Precursors to language: Social cognition and pragmatic inference in primates

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Abstract Despite their differences, human language and the vocal communication of nonhuman primates share many features. Both constitute forms of coordinated activity, rely on many shared neural mechanisms, and involve discrete, combinatorial cognition that includes rich pragmatic inference. These common features suggest that during evolution the ancestors of all modern primates faced similar social problems and responded with similar systems of communication and cognition. When language later evolved from this common foundation, many of its distinctive features were already present.

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 the common ancestor of these two very different systems?

The qualitative differences between language and nonhuman primate communication are well known (Fitch, 2010). All languages are built up from a large repertoire of learned, modifiable sounds. These sounds are combined into syllables, 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, standalone meaning and from its functional role as a noun, verb, or modifier. Grammatical rules allow a finite number of elements to convey an infinite 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 (Jackendoff, 1994; Pinker, 1994).

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 (Hammerschmidt & Fischer, 2008), and although animals can give or withhold calls voluntarily and modify the timing of vocal production (Seyfarth & Cheney, 2010), different call types are rarely given in combinations (but see Shlenker et al., 2016). 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 (Bickerton, 1990; Fitch, 2010; Hurford, 2007).

The differences between human language and nonhuman primate communication are clearest in call production. Continuities are more apparent, however, when one considers the underlying 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 responses 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,

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in its underlying perception and cognition, is discrete, combinatorial, rule-governed, and open-ended. It also relies on a rich system of knowledge derived from the social context, or pragmatic inference. 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 in primate receivers.

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 (Freiwald, Tsao, & Livingston, 2009; Kanwisher, McDermott, & Chun, 1997; Tsao, Freiwald, Tootell, & Livingston, 2006) and voices (Belin & Zattore, 2003; Petkov et al., 2008), for the processing of auditory sequences (Wilson et al., 2015), and for the multisensory integration of bimodal stimuli, specifically voices and concurrent facial expressions (Ghazanfar & Eliades, 2014). In both humans and macaques, neurons in the ventral premotor cortex exhibit neural activity both when performing a specific action and when observing another perform the same action (de Waal & Ferrari, 2010; Ferrari, Bonini, & Fogassi, 2009). 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 (Gifford, MacLean, Hauser, & Cohen, 2005).

These shared mechanisms are unlikely to have arisen by accident. Instead, it seems likely that during their common evolutionary history (from roughly 30 to 5 million years ago: Steiper, Young, & Sukarna, 2004) 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: Glazko & Nei, 2003) built upon these shared mechanisms. What were these common communicative problems?

Similar social functions

Clark (1996) examined language as a form of coordinated activity, used by people in face-to-face interactions to facilitate their activities. He emphasized that language users are not "generic speakers and addressees, but real people, with identities, genders, histories, personalities, and names" (p. xi). Clark's analysis is important because, unlike discussions that emphasize language's formal semantic and syntactic structures, it focuses on how language functions in the daily social

life 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, drawing on recent research with wild baboons. We suggest that language and nonhuman primate communication, superficially so different, share many 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 to 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 (e.g., matriline B) outrank or are outranked by all members of another (e.g., matrilines C and A, respectively). Ranks are extremely stable, often remaining unchanged for decades (Cheney & Seyfarth, 2007; Silk, Altmann, & Alberts, 2006a, 2006b). 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 (Cheney & Seyfarth, 2007). Figure 1 illustrates the matrilineal hierarchy found in a typical baboon group.

Baboon vocalizations are individually distinctive (Owren, Seyfarth, & Cheney, 1997), and listeners recognize the voices of others as the calls of specific individuals (Cheney & Seyfarth, 2007). The baboon vocal repertoire contains a number of acoustically graded signals, each of which is given in predictable contexts (Fischer, Metz, Cheney, & Seyfarth, 2001). *Grunts* may be given to any other individual,
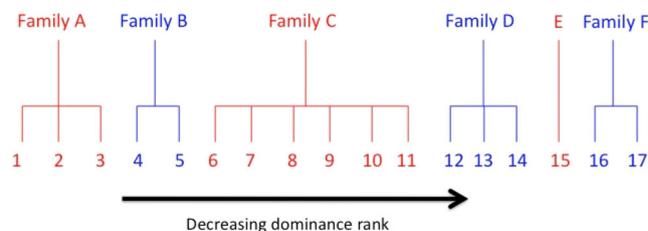
Fig. 1 The hierarchical organization of females and offspring in a typical baboon group. Matrilineal kin groups (mothers and offspring: "families") are denoted by letters and arranged from left to right in descending dominance rank order. Individuals within families are denoted by numbers and also arranged in descending rank order. Data are taken from Cheney and Seyfarth (2007). The figure is from "The Evolution of Language From Social Cognition," by Seyfarth and Cheney 2014b, *Current Opinion in Neurobiology*, *28*, p. 6. Copyright 2014 by Elsevier B.V. Reprinted with permission.

regardless of rank; *threat-grunts* are given only by higher-ranking to lower-ranking individuals; *fear-barks* and *screams* are given only by lower-ranking to higher-ranking individuals (Cheney & Seyfarth, 2007).

Field playback experiments have demonstrated 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, and 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 (Engh et al., 2006). Upon hearing a vocalization, therefore, a listener acts as if she assesses whether or not the call is directed *at her*: That is, she responds on the basis of her evaluation of the caller's intent to communicate.
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> *Calls function to facilitate social interactions*. Female baboons are strongly attracted to young infants, but the infants' mothers are often reluctant to have them touched or handled. Grunts facilitate infant handling: If a female gives a series of grunts as she approaches a mother with infant, the mother is significantly less likely to move away, and infant handling is more likely, than if the approaching female remains silent (Cheney, Seyfarth, & Silk, 1995). How do grunts achieve this outcome? Studying rhesus macaques (*Macaca mulatta*), in which females' interest in infants is also high and grunts and *girney* vocalizations facilitate infant handling, Silk, Kaldor, and Boyd (2000) found that grunts and *girneys* accurately predicted the approaching female's subsequent behavior: If she vocalized, aggression was significantly less likely and grooming was significantly more likely than if she did not. As a result, there was a contingent, predictable relation between the approaching female's vocalizations and what she did next. Presumably, mothers recognized this contingency and treated grunts and *girneys* as honest indicators of the approaching female's benign disposition. Once again, listeners' responses depend on their judgments of the signaler's intentions.
>
> *Listeners assess the meaning of calls by integrating information from multiple sources: the call type, the caller's identity, previous events, and the caller's and listener's relationships with others*. As background, recall that rank relations among females are generally stable over time, with few reversals occurring either within or between families. However, when reversals do occur, their consequences differ significantly depending on who is involved. For example, if the third-ranking female in matriline B (B3) rises in rank above her second-ranking sister (B2), the reversal affects only these two individuals. By contrast, a rank reversal between two females from

different matrilines (e.g., C1 rising in rank above B3) potentially affects entire families, since all members of the C matriline are likely to rise above all the members of the B matriline (Cheney & Seyfarth, 2007).

In one set of trials, the subjects heard an apparent rank reversal involving two members of the same matriline: for example, female B3 giving threat-grunts while female B2 screamed. Later, the same subjects heard an apparent rank reversal involving the members of two different matrilines: for example, female C1 giving threat-grunts while female B3 screamed. As a control, subjects heard a fight sequence that was consistent with the female dominance hierarchy. As in prior tests (Cheney et al., 1995), listeners responded with apparent surprise to call sequences that appeared to violate the existing dominance hierarchy, suggesting that their expectations included information about the "rules" of call delivery (see above) and the relative ranks of the individuals involved. In addition, between-family rank reversals elicited a consistently stronger response than did within-family rank reversals (Bergman, Beehner, Cheney, & Seyfarth, 2003), suggesting that expectations also included information about matrilineal kinship and the nested relationship of kinship and rank (see also Schino, Tiddi, & Polizzi di Sorrentino, 2006).

Other experiments have yielded similar results. After aggression between individuals from different matrilines (say, females C2 and D2), D2 responded to a grunt from C2 as if it signaled reconciliation. By contrast, playback of a grunt from another, higher-ranking individual not previously involved in an aggressive interaction with the victim produced no such changes in D2's behavior (Cheney & Seyfarth, 1997). The grunts of a close relative of the aggressor can also reconcile opponents: Victims of aggression were more likely to tolerate their opponent's proximity in the hour after aggression if they heard the grunt of their opponent's relative than if they heard the grunt of a more dominant individual belonging to a different matriline (Wittig, Crockford, Ekberg, Seyfarth, & Cheney, 2007). Similarly, after aggression between C2 and D2, D2 moved away from the speaker if she heard a threat-grunt from any of C2's close kin, treating this call as a sign of renewed aggression directed at her. By contrast, she showed no such response to threat-grunts from members of other matrilines (Wittig, Crockford, Seyfarth, & Cheney, 2007). These responses did not occur because members of the same matriline sound alike: In other contexts, listeners were clearly able to distinguish between closely related females' calls. Instead, listeners' responses reflected their integration of information from the call type, the caller's identity and matrilineal kin group, and the listener's memory of previous interactions with the caller or the caller's kin.

Primate communication and cognition: A discrete, computational system

Considered in isolation, baboon vocalizations are very general, nonspecific signals, broadly associated with affiliative behavior, aggression, fear, and alarm. Vocalizations, however, do not exist in a social vacuum. Each call occurs in circumstances in which the caller and recipient recognize each other, know about each other's relationships, and have a long history of interaction. When one animal vocalizes to another, the recipient is therefore free to supplement information acquired from the call itself with information acquired from the context—specifically her rich history of interaction with the caller and the caller's kin. Thanks to pragmatic inference, very general, nonspecific signals can convey highly specific information (Seyfarth & Cheney 2016).

When a baboon hears a vocalization, she forms a mental representation of the call's meaning. This representation develops instantly and is built up from several discrete pieces of information: the type of call, the caller's identity, recent events, and the caller's dominance rank and kinship affiliation. When a listener hears two animals vocalizing to each other, the meaning of this sequence includes the representation of an actor who is performing a specific action on a recipient and causing the recipient's response: If there were no attribution of causality, there would be no violation of expectation when a lower-ranking animal threatens a higher-ranking animal and the latter screams; the calls would simply have occurred together by chance. For receivers, the discrete elements of call type, caller identity, and kin group 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 (Cheney & Seyfarth, 1998; Worden, 1998) in which the assessment of meaning depends upon the call type and pragmatic inference based on social knowledge. In baboon communication, moreover, a finite number of signals can yield a nearly infinite 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. 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 new 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 semantic or syntactic properties (clearly it does not). 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 originally thought (Pinker, 1994).

It seems likely that the rich system of pragmatic inference that we have documented among baboons will be found in other species, particularly those in which individuals live long lives, interact repeatedly with the same partners, and recognize each others' relationships. If this proves correct, and if we accept the idea that communication in modern monkeys and apes provides a rough guide to the prelinguistic communication of our hominid ancestors, then that ancestral communication would be characterized by a relatively small repertoire of calls, limited semantics and syntax, but a rich system of meanings based on social knowledge and pragmatic inference. This, in turn, would suggest that, as language evolved from its prelinguistic ancestors, the relatively later appearance of semantics and syntax was built upon a foundation of social cognition.

Why should nonhuman primates have evolved such a sophisticated system of social knowledge? Long-term field studies demonstrate that an important predictor of a baboon's or a chimpanzee's reproductive success is an individual's ability to form close, long-term bonds. Doing so, moreover, would seem to require recognition of the relationships that exist among others (Gilbey et al., 2013; Mitani, 2009; Silk et al., 2009, 2010). Similar results apply to many nonprimate mammals (see Seyfarth & Cheney, 2012, for a review). Long before the evolution of language, therefore, selection favored individuals who were skilled both in the use of communication to form and maintain bonds and in the cognitive skills needed to derive, from personal experience and eavesdropping, information about other animals' relationships. Long before language, therefore, selection favored discrete, combinatorial thinking and sophisticated pragmatic inference (Cheney & Seyfarth, 2007; Seyfarth & Cheney, 2014b).

Social knowledge as a cognitive precursor to language

In many respects this proposal is not new. For example, Hockett (1960) listed "discreteness" and "productivity" as two distinctive features of language that call for an evolutionary explanation, whereas Pinker and Bloom (1990) suggested that during the course of human evolution "grammar exploited mechanisms originally used for . . . conceptualization" (Pinker & Bloom, 1990, p. 713). Similarly, Newmeyer (1991, p. 10) argued that "the conditions for the subsequent development of

language … were set by the evolution of … conceptual structure. A first step toward the evolution of this system … was undoubtedly the linking up of individual bits of conceptual structure to individual vocalizations" (see also Hurford, 2003; Jackendoff, 1987; Kirby, 1998). The present proposal is new, however, in its emphasis on social cognition (Worden, 1998, makes a similar argument), and because we can now link social cognition with reproductive success (Cheney & Seyfarth, 1990, 2007; Gilbey et al., 2013; Silk et al., 2009, 2010).

Three sorts of cognition, all well-documented in animals, have been offered as possible precursors of language (Hauser, Chomsky, & Fitch, 2002): orientation and navigation (e.g., Menzel, 2011), number (Cantlon & Brannon, 2007), and social cognition (Cheney & Seyfarth, 1990; Worden, 1998). 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 (Seyfarth & Cheney, 2014b).

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 (Seyfarth & Cheney, 2012, 2014a). The social categories of "kinship" and "dominance rank" qualify as concepts 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 (Seyfarth & Cheney, 2014b). Higher-ranking individuals do not differ in any physical respects from lower-ranking animals. Social categories also qualify as concepts because they 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 (Kitchen, Cheney, & Seyfarth, 2005). In the mind of a baboon, therefore, social categories exist independent of their 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 in which an individual's reproductive success depends on skills in forming strong social bonds and representing the relationships 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 cognitive features were already in place.

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