalizations and cerebral organization appears to be similar to what is observed in humans (Belin et al., 1998).

Asymmetry in the production of auditory communication. Only one study is available concerning lateralization in the *production* of vocalizations in non-

human primates. Hauser and Akre (2001) videotaped the timing asymmetry of both facial and vocal expressions in Cayo Santiago rhesus monkeys. They observed that for both adults and infants, the left side of the face initiated the expression before the right, thereby implicating a right hemisphere specialization. As some of the recorded expressions were related to positive/approach emotions while others were associated with negative/withdrawal emotions, emotional valence did not appear to influence the direction of this motor asymmetry. Such results are somewhat difficult to interpret, as they stand in sharp contrast with the data reported for the perception of vocalizations in macaques, a species for which a left hemispheric advantage has been systematically reported. They are also difficult to explain with respect to the laterality of the mechanisms controlling both speech perception and production in humans, which are mostly underlain by structures located in the left cerebral hemisphere (see Hauser & Akre, 2001 and Weiss et al., 2002 for hypotheses concerning potential differences between these mechanisms in human and nonhuman primates; see also the section below on the cortical control of non-human primate vocalizations).

Animal communication and intentions

A crucial issue for establishing a valid nonhuman primate model of human communication, including speech, concerns the status of the signals (vocalizations, gestures) used by primates in their spontaneous communication as well as those used in trained situations in which apes are taught forms of human language. To make a long story short, this question amounts to asking if these signals are referential and thus could be more or less equivalent to linguistic signs or if these signals exclusively convey emotionally-based information. This matter is controversial among primatologists and comparative psychologists. Some consider that these signals (vocalizations) convey information with semantic content concerning, for example, the presence of predators (Seyfarth, Cheney, & Marler, 1980), food (Dittus, 1984) or social relationships (Gouzoules, Gouzoules, & Marler, 1984), while others call for more cautious interpretations of these communications and suggest that they are likely to combine both emotionally and referentially based information (e.g., Hauser, 2000; Vauclair, 2003). Interestingly, the difficulties in interpreting nonhuman primate communicative signals culminate in discussions about auditory signals because of the implicit or explicit relation that exists between these signals and linguis-

tic signs (Vauclair, 1996). The question of the symbolic or semantic status of gestural signals seems to be less decisive because, as Leavens explains in his article (this issue), gestures rarely if ever stand for the event or object to which attention is being drawn. Thus, it is easier to propose an operational definition of gestures as referential signals in the sense of behaviors serving to direct attention. Moreover these gestures can also be viewed as intentional because (a) they are produced in a social context, (b) they imply visual contact between the partners engaged, and (c) they imply some changes in the behavior of both the signaler and the partner. For Leavens (this issue), these criteria are met for the gestures used by apes, especially for pointing.

Laterality and manual gestures in intentional communication

An interesting and novel field of inquiry has recently emerged in the comparative literature concerning the functional use of gestures in great ape communication. Wild chimpanzees are known to use communicative gestures in various contexts such as begging for food, courtship, intimidation, greetings, etc. (Goodall, 1986; Plooij, 1978). In contrast with vocalizations, the use of these gestures requires close visual contact between partners. In addition, the gestures are usually performed between only two individuals. In this respect, communicative gestures are more appropriate than vocal signals in the search for the evolutionary precursors of speech, because the latter are typically not directed to specific individuals.

A number of independent observations carried out on captive apes have shown that these communicative gestures are preferentially performed with the right hand (in gorillas: Shaffer, 1993; in bonobos: Shafer, 1997; in chimpanzees: Hopkins & Leavens, 1998). The referential and intentional status of these gestures has also been convincingly established (Leavens, this issue). Captive apes are regularly observed using manual gestures when food is placed out of their reach. If an audience is present, the apes increase the frequency of their gestures and alternate their gaze between the food object and the social agent. These behaviors suggest that the apes monitor the effect of their gestures on the social partner (a human) to whom they direct their communicative acts.

In a unique study, Hopkins and Cantero (2003) examined the spontaneous production of gestures and vocalizations in a captive group of 73 chimpanzees. The study was prompted by observations that right hand use in gestural communication was significantly higher when the gestures were accompanied by a vocalization. The procedure was simple: an experimenter stood approxi-

mately one meter from the chimpanzees' home cage and directly in front of the chimpanzee subject. The experimenter approached the cage and offered the chimpanzee a banana. Since the banana was out of the immediate reach of the ape, this condition stimulated the production of communicative behaviors by the chimpanzee subject. Note that the experimenter maintained eye contact with the subject throughout the duration of the trial in order to increase the probability that the ape would produce a communicative behavior. Begging gestures accompanied or non-accompanied by vocalizations toward the experimenter were recorded for one minute. The data showed that each chimpanzee produced on average 29 gestures (over ten trials), about seven of which were accompanied by a vocalization. Concerning laterality, right-hand population biases were found for gestures alone and for gestures associated with vocalizations. Within the entire sample of chimpanzees, 51 subjects pro-

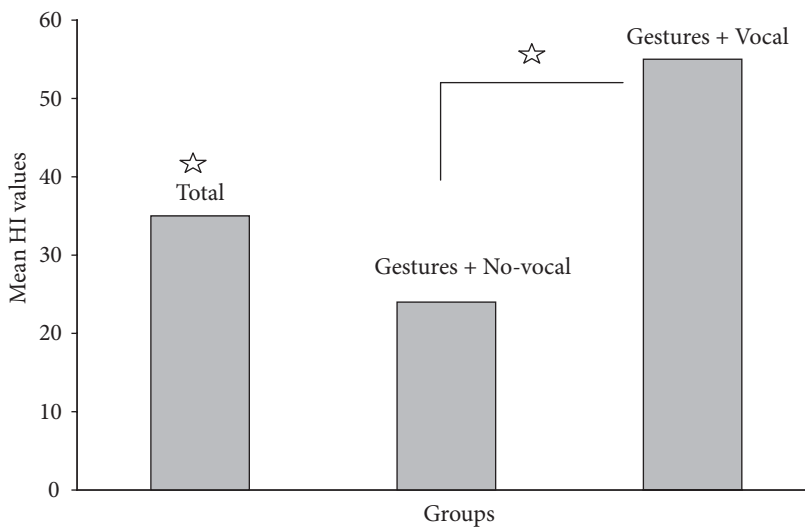


Figure 1. Mean handedness indices (HI) for the overall number of gestures, the gestures produced with a vocalization (Gesture + Vocal) and the number of gestures produced without a vocalization (Gesture + No-Vocal).

Mean handedness indices (HI) were derived by subtracting the number of left hand responses from the number of right hand responses and dividing by the total number of responses $HI = [(R-L)/(R+L)]$. Indices < 0 indicate a left bias; indices > 0 indicate a right bias. The figure shows HI values for the overall number of gestures (Total), the number of gestures produced with a vocalization (Gesture + Vocal) and the number of gestures produced without a vocalization (Gesture + No-Vocal). All were significantly different from zero. In addition, the HI values for the Gesture + Vocal responses were significantly higher than the HI values produced for the Gesture+ No-Vocal responses. (Adapted from Hopkins & Cantero, 2003)

duced gestures both with and without vocalizations. An analysis conducted on this subsample revealed that gesture + vocal right handedness scores were significantly higher than the gesture + no-vocal handedness scores (Figure 1). It is important to establish whether the use of the right hand within a communicative context generalizes to other motor tasks or is specific to gestural communication. Since the chimpanzees tested in the study are being reared in a human-designed, right-handed world, it needs to be shown that the preferential use of the right hand for gestural communication is not correlated with other measures of hand use and therefore does not reflect a bias associated with other motor functions. Hopkins and Cantero (2003) verified that this was not the case, finding that the use of the right hand in communicative contexts was independent of other measures of handedness such as hand use in simple reaching, and in bimanual feeding.

The findings from this study thus indicate that the preferential use of the right hand for gestures is significantly enhanced when the gestures are accompanied by a vocalization. Taken together, these results suggest that the neurobiological substrates for nonvocal intentional, referential gestural communication are lateralized to the left hemisphere. Moreover, these results further imply that the production of vocalizations used by chimpanzees may be lateralized to the left hemisphere because they have a facilitative effect on right but not on left hand use in gestural communication.

This set of data thus shows a remarkable convergence with the behavior of humans (children: Blake et al., 1994, and adults: Kimura, 1973) when they simultaneously produce speech and manual gesticulations.

A fascinating extension of these findings was reported by Hopkins and Cantalupo (2003). Based on their report that Brodmann's area 44 (BA44) was larger in the left compared with the right hemisphere in the great apes (Cantalupo & Hopkins, 2001), these authors looked for a possible association between the anatomical asymmetries observed in Broca's area and asymmetries in gestural communication, as well as in hand use for simple reaching. Using a subsample of the 20 chimpanzees previously examined with MRI techniques (see above), Hopkins and Cantalupo (2003) found negative correlations between the handedness index values for gestures and BA44. This result indicates that increased right hand use is associated with larger left hemisphere in Brodmann 44 values. When the correlation coefficients are adjusted for simple reaching, the index values for communicative gestures were significantly associated with the medial portion of BA44 and close to statistical significance for the total BA44. These findings need to be investigated further with a larger sample

of apes to more completely establish the association. Nevertheless, these data reveal for the first time that structural asymmetries in the brain of the great ape have functional counterparts in the asymmetry of hand use and notably with respect to the production of intentional vocal and gestural communications.

Other kinds of evidence in nonhuman primates

Mirror neurons in the monkey brain

The discovery of neurons in the monkey's premotor cortex that discharge both when the monkey makes a particular action and when it observes another individual, monkey or human, making a similar action (Gallese et al., 1996) offers converging evidence of the importance of manual actions and gestures in understanding actions made by others. The existence of such mirror neurons that map perception onto execution could provide one of the keys for understanding the origin of language. Note that these mirror neurons are located in area F5, a homologue of Broca's area in the monkey brain. Such mirror neurons have also been described in Broca's area in humans (e.g., Nishitani & Hari, 2000), suggesting that the representation of actions and speech is processed by the same cerebral structures. In a recent study, Kohler et al. (2002) reported that in area F5 of the macaque brain, there are not only visual mirror neurons but also auditory mirror neurons. These neurons discharge when the animal performs a specific action, as well as when it hears the sounds produced by such an action (e.g., ripping a piece of paper or dropping a stick). It thus seems that area F5 of the monkey brain is predisposed to managing not only visuo-gestural but also auditory-visual systems of communication.

From the above findings, the perspective proposed here is that the development of the human lateral speech circuit resulted from the fact that the precursor of Broca's area was endowed, before the appearance of speech, with a mechanism for recognizing actions made by others. This mechanism was the neural prerequisite for the development of inter-individual communication and finally of speech. In this respect, language needs to be viewed in a more general setting than one that considers speech as its complete basis, as it is involved in both action recognition (including gestures) and speech processing (Rizzolati & Arbib, 1998).

Some functional differences between animal communication and human language

A consideration of the specific modalities underlying speech and a comparison between these modalities and nonhuman communication may also help shed light on the question of the gestural origin of language.

Developmental psychologists distinguish two main modalities or functions in linguistic as well as prelinguistic communication among humans (Bates, 1979). The primary function of language is to exchange information about the world. Such an *informative function* takes two forms: a declarative form used in representing states of the world (e.g., “John is coming”) and an interrogative form. The other function is *injunctive* (imperative) and *exclamatory* and mostly expresses itself with requests and demands (e.g., “Come here!”). Developmental studies with young children have shown that the use of declaratives (see references in Vauclair, 2003) becomes the dominant mode of communication between one and two years of age (about 60% of all utterances).

It happens that a major difference between humans and nonhuman primates lies in the fact that the use of signals and learned symbols by the nonhumans is largely restricted to their imperative function, whereas humans use them predominantly for declarative purposes. These declaratives can be words or gestures, and they function not primarily to obtain a result in the physical world, but to direct another individual’s attention (his or her mental state) to an object or event, as an end in itself. Thus, a human toddler might say “Bird!” apparently to mean, “It’s a bird!” or, “Look! A bird,” and so on. In such cases, the child communicates simply to share interest in something that he or she sees, that this object is a bird and that the child has identified it and finally that he or she wants the partner to look at it.

It can be asserted with some confidence that the use of protoimperative signals is the exclusive mode of communication by animals of different phyla. When, for example, your cat meows at you in the vicinity of the window and at the same time glances back and forth from the window to you, the cat is using a protoimperative signal that can be interpreted as “I want to go out.” But it is very unlikely that your cat would use these same communicative signals to let you know that it has noticed something interesting in the garden and that it wants to share its discovery with you.

I have claimed (Vauclair, 1982, 1984, 1996, 2003; see also Tomasello & Camaioni, 1997) that this imperative function also appears to be the predominant (if not exclusive) mode used by “linguistically” trained apes. For example, an analysis of the combinations of visual productions made by the famous bonobo

Kanzi (Savage-Rumbaugh, Rumbaugh, & McDonald, 1985) reveals that 96% of this ape's productions were requests. Interestingly, these productions mostly consisted of combinations of visual signals (lexigrams punched on a keyboard) and *gestures* directed to the human partner. Thus, the difference between Kanzi's modality of communication and the typical declarative mode observed by humans is striking. In effect, communication in apes has essentially an imperative function. This appears to be the rule for all animal species and this mode fulfills biological requirements, for example warning against predators, as in vervet monkey alarm calls (Seyfarth et al., 1980). By contrast, humans use not only speech but also prelinguistic communication means such as gestures (e.g., pointing) for both imperative and declarative purposes (for example, two persons sharing an interest toward a third person, an object, or an event).

Place (2000) has argued that there was in humans an ontogenetic primacy of the use of the system of "mands" in the sense of Skinner (1957) compared to the system of "tacts." Mands can be broadly defined as commands, requests or questions that the speaker addresses to a listener. A mand serves to specify an action to be performed by the listener, the realization of which operates primarily for the benefit of the speaker. By contrast, tacts constitute more complex forms of behaviors in the sense that "they are reinforced, not, as in the case of the mand, by the behavior they call for from the listener, but by a variety of specialized reinforcers, responses such as gratitude for information supplied, agreement with opinions given, sympathy for troubles told, surprise at and interest in news reported, or laughter at jokes" (Place, 2000, II.iii). It follows from this distinction that "in the evolution of language it [the tacts] must have developed later [than the mands], as it does in the child. Moreover, since interrogative mands presuppose the availability of the tacts they solicit from the listener, it follows that the first sentences must all have been imperatives" (Place, 2000, II.iii).

The parallel between mands and tacts with imperatives and declaratives and their respective functions is striking. It is thus tempting to speculate that the mands and protoimperative actions are the dominant actions both in the nonhuman primates and in the developing human infant and child. It is also likely that these systems function best by means of mimed movements and by pointing gestures. This view is reminiscent of the scenario offered long ago by Condillac (1746) in his theory of a "language of action." He stressed that man's first efforts at communication required signals (gestural, pantomimes and then vocal signs) produced in a context in which they unambiguous and self-explanatory.

Cortical control of nonhuman primates' vocalizations

In the section devoted to the presentation of asymmetries in the production of auditory communications in nonhuman primates, I reported that these productions were lateralized to the right cerebral hemisphere in the macaque (Hauser & Akre, 2001). This finding is somewhat troubling in light of the human data concerning speech control. Steklis and Harnad (1976) wrote some years ago that that "the neural control of the vocal activity of nonhuman primates is somehow not adapted to the kind of activity involved in language. These vocalizations are controlled by evolutionarily primitive regions of the brain which are involved in stereotyped species-typical communicative behaviors and emotion" (p. 447). They added that "primate calls are a relatively restricted and predictable set for a particular species, and even if they depend upon experience for acquisition, the amount of variation in the final product is negligible compared to the variety of learned complex behaviors of which the limbs, the most qualified candidates of all, are capable" (p. 445). What explanations could be offered to explain the findings on comprehension/production systems and their lateralization in nonhuman primates? First we must dissociate comprehension from production in terms of the evolutionary pressures that have acted on the processes and on their cerebral organizations. As observed by Hauser (1996), the cortical component in primate vocalization may be more pronounced with respect to perception than with respect to production. In the former case, several demonstrations mentioned earlier in this paper suggest that the cortical system for the perception of species-specific calls in nonhuman primates is lateralized to the left. For production systems which appear to be lateralized to the right side of the brain in monkeys, a simple explanation is to consider that the production of these calls occurs in emotional situations, such as danger to the group. In this respect, it is not surprising, given the content and nature of the information conveyed, to observe a control by the right hemisphere. In addition, the lack of intentional control over these calls may be adaptive because it makes them impossible to fake (Knight, 1998).

The picture is very different for chimpanzees and possibly for other great apes. In chimpanzees, there is good evidence for the existence of both structural asymmetries in Broca's area and Wernicke's area (see above) and functional lateralization in the association of gestures and vocalizations during intentional communicative actions (see Hopkins & Cantero, 2003 and above). It is noteworthy that, to my knowledge, only one study is available concerning cerebral control of vocalizations in apes. Bernston, Boysen, and Torello (1993) recorded ERP measures in chimpanzees during the presentation of simple

non-signal stimuli as well as conspecific and human vocalizations and found a right hemisphere laterality in the processing of the significant vocal stimuli. This study concerned only a single chimpanzee and in no way permits us to draw a definite conclusion. Data on volitional control of vocalizations both for comprehension and production are thus badly needed. Such data will help us to better understand the neural systems involved in higher cognitive and communicative abilities in chimpanzees and other ape species.

Theoretical implications

I wish to point to the implications of the results reviewed here to the use of a primate model in support of the gestural theory of the origin of speech. Firstly, there is now some evidence that chimpanzees not only possess brain asymmetries in speech-related areas but also use gestures in an intentional and referential way. Such findings offer clear support for theories proposing gestural origins of human language and speech (e.g., Kendon, 1995; Corballis, 2003). A safe hypothesis is to consider that this asymmetry was also present in the common ancestor of humans and chimpanzees, at least 5 million years ago when the ape-human lineage split. Secondly, given the available evidence, it might be wise to distinguish handedness from a lateralized hand use within a communicative context. The argument can be described with respect to two issues. The first point concerns the systematic report of left hemispheric control of vocalizations in an impressive range of animal species (from frogs to mice, and from birds to dolphins and monkeys: for reviews, see Rogers & Andrew, 2002). This robust coherence of left hemispheric control in vocal communication in the animal kingdom most likely reflects the necessity to fulfill basic needs in relation to the acoustical relevant features of the calls. In this respect, this left hemisphere control in vocal animals might be similar to its involvement, in humans, in the temporal and spectral analysis of speech (Fitch, Miller, & Tallal, 1997; Schwartz & Tallal, 1980). Thus, vocal communication in animals also relies heavily on the use of small and rapid changes in the sound produced. For example, Charrier, Mathevon, and Jouventin (2001) have reported that frequency modulation appears to be a key component for individual recognition in the sub-Antarctic fur seal. Similarly, Hauser et al. (1998, and see above) manipulated interpulse interval in rhesus monkey calls and showed that this change provoked either an elimination of the left hemispheric bias or a shift from left to right bias. Aside from monkeys and apes, the species mentioned

above do not possess limbs equivalent to hands but nevertheless show a left hemispheric control of the reception and sometimes of the production of their vocal communications.

A second argument envisions that the relation between handedness and language is not total. This view comes from the obvious fact that about 70% of left-handers are also left-cerebrally dominant for language. From a brain imaging study of word generation on a large sample of right-handed participants, Knecht et al. (2000) concluded that the association between handedness and language dominance “is not an absolute one” (p. 78). These facts and the finding that about 65% of individuals belonging to large groups of chimpanzees exhibit right-hand preferences during bimanual coordination tasks (e.g., Hopkins, 1994) led Hopkins and Cantalupo (2003) to suggest that “from an evolutionary perspective, right-handedness may have evolved after the emergence of asymmetries associated with gestural communication, as Corballis [2003] has proposed, but handedness may not have been a direct consequence of selection for motor systems associated with language and speech in modern humans” (p. 225).

In the article “From mouth to hand: Gesture, speech, and the evolution of right-handedness,” Corballis (2003) responds to the commentaries on his article. He defends the view that language has its origins in the gestural system, writing, “I also think it likely, despite the doubts of some commentators, that there is indeed a link between handedness and the left-cerebral control of speech, and the balance of evidence still seems to me to support the idea that it was an asymmetry in the control of the organs of speech that provided the nudge. Whether this asymmetry originated in the lateralized control of vocalization itself and whether it has ancient roots, *now seem more problematic* [my italics]. I think we need more evidence about the control of vocalization, from both evolutionary and neurological perspectives” (p. 250).

I believe that the kind of evidence Corballis (2003) asks for is exactly what the recent ape studies on neuroanatomical asymmetries and on laterality in gestures suggest, namely that the neurobiological basis for intentional, referential communication was present prior to hominid evolution. Of course, a number of important issues need to be resolved to establish solid ground for the nonhuman primate model of speech and language origins. Although apes appear to represent particularly appropriate phylogenetic models for addressing these issues, there are still two serious problems that limit their use in the debate over the question of the origin of language. The first main problem, as I have stressed above, concerns the urgent need to obtain detailed information

on the neural systems involved in the processing of communicative and cognitive abilities in these species. The introduction of novel brain imaging techniques for investigating animals, including nonhuman primates, while they are awake (Logothetis, 2003), is very promising in this respect. The second main problem that cannot be solved by technical progress only relates to the determination of the nature of the vocal signals used by nonhuman primates. As I have noted earlier, the question of whether these vocalizations refer only to emotional states or convey semantic information is still controversial.

In addition to the demonstrations offered earlier in this article, recent studies on Diana monkeys reinforce the view that the alarm calls of these monkeys are modulated in such a way that they provide information related not only to the class of predators signaled (the leopard or the crowned eagle) but also to the distance of the predator from the caller (Zuberbuhler, 2000). A detailed analysis of the calls of free-ranging Diana monkeys has also revealed that the modulation of the formants of the monkey calls results from an active vocal filtering (Riede & Zuberbuhler, 2003). Riede and Zuberbuhler argue that this filtering is used by the monkeys in order to encode semantic information. Of course, the underlying neural systems controlling this kind of signal in this species must still be explained.

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