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The Phylogenetic Roots of Language

Evidence From Primate Communication and Cognition

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ABSTRACT—*The anatomy of the nonhuman primate vocal tract is not fundamentally different from the human one. Notwithstanding, nonhuman primates are remarkably unskillful at controlling vocal production and at combining basic call units into more complex strings. Instead, their vocal behavior is linked to specific psychological states, which are evoked by events in their social or physical environment. Humans are the only primates that have evolved the ability to produce elaborate and willfully controlled vocal signals, although this may have been a fairly recent invention. Despite their expressive limitations, nonhuman primates have demonstrated a surprising degree of cognitive complexity when responding to other individuals' vocalizations, suggesting that, as recipients, crucial linguistic abilities are part of primate cognition. Pivotal aspects of language comprehension, particularly the ability to process semantic content, may thus be part of our primate heritage. The strongest evidence currently comes from Old World monkeys, but recent work indicates that these capacities may also be present in our closest relatives, the chimpanzees.*

KEYWORDS—*primate cognition; evolution of language; vocal communication*

The evolution of language poses one of the great problems of modern science. Comparative studies of communication in animals, particularly nonhuman primates, are playing an increasingly important role in what has become a truly interdisciplinary endeavor (e.g. Hauser, Chomsky, & Fitch 2002). One key assumption is that, by investigating the communicative abilities of our closest living relatives, it may be possible to identify important physical and behavioral adaptations that made it possible for language to evolve in humans. Studies of primate vocal communication may reveal how humans' common ancestors with other living primates communicated and how and why human language originated from those early forms of communication. The mechanisms with which living nonhuman primates produce and perceive vocalizations, as well as the underlying cognitive processes of these mechanisms, are thus of particular scientific interest.

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PHYLOGENETIC ROOTS OF ACOUSTIC FLEXIBILITY

Among the 250 primate species, humans have exceptional vocal abilities. From early on, young children produce a rich array of sounds, a manifestation of their potent urge to engage in social activities, obtain goods, and affect the behavior of other people. The International Phonetic Alphabet lists over 100 acoustically unique phones, the most basic sound units of human speech and the acoustic basis for the world's 6,000 languages. These basic sound units are rarely produced singly, but are commonly combined into rapid sequences, which serve as the main carriers of meaning. These two characteristics—a rich acoustic portfolio and the predisposition to combine basic units into more complex acoustic strings—appear to be uniquely human traits, and call for an evolutionary investigation. Why are humans different from the other primates in their vocal abilities?

One explanation has been provided by research on psychological differences between human and nonhuman primates. Various studies have shown that, when vocalizing, nonhuman primates do not actively or intentionally try to inform one another, probably because they are unaware of each other's mental states (Seyfarth & Cheney, 2003). For example, in the presence of a predator, mother vervet monkeys do not attempt to alert ignorant offspring more than knowledgeable ones. Nonhuman primates vocalize in response to important events, irrespective of how potential recipients may view the situation. Humans are clearly different in this respect. People take each other's mental states into account and perceive behavior as caused by beliefs, desires, or knowledge. Although nonhuman primates probably experience a rich array of mental states, they do not seem to appreciate that their own experience may differ from that of other individuals. This cognitive limitation is likely to make their social world much less complex than that of humans. Moreover, it may also remove a powerful selection pressure to evolve more complex and flexible vocal abilities. Without the perceived need to share mental states, there are considerably fewer incentives for communication.

Nevertheless, various lines of research have demonstrated that nonhuman primate vocal behavior is much less rigid than has been thought. Vocal flexibility often remains hidden during routine life for nonhuman primates, only manifesting itself under specific circumstances, particularly after changes in the social fabric of a group. For example, observations at various zoos have shown that, over time, male chimpanzees may converge on acoustically unique pant-hoot vocalizations that are unique to particular zoos. In marmosets, the acoustic structure of certain call types alters in response to changed social environments, even during adulthood (Snowdon & de la Torre, 2002). Similarly, if baboon males fall in rank, their calls shorten within a period of months (Fischer, Kitchen, Seyfarth, & Cheney, 2004). 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 (Lemasson, Hausberger, & Zuberbühler, 2005). Although relatively difficult to detect, these and other examples of vocalization changes demonstrate subtle flexibility in adult vocal production in nonhuman primates. This flexibility may have acted as an important pre-adaptation for the evolution of modern humans' speech capacities. In sum, the old dichotomy of innately determined primate vocalizations and flexible human speech is no longer accurate.

TRANSITIONS TO SPEECH

The basic anatomy and principles of sound production are the same for all primates, although humans show a number of special adaptations, particularly a permanently lowered larynx (Lieberman 2000). Sounds from the larynx enter the adjoining vocal tract, where various structures that modify sound, such as the lips, tongue, jaw, and other articulators, form constrictions that determine the final acoustic structure of the vocal signal. Nonhuman primates use the same mechanisms to produce calls, but in a much less sophisticated manner (Riede, Bronson, Hatzikirou, & Zuberbühler, 2005).

The main reason why humans are so skillful in vocal production is that they have extraordinary motor control over their articulators. Development of human facial and mouth control is linked to a particular gene called FOXP2; damage to this gene causes severe speech disorders (Marcus & Fisher 2003). Although FOXP2 is found throughout the animal kingdom, the human version is slightly different and is very young in evolutionary terms; it did not become established in the human population until about 200,000 years ago (Enard et al., 2002). Given this gene's crucial role in speech production, one possible scenario is that, before this time, our ancestors lacked modern articulatory abilities or had abilities more resembling today's nonhuman primates. A related implication is that older hominids, including *Homo erectus*, were probably not able to produce speech like modern humans. Thus human linguistic abilities must have evolved as part of older communication systems, since it is simply inconceivable that they evolved in just 200,000 years, the equivalent of about 10,000 generations. Of particular interest are semantic (meaning-related) and syntactic (rule-related) abilities, as they are central to virtually every definition of language.

COGNITIVE PROCESSES OF CALL PRODUCTION AND COMPREHENSION

The first evidence for semantic competence in nonhuman primates came from studies on East African vervet monkeys. In this species, individuals produce acoustically distinctive alarm calls in response to at least five different types of predators. When tape-recorded exemplars of these alarm calls were played back from a hidden speaker, nearby listeners responded as if they had spotted the corresponding predator themselves, suggesting that the calls were meaningful to them (Seyfarth & Cheney 2003). Meanwhile, comparable findings have also been reported from other primates, notably West African Diana and Campbell's monkeys (Zuberbühler 2003). However, the fact that monkeys are capable of producing different types of alarm calls is not a particularly exciting finding; it has been demonstrated in many other groups of animals. Less well known are what sorts of mental representations individual animals experience during call production and perception. In some bird and ground squirrel species, alarm calls may simply reflect the caller's perception of the degree of threat, rather than referring to a particular class of predator. These threat-related factors, however, do not seem to explain the use of alarm calls in nonhuman primates. For example, Diana monkeys produce eagle alarm calls regardless of whether the predator is close or far or whether it is likely to attack from above or from the ground (Zuberbühler 2005).

Concerning call comprehension, one central question is what cognitive processes are activated when nonhuman primates listen to the calls of other individuals. For example, when hearing a leopard alarm call, do monkeys simply respond to the physical features of the call or are they capable of generating a mental representation of a leopard? One way of teasing apart these two possibilities under field conditions is to expose animals to sequences of calls that differ both in acoustic structure and in the underlying meaning—so-called habituation–dishabituation experiments. The results of one such experiment are shown in Figure 1: In Diana monkeys, individuals are indeed able to attend to the associated semantic content rather than simply responding to the acoustic features of calls.

Compared to the evolution of semantic abilities, the evolution of syntax is less well understood. Languages are grounded in phonological and syntactic rules, which enable speakers to construct an infinite number of messages from a finite group of sounds. During the first few years of their lives, and with vast amounts of exposure, children gradually learn to extract the syntactic rules of their native language and start applying them correctly (Tomasello 2003).

Given that our linguistic abilities may have old evolutionary roots, is there any evidence for syntax in primate communication? In one study, cotton-top tamarins' ability to extract rules from artificial auditory patterns was not particularly impressive (Fitch & Hauser 2004). However, when signals are communicatively relevant, nonhuman primates have demonstrated some understanding of simple syntactic rules. For example, wild Campbell's monkeys can produce sequences of calls consisting of different types of vocalizations. Experiments have shown that the ordering of the calls determines the meaning of the entire sequence; that is, the meaning of the sequence is not merely a blending of the individual calls' meanings (Zuberbühler 2003).

Nonhuman primates routinely use their knowledge of their world when responding to other individuals' vocalizations. A number of illustrative examples have been provided in the context of communication between species. For example, crested guinea fowls are ground-dwelling forest birds that are hunted by a variety of predators, including leopards and humans; in response to such threats, the birds produce a single type of alarm call that covers all ground predators. Diana monkeys gauge their vocal response to the birds' alarm calls depending on the most likely cause for the calls—that is, whether the birds called in response to a leopard or a human—rather than responding to the alarm calls themselves (Zuberbühler 2003). The monkeys responded with many alarm calls of their own if a leopard was the likely cause, while they remained mostly quiet if a human was the likely cause (Zuberbühler 2003). Humans hunt monkeys with shotguns and the most adaptive response for a monkey is to hide silently.

When the monkeys are confronted with a nearby group of chimpanzees—dangerous predators that hunt monkeys in the trees—their best response is to flee and hide silently. Chimpanzees are sometimes attacked by leopards, and if that happens, individuals often respond with loud alarm screams. In one experiment, Diana monkeys heard recordings of chimpanzee alarm screams, and it was found that half of the groups of monkeys

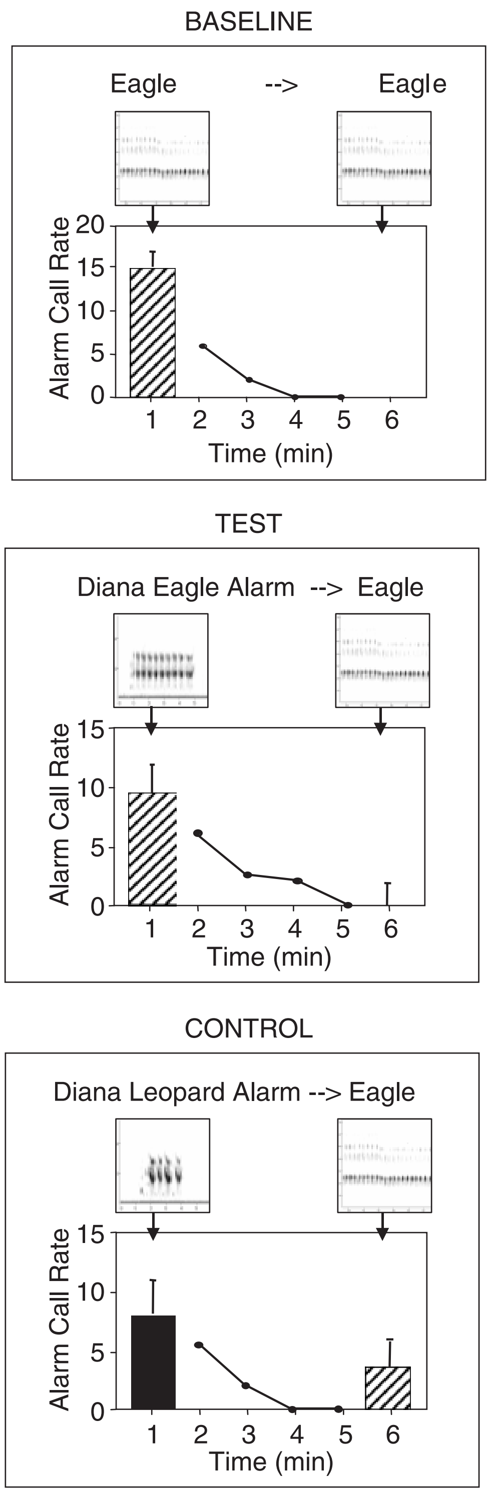

Fig. 1. Field experiment to investigate whether primates are able to process the semantic properties associated with alarm calls. Wild groups of Diana monkeys in the Taï forest, Ivory Coast, were first exposed to a prime stimulus, either a predator vocalization (e.g. shrieks of a crowned eagle; top condition) or a conspecific's alarm call (e.g. Diana eagle or leopard alarms; middle and bottom conditions). Five minutes later, the same group heard a probe stimulus, a predator vocalization (e.g., eagle shrieks) that either did or did not correspond to the previous alarm call. (The study included three additional conditions, not depicted here, in which leopard growls were used instead of eagle shrieks.) Results showed that the semantic content of the prime stimuli, not their acoustic features alone, explained the response patterns of the monkeys: Predator vocalizations did not elicit new alarm calls when monkeys were previously primed with the alarm call corresponding to that predator (middle condition), but did elicit alarm calls when the previous alarm call had been for a different predator (bottom condition; Zuberbühler 2003). Copyright (c) 1999 by the American Psychological Association. Adapted with permission.

studied abandoned their default response to chimpanzees (hiding silently) and instead began to produce conspicuous leopard alarm calls of their own, as if they assumed the presence of a leopard. Groups whose home range was in the core area of a resident chimpanzee community were significantly more likely to respond this way than were peripheral groups. Presumably, peripheral groups had less experience with chimpanzee alarm screams and, due to their less developed discrimination abilities, were more likely to hide silently in response to any type of chimpanzee vocalization. These data further underscore the general point that primates do not respond directly to the acoustic features of vocal signals but to the pragmatic circumstances under which calls are produced—in this case, the likely cause of the calls (Zuberbühler 2005).

VOCAL COMMUNICATION IN GREAT APES

The studies reviewed so far all involve various monkey species. Currently, comparable data from the natural communication of apes are conspicuously lacking. This is particularly puzzling given the apes' close evolutionary link to humans and their well-established skills in acquiring artificial communication systems (e.g. sign language). Recent work suggests that some important facts may have been overlooked, though. For example, wild chimpanzees have been documented to produce different types of barks depending on the environmental context (Crockford & Boesch, 2003). Wild chimpanzees also produce different types of screams depending on the social role they are playing during a conflict; these different screams may provide important information for nearby allies and relatives (Slocombe & Zuberbühler, 2005). More systematic experimental work is needed to determine whether apes use vocalizations to convey information about events in their environment the way monkeys have been demonstrated to do.

CONCLUSION

Studies of nonhuman primate vocal abilities play a key role in understanding human language evolution. Humans share a long evolutionary history with the nonhuman primates and comparative research has revealed a number of important similarities and differences. In terms of vocal production, humans are unique in their superior ability to rapidly change the geometry of their vocal tracts, the biological basis of complex speech utterances. Although nonhuman primates can produce many of the mouth and face maneuvers required for complex articulation, their overall performance is slow and unimpressive. These differences between human and nonhuman primates in mouth and face control have been linked to genetic differences, although there are also important differences in social intelligence. Humans appear to be the only primates that are aware of each other's mental states, creating a social reality of high complexity that may have generated intense selection pressure for elaborate communicative skills.

Nonhuman primates perform much better in comprehension-related tasks. Some basic linguistic capacities, such as the ability to assign meaning to arbitrary sounds and the ability to adjust meaning as a function of simple rules, are part of primate cognition. These linguistically important abilities must thus be very old, having emerged in the primate lineage long before the advent of modern humans. Future work will have to determine whether primate semantic signals and human speech are processed by related brain structures.

One problem with the comparative literature is that strong evidence is only available for monkeys, while the natural vocal abilities of apes are still understudied. Some observational work with chimpanzees points to comparable abilities, but there is a clear need for experimental work of great-ape vocal communication, given their importance as living links to human evolution.

Finally, meaningful progress on primate communication and cognition will largely depend on whether research questions can be addressed in an ecologically and socially relevant context—that is, with individuals interacting with each other in their natural environments. Yet, the survival of the world's primates is severely threatened by human activity, directly by the bush meat trade and habitat destruction and indirectly by international agricultural practices. Scientific progress in understanding our cognitive past is closely tied to the survival of these species in their natural habitats.

Recommended Reading

Cheney, D.L., & Seyfarth, R.M. (1990). *How monkeys see the world: Inside the mind of another species*. Chicago: Chicago University Press.

Lieberman, P. (2000). (See References)

Tallerman, M. (2005). *Language origins: Perspectives on evolution*. Oxford: Oxford University Press.

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REFERENCES

Crockford, C., & Boesch, C. (2003). Context-specific calls in wild chimpanzees, *Pan troglodytes verus*: analysis of barks. *Animal Behaviour*, *66*, 115–125.

Enard, W., Przeworski, M., Fisher, S.E., Lai, C.S.L., Wiebe, V., Kitano, T., Monaco, A.P., & Pääbo, S. (2002). Molecular evolution of FOXP2, a gene involved in speech and language. *Nature*, *418*, 869–872.

Fischer, J., Kitchen, D.M., Seyfarth, R.M., & Cheney, D.L. (2004). Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion. *Behavioral Ecology and Sociobiology*, *56*, 140–148.

Fitch, W.T., & Hauser, M.D. (2004). Computational contraints on syntactic processing in a nonhuman primate. *Science*, *303*, 377–380.

Hauser, M.D., Chomsky, N., & Fitch, W.T. (2002). The faculty of language: What is it, who has it, and how did it evolve? *Science*, *298*, 1569–1579.

Lemasson, A., Hausberger, M., & Zuberbühler, K. (2005). Socially meaningful vocal plasticity in adult Campbell's monkeys (*Cercopithecus campbelli*). *Journal of Comparative Psychology*, *112*, 220–229.

Lieberman, P. (2000). *Human language and our reptilian brain: The subcortical bases of speech, syntax, and thought*. Cambridge, MA: Harvard University Press.

Marcus, G.F., & Fisher, S.E. (2003). FOXP2 in focus: What can genes tell us about speech and language? *Trends in Cognitive Sciences*, *7*, 257–262.

Riede, T., Bronson, E., Hatzikirou, B., & Zuberbühler, K. (2005). The production mechanisms of Diana monkey alarm calls: Morphological data and a model. *Journal of Human Evolution*, *48*, 85–96.

Seyfarth, R.M., & Cheney, D.L. (2003). Signalers and receivers in animal communication. *Annual Review of Psychology*, *54*, 145–173.

Slocombe, K., & Zuberbühler, K. (2005). Agonistic screams in wild chimpanzees vary as a function of social role. *Journal of Comparative Psychology*, *119*, 67–77.

Snowdon, C.T., & de la Torre, S. (2002). Multiple environmental contexts and communication in pygmy marmosets (Cebuella pygmaea). *Journal of Comparative Psychology*, *116*, 182–188.

Tomasello, M. (2003). Constructing a language: A usage-based theory of language acquisition. Cambridge, MA: Harvard University Press.

Zuberbühler, K. (2003). Referential signalling in non-human primates: Cognitive precursors and limitations for the evolution of language. *Advances in the study of behavior*, *33*, 265–307.

Zuberbühler, K. (2005). Alarm calls: Evolutionary and cognitive mechanisms. In K. Brown (Ed.), *Encyclopedia of Language and Linguistics* (Vol 2). Oxford: Elsevier.