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The evolution of language from social cognition

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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.

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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].

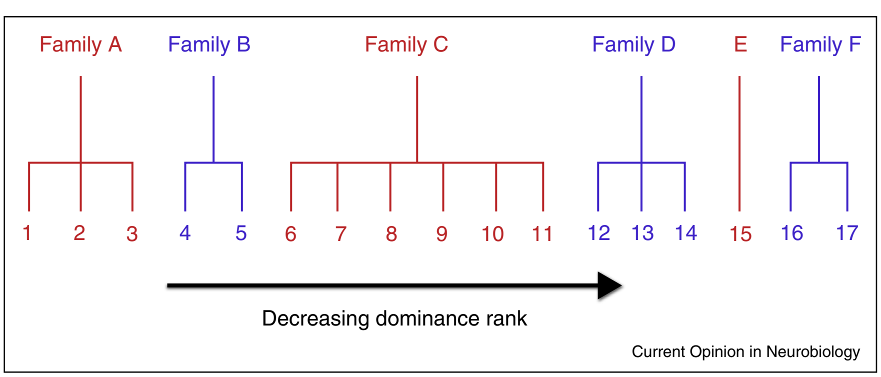
Baboon vocalizations are individually distinctive [24] and listeners recognize the voices of others as the calls of specific individuals [23]. The baboon vocal repertoire contains a number of acoustically graded signals, each of which is given in predictable contexts [25]. Field playback experiments 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).

matrilines (say, females C2 and D2), D2 will treat a grunt from C2 or any of C2's close kin as a reconciliatory signal, but will show no response to a grunt from a member of another matriline (say, A2) [29]. Similarly, after aggression between C2 and D2, D2 will treat a threat-grunt from any of C2's close kin as a sign of renewed aggression directed at her, but will show no response to threat-grunts from members of other matrilines [30]. These responses do not occur because members of the same matriline sound alike: in other contexts, listeners are clearly able to distinguish between closely related females' calls. Instead, listeners appear to treat the calls as equivalent because they recognize that close kin are close social allies.

Communication reveals what individuals know about each other. Listeners respond significantly more strongly to a sequence of threat-grunts and screams that mimic a rank reversal between families than to one that mimics a rank reversal between individuals within the same family [31•], indicating that they classify individuals simultaneously according to both kinship and rank [32]. Notice that, in their production, these call sequences are fundamentally different from human sentences: they are made by two individuals, each producing only one type of vocalization. Nonetheless, listeners parse the sequence as a narrative in which there is an actor, an action, and an individual who is acted upon.

Primate communication and cognition: a discrete, combinatorial system

Baboon communication is embedded in a sophisticated system of social knowledge. When a baboon hears vocalizations, she forms a mental representation of call meaning. This representation develops rapidly and is built up from several discrete pieces of information: the type of call, the caller's identity, recent events, and the caller's rank and kinship affiliation. The meaning of a call sequence includes the representation of an actor who performs a specific action on a recipient and causes the recipient's response. These discrete elements are combined according to the 'rules' of call delivery to create a message whose meaning is more than just the sum of the meanings of its constituent elements.

A baboon's assessment of call meaning thus constitutes a *discrete*, *combinatorial*, *rule-governed*, *and open-ended* system of communication [33,34] in which a finite number of signals can yield a nearly unlimited number of meanings. If a listener recognizes the difference between [A threatens B and B screams] and [B threatens A and A screams], and can make this distinction for every dyad in a group of 70–80 individuals, a simple system of signals can generate a huge number of meanings. The discrete, combinatorial system arises even though the calls themselves may be acoustically graded. Finally, the communicative system is effectively open ended, because baboons learn to recognize the calls of new infants, new male immigrants — indeed *any* new individual — and assign meaning to these calls depending on the individuals' ranks and kinship affiliations.

This does not mean that vocal communication in baboons constitutes a language, or even that baboon communication has many of language's formal, structural properties. Instead, we suggest that several of the cognitive mechanisms that have long been thought to mark a clear separation between language and nonhuman primate communication can, in fact, be found — in admittedly simpler form — in the communication and social cognition of nonhuman primates. As a result, the earliest steps toward the evolution of language may not be as difficult to imagine as often thought.

Why should such a system have evolved? Long-term field studies demonstrate that the best predictor of a baboon's or chimpanzee's reproductive success is an individual's ability to form close, long-term bonds and to recognize the relations that exist among others [35,36••,37•]. Selection should thus favor individuals who are skilled both in the use of communication to form and maintain bonds and in the ability to derive, from overheard signals, information about other animals' relations. Discrete, combinatorial communication and cognition has thus been favored by natural selection.

Social knowledge as a cognitive precursor to language

In many respects this proposal is not new. For example, Hockett [38] listed 'discreteness' and 'productivity' as two 'design features' of language that call for an evolutionary explanation, while Pinker and Bloom [39] suggested that during the course of human evolution 'grammar exploited mechanisms originally used for . . . conceptualization' ([38], p. 713), and Newmeyer ([40], p. 10) argued that 'the conditions for the subsequent development of language . . . were set by the evolution of . . . conceptual structure. A first step . . . was undoubtedly the linking up of individual bits of conceptual structure to individual vocalizations' (see also [41–43]). Our proposal is new, however, in its emphasis on social cognition (Worden [34] makes a similar argument), and in our ability to link social cognition with reproductive success [23,35,36••,37•,47].

Three sorts of cognition, all well documented in animals, have been offered as possible precursors of language [44]: orientation and navigation (e.g. [45]); number [46]; and social cognition [34,47]. All involve discrete elements and rule-governed computations. In three respects, however, social cognition seems the most likely candidate as a precursor of language. First, only in social cognition do the discrete elements include living creatures, to which listeners can reasonably attribute motives and goals, and context-specific vocalizations that are also associated with a caller's motivation to interact with another in specific ways. Only social cognition, therefore, deals with agents, actions, and patients.

Second, only in social cognition are the discrete elements explicitly linked to vocalizations, so that the system of communication and the system of cognition on which it is based are tightly coupled. This merging of communication and cognition does not occur in animal orientation, navigation, or systems of number.

Third, only in social cognition are the discrete elements linked — as in language — to the organization of items into concepts. Because the meaning of a baboon's call is inseparable from the identity of the caller, her dominance rank, and her family membership, baboon communication relies on a form of concept formation based on socially defined categories [48,49•]. The social categories of 'kinship' and 'dominance rank' qualify as concepts, first, because they cannot be reduced to any one, or even a few, sensory attributes. Family members do not always look alike, sound alike, behave alike, or share any other physical or personality features that make them easy to classify together [48]. Second, social categories persist despite changes in their composition. Among females and juveniles, the recognition of families is unaffected by births and deaths; among adult males, the recognition of a linear, transitive hierarchy persists despite frequent changes in the individuals who occupy each position [50]. In the mind of a baboon, therefore, social categories exist independent of their specific members. And because the meaning of a vocalization cannot be divorced from the caller's identity, and the caller's identity cannot be separated from her placement in a conceptual structure based on kinship and rank, communication and conceptual structure are inextricably bound together — just as we might expect in a system of communication that served as a precursor to human language and thought.

Conclusions

Nonhuman primates live in complex social groups where an individual's reproductive success depends on her skills in forming relationships and representing the relations of others. In response, animals have evolved systems of communication and cognition that are discrete, combinatorial, rule-governed, and open-ended. As a result, when language first evolved from the communication of nonhuman primates, many of its distinctive features were already in place.

Conflict of interest statement

The authors declare no conflict of interest.

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