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The Primate Mind before Tools, Language, and Culture

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Plato says in Phaedo that our "necessary ideas" arise from the preexistence of the soul, are not derivable from experience—read monkeys for preexistence.

We can thus trace causation of thought…it obeys the same laws as other parts of structure.

— Charles Darwin, 1838 [1987]: Notebook M

INTRODUCTION

Beginning with the arrival of the first stone tools, roughly 2.3 million years ago (Semaw 2000), the archaeological record provides a rich source of data from which to reconstruct the evolution of human mind and behavior. Supplementing these historical data, some living monkeys and apes, particularly chimpanzees, make tools (McGrew 1994, Matsuzawa 1994, Yamakoshi 2001) and exhibit a limited form of culture (Whiten et al. 1999), allowing these species to be used as points of comparison when developing theories about human cognitive evolution.

But what about the period before tools and culture appeared? Regardless of whether they were made by early hominids or modern chimpanzees, tools and culture did not emerge *de novo*—they were, instead, the product of minds that had been evolving for millions of years in response to a variety of selection pressures. What were these selective forces and what kind of cognition did they produce? To reconstruct the evolution of mind before tools and culture, our hypotheses must come primarily from the behavior and cognition of modern primates—a much more speculative enterprise since these species have themselves undergone their own evolutionary changes during the millions of years since they diverged from the common ancestor of monkeys, apes, and humans (the anthropoid primates).

Baboons and other Old World monkeys rarely if ever manufacture tools. Unlike chimpanzees, they have few if any traits that could be called cultural. Yet they, like other primates, have larger brains than non-primate mammals of a similar size (Martin 1990). Why? In *Baboon Metaphysics* (Cheney and Seyfarth 2007), we argue that the baboon mind—and, by extension, that of other nonhuman anthropoid primates—has been shaped by natural selection acting in a complex social environment. Baboons live in a society where reproductive success depends on social skills. As a result, natural selection has favored a mind that is specialized for observing social life, computing social relations, and predicting other animals' behavior.

Here we offer three additional speculations concerning the evolution of human cognition, based on our research on baboons. First, long before the evolution of language and culture, the demands of social life created primates who recognized others as individuals and arranged them into groups according to an implicit set of rules. These ancestors had, in effect, a theory of social organization. Second, the prior evolution of social cognition created individuals who were, in some important respects, preadapted to develop the cognitive skills that would eventually underlie language. The discrete, compositional structure we find in modern language did not first appear there, but arose instead because understanding social life and predicting others' behavior requires discrete, compositional thinking. Third, as Alison Jolly first proposed in 1966, the technological skills and cultural traits evident in rudimentary form in chimpanzees—and hyperbolically so in humans—have their historical roots in the evolution of social skills. In this chapter we review some of the data that lead to these speculations and discuss them in greater detail.

SOCIAL KNOWLEDGE IN BABOONS

Baboons (*Papio hamadryas*) are Old World monkeys that shared a common ancestor with humans roughly 30 million years ago (Steiper, Young, and

Sukarna 2004). They 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 (Silk, Seyfarth, and Cheney 1999, Silk, Altmann, and Alberts 2006a, 2006b). 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). Ranks within matrilines are as stable as those between matrilines: for example, A1>A2>A3>B1>B2>C1, where letters are used to denote matrilineal kin groups and numbers denote the different individuals within them (Cheney and Seyfarth 2007).

Baboon vocalizations, like those of many other primates, are individually distinctive (e.g., Owren, Seyfarth, and Cheney 1997; Rendall 2003), and playback experiments have shown that listeners recognize the voices of others as the calls of specific individuals (reviewed in Cheney and Seyfarth 2007). The baboon vocal repertoire contains a number of acoustically graded signals, each of which is given in predictable contexts. Because calls are individually distinctive and each call type is predictably linked to a particular social context, baboon listeners can potentially acquire quite specific information from the calls that they hear. Experiments that test what information actually is obtained are thus, in effect, tests of social cognition.

Throughout the day, baboons hear individuals giving vocalizations to each other. Some interactions involve aggressive competition; for example, when a higher-ranking animal gives a series of threat-grunts to a lower-ranking animal and the latter screams. Threat-grunts are aggressive vocalizations given by higher-ranking to lower-ranking individuals, whereas screams are submissive signals, given primarily by lower-ranking individuals to higher-ranking ones. A threat-grunt-scream sequence, therefore, potentially provides information not only about the identities of the opponents involved but also about who is threatening whom. Baboons are sensitive to both types of information. In playback experiments, listeners respond with apparent surprise to sequences of calls that appear to violate the existing dominance hierarchy. They show little response upon hearing the sequence "B2 threat-grunts and C3 screams", but respond strongly—by looking toward the source of the call—when they hear "C3 threat-grunts and B2 screams" (Cheney, Seyfarth, and Silk 1995a). In addition, between-family rank reversals (C3 threat-grunts and B2 screams) elicit a stronger violation of expectation response than do within-family rank reversals (C3 threat grunts and C1 screams) (Bergman et al. 2003).

A baboon who ignores the sequence "B2 threat-grunts and C3 screams" but responds strongly when she hears "C3 threat-grunts and B2 screams" reveals, by her responses, that she recognizes the identities of both participants, their relative ranks, and their family membership. Baboons who react more strongly to call sequences that mimic a between-family rank reversal than to those that mimic a within-family rank reversal act as if they classify individuals simultaneously according to both rank and kinship (Bergman et al. 2003). In both of these cases, listeners act as if they assume that the threat-grunt and scream have occurred together not by chance, but because one vocalization caused the other to occur. Without this assumption of causality there would be no violation of expectation when B2's scream and C3's threat-grunt occurred together.

Baboons' ability to deduce a social narrative from a sequence of sounds reveals a cognitive system in which listeners extract a large number of complex, nuanced messages from a relatively small, finite number of signals. A baboon who understands that "B2 threat-grunts and C3 screams" is different from "C3 threat-grunts and B2 screams" can make the same judgment for all possible pairs of group members as well as any new individuals who may join. This open-ended system of classification is, in at least one respect, abstract, because the categories of rank and matrilineal kinship persist despite changes in the individuals who comprise them (Cheney and Seyfarth 2007: chaps. 6, 7).

In addition to making judgments based on social causation, rank, and kinship, baboons appear to recognize other individuals' intentions and motives. Baboon groups are noisy, tumultuous societies, and a baboon would not be able to feed, rest, or engage in social interactions if she responded to every call as if it were directed at her. In fact, baboons seem to use a variety of behavioral cues, including gaze direction and the memory of recent interactions with specific individuals when making inferences about the target of a vocalization. For example, when a female hears a recent opponent's threat-grunts soon after fighting with her, she responds as if she assumes that the threat-grunt is directed at her, and she avoids the signaler. However, when she hears the same female's threat-grunts soon after grooming with her, she acts as if the calls are directed at someone else and ignores the calls (Engh et al. 2006a).

The attribution of motives to others is perhaps most evident in the case of 'reconciliatory' vocalizations. Like many other group-living animals, baboons incur both costs and benefits from joining a group. In an apparent attempt to minimize the disruptive effects of within-group competition, many primates 'reconcile' with one another, by coming together, touching, hugging, or grooming after aggression (Cheney, Seyfarth, and Silk 1995b). In baboons, reconciliation among females occurs after roughly 10% of fights, and typically occurs when the dominant animal grunts to the subordinate (Cheney, Seyfarth, and Silk 1995b, Silk, Cheney, and Seyfarth 1996). Playback experiments have shown that, even in the absence of any other behavior, grunts alone function to restore former opponents' behavior to baseline levels. When a subordinate female hears her opponent grunt soon after a fight, she approaches her opponent and tolerates her opponent's approaches at a rate that is even higher than baseline rates (Cheney and Seyfarth 1997). In contrast, hearing the grunt of another, previously uninvolved high-ranking female unrelated to her opponent has no effect on the subordinate's behavior.

In some cases, the behavior of subordinates after aggression seems to involve more complex and indirect causal reasoning about both other animals' motives and their kinship bonds. Playback experiments have shown that baboons will accept the 'reconciliatory' grunt by a close relative of a recent opponent as a proxy for direct reconciliation by the opponent herself (Wittig et al. 2007). If individual D1 has been threatened by individual A1 and then hears a grunt from A2, in the hour that follows she is more likely to approach, and more likely to tolerate the approaches of, A1 and A2 than if she had heard no grunt or a grunt from another high-ranking individual unrelated to the A matriline. Intriguingly, D1's behavior toward other members of the A matriline does not change. Subjects in these experiments act as if they recognize that a grunt from a particular female is causally related to a previous fight, but only if the caller is a close relative of her former opponent.

THE FUNCTION OF SOCIAL COGNITION

Baboons live in a society where reproductive success depends upon social skills. Among female baboons living in Kenya, longevity and infant survival are the best predictors of reproductive success, and the best predictor of infant survival is the extent of a female's social integration (Silk, Alberts, and Altmann 2003). Females are strongly motivated to form close social bonds (as measured by frequent proximity and grooming) with others, particularly their matrilineal kin. When a mother dies, females respond by strengthening their bonds with other matrilineal kin. When few or no matrilineal kin are available, they form bonds with paternal sisters and/or unrelated individuals (Silk, Altmann, and Alberts 2006a, 2006b).

In our study group, females experienced the greatest stress (as measured by elevated glucocorticoid levels; Sapolsky 2002) from predation and infanticide—the two events that exert the greatest effect on their own and their infants' survival and reproduction. When infants were threatened with infanticide, their mothers alleviated stress by forming a temporary pair bond, or 'friendship' with an adult male; when a close female companion was killed by a predator, females alleviated stress by broadening and extending their network of bonds with other females (Beehner et al. 2005, Engh et al. 2006b, 2006c). During a "calm" period without infanticide or predation, females whose grooming networks focused on a few preferred partners had lower baseline glucocorticoid levels than did females whose grooming was spread more widely among others (Crockford et al. 2008). When the same females were subsequently challenged by the threat of infanticide, individuals with the most focused grooming networks and the lowest baseline levels showed the smallest increase in glucocorticoid levels (Wittig et al. 2008).

A female's ability to form stable, persistent bonds with other females had a direct effect on her reproductive success. Lifetime reproductive success was most strongly influenced by a female's lifespan and the survival of her infants (Cheney et al. 2004). Females with stronger, more stable, and more enduring social bonds exhibited significantly higher infant survival (Silk et al. 2009) and lived longer (Silk et al. 2010) than females with weaker, less stable social bonds. Dominance rank also affected females' longevity (high-ranking females lived longer), however, the strength of a female's social bonds and her dominance rank had independent effects on longevity. Results suggest that the ability to form strong, enduring social bonds—an indication of social intelligence (see below)—may have allowed low-ranking females to overcome at least some of the limitations imposed by their social status.

In sum, a female baboon's social skills affect her reproductive success. Under these conditions, an individual must know as much as possible about other animals' relations—that is, she must have a sophisticated understanding of the individuals in her group, their long-term associations, short-term bonds, and the motivations that underlie them. Natural selection has thus favored the evolution of skills in identifying and classifying conspecifics because these skills are essential to survival and reproduction (Cheney and Seyfarth 2007).

THE ORIGIN OF SOCIAL CONCEPTS

A variety of research suggests that the mind of a human infant is not a *tabula rasa*. Instead, infants begin life with what Carey (2011:113) has called "a set of innate conceptual representations…that guide an infant's expectations of which objects go together and how they are likely to behave." In Keil's words, they "embody systematic sets of beliefs [that are] largely causal in nature" (1989:1).

How do infants bring together their knowledge of 'what objects go together' and how these objects behave? Reviewing studies of children's cognitive development, Keil (1994) distinguishes between two broadly different hypotheses: "One strongly empiricist account argues that early concepts are devoid of a theory, which then gradually gets overlaid. The other view, which will be called the primal theories account, argues that concepts are embedded within theorylike relations from the start" (1994:235). According to the latter hypothesis, "even in infancy, some very crude theoretical biases start to be abstracted away" from the regularities observed in the social and physical world (1994:238). In Gopnik and Wellman's (1994) terms, an empiricist child may be able to make generalizations that allow her to predict behavior, but these generalizations do not yet constitute a theory because they "are not far removed from the evidence itself." Theories, in contrast, make "predictions about a wide variety of evidence, including evidence that played no role in the theory's initial construction" (1994:261).

Of course, it would go far beyond the evidence to suggest that baboons have the same kind of theories or concepts we see in young children. Nonetheless, there are points at which baboons appear to make deductions that go beyond the mere observations of behavior—deductions that suggest that they have some underlying theory about individuals, their motives, and how these motives are likely to be expressed.

For example, consider the phenomenon of individual recognition, which is widespread among animals (Tibbetts and Dale 2007). Nonhuman primates—and perhaps many other species—have neural structures that appear to be specialized for identifying individual faces and voices (reviewed in Seyfarth and Cheney 2008). Individual recognition is also cross-modal: when a female baboon hears her offspring's call she looks toward the source of the sound (e.g., Cheney and Seyfarth 1999), as if the sound has created an expectation of what she will see if she looks toward its source. Dogs and squirrel monkeys associate the faces and voices of their caretakers (Adachi, Kuwahata, and Fugita 2007, Adachi and Fujita 2007), while horses associate the whinny of a specific herd member with the sight of that individual (Proops, McComb, and Reby 2008). Humans, of course, do this routinely, integrating information about faces and voices to form the rich, multimodal percept of a person (Campanella and Belin 2007).

Taken together, these results suggest that individual recognition in many animals involves the formation of a concept—the concept of animal X—that cannot be reduced to or defined in terms of any single sensory attribute. It involves, instead, the integration of many different attributes into a single percept, such that the sound of X's voice creates an expectation of what one will see and the sight of X creates an expectation of what one will hear. These concepts are formed without language: animals do not give names to each other. How they develop is unclear. Obviously, animals require experience to recognize the members of their group and any new animals who join or are born into it. But neural structures specialized for the recognition of individual faces, voices, and their cross-modal integration suggest that animals in some species have an innate predisposition to form the concept of an individual—an innate conceptual representation that parallels those found in human infants. Finally, individual recognition has a long evolutionary history, appearing throughout the animal kingdom. Perhaps one of the earliest concepts—whenever it appeared—was a social one: what in our species we call the concept of a person.

Building on the recognition of individuals, baboons go on to recognize what human observers describe as "close associates." Here the animals act as if they have a theory: one that is causal because it is based on assumptions about why individuals behave the way they do ("because they are members of the same matriline, or close associates"), and one that has generality because it makes predictions about a wide variety of evidence, some of which played no role in the theory's initial construction. On the basis of some minimal observations (as yet unknown), baboons conclude that, if A1 and A2 interact in certain ways in some contexts (when feeding, for example), they can therefore be counted on to behave in predictable ways in many other contexts—when forming an alliance, or grooming, or reconciling with each other's former opponents. In apparently predicting how matrilineal kin will interact under a wide variety of circumstances, baboons act as if they have a theory about "matrilineal families"—how they should be recognized and how, once identified, individuals within them are likely to behave. The baboons then use this theory to predict behavior.

When it comes to recognizing matrilineal kin groups, baboons are "essentialists" (Gelman, Coley, and Gottfried 1994). They act as if the members of kin groups "have essences or underlying natures that make them the things that they are." These essences cannot be based on physical appearance, because members of the same matriline do not look alike (think of mothers, their infants, and their adolescent sons) or share any other physical features that distinguish them from the members of other matrilines. Baboons' classification of others must be based on something more abstract. It constitutes a kind of implicit theoretical knowledge because "one of the things that theories do is to embody or provide causal linkages from deeper properties to more superficial or surface properties" (Medin 1989:1476).

Consider, as another example, the baboons' ascription of motives to others. When a baboon hears the sequence "Sylvia threat-grunts and Hannah screams," she responds as if she assumes a causal relation between the two events: the threat-grunt and the scream occurred together not by chance but because the former caused the latter. The listener has no other evidence on which to base this assumption because she cannot see the animals interacting. Only her memory of past interactions can guide her perception of current events. And yet she makes the assumption of causality not just for Sylvia and Hannah but for every combination of females whose calls she hears. The listener acts as if she has a general theory about how individuals—all individuals—interact.

In much the same way, recall that, in several experiments, a baboon who grooms with X and then, some minutes later, hears X's threat grunt shows little if any response. She acts as if the threat grunt is not directed at her. In contrast, if the baboon has recently fought with X and then hears X's threat grunt, she responds strongly, as if the threat is meant for her. These results hold across many different trials in which many different individuals were substituted for X (see references above). The subject, in other words, acts as if she has a theory that can be applied to all individuals in her group—not just X. Individuals with whom you groom are kindly motivated toward you and this motivation is likely to persist over time, whereas individuals who have recently threatened you are not kindly motivated and this, too, predicts their subsequent behavior. Of course, these expectations probably begin with the formation of relatively simple, Pavlovian associations between, say, grooming with X and subsequent friendly behavior with X. But these associations are not enough to explain the baboons' behavior. Instead, as they develop into adults baboons seem to develop some very crude generalizations—or "theoretical biases" (Keil 1994) that allow them to organize what they know about other individuals.

Lastly, it is interesting to note that as children's conceptual skills develop they begin to formulate many different concepts in parallel—concepts that can differ widely in both the objects they include and the causal mechanisms that underlie them (Carey 1985). The formation of multiple concepts helps elucidate the children's growing skill because, as Keil (1989:1) points out, "no individual concept can be understood without some understanding of how it relates to other concepts." Here again, baboons provide us with a rich source for speculation because they appear to have different social concepts that follow different rules. Individuals grouped together in the same matriline are assumed, by virtue of this grouping, to behave in certain ways toward each other. Individuals arranged in a linear dominance hierarchy follow different rules. The concepts 'matrilineal kin group' and 'dominance hierarchy' thus differ in their essential properties, but they can also be merged to form a more complex concept of 'ranked matrilines' (Bergman et al. 2003).

IMPLICATIONS FOR RESEARCH ON THE EVOLUTION OF HUMAN COGNITION

We propose that, long before the evolution of human language and culture, natural selection favored individuals who could predict each other's behavior and form social relationships that returned the greatest benefit to them. In doing so, selection favored skills in recognizing and classifying individuals along multiple abstract dimensions (rank, kinship, and so on). Because these skills evolved long before the appearance of tools, culture, or language, they acted as important "prime movers" in human evolution, preadapting individuals for the evolution of more advanced abilities, such as shared attention, a full-blown theory of mind, teaching, and cultural transmission.

PREADAPTATIONS FOR LANGUAGE

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 the vocalizations of non-human anthropoid primates. But this technique has not proved very successful, because the two sorts of communication are so different that comparison between them reveals little about their common ancestry. The differences are most pronounced in call production. Nonhuman primates have a relatively small repertoire of calls, each of which is closely linked to particular social circumstances and shows little modification during development (see Hammerschmidt and Fischer 2008 for a review). With some intriguing exceptions (Zuberbuhler 2002, Arnold and Zuberbuhler 2006), nonhuman primate signalers do not combine different call types to create new meaning.

We suggest, however, that for those interested in reconstructing the evolution of language these differences in production have been overemphasized, distracting attention from studies of perception and cognition where continuities with language are more apparent. Here nonhuman primates have a much larger repertoire and an almost open-ended ability to learn new sound-meaning pairs throughout their lives (Seyfarth and Cheney 2008). And while, for the most part, they do not create call combinations, nonhuman primates hear them all the time, whenever two individuals vocalize to each other. Their interpretation of the information contained in these call sequences reveals a discrete, computational mode of thinking that shares several properties with human language processing.

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 Noam Chomsky has 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 2002:447; Chomsky 1982:119). 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) suggests that "[t]he 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 hominin ancestors, are widely accepted but rather vague. What kind of conceptual thinking? Concepts about what? We propose that nonhuman primate social knowledge shares several properties with human language that may be relevant to theories of language evolution.

First, primate social knowledge is representational. When one baboon 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, social knowledge is based on properties that have discrete values (Worden 1998). At least in baboons, each individual is unique and unambiguously associated with a specific dominance rank. Ranks are not "fuzzy" categories: an individual ranked third always defers to those ranked first and second but never defers to those ranked fourth or below. Matrilineal kin associations have boundaries that are slightly less precise (e.g., Dasser 1988), but they still constitute a category to which an individual either belongs or does not.

Third, nonhuman primates 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, loosely speaking, 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.

Some Caveats

There are important limits to the parallel we have drawn between nonhuman primate social cognition and the cognitive operations that underlie language. Note, for example, that agents, actions, and recipients in a baboon call sequence are not coded in the way we usually encounter them in language. For baboon listeners, agent and action are coded in the threat-grunts, which are recognizable as aggressive vocalizations and identifiable as Sylvia's. The same holds for Hannah's screams. Although the precise order of calls seems relatively unimportant in listeners' assessment of the event, their temporal and spatial juxtaposition is not. Listeners behave as if they assume that the calls do not occur together by chance, but instead are juxtaposed because Sylvia's threat-grunt *caused* Hannah's scream. We suggest, therefore, that the propositional information baboons acquire when they hear vocalizations includes an understanding of the causal relations that link an actor's threat-grunts and a recipient's screams.

Perhaps more important, none of the call sequences we describe was produced by a single individual. In their manner of production, therefore, baboon vocalizations could hardly be more different from language. Despite this difference, however, listeners interpret the meaning of a sequence 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 by humans initially built upon our pre-linguistic ancestors' knowledge of social relations (Cheney and Seyfarth 1998, Worden 1998). Indeed, as Worden (1998:156) argues, "no other candidate meaning structure has such a good fit to language meanings."

Lastly, we are not suggesting that all of the syntactic properties found in language are present in nonhuman primate social knowledge. Such a claim would be entirely unjustified, given the many features of language—like case, tense, subject-verb agreement, open- and closed-class items, and recursion—that have no counterpart in the communication or cognition of any nonhuman primate and almost certainly evolved long after the divergence of the hominin line from the common ancestor of humans and chimpanzees (for recent discussions see Jackendoff 1999, Calvin and Bickerton 2000, Hauser, Chomsky, and Fitch 2002, Burling 2005, Johansson 2005, Hurford 2007). Instead, focusing on the early, prelinguistic stages of language evolution, we suggest that primates—including Old World monkeys, apes, and our hominin ancestors—evolved in a social environment that created selection pressures favoring structured, hierarchical, rule-governed intelligence.

Because this social intelligence exhibits, in simpler form, several language-like features, many of the rules and computations found in human language first appeared as an elaboration of the rules and computations underlying social interactions.

First Thought, Then Language

The "social cognition" 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 prelinguistic ancestors. In a widely cited hypothesis, Bickerton has proposed that language evolved in two stages: first "proto-language" and then modern language (1990, 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 cognition 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 cognition hypothesis may in some respects help to alleviate this problem.

The social cognition 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.

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.

SOCIAL COGNITION AND THE EVOLUTION OF TECHNOLOGY

Finally, the social cognition hypothesis may help explain how social complexity and technological complexity—the use and manufacture of tools, for example—may have interacted to shape human evolution. Extrapolating from our research on baboons, it 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 found in chimpanzees (and greatly elaborated 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.