



Tonkean macaques communicate with their right hand



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ABSTRACT

There are two conflicting hypotheses to explain the origins of language. Vocal origin theory states that language results from the gradual evolution of animals' vocal communication, but gestural origin theory considers that language evolved from gestures, with the initial left-hemispheric control of manual gestures gradually encompassing vocalizations. To contribute to this debate, we investigated functional hemispheric specialization related to hand biases when grasping or showing an object through manual gesture in Tonkean macaques. The results of this study, the first quantitative study on Tonkean macaques' handedness, showed a remarkable convergence of the Tonkean macaques' handedness patterns with those of baboons and human infants, with hand preferences for manual communicative gestures significantly favoring the use of the right hand. Our findings support the hypothesis that left hemispheric lateralization for language is derived from a gestural communication system that was present in the common ancestor of macaques, baboons and humans.

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1. Introduction

Human speech constitutes a particular communication system in the animal kingdom. Our language is characterized by the flexible acquisition of shared conventions, and is cognitively very complex, requiring specific abilities such as intentionality or empathy (Pinker, 1998). It allows us to express an infinity of semantic nuances and to transcend the spatiotemporal context in which speech takes place (Kirtchuk, 2000). Our language is also the most obvious expression of hemispheric specialization and has often been linked to the fact that humans are mainly right-handed for many actions (Annett, 1985). It has been shown, for example, that humans predominantly use their right hand for manual movements when they are talking (Kimura, 1973) and that the degree of right-hand asymmetry for manual communication (e.g., pointing) increases during the development of speech in young children (e.g., Blake, O'Rourke, & Borzellino, 1994; Vauclair & Imbault, 2009).

The origins and lateralization of language have been debated for more than a century, but remain extremely controversial (e.g., Christiansen & Kirby, 2003). Up to the 1980s, language was commonly assumed to be unique to humans, suddenly emerging with *Homo sapiens* about 100,000 years ago. This theory has since fallen by the wayside and current theories include continuity between humans and other animals and more ancestral origins (e.g., Fitch,

2010). Researchers therefore tend to adopt a phylogenetic approach, and in this context nonhuman primates would appear to be an ideal model for clarifying hypotheses on language origins. There are two main hypotheses: the vocal origin hypothesis states that language results from the gradual evolution of animals' vocal communication (Lemasson, Gautier, & Hausberger, 2003; Lemasson, Hausberger, & Zuberbühler, 2005; Snowdon, 2002; Zuberbühler, 2005), whereas the gestural origin hypothesis considers that language evolved from gestures (Corballis, 2002; Hewes, 1973; Vauclair, 2004). According to the latter, the left hemisphere initially controlled manual gestures, and later came to encompass vocalizations, too. The close proximity between gestures and language raises the question of what role manual motor and communicative functions played in the evolution of communicative systems in humans (Gentilucci & Dalla Volta, 2008; Gentilucci, Dalla Volta, & Gianelli, 2008). Observations of the gestural communication systems of nonhuman primates have highlighted their numerous similarities with human language. Several species of nonhuman primates spontaneously use their hands to communicate with their conspecifics in a variety of social contexts. This behavior has mostly been studied in great apes (e.g., chimpanzees: Liebal, Call, & Tomasello, 2004; Pollick & De Waal, 2007; gorillas: Pika, Liebal, & Tomasello, 2003; bonobos: Pika, Liebal, & Tomasello, 2005), while it also seems to be present in Old World monkeys (e.g., mandrills: Laidre, 2011; baboons: Kummer, 1968; Meguerditchian & Vauclair, 2006) and New World monkeys (e.g., squirrel monkeys: Anderson, Kuwahata, & Fujita, 2007; capuchins: Mitchell & Anderson, 1997). Maestripietri (2005) found that communicative gestures varied between different species of macaques and most of

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these gestures appear in dominance and submission contexts (Maestriperi, 2005). Unlike vocalizations, these communicative gestures are directed towards a particular recipient and require an appropriate behavioral response from that recipient. These two characteristics suggest an intentional use of the gesture by the sender (Arbib, Liebal, & Pika, 2008).

The study of manual communicative gestures and their asymmetries, providing information on underlying hemispheric specialization, in nonhuman primates, thus constitutes an ideal framework for clarifying the hypothesis of the gestural origin of language and its cerebral lateralization (Corballis, 2002; Vauclair, 2004). However, most studies of lateralization in nonhuman primates have focused on noncommunicative motor actions. MacNeillage, Studdert-Kennedy, and Lindblom (1987) for example proposed a specialization of the left hand for visually guided movements and of the right hand for more complex and/or bimanual movements. But Papademetriou, Sheu, and Michel's (2005) meta-analysis of primate hand preferences for reaching underlined the current impossibility of forming empirically based theories from which to generate worthwhile hypotheses about the evolution of human brain–behavior relations. There is a clear lack of consistency between studies, and the considerable variability between findings could be due mainly to the variability (e.g., in complexity) of the tasks used to assess hand preference (Fagot & Vauclair, 1991). Tasks vary in terms not only of the reaching patterns that are assessed but also of the individuals' postures (e.g., sitting or moving). McGrew and Marchant (1997) noted that tasks testing primate handedness often involved reaching from an upright posture, which is a highly unusual posture for nonhuman primates. The current literature highlights the need to collect more handedness data using similar, or at least comparable, tasks administered to relatively large samples of individuals in the field and in captivity. The biology of the species must, of course, be taken into account before defining the degree of difficulty or complexity of a given task. For example, a hanging task is easier for arboreal species than for terrestrial ones (Blois-Heulin, Bernard, & Bec, 2007; Blois-Heulin, Guitton, Nedellec-Bienvenue, Ropars, & Vallet, 2006).

Bishop, Ross, Daniels, and Bright (1996) were the first to propose a standard method for quantifying handedness in humans to ensure uniformity in a field where failure to replicate is a major problem. They proposed a behavioral measure for quantifying the consistency of hand preference (the so-called QHP task). This task fosters the use of both hands by varying the spatial position of the object to be reached for in relation to the body midline, the idea being to determine where, in the preferred hand's contralateral space, the individual shifts to using the non-preferred ipsilateral hand. The stronger our preference for our right hand, the further we are likely to go into its contralateral space before switching to our left hand, and *viceversa*. Meunier, Blois-Heulin, and Vauclair (2011) successfully adapted this task to Olive baboons (*Papio anubis*) to assess their handedness for a simple reaching task. However, it has been demonstrated that manual asymmetry is not always a reliable cue for inferring hemispheric language specialization (Knecht et al., 2000a; Knecht et al., 2000b). One can assume that the study of hand preferences for communicative gestures (versus noncommunicative gestures such as simple reaching) constitutes a more relevant approach to considering lateralization and language origin (Meguerditchian & Vauclair, 2009). The first studies to investigate the lateralization of such behaviors in nonhuman primates showed that (i) great apes as well as baboons have a comparable population-level bias in favor of their right hand when communicating with a human partner through manual gesture (chimpanzees: Hopkins & Cantero, 2003; Hopkins & Wesley, 2002) or when threatening a conspecific or a human through hand-slapping (Olive baboons: Meguerditchian & Vauclair, 2006) and (ii) for both chimpanzees and baboons, hand preference strength is significantly

greater for communicative tasks than for noncommunicative ones (Hopkins et al., 2005; Vauclair, Meguerditchian, & Hopkins, 2005), especially complex coordinated bimanual tasks (i.e., the tube task; see Hopkins, 1995, for more details; Meguerditchian, Molesti, & Vauclair, 2011).

One advantage of the standardized apparatus designed by Bishop et al. (1996) and adapted to nonhuman primates by Meunier et al. (2011) is that it can be used in other tasks besides simple reaching, such as communication tasks involving pointing and manual gesture (human infants: Jacquet, Esseily, Rider, & Fagard, 2012; Olive baboons: Meunier, Vauclair, & Fagard, 2012). In the present study, we used this apparatus to explore handedness patterns for a communicative gesture with Tonkean macaques (*Macaca tonkeana*). In addition to this manual gesture, we also recorded hand biases for grasping in several spatial positions. Assuming that language, and thus its associated left-hemispheric control, does indeed have its roots in gestural communication, we predicted that the Tonkean macaques would exhibit patterns of handedness comparable to those of human infants and baboons. Furthermore, these patterns would differ according to the type of task, with the macaques being more right-hand/left-hemisphere specialized when they communicated through manual gesture than when they simply grasped objects. The present study was the first of its kind to test macaques with the same setup as for both human infants and baboons, and on the same communicative task.

2. Methods

All the experiments were carried out in accordance with the Principles of Laboratory Animal Care, and with CNRS guidelines on animal care.

2.1. Subjects

Data were collected from February to June 2011 at the Primatology Centre of Strasbourg University, France. The subjects were 13 captive Tonkean macaques (*M. tonkeana*) including 5 adult males, 4 adult females, 3 subadult males and 1 subadult female. All the subjects lived in the same social group of 22 individuals and were housed in a one-acre wooded area at the primatology center. They had free access from the outdoor area to an indoor shelter. The macaques were fed with commercial primate pellets twice a day, fresh fruits and vegetables once a day, and seeds three times a week. Water was available *ad libitum*, except during testing.

3. Experimental procedure

The experimental procedure was an adaptation of Bishop's QHP task, originally designed by Bishop et al. (1996) to evaluate the degree of hand preference in human children. These authors originally placed seven picture cards, all 30° apart one from another, within the children's reach. Children stood in front of the template at the center of the baseline and were asked to pick up a specific, named card and place it in a box located directly in front of them. The experimenter recorded the hand used to pick up each card. The card order was random but the sequence of positions was the same for all participants (Bishop et al., 1996). We adapted this apparatus to nonhuman primates for two tasks that differed only in their nature: a noncommunicative, simple reaching task and a task involving a communicative gesture.

The apparatus (see Fig. 1), composed of an experimental table (for the reaching task) and five platforms (for the communicative task), was fixed to the wire mesh of a cage, next to the outdoor enclosure. To adjust the horizontal position of the subject, a concrete block was placed inside the cage, perpendicular to the wire

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