

NON-HUMAN PRIMATES AND COMMUNICATION

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Keywords: language, thought, cognition, mental representation, speech, semantic, evolution, alarm calls, monkeys, chimpanzees, vocalizations, social complexity, intelligence, concept, syntax, predator.

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Summary

We share a long evolutionary history with the other non-human primates. Comparative research has revealed a number of similarities and some key differences between them and us, some of which are relevant in understanding the evolution of human language. Humans are unique in their superior ability to rapidly change the geometry of their vocal tracts, the biological basis of complex speech utterances. This may be the result of recent genetic changes in the hominid lineage, which have led to increased oro-facial motor control. Although non-human primates can produce many of the maneuvers required for complex articulation, their overall performance is slow and unsophisticated. In addition, there is no evidence that non-human primates are able to vocally imitate one another. However, sophisticated articulatory abilities are insufficient to explain human-animal differences. Non-human primates routinely use gestural signals to communicate with one another, but they have not revealed any kind of referential abilities in this domain. There are important differences in social intelligence. Humans appear to be the only primates that are aware of each other's mental states and that are motivated to share intentions with one another. This propensity may create a social reality in which individuals experience the desire to point things out and to describe the world to one another. The ability to generate elaborate vocal signals may have been an enormously

advantageous invention in the evolutionary history of modern humans. Even though non-human primates are not able or motivated to inform one another about their own experiences, they still perform quite well in comprehension-related tasks. In this context, some basic linguistic capacities have been identified, particularly the ability to assign meaning to arbitrary sounds and the ability to adjust meaning as a function of simple rules. These cognitive capacities must thus be phylogenetically old, having emerged in the primate lineage long before the advent of modern humans. It may thus be of interest whether primate semantic signals and human speech are processed by homologous brain structures. Currently, strong evidence for semantic abilities is only available for monkeys, while the natural vocal abilities of apes are still underdescribed. There is a clear need for experimental work on great ape vocal communication, given their importance as living links to human evolution. Meaningful progress on primate communication and cognition will largely depend on whether questions can be addressed in an ecologically and socially relevant context, ideally with individuals interacting with each other in their natural habitats. Scientific progress is thus closely related to the survival of these species in their natural habitats.

1. Introduction

The evolution of language poses one of the great problems of science. It is unclear why humans are the only species that have evolved a highly complex communication system, language, which is capable of describing an unlimited range of objects or events. Numerous evolutionary scenarios have been put forward to account for this biological and cognitive specialization, many of which are difficult to test empirically. Traditionally, comparative studies of animal communication have played a minor role in understanding language evolution. This is partly rooted in a widespread belief that human language is simply too complex, unique, and specialized to warrant meaningful comparisons with any animal communication system.

In recent years, numerous primate studies have produced empirical material of significant relevance for questions concerning the origins of language. The assumption underlying this research is that, by investigating the communicative abilities of our closest living relatives, it may be possible to identify important morphological, behavioral, and cognitive pre-adaptations and precursors for human language.

The goal of this chapter is to review some of this evidence, with a particular focus on studies that investigated cognitive capacities underlying the spontaneous natural communication of non-human primates, as they are most likely to elucidate the nature of the cognitive stockpile that has led to the origins of language.

2. Primate Vocal Production Abilities

Humans have exceptional vocal abilities. From early on, young children produce a rich array of sounds, which they use to engage in social activities, to obtain goods, or to affect other's behavior. As many as 200 vowels and 600 consonants have been distinguished in the world's 6,000 languages. These basic sound units are rarely produced singly, but commonly combined into rapid and long sequences, the principal carriers of meaning. Young infants quickly develop considerable control over their

vocal tract, allowing them to generate and imitate the vocal patterns they perceive from others. These aspects, the richness of the acoustic portfolio and a predisposition to combine basic units into more complex acoustic strings, are uniquely human traits, calling for an evolutionary investigation. Why are humans different from the other primates concerning these abilities and what are their phylogenetic roots?

The basic anatomy and principles of sound production are similar in most primates although humans show a number of special adaptations, particularly a permanently lowered larynx. There is an inherent relationship between the geometry and flexibility of a vocal tract and the acoustic properties of the vocalizations produced. The principal mechanism is that sounds generated by the larynx enter the adjoining vocal tract where various articulators, such as the lips, tongue, mandible, and velum, form constrictions that determine the final acoustic structure of the vocal signal. All primates rely on this mechanism during vocal production. For example, similar to human vowel production, Diana monkeys engage in articulation using lip rounding, laryngeal lowering, and mandible movements to create formant frequency transitions. In this monkey species, moreover, these maneuvers are essential for labeling two different types of predators, the crowned eagle and the leopard (Fig. 1).

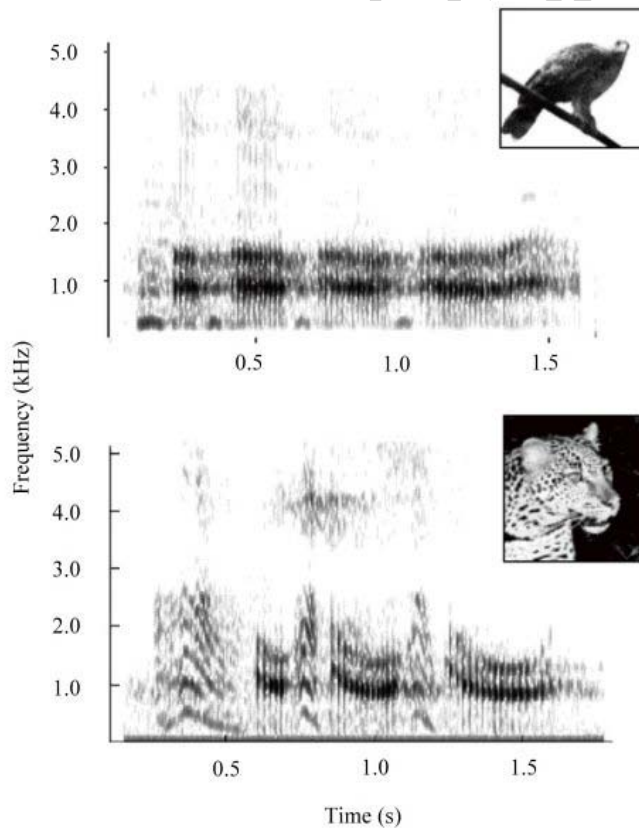


Figure 1. Alarm calls given by two male Diana monkeys to a crowned eagle and a leopard.

The main acoustic difference between the two alarm calls is the degree of frequency transition present in the two calls. Alarm calls to leopards exhibit a strong transition, alarm calls to eagles very little (Fig. 1). Playback experiments have demonstrated that

these subtle acoustic differences are meaningful to other monkeys because they convey information about the predator type spotted by the caller.

Currently, there is no strong evidence for vocal imitation in primates, apart from humans (but humans are not the only mammals capable of vocal learning). Nevertheless, non-human primates appear to have some control over their vocal production. However, vocal flexibility is subtle and often remains hidden during an individual's routine life. For example, the trill vocalizations of pygmy marmosets change in acoustic structure after pairing and remain highly stable thereafter. In marmosets, the acoustic structure of certain call types alters in response to changed social environments, even during adulthood. If chacma baboon males fall in rank, the acoustic structure of their calls changes within a period of months, independent of body size. Pant hoot vocalizations of chimpanzees are more similar within than between groups, regardless of the individuals' genetic relatedness. A variety of other aspects of evidence similarly suggests that non-human primates may have some control over elements of their vocal repertoire. In adult Campbell's monkeys, the acoustic structure of contact calls changes with an individual's social relations, and individuals remember and distinguish past and present call variants of familiar group members. Although relatively difficult to detect, these and other examples demonstrate that important pre-adaptations for the evolution of modern speech capacities are part of primate behaviors.

Nevertheless, vocal flexibility of modern humans is clearly more sophisticated. Recent genetic work has provided some interesting insights for why humans may be special in this respect. In humans and possibly other animals, development of oro-facial motor control appears to be crucially governed by a gene located on Chromosome 7, the FOXP2. Damage to this gene causes severe and irreversible speech disorders in adult life although other aspects of cognition remain unaffected. Although FOXP2 is found throughout the animal kingdom, the human version is slightly different from those of other animals, including our closest living relatives, the great apes. This is due to some recent mutations, which did not become stabilized in the human population until about 200,000 years ago. Thus, one possible scenario is that, prior to this event, humans did not have modern articulatory abilities, perhaps more resembling those of the extant apes. One direct implication from these findings is that the cognitive apparatus required for language processing must thus be much older than speech itself. This is because it is simply inconceivable that the entire set of cognitive abilities required for language acquisition and processing evolved in just 200,000 years, the equivalent of about 10,000 or so generations. It is more likely that early hominids possessed the cognitive skills required for language, but lacked the vocal abilities to produce speech.

Of course, these individuals also communicated, although vocal communication may have remained simple. It is also likely that these individuals made use of non-vocal ways of communication. Deaf children, who grow up with little acoustic stimulation, inevitably develop alternative means of communication, for example by expressing themselves with gestures. The case of Nicaraguan sign language (NSL) is a particularly interesting example. NSL emerged as spontaneous alternative communication system amongst deaf pupils who underwent formal training in lip-reading and speech production. They began to show signs of linguistic complexity comparable to normal early spoken language after a few generations. Based on these data it may be reasonable

to assume that early humans used tactile and visual modes of communication, in addition to an allegedly unsophisticated vocal communication system.

3. Social Cognition

Although the NSL findings are remarkable in their own right, they raise an important additional point: If non-human primates do not have the oro-facial control to produce complex vocal signals why do they not simply communicate with gestural signals? Gestures clearly do play an important role in primate communication and a number of recent studies have catalogued and elucidated the nature and repertoire of gestural signals in various ape species. For example, 20 distinct auditory, tactile, and visual gestures have been distinguished in bonobos. This repertoire was flexible and adapted to various communicative circumstances, including the attentional state of the recipient. Similarly, the entire repertoire of tactile and visual gestures in captive chimpanzees has now been catalogued. Individuals sometimes used gestures in sequences, although mainly in the form of repetitions caused by a recipient's lack of responsiveness. Gorillas also possess a multifaceted gestural repertoire, characterized by flexibility with accommodations to the attentional state of the recipient. Despite this richness in behavioral form, one important outcome of this research has been the lack of evidence of any sort of referential function of these signals. It appears that apes do not use their gestures to draw attention to events in the environment, nor to label a particular external object of interest. Unlike deaf children they do not develop idiosyncratic ways of describing events to one another. Ape gestures, in other words, are not used as declaratives, they primarily serve to alter the behavior of a conspecifics in a desired way, for example to initiate play. The conspicuous absence of referential signals in non-human primate gestural communication is important and could be the result of several causes.

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Biographical Sketch

Klaus Zuberbühler is a Reader in Psychology at the University of St Andrews, Scotland. His research interests include the evolution of primate intelligence and its manifestation in communication. His current research focus is on the cognitive processes that enable non-human to communicate about important external events, such as the appearance of a predator, food, or social event. He is the director of the Tai Monkey Project, a tropical research station in the Tai National Park, Ivory Coast, where he conducted most of his fieldwork. In 2004 he received the Distinguished Scientific Award for Early Career Contribution to Psychology by the American Psychological Association for his studies on non-human primate communication and cognition.