ORIGINAL ARTICLE

Primate social knowledge and the origins of language

Robert M. Seyfarth · Dorothy L. Cheney

Abstract   Primate vocal communication is very different from human language. Differences are most pronounced in call production. Differences in production have been overemphasized, however, and distracted attention from the information that primates acquire when they hear vocalizations. In perception and cognition, continuities with language are more apparent. We suggest that natural selection has favored nonhuman primates who, upon hearing vocalizations, form mental representations of other individuals, their relationships, and their motives. This social knowledge constitutes a discrete, combinatorial system that shares several features with language. It is probably a general primate characteristic whose appearance predates the evolution of spoken language in our hominid ancestors. The prior evolution of social cognition created individuals who were preadapted to develop language. Several features thought to be unique to language—like discrete combinatorics and the encoding of propositional information—were not introduced by language. They arose, instead, because understanding social life and predicting others' behavior requires a particular style of thinking.

R. M. Seyfarth (✉)
Department of Psychology, University of Pennsylvania, Philadelphia, PA 19104, USA
e-mail: seyfarth@psych.upenn.edu

D. L. Cheney
Department of Biology, University of Pennsylvania, Philadelphia, PA 19104, USA
e-mail: cheney@sas.upenn.edu

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We can thus trace causation of thought…it obeys the same laws as other parts of structure." Charles Darwin, 1838: *M Notebook*.

1 Introduction

Darwin believed that the course of evolution could be revealed through the comparative method—by contrasting similar traits in related species, examining their common properties, measuring their differences, and searching for branching points in the fossil record. When the trait in question is language, the Darwinian approach might logically begin with a comparative study of human language and non-human primate vocalizations. But this technique has not proved very successful. The two sorts of communication are so different that comparison between them reveals little about their common ancestry. There is, however, another, more indirect, approach—one that examines the evolution of language through its links with cognition.

In humans, language and cognition are inextricably bound together. Through language, we express our thoughts and reveal how we see the world. Language thus offers a window into the mind, a view of mental content. When we use language we perform some of the most complicated mental gymnastics of which humans are capable. Language therefore tells us something about how the mind works.

The vocal communication of monkeys and apes is very different from language. Differences are particularly striking in the area of vocal production. Nonhuman primates make use of a relatively small repertoire of calls that appear fully formed early in life and are, for the most part, not modified as a result of experience (see Seyfarth and Cheney 1997 for review). With some intriguing exceptions (Zuberbuhler 2002; Arnold and Zuberbuhler 2006), nonhuman primate signalers do not combine different call types to create new meaning. Nonetheless, communication in monkeys and apes is clearly linked to their cognition. As a result, we can use their vocalizations to study the content of their knowledge and learn how their minds work. One goal of this paper is to describe some experiments that use vocal playback experiments to examine mental content and cognition in free-ranging baboons (*Papio hamadryas ursinus*).

The close links in both humans and baboons between communication and cognition raise the possibility that we can apply Darwin's comparative method not by contrasting primate vocalizations directly with language but instead by comparing the mental representations that underlie primate communication with some of the cognitive operations that are central to human language. A second goal of this paper is to make such a comparison, perhaps shedding some light on the earliest stages of language evolution.

It is now well accepted that before a child can learn language she must have some experience with the objects, events, and relations that make up her world. As several linguists have put it, "If you couldn't pick pieces of meaning out of the world in advance, before you learned a language, then language couldn't be learnt" (Fisher and Gleitman 2002, p. 447, quoting Chomsky 1982, p. 119). The same argument

appears in theories of language evolution. Pinker and Bloom (1990), for example, propose that "grammar exploited mechanisms originally used for…conceptualization", and Newmeyer (1991) states 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" (for similar views, see Jackendoff 1987, 2002; Kirby 1998; Newmeyer 2003; Hurford 1998, 2003).

The hypotheses that a certain kind of thinking appears before the emergence of language in young children, and evolved before spoken language in our hominid ancestors, are part of a broader intellectual tradition that can be traced to Plato, who believed that one could not acquire a concept that one could not antecedently entertain. More recently, this view has been articulated in Fodor's influential book, *The Language of Thought* (1975). Fodor proposed that human knowledge and reasoning is couched in a "language of thought" that is distinct from external languages like English or Tsetswana. It contains symbols that pertain to people, objects, events, and the categories to which they belong, and causal relations that govern how objects behave in space and time and how people interact with one another.

The language of thought is distinguished from natural languages because of at least two prominent cases in which thought occurs without language. First, animals think, yet they have no language. Once we reject the behaviorist view that mental activities are an "explanatory fiction" (Skinner 1974) and accept the proposition that animals possess information about each other, objects, events, and the relations between them, we commit ourselves to the existence of cognitive processes that are mediated by representational systems other than natural languages (Fodor 1975, p. 57). Second, it is now widely accepted that before they learn language human infants possess "core knowledge" that enormously aids their first categorization of objects, properties, and events in the world (Carey and Spelke 1996). As with animals, the question then becomes how richly specified this private language (or "mentalese") may be, and how experience refines, enhances, and transforms it (Gleitman and Papafragou 2005).

At the same time, the language of thought is called a *language* of thought because it shares many properties with natural languages. Like natural languages, it includes some mental representations that correspond to objects in the world and others that specify the relation between these objects. Applied to humans, the language of thought hypothesis assumes that people—even pre-verbal infants— have "propositional attitudes": mental states with representational content. To have a certain propositional attitude is to be in a specified relation to an internal representation: to know, believe, or fear that something is the case (Fodor 1975; Stalnaker 1999). In both the language of thought and language, propositional attitudes are expressed in the form "thinks that…", "wants that…", and so on.

Applied to theories of language evolution, the language of thought hypothesis predicts that knowledge of objects, events, and conceptual and causal relations preceded language, and that language evolved later as a means to express this knowledge (e.g., Jackendoff 2002, p. 238). Obviously, we cannot test this view

using modern humans, but we can approach the problem indirectly, as Darwin originally suggested, through the study of nonhuman primate communication and cognition. That is what we propose to do here.

But first let us be clear about our methods. Because we are testing the language of thought hypothesis using baboons as our subjects, it might at first appear that we are treating them as living replicas of the 30 million year-old common ancestor of Old World monkeys, apes, and humans. Clearly this would be a mistake. After all, monkeys and apes have undergone their own evolutionary changes in the years since they and we diverged from our common ancestor. Fortunately, though, reconstructing the common ancestor is not our primary goal. Instead, we study baboons in order to learn how, in primates generally, evolution has acted on the communication and cognition of animals that live in large social groups. If we can find general rules that specify how social complexity affects cognition and cognition affects reproductive success, then these rules might usefully be applied to research on the evolution of communication and cognition in other species, including our own.

In the sections below, we hope it will be clear that we are *not* arguing that baboons have a language or that they are capable of anything close to linguistic communication. Instead, we draw attention to some intriguing similarities between the social knowledge of baboons and the organization of word meaning in language. Baboons' social knowledge is directly linked to their survival and reproduction: it represents a set of cognitive skills that has evolved through natural selection. Baboons thus illustrate how some of the mental representations and cognitive skills that underlie language may have first emerged, in rudimentary form, in our pre-linguistic primate ancestors.

Our focus on the early, prelinguistic period of language evolution means that we will not be discussing many features of modern languages whose evolution is hotly debated—features like case, tense, subject–verb agreement, open- and closed-class items, long-distance dependency, subordinate clauses, the subjunctive, subjacency, and the empty category principle. Nothing like these grammatical constructions exists in the communication of any nonhuman primate, including chimpanzees. They undoubtedly emerged during the later stages of language evolution, long after the divergence of the human lineage from the common ancestor of humans and chimpanzees.

So, rather than starting with modern language in all of its complexity and working backward—or, as Jackendoff (2002) puts it, searching within language for traces of its past—we begin instead with a system of communication that is clearly not a language but nonetheless shares some of its features. If we can show that at least some of the properties found in language can also be found in the social intelligence of non-human primates, we may gain a better idea of the cognitive foundations on which language was built.

Finally, some linguists believe that there is a fundamental problem in the application of evolutionary theory to language. For instance, Jackendoff (1990) states "All the characteristics of organisms that have been examined for evidence of natural selection have been either physical structures or patterns of behavior. …Linguistic theory, however, is not [just] about behavior, but rather about the

mental representations that help determine perception and behavior." Here Jackendoff (2002) seems to be arguing that language is not so much a system of communication, on which selection pressures might have acted, as it is a system for mental representation and thought, where the role of evolutionary pressures is more difficult to imagine (Knight et al. 2000).

There is no doubt that language functions as both a means of communication and a tool for organizing and manipulating thoughts. But this, in itself, does not make it different from many other complex behaviors, nor does it make language immune to evolutionary explanations. Whenever an animal can gain a selective advantage by performing a particular behavior, natural selection will simultaneously favor both the behavior itself and whatever morphology, physiology, or cognitive processes are needed to support it. If jays and nutcrackers, for example, can gain an evolutionary advantage by storing and recovering seeds from a huge number of locations, selection will simultaneously favor seed-hiding behavior, memory, and the necessary neurophysiology to support it. And if the ability to represent, organize, and classify other individuals' relationships enables baboons to perform the mental calculations necessary for negotiating their social world, natural selection will favor whatever skills in communication, cognition, and neural machinery are needed to do so.

2 The social background

Baboons are Old World monkeys that shared a common ancestor with humans approximately 30 million years ago (Boyd and Silk 2000; Steiper et al. 2004). They 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. Offspring acquire ranks similar to those of their mothers. Baboon social structure can therefore be described as 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 within matrilines are as stable as those between matrilines (Silk et al. 1999; Cheney et al. 2004), for example $A_1 > A_2 > B_1 > B_2 > B_3$, where letters are used to denote matrilineal families and numbers to denote the ranked individuals within them. The research described here was conducted on a group of approximately 80 individuals, including 20–25 adult females, living in the Okavango Delta of Botswana. The group has been observed for 25 years (for review see Cheney and Seyfarth 2007).

Baboon vocalizations exhibit two properties that make them ideal for experimental studies of social cognition: calls are individually distinctive (Owren et al. 1997; Snowdon 1990) and different call types are given in highly predictable circumstances. During aggressive interactions, for example, acoustically distinctive "threat-grunts" are given only by higher-ranking individuals to those of lower rank, whereas screams and "fear barks" are given only by lower-ranking individuals to those of higher rank. Grunts may be given either "up" or "down" the hierarchy.

3 Baboon social knowledge

Given the complexity of their society, it seems reasonable to ask whether baboons themselves recognize the rank and kin relations that are so apparent to a human observer. To test whether baboons recognize each other's dominance ranks, we first built a library of tape-recorded calls from known individuals and then used a "violation of expectation" paradigm. As a subject went about its daily life, foraging, resting, or feeding, it heard from a concealed loudspeaker either a naturally occurring sequence of calls consistent with the existing dominance hierarchy (e.g., B_2 grunts and C_3 fear-barks) or, on another day, a call sequence that violated the hierarchy (C_3 grunts and B_2 fear-barks). As an additional control, this abnormal sequence was maintained but we added calls from a third female, higher-ranking than the other two, to create a sequence that, interpreted in a particular way, would not violate the hierarchy (C_3 grunts, A_1 grunts, and B_2 fear-barks). Regardless of their own relative ranks, subjects looked toward the speaker for significantly longer durations to call sequences that violated the existing hierarchy than to those that did not (Cheney et al. 1995a). As in experiments with human infants, a significantly longer duration of looking is here interpreted as a "violation of expectation" (Kelman and Spelke 1983; Wang et al. 2004), indicating that the sequence of calls presented subjects with information that was different from their expectations.

To test whether baboons recognize the close associations among individuals in the matrilineal "families" that make up their group, we waited until two adult females, say A_1 and B_1, were sitting together and played them a sequence of calls that mimicked a fight between two other members of their group. When the fight appeared to involve individuals unrelated to the subjects, they showed little change in behavior. However, when the fight involved a relative of A_1, B_1 responded by looking at A_1, and when the simulated fight involved a relative of A_1 and a relative of B_1, the subjects responded by looking at each other. Moreover, in this third condition A_1 (the higher-ranking subject) was significantly more likely to approach and supplant B_1 in the minutes after playback. Subjects responded, in other words, as if they recognized each other's close associates (Cheney and Seyfarth 1999).

Further evidence that baboons recognize the close associations that exist among matrilineal kin comes from research on baboons' "reconciliatory" grunts. Female baboons often behave aggressively toward one another, but after roughly 13% of all fights the dominant individual will give a friendly grunt to the subordinate (Cheney et al. 1995b). Playback experiments have shown that such grunts produce changes in the subordinate's behavior, making her more likely to approach the dominant in a friendly manner or to tolerate the dominant's approach than she would have been if the grunt had not occurred (Cheney and Seyfarth 1997).

A dominant female's attempt to reconcile may be thwarted, however, if her aggression causes the victim to avoid the dominant, fearing further aggression. Baboons, we speculate, may use grunts to reconcile in part because these calls allow an aggressor to reconcile from a distance. We also noted, however, that in some cases aggression between two individuals was followed by a grunt to the victim from a close relative (mother or matrilineal sister) of the aggressor. To test the hypothesis that victims treat such grunts as a "proxy" for reconciliation by the aggressor herself,

Wittig et al. (2007) designed an experiment in which female subjects who had recently been threatened heard grunts from one of their aggressor's close relatives. In the control condition, subjects heard the grunt from a high-ranking female in another matriline. Upon hearing a grunt from one of their aggressor's close relatives, victims looked toward the speaker more often and for longer durations than in the control condition. Moreover, in the next hour subjects were significantly less likely to behave submissively toward both their former aggressor and the aggressor's relative whose grunt they had heard. Their behavior toward control females and other members of the aggressor's matriline was unaffected (Wittig et al. 2007). This experiment provides further, independent support for the hypothesis that baboons can recognize other individuals' matrilineal kin. After receiving aggression, baboons respond differently to a grunt depending upon whether it comes from a relative of their former opponent or another individual. This difference requires that victims be able to identify their opponents' matrilineal kin.

Having shown that baboons recognize each other's ranks and their kin-based associations, we asked whether baboons classify others simultaneously according to rank and kinship, and thus recognize that their group is composed of a hierarchy of families. In this experiment, adult females heard sequences of threat-grunts and screams that mimicked a fight between two unrelated females. One sequence consisted of an anomalous threat-grunt–scream sequence mimicking a *within-family* rank reversal (e.g., B_3 threat-grunts and B_1 screams, Fig. 1). A second consisted of an anomalous sequence mimicking a *between-family* rank reversal (e.g., C_3 threat-grunts and B_1 screams). The third consisted of a no-reversal control sequence consistent with the female dominance hierarchy (e.g., B_1 threat-grunts and B_3 screams, or B_3 threat-grunts and C_1 screams).

If baboons classify others simultaneously according to both individual attributes (rank) and membership in a higher-order class (matriline), they should have
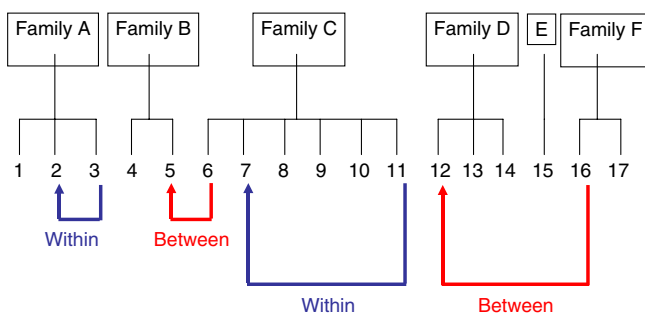

Fig. 1 Hierarchical organization of a baboon group and the design of playback experiments. Matrilineal families are listed left to right in descending rank order. In Bergman et al. (2003), a within-family rank-reversal was simulated by combining a threat-grunt from a lower-ranking member of one family (for example individual A_3) with a scream from a higher-ranking member of the same family (A_2). A between-family rank reversal was simulated by combining a threat-grunt from a lower-ranking member of one family (C_6) with a scream from a higher-ranking individual in a higher-ranking family (B_5). By selecting calls from subjects in large and small families, it was possible to control for rank distance between subjects

responded more strongly to the apparent between-family rank reversal than to the within-family rank reversal. A between-family rank reversal is potentially much more significant than a within-family rank reversal because it signals a possible change in the dominance relations of two entire matrilines rather than just two individuals within the same family. This was indeed the case (Bergman et al. 2003). In contrast, subjects responded relatively weakly both to sequences that mimicked a within-family rank reversal and to those in which no reversal took place.

4 The syntax of social cognition

The vocalizations of monkeys clearly lack any properties that we would be tempted to call syntactic. Nevertheless, the social knowledge of baboons, their assessment of call meaning, and their parsing of call sequences display a number of syntactic properties.

First, primate social knowledge is *representational*. When one monkey hears another's vocalization she acquires information that is highly specific—about a particular sort of predator, or about a particular individual and her motivation to interact in specific ways (threaten, appease, or reconcile) with another.

Second, the social knowledge thus acquired is based on properties that have *discrete values* (Worden 1988). At least in baboons, each individual is unique and unambiguously associated with a specific dominance rank: an individual ranked third always defers to those ranked 1 and 2, and never defers to those ranked 4 and below. Ranks are not "fuzzy" categories. Matrilineal kin associations are equally clear and unambiguous, at least among the close kin (mothers, daughters, and sisters) who formed the subjects of our experiments. Similarly, each call type is recognized as a distinct vocalization and is associated with a specific motivation to interact in a particular way.

Third, animals combine these discrete-valued traits to create a representation of social relations that is *hierarchically structured*. Baboons, for example, create a nested hierarchy in which others are placed in a linear rank order and simultaneously grouped according to matrilineal kinship in a manner that preserves ranks both within and across families.

Fourth, social knowledge is *rule-governed and open-ended*. Baboons recognize that vocalizations follow certain rules of directionality that must, for instance, correspond to the current dominance hierarchy. Threat-grunts are given only by dominant animals to subordinates, *fear* barks are given only by subordinates to dominants, but grunts can be given in either direction. Knowledge is open-ended because new individuals can be added or eliminated without altering the underlying structure, and because the set of all possible interactions is very large (Worden 1998; Seyfarth and Cheney 2003). Taken together, the rule-governed and open-ended properties of primate social knowledge lead to a cognitive system that allows animals to comprehend a huge number of messages from a finite number of signals. If a baboon understands that *Sylvia threat-grunts and Hannah screams* carries a different meaning from *Hannah threat-grunts and Sylvia screams*, she can make the same judgment for all possible pairs of individuals in the group, including any new individuals who may join.

Fifth, knowledge is *propositional*. Baboons evaluate the meaning of call sequences in terms of other individuals' identities, motives and the causal relations that link one individual's behavior with another. That is, they represent in their minds (albeit in a limited way) the individuated concepts of "Sylvia", "Hannah", "threat-grunt", and "scream", and they combine these concepts to create a mental representation of one individual's intentions toward another. In so doing, they interpret a stream of sounds as a dramatic narrative: "Sylvia is threatening Hannah and causing her to scream" (for an empirical test of the hypothesis that baboons listeners know when a vocalization is directed *at them*, and hence recognize another's intention to communicate, see Engh et al. 2006c).

Sixth, knowledge is *independent of sensory modality*. While playback experiments allow us to explore the structure of primates' social knowledge and demonstrate that such knowledge can be acquired through vocalizations alone, social knowledge is also obtained visually. Indeed, we now know that, at the neurophysiological level, visual and auditory information are integrated to form a multimodal representation of call meaning (Ghazanfar and Logothetis 2003; Gil da Costa et al. 2004; Ghazanfar et al. 2005; Barsalou 2005).

In sum, when they hear and interpret a sequence of calls, baboons recognize individuals, assess their motives and behavior, and evaluate the entire call sequence in light of what they know about the dominance hierarchy in their group. Elements of the sequence—the individual calls—retain their own separate meaning, but taken together they convey a meaning that is more than the sum of its parts. Of course, none of these call sequences was produced by a single individual. In their manner of production, they could hardly be more different from language. Nonetheless, baboon listeners interpret the meaning of a sequence of vocalizations in ways that bear important resemblances to the meanings we express in language, which are built up by combining discrete-valued entities in a structured, hierarchical, rule-governed, and open-ended manner. This leads to the hypothesis that the internal representations of language meaning in the human brain initially built upon our pre-linguistic ancestors' knowledge of social relations (Cheney and Seyfarth 1998; Worden 1998). Indeed, as Worden (1998) argues, "no other candidate meaning structure has such a good fit to language meanings."

5 Social cognition and the evolution of language

We are not suggesting that all of the syntactic properties found in language are present in primate social knowledge. Such a claim would be entirely unjustified, given the many features of language (grammatical features in particular—see "Introduction") that have no counterpart in the communication or cognition of any nonhuman primate and that almost certainly evolved long after the divergence of the hominid line from the common ancestors of humans and chimpanzees (for recent discussions, see Jackendoff 1999; Calvin and Bickerton 2000; Hauser et al. 2002; Burling 2005; Johansson 2005). Instead, focusing on the early, prelinguistic stages of language evolution, we suggest that primates—including Old World monkeys, apes, and our hominid ancestors—evolved in an environment characterized by

social challenges and that such competition created selection pressures that favored structured, hierarchical, rule-governed intelligence. Because this social intelligence exhibits, in simpler form, several language-like features, we suggest that many of the rules and computations found in human language may have first appeared as an elaboration of the rules and computations underlying social interactions.

What selection pressures gave rise to social intelligence? Recent data from baboons are beginning to answer this question. In the longest-running study of baboons to date, Silk et al. (2003) found that a female's lifetime reproductive success depended primarily on the rate at which her infants survived, and infant survival was best predicted not by the female's dominance rank (as some might expect) but by the extent of her social networks. Females with more extensive grooming networks had higher infant survival.

Our own long-term study of baboons has combined data on social behavior with concurrent measurement of glucocorticoids, a class of hormones secreted in response to stress. When a baboon, human, or any other mammal faces an acute emergency—like being chased by a lion—the body mounts a stress response. Minutes after the emergency is detected, the adrenal cortex begins to pump glucocorticoids into the blood. The elevated levels of glucocorticoids act both to mobilize energy reserves and to curtail non-essential metabolic activity (Sapolsky 2002, 2004). While adaptive over the short term, this flight-or-fight response is physiologically costly if it persists. Occasional stressors can be tolerated, but long-term, chronic stress drains the body of essential reserves and has many other deleterious consequences. Some hallmarks of prolonged stress are atherosclerosis, cardiovascular disease, and a compromised immune system.

Over a 5-year period, females experienced the greatest stress in response to three events: predation, especially the loss of a close companion (Engh et al. 2006a); the threat of infanticide by new immigrant males (Palombit et al. 1997; Beehner et al. 2005: Engh et al. 2006b); and instability in the female dominance hierarchy (Engh et al. 2006b). In each case, however, after an initial surge in glucocorticoids, females' stress levels returned to baseline. Females' ability to respond to stress in this adaptive way seemed to depend on the formation and maintenance of social relations. For example, females who lost a close companion to predation increased the number of their grooming partners and their time spent grooming in the weeks thereafter. Perhaps as a result, their glucocorticoid levels returned to normal. Females who did not lose a close companion showed no such change in behavior (Engh et al. 2006a). Many females whose infants were threatened by infanticidal males formed a close bond with an adult male "friend", who helped to care for and protect the female and her infant (Palombit et al. 1997). Perhaps as a result, their glucocorticoid levels were lower than those of females who did not form a friendship (Beehner et al. 2005; Engh et al. 2006b). Females whose ranks were threatened by aggression from lower-ranking families formed aggressive alliances with kin, thereby retaining their ranks in most cases (Engh et al. 2006b).

In sum, skills in forming and maintaining social relations are correlated with both increased reproductive success and the ability to mount an adaptive response to stressful stimuli. Skills in communication and cognition are thus linked to fitness. To survive, avoid stress, reproduce, and raise offspring who are themselves

successful, individuals need both a system of communication that allows them to influence other animals' behavior and a system of mental representations that allows them to recognize and predict other animals' behavior—in other words, a representation of social relations that is discretely coded, combinatorial, hierarchically structured, rule-governed, and propositional. The demands of social life have thus led to the evolution of animals who represent their world not just as a collection of different individuals but as a collection of actors, each one of whom is predisposed to behave in certain ways toward each of her possible partners following a number of (usually) predictable rules. Evolution has produced individuals who, despite their limited vocabulary, have propositional attitudes encoded in a language of thought (Cheney and Seyfarth 2007).

The "social origins" hypothesis adds a slightly new wrinkle to theories of language evolution because it proposes that some precursors of grammar may have been part of the cognitive abilities of our pre-linguistic ancestors. In a widely-cited hypothesis, Bickerton (1990) has proposed that language evolved in two stages: first "proto-language" and then modern language (Calvin and Bickerton 2000). Bickerton's model of proto-language is drawn from four sources: pidgin languages (Bickerton 1981), the language of individuals who have been isolated from adults during childhood (Curtiss 1977), children's language at the one-word stage; and the signing of captive apes (e.g., Savage-Rumbaugh 1986). In essence, proto-language is language without syntax (Jackendoff 1999, 2002). By contrast, the social origins hypothesis suggests that some of the cognitive operations that underlie modern syntax were among the earliest precursors of language. Specifically, before language appeared, natural selection favored individuals who, upon hearing a sequence of calls, could combine several discrete, meaningful elements in a rule-governed manner to create a complex, propositional representation of events. In Bickerton's hypothesis, proto-language is grammatically impoverished, making it difficult to imagine a gradual transition from proto-language to language. The social origins hypothesis may in some respects help to alleviate this problem.

The social origins hypothesis also makes chronological sense. If we assume that social complexity favored increasingly sophisticated cognitive abilities, we can imagine how these skills might have created an environment in which natural selection favored more flexible articulation, a full-blown theory of mind, the ability to generate new words, and the ability to create sentences. By contrast, it is difficult to imagine how—or why—these uniquely human skills would have evolved if humans had not first possessed the conceptual capacity that made them adaptive. Indeed, if one accepts the view that there are parallels between primate social cognition and the mechanisms that encode meaning in language, and agrees that the former is a generalized primate trait while the latter are unique to humans, it is hard to imagine that the earliest forms of human syntax did *not* build upon these pre-existing cognitive skills. Before hominids produced syntactic utterances, they assigned meaning to other individuals' calls and extracted syntactic, rule-governed, propositional information from the vocal interactions of others.

The social origins hypothesis also helps explain how social complexity and technological complexity (tool use, for example) may have interacted to shape human evolution. Extrapolating from our research on baboons, it now seems likely

that social complexity and social intelligence are widespread among monkeys and apes. By contrast, the use and manufacture of tools is restricted almost entirely to two of the great apes, chimpanzees and orangutans. With the exception of one New World monkey species, the capuchin, tool use among monkeys is decidedly unimpressive. It therefore seems probable, as Jolly (1966) first proposed, that the technological and innovative skills evident in rudimentary form in chimpanzees (and hyperbolically so in humans) have their roots in the selective forces that originally favored the evolution of social skills. Although innovation, tool use, and technological invention may have played a crucial role in the evolution of ape and human brains (Reader and Laland 2002), these skills were probably built upon mental computations that had their origins and foundations in social interactions.

In sum, we suggest that language-like perception and cognition preceded and set the stage for language-like production. Long before our ancestors spoke in sentences they had a language of thought in which they represented the world—and the meaning of call sequences—in terms of actors, actions, and those who are acted upon.

Talmy (2006) suggests that during the course of evolution a crucial bottleneck was overcome when our ancestors' vocal communication changed from analog to digital, and he poses the question: Where did language get its digitalness from? The answer, we believe, lies in social cognition. Long before they could engage in the computations that underlie modern grammar they performed the computations needed to understand their societies. As a result, the discrete, compositional structure we find in spoken language did not first appear there. It arose, instead, because understanding social life and predicting others' behavior requires discrete, compositional thinking.

Similarly, Hurford (1990) asks whether propositional structures (among other features) are "elements of the structure of languages" or whether they "somehow existed before language" in another domain. Here again, data on primate social cognition provide an answer: the propositions that are expressed in language did not originate with language. They arose, instead, because to succeed in a social group of monkeys or apes one must understand an elementary form of propositional relations.

The linguistic revolution thus occurred when we began to express this tacit knowledge, and to use our cognitive skills in speaking as well as listening. The earliest syntactic utterances, however, were not entirely original. They described relations that their speakers already understood and had a formal structure that grew out of their speakers' knowledge of social relationships.

References

Arnold K, Zuberbuhler K (2006) Language evolution: compositional semantics in primate calls. Nature 441:303

Barsalou L (2005) Continuity of the conceptual system across species. Trends Cog Sci 9:309–311

Beehner JC, Bergman TJ, Cheney DL, Seyfarth RM, Whitten PL (2005) The effect of new alpha males on female stress in free-ranging baboons. Anim Behav 69:1211–1221

Bergman TJ, Beehner JC, Cheney DL, Seyfarth RM (2003) Hierarchical classification by rank and kinship in baboons. Science 302:1234–1236

Bickerton D (1981) Roots of Language. Karoma, Ann Arbor, MI

Bickerton D (1990) Language and species. University of Chicago Press, Chicago

Boyd R, Silk JB (2000) How humans evolved. W.W. Norton, New York

Burling R (2005) The talking ape. Oxford University Press, Oxford

Calvin WH, Bickerton D (2000) Lingua ex machina: reconciling Darwin with the human brain. MIT Press, Cambridge, MA

Carey S, Spelke E (1996) Science and core knowledge. Phil Sci 63:515–533

Cheney DL, Seyfarth RM (1997) Reconciliatory grunts by dominant female baboons influence victims' behaviour. Anim Behav 54:409–418

Cheney DL, Seyfarth RM (1998) Why monkeys don't have language. In: Petersen G (ed) The Tanner lectures on human values, vol 19. Utah University Press, Salt Lake City, pp 175–219

Cheney DL, Seyfarth RM (1999) Recognition of other individuals' social relationships by female baboons. Anim Behav 58:67–75

Cheney DL, Seyfarth RM (2007) Baboon metaphysics. University of Chicago Press, Chicago

Cheney DL, Seyfarth RM, Silk JB (1995a) The responses of female baboons to anomalous social interactions: evidence for causal reasoning? J Comp Psych 109:134–141

Cheney DL, Seyfarth RM, Silk JB (1995b) The role of grunts in reconciling opponents and facilitating interactions among adult female baboons. Anim Behav 50:249–257

Cheney DL, Seyfarth RM, Fischer J, Beehner JC, Bergman TJ, Johnson SE, Kitchen DM, Palombit RA, Rendall D, Silk JB (2004) Factors affecting reproduction and mortality among baboons in the Okavango Delta, Botswana. Int J Primatol 25:401–428

Chomsky N (1982) Noam Chomsky on the generative enterprise: a discussion with Riny Huybregts and Henk van Riemsdijk. Foris, Dordrecht

Cohen YE, Hauser MD, Russ BE (2006) Spontaneous processing of abstract categorical information in the ventrolateral prefrontal cortex. Bio Lett 2:261–265

Curtiss S (1977) Genie: a linguistic study of a modern-day 'wild child'. Academic Press, New York

Engh AL, Beehner JC, Bergman TJ, Whitten PL, Hoffmeier RR, Seyfarth RM, Cheney DL (2006a) Behavioural and hormonal responses to predation in female chacma baboons (*Papio hamadryas ursinus*). Proc R Soc Lond B 273:707–712

Engh AL, Beehner JC, Bergman TJ, Whitten PL, Hoffmeier RR, Seyfarth RM, Cheney DL (2006b) Female hierarchy instability, male immigration, and infanticide increase glucocorticoid levels in female chacma baboons. Anim Behav 71:1227–1237

Engh AE, Hoffmeier RR, Cheney DL, Seyfarth RM (2006c) Who, me? Can baboons infer the target of vocalisations? Anim Behav 71:381–387

Fisher C, Gleitman LR (2002) Language acquisition. In: Pashler HF, Gallistel CR (eds) Stevens handbook of experimental psychology, vol 3: learning and motivation. Wiley, New York, pp 445–496

Fodor JA (1975) The language of thought. Crowell Press, New York

Ghazanfar A, Logothetis N (2003) Facial expressions linked the monkey calls. Nature 423:937–938

Ghazanfar AA, Maier JX, Hoffman KL, Logothetis N (2005) Multisensory integration of dynamic faces and voices in rhesus monkey auditory cortex. J Neurosci 25:5004–5012

Gil da Costa R, Braun A, Lopes M, Hauser MD, Carson RE, Herskovitch P, Martin A (2004) Toward an evolutionary perspective on conceptual representation: species–specific calls activate visual and affective processing systems in the macaque. Proc Natl Acad Sci USA 101:17516–17521

Gleitman LR, Papafragou, A (2005) Language and thought. In: Holyoak K, Morrison R (eds) Cambridge handbook of thinking and reasoning. Cambridge University Press, Cambridge, pp 633–661

Hauser MD, Chomsky N, Fitch W (2002) The faculty of language: what it is, who has it, and how did it evolve. Science 298:1565–1568

Hurford JD (1990) Beyond the roadblock in linguistic evolution studies. Behav Brain Sci 13:736–737

Hurford JD (1998) Introduction: the emergence of syntax. In: Hurford JR, Studdert-Kennedy M, Knight C (eds) Approaches to the evolution of language. Cambridge University Press, Cambridge, pp 299–304

Hurford JD (2003) The neural basis of predicate-argument structure. Behav Brain Sci 26:261–316

Jackendoff R (1987) Consciousness and the computational mind. Basic Books, New York

Jackendoff R (1990) What would a theory of language evolution have to look like? Behav Brain Sci 13:737–738

Jackendoff R (1999) Possible stages in the evolution of the language capacity. Trends Cog Sci 3:272–279

Jackendoff R (2002) Foundations of language. Oxford University Press, Oxford

Johansson S (2005) Origins of language: constraints on hypotheses. John Benjamins, Philadelphia

Jolly A (1966) Lemur social behavior and primate intelligence. Science 153:501–506

Kellman PJ, Spelke ES (1983) Perception of partially occluded objects in infancy. Cog Psych 15:483–524

Kirby S (1998) Fitness and the selective adaptation of language. In: Hurford JR, Studdert-Kennedy M, Knight C (eds) Approaches to the evolution of language. Cambridge University Press, Cambridge, pp 359–383

Knight C, Studdert-Kennedy M, Hurford JR (2000) Language: a Darwinian adaptation? In: Knight C, Studdert-Kennedy M, Hurford JR (eds) The evolutionary emergence of language. Cambridge University Press, Cambridge, pp 1–15

Newmeyer F (1991) Functional explanations in linguistics and the origins of language. Lang Commun 11:3–28

Newmeyer F (2003) Grammar is grammar and usage is usage. Language 79:682–707

Owren MJ, Seyfarth RM, Cheney DL (1997) The acoustic features of vowel-like grunt calls in chacma baboons (*Papio cynocephalus ursinus*): implications for production processes and functions. J Acoust Soc Am 101:2951–2963

Palombit RA, Seyfarth RM, Cheney DL (1997) The adaptive value of friendships to female baboons: experimental and observational evidence. Anim Behav 54:599–614

Pinker S, Bloom P (1990) Natural language and natural selection. Behav Brain Sci 13:713–783

Reader SM, Laland KN (2002) Social intelligence, innovation, and enhanced brain size in primates. Proc Natl Acad Sci USA 99:4436–4441

Sapolsky R (2002) Endocrinology of the stress response. In: Becker JB, Breedlove SM, Crews D, McCarthy MM (eds) Behavioral endocrinology. MIT Press, Cambridge, MA, pp 409–450

Sapolsky RM (2004) Social status and health in humans and other animals. Annu Rev Anthropol 33:393–418

Savage-Rumbaugh ES (1986) Ape language: from conditioned response to symbol. Columbia University Press, New York

Seyfarth RM, Cheney DL (2003) Signalers and receivers in animal communication. Annu Rev Psychol 54:145–173

Silk JB, Seyfarth RM, Cheney DL (1999) The structure of social relationships among female savannah baboons in Moremi Reserve, Botswana. Behaviour 136:679–703

Silk JB, Alberts SC, Altmann J (2003) Social bonds of female baboons enhance infant survival. Science 302:1231–1234

Skinner BF (1974) About behaviorism. Knopf, New York

Snowdon CT (1990) Language capacities of nonhuman primates. Yearbk Phys Anthropol 33:215–243

Stalnaker R (1999) Propositional attitudes. In: Wilson RA, Keil FC (eds) The MIT encyclopaedia of the cognitive sciences. MIT Press, Cambridge, MA, pp 678–679

Steiper ME, Young NM, Sukarna TY (2004) Genomic data support the hominoid slowdown and an Early Oligocene estimate for the hominoid–cercopithecoid divergence. Proc Natl Acad Sci USA 101:17021–17026

Talmy L (2006) Recombinance in the evolution of language. Paper presented at the 6th International Conference on the evolution of language, Rome

Wittig RM, Crockford C, Wikberg E, Seyfarth RM, Cheney DL (2007) Kin-mediated reconciliation substitutes for direct reconciliation in baboons. Proc R Soc Lond B 274:1109–1115

Wang S, Baillargeon R, Brueckner L (2004) Young infants' reasoning about hidden objects: evidence from violation-of-expectation tasks with test trials only. Cognition 93:167–198

Worden R (1998) The evolution of language from social intelligence. In: Hurford JR, Studdert-Kennedy M, Knight C (eds) Approaches to the evolution of language. Cambridge University Press, Cambridge, pp 148–168

Zuberbuhler K (2002) A syntactic rule in forest monkey communication. Anim Behav 63:293–299