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The evolution of language from social cognition Robert M Seyfarth¹ and Dorothy L Cheney²

Despite their differences, human language and the vocal communication of nonhuman primates share many features. Both constitute a form of joint action, rely on similar neural mechanisms, and involve discrete, combinatorial cognition. These shared features suggest that during evolution the ancestors of modern primates faced similar social problems and responded by evolving similar systems of perception, communication and cognition. When language later evolved from this common foundation, many of its distinctive features were already in place.

Addresses

¹ Department of Psychology, University of Pennsylvania, 3720 Walnut Street, Philadelphia, PA 19104, USA

² Department of Biology, University of Pennsylvania, Philadelphia, PA 19104, USA

Corresponding author: Seyfarth, Robert M (seyfarth@psych.upenn.edu)

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Introduction

Human language poses a problem for evolutionary theory because of the striking discontinuities between language and the communication of our closest animal relatives, the nonhuman primates. How could language have evolved from something so very different?

The qualitative differences between language and nonhuman primate communication are well known [1°]. All languages are built up from a large repertoire of learned, modifiable sounds. These sounds constitute phonemes, which are combined into words, which in turn are combined according to grammatical rules into sentences. In sentences, the meaning of each word derives both from its own, stand-alone meaning and from its functional role as a noun, verb, or modifier. Grammatical rules allow a finite number of elements to convey an unlimited number of meanings: the meaning of a sentence is more than just the summed meanings of its constituent words. Languages derive their communicative power from being discrete, combinatorial, rule-governed, and open-ended computational systems (see [2,3] for review).

By contrast, nonhuman primates (prosimians, monkeys, and apes) — and indeed most mammals — have a relatively small repertoire of calls. Their vocalizations exhibit only slight modification during development [4], and while animals can give or withhold calls voluntarily and modify the timing of vocal production [5], different call types are rarely given in combinations (but see [6]). When call combinations do occur, there is little evidence that individual calls play functional roles as agents, actions, or patients. As a result, primate vocalizations, when compared to language, are believed to convey only limited information [1°,7,8].

Differences between human language and nonhuman primate communication are clearest in call production. Continuities are more apparent, however, when one considers the neural mechanisms that govern call perception; the complex pragmatic inferences that listeners make when interpreting calls; and the function of vocal signals in the daily lives of individuals. Here we focus on nonhuman primates as perceivers, and on the perceptual and cognitive mechanisms that underlie their response to signals. In these contexts, we argue that human and nonhuman primates exhibit many homologous brain mechanisms that have evolved to serve similar social functions. We suggest that vocalizations and social knowledge combine to form a system of communication that, in its underlying perception and cognition, is discrete, combinatorial, rule-governed, and open-ended. We conclude that, long before language evolved, a discrete, combinatorial system of communication, perception, and cognition — with many of language's supposedly unique features — was already in place.

Homologous neural mechanisms

Human and nonhuman primates share many neurological mechanisms for perceiving, processing, and responding to communicative signals. These include mechanisms for the recognition of faces [9–11] and voices [12,13], and for the multisensory integration of bimodal stimuli, specifically voices and concurrent facial expressions [14]. In both humans and macaques, neurons in the ventral premotor cortex exhibit similar neural activity when performing a specific action and when observing another perform the same action [15,16]. Moreover, in both humans and macaques the ventrolateral prefrontal cortex plays an important role in the classification of conspecific calls with different acoustic properties that either are or are not associated with the same events [17].

These shared mechanisms are unlikely to have arisen by accident. Instead, it seems likely that during their common evolutionary history (roughly 30 to 5 million years ago: [18]) Old World monkeys, apes, and early hominids faced similar problems in communication and evolved similar mechanisms to deal with them. The more recent evolution of language in the human lineage (during the past 5–6 million years: [19]) built upon these shared mechanisms. What were these common communicative problems?

Similar social functions

Clark [20**] examines language as a form of joint action, used by people in face-to-face interactions to facilitate and coordinate their activities. He emphasizes that language users are not 'generic speakers and addressees, but real people, with identities, genders, histories, personalities, and names' [(20, p. xi)]. Clark's analysis is important because, unlike discussions that emphasize language's formal structure, Clark focuses on how language functions in the daily lives of individuals, many of whom have a long history of past interaction. Clark therefore provides an ideal background against which to compare the social function of language with the social function of vocalizations in nonhuman primate groups. Here we make such a comparison and, drawing on recent research with wild baboons, suggest that the two systems of communication, superficially so different, share many biologically important functions. These shared functions help explain the evolution of the homologous neural mechanisms listed above.

Baboons live throughout the savannah woodlands of Africa in groups of 50–150 individuals. Although most males emigrate to other groups as young adults, females remain in their natal groups throughout their lives, maintaining close social bonds with their matrilineal kin. Females can be ranked in a stable, linear dominance hierarchy that determines priority of access to resources.

Daughters acquire ranks similar to those of their mothers. The stable core of a baboon group is therefore a hierarchy of matrilines, in which all members of one matriline (for example, matriline B) outrank or are outranked by all members of another (for example, matrilines C and A, respectively: Figure 1). Ranks are extremely stable, often remaining unchanged for decades [21–23]. When rank reversals occur within a matriline, they affect only the two individuals involved. However, when rank reversals occur between individuals in different matrilines, most members of the lower-ranking matriline rise in rank together above all members of the previously higher-ranking matriline [23].

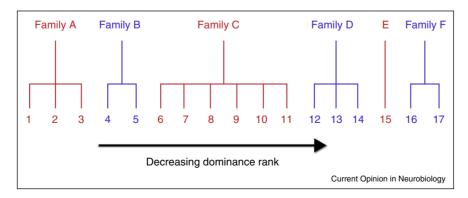
Baboon vocalizations are individually distinctive [24] and listeners recognize the voices of others as the calls of specific individuals [23]. The baboon vocal repertoire contains a number of acoustically graded signals, each of which is given in predictable contexts [25]. Field playback experiments demonstrate that the baboons' system of communication has the following properties:

An individual who hears a vocalization assesses the caller's intention to communicate to her. If two animals engage in aggression, then separate, then one hears a threat-grunt from the other, the listener responds as if the threat is directed at her, but if the threat-grunt is heard after a recent grooming interaction, the listener responds as if the call is directed at another individual [26].

Calls function to facilitate social interactions. When one female approaches another, friendly behavior is significantly more likely if the approaching female grunts than if she does not [27,28°].

Listeners assess the meaning of a call by integrating information from multiple sources: the call type, caller's identity, previous events, and the caller's and listener's relationships with others. After aggression between individuals from different

Figure 1



The hierarchical organization of females and offspring in a typical baboon group. Matrilineal kin groups (mothers and offspring: 'families') are denoted by letters and arranged from left to right in descending dominance rank order. Individuals within families are denoted by numbers and also arranged in descending rank order. Source: Data taken from Cheney and Seyfarth (2007).

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