

Pre-Hunt Communication Provides Context for the Evolution of Early Human Language

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Abstract

The origin of human language is one of the most fascinating and most difficult problems of evolution. Here I argue that pre-hunt communication was the starting context of the evolution of human language. Hunting of big game created a shared interest; animals and hunting actions are easy to imitate; the need to plan created a pressure for increasing complexity; and finally, cultural inheritance of hunting tools and know-how made the transition unique. I further argue that this “first step” was actually a two-stage process where first indexical and iconic signs evolved to coordinate recruitment for the hunt; then later, in the second stage, the complexity of this communication system increased as a response to the increased demand to coordinate group-hunting effort (including division of labor). I provide a review of the fossil record and show that the available evidence is fully compatible with the theory.

Keywords

big-game hunting, coordination of group activity, evolution of early human language, pre-hunt communication, transmission of know-how

There are two sharply conflicting views regarding the origin of human language. The first considers language as a unique human feature that cannot be accounted for in terms of natural selection (Chomsky 1986; Hauser et al. 2002). The second view accepts the uniqueness of human language in terms of communication (Hockett 1963) and views it as a complex biological organ that could evolve only by means of natural selection (Darwin 1871; Hockett 1963; Bickerton 1990, 1995; Givón 2002; Pinker and Bloom 1990; Pinker 1994; Maynard Smith and Szathmáry 1995; Hurford 2007). One of the key difficulties faced by the proponents of natural origins is to identify the context in which the evolution of language started, that is, to identify the ultimate evolutionary forces that triggered that evolution. A wide variety of theories exists, ranging from sexual selection (Darwin 1871; Miller 2001) through tool making (Greenfield 1991) to the maintenance of group identity (Knight 1998) and social cohesion (Dunbar 1998; see Számadó and Szathmáry 2006 for a review). However, none of these theories is widely accepted as a satisfactory explanation. The aim of this article is to identify the context and the possible selective forces that drove the evolution of early human language. I suggest that this context was pre-hunt communication serving recruitment and the coordination of group hunting. This suggestion is not new and can be traced back to the hallmark paper of Washburn and Lancaster (1968). The idea was later elaborated and connected with the gestural theory of the origin of language by Hewes (1973). However, neither attempt was successful in establishing the “hunting origin” of human language. This was a result of several factors ranging from political correctness (i.e., it was not acceptable to propose a scenario in which women had no role in the origin of language) to the fascinating new discoveries highlighting the complexity of primate social life and social organization (Goodall [1971] 1996, 1990; de Waal 1982). These discoveries led to new theories that centered on social pressures that might have selected for language, including mate choice, mate bonding, gossip, trading information for position, and group bonding (Deacon 1997; Dessalles 1998; Dunbar 1998; Knight 1998; Power 1998; Miller 2001; Burling 2005). This new wave of theories made hunting theories look like obsolete remnants of the past, outdated and overthrown. However, these new theories could not give a consistent account either. As a result there is an increasing amount of skepticism toward such theorizing (Bickerton 2003; Hauser and Fitch 2003). Moreover, none of these new theories can give a selective scenario that would explain the honesty, uniqueness, expressive power, and groundedness of human language—conditions that were identified as necessary for any theory that tries to explain the origin of human language (Számadó and Szathmáry 2006).

Why should anyone risk reviving an old account of language origin under these circumstances? There are four reasons for this revival: (1) There has been a huge advance in

knowledge since the original publication of Washburn and Lancaster (1968); (2) the proposed theory fulfills all the relevant criteria that one could demand (Számadó and Szathmáry 2006); (3) it can explain the fossil record; and (4) it has testable predictions.

What Has to Be Explained?

Számadó and Szathmáry (2006) gave a list of requirements that one would expect from a theory that tries to explain the origin of early human language. Here I only give a brief summary of these requirements, namely honesty, groundedness, power of generalizations, and uniqueness. Honesty assumes a situation in which there is no conflict of interest between the participants. Groundedness assumes that potential words can be grounded in reality; that is, named objects and concepts can be referred to by other means (for example, by pointing) and not by just vocal means. Power of generalization implies that the scenario should be rich enough to demand an increasing complexity of communication. Last but not least, uniqueness means that the scenario should be able to explain why only humans and not other animals living under somewhat similar conditions evolved language.

Számadó and Szathmáry (2006) in their review surveyed all the available alternative theories and concluded that in their present form none of these theories fits all the criteria described above. Most of these theories center around a social context, such as grooming, gossip, pair bonding, sexual selection, status for information, parent–offspring contact, or group bonding. In most of these situations there are problems with honesty, groundedness, and uniqueness. Conflict of interest is almost always present in social situations; abstract concepts (such as “faithful” or “philander”) cannot be easily grounded; and mating calls, contact calls, or pair-bonding rituals are not unique, observed in countless species, and thus do not require the level of complexity that could drive the evolution of human language. Only two promising theories were found. One is Greenfield’s theory (1991) that builds on the parallel cognitive requirements necessary for tool making and language production; the other is the hunting theory put forth by Washburn and Lancaster (1968) and mentioned briefly by Hewes (1973). The problem with tool making is that it cannot account for the uniqueness of human language, as chimpanzees also make and use tools. One problem with the hunting theory is also uniqueness, as there are other group-hunting mammals such as lions, wolves, African hunting dogs, and so on, which are highly efficient hunters yet do not have a communication system comparable to human language. The other main problem was the lack of detail, which is understandable as most of the groundbreaking information was published after the original paper. Unfortunately, no one took up the gauntlet for more than 30 years to re-evaluate the hunting theory in the light of new

discoveries. Here I do this and argue that it is the only scenario that fits all the criteria put forth by Számadó and Szathmáry (2006).

Proposition

The role of early human language was recruitment and the coordination of group-hunting behavior. In order to show the validity of this proposition the following points have to be shown:

1. Hominids hunted big game that could not be killed by a lone hunter, and hunted for a reasonably long time (i.e., sufficiently long to have enough time to evolve a complex communication system such as human language).
2. The ability to recruit large hunting parties gave a selective advantage.
3. There was a need for pre-hunt communication to coordinate hunts. That is, the situation required the power of generalization.
4. All the necessary signals could arise by means of imitating the actions of the hunters or the animals involved. That is, the situation fits the groundedness criteria.
5. There was a shared interest. In addition, even though cheating could not be ruled out (i.e., one agrees to participate in the hunt but does something else), the situation was such that signals (promises) could be cross-checked (see Lachmann et al. 2001), thus cheating was not a viable strategy.
6. In addition, one has to be able to show why other social carnivores did not evolve the language-like communication.

In the following sections I will discuss these points.

Big-Game Hunting in Early Hominids

There is abundant evidence that the global climate became generally colder during the Plio-Pleistocene starting around 2.8 Mya; in parallel with this, environments became colder and drier in Africa, which favored the spread of open savannah (Bobe et al. 2002; Alemseged 2003; Bobe and Behrensmeyer 2004; deMenocal 2004; Fernandez and Vrba 2006). This in turn resulted in a change in the mammalian fauna, favoring the spread of species adapted to this new environment. According to Bobe and Behrensmeyer (2004), there were four pulses of high faunal turnover in the Turcana basin that occurred in the following intervals: 3.4–3.2, 2.8–2.6, 2.4–2.2, and 2.0–1.8 Mya. Taxa associated with closed woodland show a steady decline after 3.2 Mya. The abundance of bovid species adapted to open grassland increased during 2.5–2.0 Mya. The origin of *Homo* and lithic technology coincides with the moderate expansion of savannah beginning at 2.5 Mya. Significant expansion of open grassland occurred after 2.0 Mya during the appearance of *Homo erectus*. Correspondingly, taxa adapted to arboreal or closed setting died out during 2.0–1.8 Mya.

Thus, while earliest *Homo* probably lived in a mosaic environment of closed, riparian woodland and grassland, *Homo erectus* lived in a habitat dominated by open grassland. Accordingly, *H. erectus* shows adaptations to a hot and dry environment in a long and narrow body, and also shows clear adaptations to long-distance running (Bramble and Lieberman 2004), which was probably one of the key adaptations to the new environment.

This habitat change was paralleled by a change in diet. Meat started to play an increasing role (Lewin 1998; Stanford 1999). While there is a still ongoing debate about the relative importance of scavenging versus hunting in early hominid evolution (Binford 1981, 1986, 1988; Bunn 1981, 1983, 1991; Bunn and Kroll 1986, 1988; Blumenshine 1985, 1987, 1989, 1991; Speth 1989; Capaldo 1997; Dominguez-Rodrigo 1997, 2002, 2003; Selvaggio and Wilder 2001; Lupo and O’Connell 2002; O’Connell et al. 2002, 2003; O’Connell and Lupo 2002; O’Connell et al. 2003; Engeland et al. 2004; Dominguez-Rodrigo et al. 2005; Dominguez-Rodrigo and Barba 2006, 2007; Blumenshine et al. 2007; Pobiner et al. 2008), several lines of evidence point toward the conclusion that hunting played a dominant role.

The first line of evidence is the use of stone tools by early hominids. Stone tools are the oldest evidence that can be related to hunting. These appear in the fossil record around 2.6 Mya (Semaw et al. 1997, 2003; Semaw 2000) and it is well established that these were used to butcher large-sized mammals (de Heinzelin et al. 1999; Dominguez-Rodrigo et al. 2005). The abundance of these stone tools is somewhat baffling (Semaw 2000) but it suggests that they were widely needed and used. Semaw et al. (2003: 176) conclude: “The need for cutting tools—as well as the knowledge how to manufacture them—was firmly in place by 2.6 Myr.” A recent finding may extend the antiquity of stone tools even further as McPherron et al. (2010) present evidence for stone-tool-inflicted cut marks on bones that can be dated between 3.42 Mya and 3.24 Mya. We also know that the production of these stone tools was a complex process requiring motor precision and coordination (Roche et al. 1999), and that early toolmakers had a mastery of this process, that is, “selecting raw material with good flaking quality, sought for acute angles when striking cobbles and produced sharp-edged implements used for cutting” (Semaw 2000: 1211). It is also known that the makers of these early artifacts traveled long distances to collect suitable raw material (Semaw 2000), and that stone tools were transported to the site of carcass manipulation (de Heinzelin et al. 1999). This strongly suggests a conscious and elaborate tool-using strategy. These facts taken together, the abundance, the fact that it was firmly in place by 2.6 Mya, and the conscious nature and the complexity of the process, strongly suggest that there was an important selection pressure behind the evolution of this technology. This makes opportunistic scavenging highly

unlikely. The fact that they were consciously gathering suitable raw material, processing raw material in a complex way, and transporting tools with themselves shows that the makers of these tools knew very well that they needed these tools. Finding a carcass here and there by chance is highly unlikely to exert such strong selective pressure; but hunting big game can deliberately exert such pressures. Tooby (1987: 400) provides the following argument:

It seems implausible and inconsistent with foraging theory to posit that hominids would have transported lithic materials across large distances and manufactured stone tools exclusively to exploit relatively unrewarding and rare scavenging opportunities while ignoring far more abundant hunting opportunities.

The very fact that they had stone tools in abundance strongly suggests that these hunters had access to big carcasses on a regular basis, given the fact that small prey can simply be torn apart (as is the practice of chimpanzees) and require no tools for processing.

The second and perhaps the most contested line of evidence comes from the cut-mark studies on bone assemblages associated with early human fossils (Bunn 1981; Potts and Shipman 1981). The earliest interpretations suggested hunting; Bunn and Kroll (1986) explicitly argue that “coordinated group activity, repeated participation in dangerous subsistence pursuits, and a significant amount of meat and marrow eating were probably habitual components of the lives of some ancient hominids by 1.75 million years ago.” This interpretation was contested immediately (Binford 1981, 1986, 1988), and later reinterpretations along with taphonomic experiments suggested scavenging as a more likely explanation (Blumenschine 1985, 1987, 1989, 1991), whereas the latest studies come out in favor of hunting again (Dominguez-Rodrigo 1997; Dominguez-Rodrigo et al. 2005; Dominguez-Rodrigo and Barba 2006). Needless to say, these later studies were hotly contested as well (Lupo and O’Connell 2002; O’Connell et al. 2003; Blumenschine et al. 2007 versus Dominguez-Rodrigo 2003; Dominguez-Rodrigo and Barba 2007). These debates mostly center around the famous FLK Zinj site (Olduvai); however, even opponents of the hunting theory admit that “at FLK Zinj, high cut-mark counts rule out passive scavenging as the primary mode of carcass access” (O’Connell et al. 2002). More importantly, a recent comparative study of three other sites from Koobi Fora, ranging from 1.65 to 1.39 Mya (Pobiner et al. 2008: 121), concludes that “the taphonomic data relevant to distinguishing between these scenarios are tooth mark data, which at these sites do not support the scenario of hominids butchering scavenged felid kills.” While the authors do not argue explicitly in favor of hunting, the fact that hominids at these sites had access to large-sized mammals (size 3 being the most abundant: 50% or higher at all sites),¹ to well-fleshed carcasses, and to the meatier part of the ribs, and that they also

disarticulated, transported, and fully butchered the transported parts, and finally that these carcasses did not come from scavenged felid kills, leaves hunting the most likely explanation.

The third line of evidence, interestingly, comes from the study of tapeworms. There are three species of human tapeworm: *Taenia solium*, *T. saginata*, and *T. asiatica*. While *T. saginata* and *T. asiatica* are sister species, they do not form a clade with *T. solium* (Hoberg et al. 2001). This means that there must have been at least two independent host shifts to hominids. Phylogenetic analyses indicate that *T. solium* and its closest relative *T. hyaenae* used hyaenids as a definitive host, and bovids (but not *Bos* spp.) as an indefinite host, and that the host switching occurred in sub-Saharan Africa. The most recent common ancestor of *T. saginata*, *T. asiatica*, and their closest relative, *T. simbae*, used felids as a definitive host, and bovids (but not *Bos* spp.) as an indefinite host (Hoberg et al. 2001). Thus, early hominids ate the same bovid species as lions and hyenas on a regular basis, so much so that the host shifts could occur. The estimated divergence time for *T. saginata* and *T. asiatica* range from ca. 0.78–1.71 Mya (Hoberg et al. 2001), which means that even by the most “pessimistic” estimates hominids acquired tapeworms (and hence had access to bovids on a regular basis) at least ca. 0.8 Mya. The other end of the range (1.71 Mya) points to the possibility that the acquisition of tapeworms coincides with the emergence of *H. erectus*, which indicates that *H. erectus* was able to secure enough meat on a regular basis to provide a suitable target for a host shift (which fits the conclusion of the above-discussed cut-mark study by Pobiner et al. 2008).

The fourth line of evidence comes from carbon isotope studies. Van der Merwe and Tschauner (1999) argue that meat was an important element of the diet of hominids as early as 3 Mya based on the similarity between hominid and hyena carbon profiles. While this conclusion is contested by Peters and Vogel (2005), even the latter authors admit that C4 plant food was not available to a degree that could explain the observed C4 ratios. All in all, while the C4 ratio in itself might not be enough proof for hunting, it does not contradict hunting either. The evidence is perfectly reconcilable with a theory that assumes that hominids hunted big game perhaps as early as 2.6 Mya.

The fifth line of evidence comes from the fact that *H. erectus* is the first hominid adapted to long-distance or endurance running (Bramble and Lieberman 2004; Lieberman et al. 2007). Moreover, *H. erectus* was not just a capable long-distance runner but had a flexible optimum speed as well (Bramble and Lieberman 2004). This makes the most sense if *H. erectus* hunted different prey species with different optimum running speeds. While Pickering and Bunn (2007) contest the idea that endurance running could have evolved for hunting, Lieberman et al. (2007) point out that data from modern hunter-gatherers who hunt with bows and arrows, poisons,

tipped spears, and dogs (i.e., have more efficient means to hunt) cannot be used to disprove this idea. The very fact that modern humans are still good runners (unlike any of our close relatives), the performance of humans can match or exceed those mammals adapted to a cursorial niche (like dogs and equids; Lieberman et al. 2007), and humans possess a series of adaptations that can be explained only in terms of endurance running (like the abundance of eccrine sweat glands) show the importance of endurance running as a hominid adaptation. As *H. erectus* already shows the adaptations for long-distance running, while australopithecids were probably habitual bipeds but not good runners (Ward 2002; Bramble and Lieberman 2004), running, and specifically long-distance running, should have evolved during the transition from australopithecids to *H. erectus*. This assumes a strong selection pressure for long-distance running with flexible optimum speed. Hunting of big game, where prey species have different optimum speeds, is the most likely candidate.

The sixth line of evidence comes from the weapons used to hunt. There is the famous finding of fossilized spears in Germany, which was dated as 400,000 years old (Thieme 1997). According to Thieme, these spears were used to kill horses. Arguably, if hominids hunted with spears 400 Kya, then hunting must have evolved even earlier.

The seventh line of evidence comes from the fact that both humans and chimpanzees (Mitani and Watts 1999; Watts and Mitani 2002; Boesch 2005; Gilby et al. 2006) are good hunters. Thus, the most parsimonious assumption is that the ancestor of these species hunted as well. In sharp contrast with this, chimps ignore scavenging possibilities (Watts 2008). Thus, the hunting scenario does not require qualitative changes, whereas a scavenging scenario requires two transitions, one from hunting to scavenging, and another from scavenging back to big-game hunting. Both transitions require special explanations, which puts the burden of proof on those who wish to argue in favor of dominance of a scavenging scenario as opposed to hunting.

All in all, while these lines of evidence might not be persuasive in separation, taken together the facts of (1) tool use in place by 2.6 Mya; (2) the latest cut-mark study showing carcass acquisition ca. 1.5 Mya, which definitely did not come from scavenging from felids; (3) carbon isotope studies showing similar C4 ratios to predators; (4) the origin of two species of tapeworm perhaps as early as 1.7 Mya, which used hominids as a definitive host; and (5) the evolution of long-distance running in *H. erectus*, strongly suggest that cooperative hunting of prey species that could not be killed by a lone hunter and required tools to process could have started as early as 2.6 Mya, and that big-game hunting was strongly in place by the time *H. erectus* emerged—*H. erectus* being the first specialized hominid big-game hunter. In accordance with this conclusion, Shipman and Walker (1989: 389), invoking a complex set of criteria, including locomotion, dentition, diet,

and gestation period, conclude that “on the whole the evidence suggests that carnivory, or hunting to a biologically significant degree probably first occurred in *H. erectus*.”

Of course, this is a fairly revolutionary conclusion, and most authors would prefer a more conservative estimate. For example, Stiner (2002) in her review of carnivory argues that hunting of prime adult ungulates (bovids and cervids) was well established by the late Pleistocene, and thus probably started in the middle Pleistocene. She argues that accordingly a more basic adaptation for ungulate hunting (i.e., not for prime adults but for weak/young individuals) had evolved in hominids by about 500 Kya. However, importantly, she also argues that hunting of medium-sized and large ungulates started long before stone-tipped and bone-tipped weapons were widely used, and this strongly suggests that cooperation amongst hunters was essential for the capture of large game.

Later stages are less controversial. It is well established and several studies show that middle Palaeolithic hominids were already competent hunters, hunted prime age herbivores (Conard and Prindiville 2000; Gaudzinski and Roebroeks 2000; McBrearty and Brooks 2000; Lombard 2005; Yeshurun et al. 2007), and most likely used strategies that required high levels of cooperation within the group, like corralling and then killing a groups of horses (Olsen 1989).

All in all, hunting of large prey by early hominids is well established by the late Pleistocene, and the available evidence strongly suggests that it started as early as the lower Pleistocene with *H. erectus* being the first specialized hominid big-game hunter. Moreover, hominids hunted not just large game, but prime adult individuals, which is clearly unique even amongst group-hunting predators (because they usually target the weak, the ill, and the young). This suggests a level of cooperation and coordination and/or technological development not found in other group-hunting species. One may wonder how such cooperation can be achieved. The obvious answer is pre-hunt communication, which, as I argue, was the cradle of human language.

Function of the Very First “Words”

Here I propose that the function of the very first “word” was recruitment. In order to understand the selection pressure behind recruitment one has to look at how and when chimpanzees hunt. First, chimpanzees are good hunters of small prey (Mitani and Watts 1999; Watts and Mitani 2002). The chimpanzees at Ngogo have a success rate of 85% when hunting for red colobus (Watts and Mitani 2002). This is a much higher success rate than that of lions (30%; Estes 1991), or even than that of hunting dogs (39% or 70%, according to two separate studies; Estes 1991). Of course, not all chimpanzee groups have a success rate as high as this (though all of the reported rates are above 50%; see Mitani and Watts 1999 for

comparison); but the reasons are telling. The Ngogo group is the largest of all the groups under study and can field the most males for hunting expeditions (successful hunting parties included an average of 26 individuals and 14 adult males; Mitani and Watts 1999). In fact Watts and Mitani (2002) were able to show that hunting success (i.e., the number of monkeys killed per hunt) positively correlates with the number of males, and in general it is not efficient to hunt below a group size of 5. The finding that hunting success positively correlates with the size of the hunting party was further confirmed by other studies (Gilby et al. 2006). All in all, given sufficient numbers, chimpanzees are highly efficient hunters of small prey. It is reasonable to assume the same about early hominids. Whether they had the numbers, and how, will be discussed later on. In addition, chimpanzees hunt duikers (Mitani and Watts 1999; Watts and Mitani 2002). It is not unreasonable to assume that early hominids could have done the same in the tropical forest environment. Thus, hunting small- or medium-sized antelopes in their new environment would have been a natural continuation of an already existing behavioral strategy.

Second, the Ngogo chimpanzees hunt the most at times of ripe fruit crops (Mitani and Watts 2001; Watts and Mitani 2002). Firstly, this means that chimpanzees can cover the energetic requirement of a hunt from fruits. Second, more importantly, this means that the group is together, and hence a high number of hunters is guaranteed. In other words, fruit crops serve *as a natural recruitment system* for the Ngogo chimpanzees. Early hominids could have faced a similar situation. In their tropical forest environment ripe fruit crops could have served as a natural recruitment system for the hunt, which would have enabled them to be successful hunters of small-sized mammals (including monkeys and small antelopes). However, living in a more open environment like the savannah or forested woodland meant the lack of suitable ripe fruit crops, which could have served as recruitment. Hunting, of course, would have been practiced, very much like chimpanzees at Gombe hunt; but the success rate would have been lower. Thus, on one hand there was a selective pressure to supplement the missing “natural recruitment” system with other ways of recruiting. On the other hand, the increasing abundance and size of suitable prey (i.e., that of bovid species) gave another reason why efficient recruitment was selected. In this situation any mechanism that could have resulted in a higher number of hunters could have given a selective advantage to those individuals who possessed this mechanism.

Note that chimpanzees have a hunting call, which is emitted on sight of their prey (Mitani and Watts 1999). This call can apparently mobilize other potential hunters into action. From the point of view of recruitment, there are two problems with this call. First, it depends on seeing the prey, i.e., it is not voluntary. Second, it can mobilize only those chimpanzees that are already in the vicinity, i.e., within hearing distance. In

contrast to this, early hominids “needed” a recruitment signal that was voluntary, did not depend on the prey being visible (i.e., displaced reference), and could serve the purpose of gathering and keeping together the critical number of adult males needed for a successful hunt.

Form of the Possible First “Words”

Bickerton (2005) notes the following:

If for any given selective pressure it proves impossible even to hypothesize a plausible first exchange of meaningful items (plausible both in terms of interpretation and number of items involved), this alone should suffice to rule out the selective pressure concerned.

In light of this remark, what can we say about the possible first words in the pre-hunt coordination scenario? Probably that they were not words at all—and not even gestures. As we have seen, it is the most likely that first “words” served the function of recruitment to hunt. How can group members be motivated to hunt? The simplest solution is the sight of the prey species. The sight of red colobus, their regular prey, excites chimpanzees. What can be done, however, when the prey species is not in sight? A substitute must be used. Here I propose that the simplest substitute is a body part of the prey species that cannot be eaten and remains intact for many days, even weeks or months. For example, horns of hunted gazelles (attached to heads) could have been the first substitutes of this kind, that is, horns of the prey species were the “first words” of humankind. This was simple indexical communication. What happened when horns were not present but some members wanted to hunt (assuming that dragging/showing around heads with horns was already established as a signal to call for hunt)? Missing horns had to be imitated somehow, either by mimicking their form, or by drawings. If there were several prey species that had to be differentiated, then there was a selective pressure for precise imitation, drawing skills, which allowed the signaler to communicate the selected prey species with great fidelity. Therefore, the next generation of “words” was probably icons, mimicking recognizable feature of the prey species (i.e., horns). Once this stage was established, and different hunting tactics were evolved (if at all), hunting tactics could be communicated by mimicking the involved actions (i.e., running, throwing, hiding, very much like in today’s game of charades).

Please note that it is not necessary for this scenario to have horns as the first “words.” Anything that was conspicuous enough, lasted long enough, and could be related to the prey animal could have served the function. However, given the circumstances, horns with skulls are the most likely candidates: Horns are the most conspicuous feature of antelopes, as witnessed by the fact that in most sign languages the sign for hoofed mammals—bulls, cows, and so on—derives from the

shape of horns; also !Kung hunters (Marshall 1976) use hands to mimic bovid prey heads with horns such as wildebeest or hartebeest; horns cannot be eaten; they last long enough; and finally, the shape and size of horns unambiguously relate to the given prey species (see again !Kung hunters in Marshall 1976).

The evolution of various recruitment systems in bees gives an example of how to solve the problem of recruitment with indexical signs, and how such a system can evolve into an iconic/symbolic system of communication. One stage present both in bumblebees (*Bombus terrestris*) and honeybees (*Apis mellifera*) is when workers bring back the odor of the flower they encountered to the hive (Dornhaus and Chittka 1999). This is clearly an indexical communication, where the odor serves to identify the flower species. This indexical stage can evolve further into an iconic/symbolic system when the ecology of the given species selects for it. In honeybees this selective force was the highly clustered and temporal nature of flower resources (Dornhaus and Chittka 2004), which made it beneficial for the workers to evolve means to communicate not just the species but also the direction and the distance of the resource. The proposed first “word” of the human language is identical to the indexical stage of the bee language both in form and function; the skull of a bovid species refers to the species in the same indexical way as the odor of a flower refers to the flowering plant.

The evolution of the dance of bees also offers a parallel to show that such an indexical/iconic communication system will evolve into a more symbolic one given that selection pressure for efficient and fast communication is present. The process by which signs can acquire novel grammatical functions is called grammaticalization; it is well described and studied by linguists (Hopper and Traugott 1993; Zeevat 2006). Also described is that signs of iconic origin, such as in the case of sign languages, can be used for such a process (Senghas et al. 2004; Fox 2007).

That our ancestors had the cognitive abilities for the referential use of objects (such as skulls), and then gestures, is a reasonable assumption. Gestural communication appears to be limited to the *Hominoidea* (Pollick and de Waal 2007), which strongly suggests that our ancestors had this ability as well. While the majority of the gestures of great apes are dyadic (i.e., not referential), and used for imperative purposes (Liebal and Pika 2005), they seem to have the cognitive potential to learn the referential use of gestures as witnessed both by the observation of the “directed scratches” gesture in the Ngogo chimpanzee community (Pika and Mitani 2006) and by the fact that captive chimpanzees can learn the referential use of American Sign Language (ASL) gestures (Gardner et al. 1989). Last but not least, investigating the flexibility of gestural communication of chimpanzees and bonobos, Pollick and de Waal (2007: 8187) explicitly argue that “this observation

makes gesture a serious candidate modality to have acquired symbolic meaning in early hominids.”

All in all, this scenario makes possible gradual evolution from indices through icons to symbols, which fits well with a number of gestural, cognitive, and linguistic theories. There are no jumps; no words are invented “out of the blue,” thus eliminating the “popular” dilemma of how other members of the group could understand novel words. In addition, any kind of potential ambiguity (that a modern speaker might observe—another oft-cited dilemma) is resolved by the highly context-specific use of these signals.

Strictly speaking, this new communication system did not evolve out of any existing animal communication system (as mimicking other animals was probably not part of the communication of early hominids before the niche change), which explains why the attempts to identify an animal communication system that could have served as a basis for human language proved to be a failure. However, obviously, existing cognitive capabilities and skills were used. The proposed scenario fits well with the recent argument given by Arbib et al. (2008). Based on a review of monkey and ape communication they too argue against a direct evolutionary path from nonhuman primate vocalization to human speech.

As to Bickerton’s criteria (2005) of symbolism, predication, and voluntary expansion, this new communication system in its simplest form, i.e., at the index stage, was neither symbolic nor predicative (as it measured only motivational states); moreover, it was not voluntarily expandable (as it relied on body parts of the hunted species). However, despite all the theoretical skepticism, this system had the potential to *gradually evolve* into a symbolic, predicative, and voluntarily expandable system.

What drove the system to be more and more complex? I suggest that it was the need to coordinate group hunting to improve efficiency.

Power of Generalization: The Need to Coordinate Group-Level Hunting

Once the problem of recruitment was solved, large hunting party size allowed hominids to tackle larger prey. In turn, this meant that more and more species fell into the range of suitable prey for early Homo, which I propose drove the evolution of pre-hunt coordination of hunting roles and communication of hunting know-how in general.

Lions, wolves, and African hunting dogs can hunt big game very efficiently without any pre-hunt coordination, so why was it necessary for early hominids? The answer is very simple: Hunting is a biological adaptation in all the above species; they have all the tools for it (body shape, muscles, fangs, claws), and they hunt and kill the same way in all the hunts. In some of these species, viz., in lions (Stander

1992) hunting roles evolved and each individual has its favorite position. Apparently they learn these roles by watching the hunting behavior of the adults but do not imitate other pack members (Stander 1992).

As Boesch (2002) argues, hunting roles evolved in some chimpanzee populations as well. He describes “chasers,” “drivers,” “blockers,” and “ambushers.” Here, as well as in lions, individuals seem to have preferred roles (Boesch 2002). Chimpanzees have to learn hunting roles too; however, in the absence of language, it takes roughly 20 years(!) for them to learn the more complicated roles (Boesch 2002). Boesch (2002: 37) explicitly states that “the most demanding aspect of collaborative hunting is to coordinate actions both in time and in space with those of other hunters.”

One can conclude that group hunting on a difficult terrain or group hunting of large prey favors the evolution of hunting roles. Humans, however, are not born with innate knowledge of hunting roles, thus they have to acquire the know-how of hunting if they want to be successful as a group. Even today’s hunters are not born with these mental models; they have to learn it from the elders of the tribe. For example, hunting success in Ache is age-dependent (Walker et al. 2002) and only experienced hunters are allowed to participate in the more complex cooperative hunts (i.e., monkey hunts). The parallel with today’s team sports helps to highlight the argument. We are not born football or basketball players with hardwired football or basketball tactics. We have to learn these tactics available to the teams, and the usual way to learn these are the pre-match tactical briefings. These “pre-match” tactical briefings were the natural way to coordinate the hunt at the group level too. All in all, any mechanism that allowed hominids to acquire hunting roles and hunting know-how efficiently gave a selective advantage to the group and thus was selected for.

This task is beyond the usual reach of animal communication. Most of the signals used by animals are so-called self-reporting signals (Maynard Smith and Harper 1995) with which animals can communicate their intentions, internal states, and so on. Obviously, when it comes to coordinating a given action and thus sharing know-how of that action, self-reporting signals are not sufficient for the task. A simple yet famous example for group-level coordination and the use of other-reporting signals is bee dance (Michener 1974) by which bees communicate the direction, distance, and richness of a resource. Note that bees do not have to communicate about know-how, i.e., about how to collect pollen or nectar. Yet even the communication of relatively simple things like distance and direction requires other-reporting signals. As discussed above, pre-hunt communication differed from bee dance in that once hominids reached a sufficient level of cultural flexibility, they had to communicate not just about the distance or direction but also about the know-how. Tool making skills can be passed on

without language; know-how is a lot more difficult to pass on without it.

The relatively high iconicity of sign languages is a well-known phenomenon (Sandler 2005; Fox 2007). It is also known that iconicity is a useful and frequent method of sign formation (Brennan 1990; Taub 2001; Senghas et al. 2004; Fox 2007). For example, in the ASL, British Sign Language (BSL), and Hungarian Sign Language (HSL) the majority of signs used to denote animals are of iconic origin. These signs originate either from imitating some striking morphological feature (like horns of the bull) or some characteristic movement (like hopping of the frog) of the given animal. Different sign languages can choose different features or different movements; also the same feature (like the horns) can be represented in a slightly different way (e.g., in the HSL only one hand is used, as opposed to the ASL where both hands are used to sign “bull”). However, the imitative origin is easily recognizable even for humans who have never had any experience with sign languages. In the same way the sign denoting “bird” is of recognizable iconic origin in most sign languages, even though each language may choose a different characteristic of birds to imitate (wings in the International Sign Language (ISL) and beaks in the ASL; Sandler 2005). Also, the accuracy of the recognition of a given sign is higher for highly iconic signs than for less iconic signs (Campbell et al. 1992). The usefulness of iconicity, however, is not limited to referring to objects or animals. Iconic gestures can be used to describe motion (Senghas et al. 2004) and highly iconic structures (HIS; Sallandre and Cuxac 2002) can be used to reconstruct personal experience, where HIS can refer to form, size, situation, or person (Sallandre and Cuxac 2002). Even though iconicity is expected to be lost or decreased by the process of conventionalization, it can still be found on many levels even in today’s languages (Burling 2005).

All in all, one can conclude that iconicity can provide the means to recruit novel signs. These signs can either denote objects or animals or can be used to reconstruct personal experiences. Thus, mimesis offered a tool for hominids to coordinate group hunting, either by communicating desirable prey species, exchanging personal experience, or coordinating hunting roles.

Uniqueness

One has to answer the question that if coordination of hunting roles and communication of hunting know-how selected for a more and more complex pre-hunt communication in the case of early hominids, then why did neither those chimpanzees that have hunting roles nor those group-hunting species, such as lions that have hunting roles too, evolve a communication system similar to human language?

First, chimpanzees did not evolve better recruitment or communication for coordination during group hunting because there is no strong selection for it. Group hunting is more of a free-time activity for males, a kind of luxury (Mitani and Watts 2001) rather than an essential foraging method. For the same reason, there is no feedback between male hunting success and reproductive success, either in terms of sexual access nor in terms of better nutrition for the young. Males mostly do not share with females or young (Watts and Mitani 2002; Gilby and Wrangham 2007), they do not share preferentially with swollen females (Gilby 2006), and sharing does not increase the probability of mating (Mitani and Watts 2001; Gilby 2006). However, females are fine without this resource because of the availability of ripe fruit crops. All in all, meat is a luxury for chimpanzees rather than a necessity; also, fruit crops provide a natural recruitment system, therefore there was no strong selective pressure to increase the efficiency of recruitment for the hunt.

Second, the difference between humans and the other group-hunting species can be explained by the cultural nature of hunting as adaptation and by the fact that the early hominids were omnivores. First of all, lions, wolves, and hunting dogs are obligate carnivores—hunting is their only way to get food. This means that recruitment is very simple; when they feel hungry they go hunting. They do have recruitment calls but the object of the recruitment is unambiguous. In contrast, early hominids were omnivores. Feeding is not equivalent to hunting. Thus, hunger or excitement to feed is not equivalent to a hunting mood either. This in turn means that recruitment for hunting needed special signals that made it clear that the object of the mission is hunting and not some other alternative food source.

Third, lions, wolves, and hunting dogs are all specialized hunters (Estes 1991). They always hunt the same way: lions by ambush, hunting dogs by running down their prey, but never the other way round. They always kill the same way—lions by suffocating their victims, hunting dogs by bleeding them out. Experience makes the master, but they have to practice only one type of hunt and one kind of killing move, they do not have to choose from an array of possible strategies, and they do not have to coordinate different tactics. In contrast, humans have developed a large array of methods to hunt and kill prey species, and with the flexibility derived from tool use they had to find the means to coordinate group hunting.

Fourth, even if these group-hunting species such as lions would benefit from a cultural transmission of hunting roles and hunting know-how, this process cannot take off from the ground in the absence of a suitable precursor, viz., in the absence of the use of an indexical/iconical communication system for recruitment, and in the absence of the corresponding cognitive and mimetic skills.

Honesty

Evolution of conventional communication systems requires that there be no conflict of interest between the signaler and the receiver (for a detailed discussion see Számadó and Szathmáry 2006). Regarding the hunt there can be two kinds of cheating: (1) not participating in the hunt, or only pretending to do so; and (2) giving misleading signals before or during the hunt. The first one is the problem of cooperation and free riding. There are two reasons why this kind of cheating is not interesting from our point of view: It does not affect the pre-hunt coordination of the hunt, and the situation can be easily cross-checked—those participating in the hunt can easily see who is there and who is not. The second kind of cheating—giving misleading signals before or during the hunt—could undermine the hunt; however, this is not in the interest of the participants as once one decides to participate there is a shared interest in succeeding. All in all, the shared interest created by the hunt provides a scenario in which honest cost-free signals can evolve.

Relation with Other Theories

This scenario fits well with a number of gestural, cognitive, and linguistic theories. First of all, it is in line with the gestural theories proposed by Hewes (1973) and Corballis (2001). The role of gestures in the evolution of early human language has received recent attention (Pollick and de Waal 2007; Arbib et al. 2008), and as discussed above, the current proposal fits in with both arguments. It also fits Donald's (1998) theory of mimesis; Donald argues that mimesis played a crucial role in the early evolution of human language, and mimetic actions (such as "action metaphor") were the predecessors of human language, and finally that the "executive suite" provided the cognitive background both for mimesis and for human language. It follows that the current theory is also compatible with Arbib's (2005) mirror system hypothesis, including the latest version outlined by Arbib et al. (2008).

The current model also fits the linguistic approaches of Hurford and Givón (2002). Hurford (2007) argues that the first communicative acts leading to human language were purely illocutory and grammatical complexity and descriptive power grew on top of these acts. The current model proposes recruitment as a first step, which is a purely illocutory act—the need of pre-hunt coordination of the hunt drives the evolution of grammatical complexity and descriptive power. Hurford (2007: 242) further argues that "*given the right kind of environment*, the disposition to integrate deixis with symbols can be hypothesized to have increased gradually by natural selection during the few million years since australopithecines" (emphasis in original). The current model proposes that it was the coordination of the hunt, i.e., pre-hunt communication, which provided this "right kind of environment." The reason is very simple: Communication about displaced reference (i.e.,

about animals that cannot be seen and hence cannot be pointed at directly) is possible only with the integration of deixis (i.e., pointing) and symbols.

This scenario fits well with Givón's (2002) argument too. He argues for a pragmatic approach, according to which the function of language drove its evolution. He suggests that human language evolved for communication (a claim nowhere nearly as widely accepted as obvious as it may seem) testified to by the fact that the bulk of the grammatical machinery is devoted to code for declarative speech acts (as opposed to manipulative acts); displaced reference (i.e., about objects, animals, etc., which cannot be seen); perspective shifting; and providing discourse coherence for multi-propositional discourse. Pre-hunt communication just provides a context in which these features are adaptive. There is a need for declarative speech acts describing past experiences or future plans; there is a need to communicate about displaced reference, as most of this communication took place when prey was not necessarily visible; there is a need for perspective shifting as hunters exchange their experiences and plans; and finally there is a need for multi-propositional discourse, where discourse coherence—efficient and fluent communication—can greatly increase the fitness of participants.

This is not to suggest that grammar as it is known evolved exclusively in the context of pre-hunt communication; it is just that pre-hunt communication provided a context in which there was a selection pressure for all major features of grammar and where the evolution of these features could “take off from the ground” because all the other conditions were fulfilled, like groundedness (i.e., the potential for indexical, and then for iconic communication) and shared interest.

Bickerton's Scavenging Scenario

Bickerton's (2005) “recruitment model” is perhaps closest to the scenario presented here. It indeed has some similarities but there are also key differences worth noting. Bickerton proposed a scenario in which the function of first words was to recruit sufficient numbers of hominids (living in fission–fusion groups) in order to defend and utilize large carcasses. Bickerton argues that the niche occupied by early hominids was very similar to the niche occupied by many social insects in terms of resource availability, viz., resources are patchy but large enough to support a whole group (i.e., carcasses of large mammals) but can be exploited successfully only if a large number of hominids were present (due to competition of other predators, such as lions and hyenas). So, just as ants and bees evolved their own “languages” that enable them to recruit large number of workers to harvest a given patch of resource (be it flowers or large insects), Bickerton argues, early language evolved for the very same reason. Its function was to

inform and thus gather the scattered members of sub-groups to the carcass discovered by one of the sub-groups.

The following four objections can be made to Bickerton's scenario:

1. It assumes that early hominids were “potent” power scavengers, i.e., they could chase away lions, hyenas, and so on. The hypothesis of “power” or “confrontational” scavenging is a recently favored alternative to hunting (O'Connell et al. 2002); it assumes that the increased frequency of meat in the hominid diet was a result of hominids actively chasing away predators from their kill. This is not very likely, as I discuss in online Appendix 1.
2. It assumes that these large carcasses were frequently presented and utilized; this is not likely to have been the case. Blumenshine (1987) has shown that reliable scavenging opportunities are only presented in riparian woodland from felid kills, yet the latest comparative study shows that early hominids had access to carcasses that definitely did not come from felid kills (Pobiner et al. 2008).
3. Group members that found the carcass had to locate other group members engaged in other activities (e.g., digging tubers) to be able to recruit them; how did they do it and who guarded the carcass in the meantime?
4. Assuming that they stayed at the carcass (the natural assumption), a simple food call would have sufficed. Many species, including hyenas, have such food calls, and if the same selective pressure selects for similar solutions (cf. Bickerton 2005), humans could have evolved the same simple system.

Predictions

As outlined in the previous sections and as discussed further in online Appendix 2, the model predicts that *Homo erectus* possessed the set of adaptations called “the big game hunter's toolkit,” which includes morphological adaptations, tools, and a suitable system of communication. (In online Appendix 2, I discuss my arguments as to why *H. erectus* was the first hominid with this “toolkit” of adaptations.) It follows from the model that:

1. *H. erectus* possessed a communication system suitable for recruitment and for the coordination of the hunt, this should be reflected in the organization of the *H. erectus* brain. More specifically, the model predicts that *H. erectus* possessed a more human-like Broca's and Wernicke's areas that reflect the level of early human language. Available evidence supports this prediction (Holloway 1995, 1996).
2. *H. erectus* is the first hominid species that is expected to be frequently associated with middle- and large-sized mammalian fossils showing cut marks referring to active meat acquisition. Again, available evidence supports this prediction (Pobiner et al. 2008).

3. *H. erectus* is expected to be in resource competition with other savannah-dwelling big-game hunters (and bone-crackers). Available evidence supports this prediction. Lewis (1997: 282) concludes about the African paleoguild of carnivores that “the larger bone-cracking species disappeared first in eastern Africa and then in southern Africa. Next, the larger of the more specialized flesh-slicing species, such as the saber-toothed felids and *Chasmaporthetes* disappeared.” While Lewis remarks that Plio-Pleistocene carnivore paleoguilds “appear to have been more complete ecologically than modern guilds” (p. 282), this holds only if one ignores *H. erectus*. *H. erectus*, being the first specialized hominid big-game hunter, filled the niche both of the specialized flesh-slicing big-game hunters and the niche of large bone-crackers (given that hominids were also able to extract the marrow with their stone tools). Thus, as a prediction of the model one expects the same pattern (i.e., competitive exclusion of specialized big-game hunters and large bone-crackers) in Eurasia with the spread of *H. erectus*. Composition of the modern carnivore guild also supports this prediction, namely that, “larger carnivorous species that survived seem to be, for the most part, highly adaptable in terms of prey preference, carcass utilization, and habitat use” (Lewis 1997: 282). No wonder, as this was the only way to coexist with *H. erectus* and later on with more advanced hominids. The facts that the “modern” carnivore guild appeared first in Africa and its appearance, 2.0–1.8 Mya (Turner 2000), coincides with the origin of *H. erectus*, and that saber-toothed cats survived the longest in North America (the continent reached last by humans; Turner 2000), further support this prediction.

4. As *H. erectus* must have had a communication system suitable for recruitment and pre-hunt coordination, all the descendants of *H. erectus*, including *H. heidelbergensis*, *H. neanderthalis*, and of course *H. sapiens* must have had a communication system *at least of that level of complexity*. Moreover, they all must show the corresponding changes in brain structure, especially in Broca’s and Wernicke’s areas. The finding that Neanderthals carried a FOXP2 protein that was identical to that of modern humans in the only two positions that differ between human and chimpanzee (Krause et al. 2007) strongly supports this conclusion. The discovery of *H. floresiensis* provides an interesting problem. Given the possible isolation of this species from other descendant *H. erectus* populations (due to strong sea currents) and the small brain size, the question arises whether it is possible that *H. floresiensis* lost this communication system alongside the loss of big-game hunting behavior (probably due to the presence of highly unusual and “unbeatable”² competitors: the Komodo dragons). This is an empirical question; the clear prediction of the model is that the ancestors of *H. floresiensis*, i.e., the founder population of Flores, must have had this

communication system along with the corresponding brain adaptations.

5. Assuming that skulls with horns were the first indexical signs that started the evolution of human language, one would expect this to be reflected in the fossil record. Thus, a correlation between the heads of potential prey species and early hominid fossils or tools is expected. This is exactly what was found by Pobiner et al. (2008). They write:

The relatively high proportion of cut marks on crania and mandibles, including hyoids, compared with their low rank may indicate either a higher encounter rate of heads, a higher preference for processing heads, a higher survival rate for heads. (p. 115)

They gave no explanation for this finding; however, it fits well with the current model.

6. Assuming, on one hand that drawing originated in the context of pre-hunt communication to facilitate coordination of the group’s hunting effort, on the other that cultural systems have inertia, one would expect the earliest pieces of art to depict big game that can be hunted only by a coordinated group effort. Of course, the earliest (functional) pieces may have disappeared without leaving any trace. However, due to the inertia of cultural systems one would expect pieces of art to be related to big game and hunting even when these drawings/paintings were no longer functional. There are two lines of evidence to support this prediction: (1) the Bushman tradition of drawing antelopes in the sand before they go hunting (Frobenius 1981); (2) the earliest cave paintings in Europe also mostly depict large mammalian species that could be hunted only by coordinated group effort. Horses, bovinds, mammoths, rhinos (see Table 1) are the most frequently depicted groups (Steven in Haddingham 1979). There are no plants, objects, rocks, shelters, and so on among the earliest pieces of art; moreover, there are no (or very few) birds, rodents, reptiles, insects, and so on. That is, there are no representations of species that might have been hunted by early humans but could be hunted and killed by a lone hunter. Moreover, there are only a very few representations of animals dangerous to humans, such as felids, bears, wolves, and so on. All in all, both Bushman pre-hunt drawing and early cave art fit the prediction of the model. The model further predicts that if any earlier representations are found (either in Europe or in Africa), then the topic of these representations is most likely to be big game that can be hunted only by a coordinated group effort.

7. The model also predicts the lack of pre-hunting communication that serves to coordinate future action or prey type in other group hunting species. It follows from the uniqueness of human language that no other species should have pre-hunt communication for the coordination of group tactics during the hunt. This does not mean that today’s group-hunting species do not have any pre-hunt communication, as usually they do.

Table 1. The frequency of depicted animals in 40 European caves (after Stevens, in Haddingham 1979).

Animals	Number of occurrences	Frequency (%)
Horse	780	29.725
Bison	759	28.925
Large bovid	177	6.745
Small bovid	212	8.08
Reindeer	115	4.3825
Other deer	292	11.13
Mammoth	202	7.70
Rhino	20	0.7625
Bear	50	1.9
Feline	17	0.65
Total	2,624	100

For example, both wolves and hunting dogs vocalize before the hunt. However, this kind of communication serves to coordinate the motivational state of the group members (i.e., serves as recruitment) rather than to communicate about prey type or hunting tactics. Moreover, as a logical consequence this type of vocalization is rather stereotyped. An important prediction is that even if there is some kind of variation in these vocalizations, there should be no correlation between different types of vocalizations and the hunted prey species (i.e., these group hunting species do not use pre-hunt communication to coordinate on prey species or to negotiate hunting tactics).

8. There should be no genetically inherited mental models of hunting in humans—not even in contemporary hunters. It follows that even contemporary hunters have to learn both the use of weapons and the tactics of the hunt. Moreover, they have to learn it from each other, that is, there should be a cultural inheritance of hunting tactics and prey preferences. Studies of contemporary hunter-gatherers support this prediction. !Kung boys learn to hunt from a very young age (Lee 1979), first as play, then they start to hunt for small birds and reptiles, then for larger prey. They have several games that help them to acquire basic skills, such as javelin and spear throwing games (Lee 1979), and they have toy bows and arrows from a very young age (Marshall 1976; Lee 1979). Tracking skills are acquired by ongoing observation of nature; however, as Lee (1979: 236) describes the following:

Before they actually go on a hunt !Kung boys listened to dozens of hunts described in the minutest detail in the storytelling around the campfire. This is a major component of their socialization as hunters. This vast body of knowledge is a treasure house of lore and information about animals and how to kill them. And the boys listen intently.

9. It follows that pre-hunt communication should still be an integral part of hunter-gatherers. Of course, the flexibility of modern human language is such that pre-hunt communication need not be necessarily held before the actual hunt, but information exchange about previous hunts, whereabouts of prey, and the planning of future hunts are expected to be important parts of hunter-gatherer groups. Again, studies of contemporary hunter-gatherers support this prediction. Lee (1979: 205) reports the following: “Graphic description of hunts, both recent and distant, constitute an almost nightly activity of men around the camp fire. In storytelling, men can portray a hunt, step-by-step, in microscopic and baroque detail.” Marshall (1976: 130) writes as follows:

!Kung men talk endlessly about hunting as they sit together repairing their equipment or poisoning their arrows. They recount over and over memorable episodes of past hunts, hear each other’s recent news about recent hunts, and make plans.

Timeline and Summary of the Pre-Hunt Communication Scenario for the Evolution of Human Language

Here I summarize the scenario proposed for the evolution of human language and the evidence that supports it.

Observation 1. Increase of grassland and bovid species because of climate change started around 2.8 Mya. Evidence comes from mammalian fossil bone assemblages (Vrba 1985; Bobe et al. 2002; Alemseged 2003; Bobe and Behrensmeyer 2004; Fernandez and Vrba 2006), marine sediments, pollen spectra, and carbon isotope studies (for a review see deMenocal 2004).

Observation 2. Chimpanzees hunt small prey and have a natural recruitment system in the form of ripe fruits that serves to bring a sufficient number of males together. Evidence comes from chimpanzee field studies (Mitani and Watts 1999; Watts and Mitani 2002; Gilby et al. 2006).

Observation 3. Hunting success correlates with hunting party size. Evidence comes from chimpanzee, lion, and hunting dog studies (Fanshawe and Fitzgibbon 1993; Creel and Creel 1995; Creel 1997; Courchamp and Macdonald 2001; Funston et al. 2001; Watts and Mitani 2002; Gilby et al. 2006).

Inference 1. Increase in the number of suitable prey species (bovids) and the potential loss of their “natural” recruitment system put a selection pressure on efficient recruitment in hominids living in the given regions.

Observation 4. Recruitment can be solved with other-reporting signals evolving out of indexical signs. Evidence comes from the evolution of the “dance of the bees” (Michener 1974; Dornhaus and Chittka 1999).

Inference 2. Larger party size obtained by more efficient recruitment allows hominids to tackle larger prey; however, efficient handling of mid-size and large prey needs suitable

tools to open up and to disarticulate the carcass. This puts a selection pressure on tool making and tool use.

Observation 5. Evidence from archaeological studies shows that stone tools used for butchery suddenly appear in great number in the fossil record around 2.5–2.6 Mya (Semaw 2000; Semaw et al. 2003; Dominguez-Rodrigo et al. 2005).

Observation 6. Evidence from cut-mark studies that meat coming from small to large prey started to play an increasing role in hominid diet, which coincides with the appearance of stone tools (Dominguez-Rodrigo et al. 2005).

Inference 3. Hominids solved both the problem of recruitment and the problem of tool-making and hunted large enough prey (not necessarily large or the largest) that killing of that prey required coordinated group hunting and stone tools to process the carcass.

Observation 7. Evidence from lion and chimpanzee studies shows that coordinated group-hunting selects for hunting roles (Stander 1992; Boesch 2002).

Observation 8. Evidence from anthropological studies of hunter-gatherers shows that humans do not have genetically determined knowledge or preferences for hunting roles, they have to learn it (Marshall 1976; Lee 1979; Walker et al. 2002).

Observation 9. Evidence from chimpanzee studies shows that in the absence of innate knowledge, hunting roles can be either learned individually or transmitted culturally. Individual learning is slow and inefficient (Boesch 2002).

Inference 4. Given the importance of meat in early hominid diet—as opposed to its role in chimpanzee diet—there was a selection for a communication system that allows the efficient cultural transmission of hunting roles and hunting knowledge in general. The presence of a recruitment system that already used indexical or even iconic signs served as a pre-adaptation.

Observation 10. Evidence from the evolution of sign languages shows that imitation allows the origin of iconic signs (Brennan 1990; Taub 2001; Senghas et al. 2004; Fox 2007).

Observation 11. Evidence from the evolution of sign languages and from anthropological studies shows that potential prey species, hunting moves of hunters, and situations can be easily imitated (Marshall 1976; Sallandre and Cuxac 2002; Senghas et al. 2004).

Observation 12. Two independent host shifts of tapeworms occurred to hominids as definitive host around 0.8–1.7 Mya (Hoberg et al. 2001).

Observation 13. Evidence from cut-mark studies shows that hominids were frequently gaining early access to either fully fleshed carcasses or to carcasses containing substantial amounts of meat, which in some cases were very unlikely to have come from felid kills, and in other cases definitely did not, and where hominids (probably *H. erectus*) were fully in control of the process (Bunn and Kroll 1986; Dominguez-Rodrigo

2002; Dominguez-Rodrigo and Barba 2006; Pobiner et al. 2008).

Observation 14. Evidence from a set of morphological adaptations that favor long-distance running and that were in place by the time *H. erectus* emerged shows that *H. erectus* was a good long-distance runner (Bramble and Lieberman 2004).

Observation 15. Evidence from fossil endocasts shows the non-allometric increase of brain size and the reorganization of the frontal lobe involving Broca's area in *H. habilis* (Holloway 1995, 1996; Tobias 1995).

Observation 16. Evidence from paleoanthropology and modeling hominid dispersal shows quick spread of *H. erectus* in the savannah, grassland region that favors a cursorial big-game hunter (Antón et al. 2002; Hughes et al. 2007).

Conclusion 1. By the time *H. erectus* emerged, around 1.8–2.0 Mya, all key adaptations that were necessary to invade the niche of a cursorial big-game hunter were in place. This includes the suitable morphological adaptations, suitable tools, and a system of communication that allowed both efficient recruitment and the cultural transmission of hunting roles and hunting knowledge.

Summary

The context of the evolution of early human language is a long-standing enigma. Here I have shown that pre-hunt communication fits the criteria that one can demand from a scenario trying to explain the early evolution of human language. Recruitment created a need for a novel signaling system. The shared interest of the hunt created an environment in which conventional signals could evolve. The need to plan ahead and negotiate culturally mediated hunting tactics created a pressure for increasing complexity. The ease of mimicking animals and actions combined with drawings allowed the emergence of simple iconic signals from which more conventional (symbolic) forms could evolve. Last but not least, climate change combined with the cultural inheritance of both hunting tools and hunting know-how made this transition unique.

The plausibility of the requirements listed in the third section was also investigated. There is solid evidence for the habitat change and meat eating; there is compelling evidence for hunting large mammals and using tools. Moreover, the present theory can explain all the basic requirements, that is, honesty, groundedness, power of generalization, and uniqueness.

Also note that there are two kinds of selection pressure and thus two transitions involved. The first one is a selection pressure to find a substitute for the natural recruitment system that was provided by fruit crops to achieve large hunting party size. The second one is selection pressure for a communication system that allows the coordination of group-hunting behavior. The first selection pressure originates from the niche change and from the fact that hominids are omnivores, thus hunger is

not the equivalent of hunting, yet hunting success was probably correlated with the size of hunting parties. The second one originates from the need to coordinate big-game hunting and from the fact that hunting of big game is partly a cultural adaptation of hominids. The first one is a requirement for the second, and the solution of the first one is a pre-adaptation (exaptation) for the solution of the second. Without large hunting parties the big-game hunting would have been impossible; without the ability to use indexical or possibly iconical signals (for recruitment), the evolution of an iconical/symbolic communication system (for the coordination of the hunt) would have been impossible too. As discussed above, the type of solution for the first problem need not necessarily be the one presented here (i.e., skulls with horns) but, for the reasons discussed, it is the most likely solution. The order of these transitions, however, is a logical necessity, as first the problem of recruitment had to be solved, which then opened up the way for cooperative big-game hunting, which in turn created the second type of selective pressure for the coordination of the hunt. Pre-conditions for this type of linguistic transition are as follows:

- Some form of preference for meat eating.
- Rudimentary tool-making skills.
- Rudimentary cooperative skills.
- Habitat change forcing the species to exploit new resources.
 - Abundance of prey species in the new habitat that can only be hunted by means of coordinated group behavior.
 - Necessary cognitive background for multitasking, mimicking, long-term memory, and so forth.

It is easy to see that it takes a unique combination of skills and events to make such a transition. A simple habitat change is not enough, as the species has to have tool-making skills (i.e., skills that allow cultural adaptation) and predisposition toward both hunting and cooperation. Moreover, the possession of these skills is not enough either, as without the proper selective pressure (i.e., habitat change) the transition will not be selected for. For example, arguably today's chimpanzees have all the necessary skills for such a transition (linguistic, tool-making, cooperative skills); however, they are not exposed to an environment in which hunting of large mammals (larger than their size) could be a vital source of food. In contrast, relatives of the ancestors of today's chimpanzees who were exposed to such an environment did make this transition and evolved into modern humans.

Note that the current theory only explains the first stage of the evolution of human language. This stage, for obvious reasons, was highly context-dependent, as signals evolved to fit the function of coordinating group hunting behavior. It is highly unlikely that signals at this stage would have been used in other contexts. Probably this kind of proto-language had to reach a level of abstraction and complexity to be usable and

useful in other contexts. This means that probably there was a second linguistic revolution when language became context-free (i.e., when it began to be used in the context of everyday life, mating, parent–offspring communication, and so on). The current model does not deal with this transition. However, it would not be surprising if this kind of second linguistic transition were the engine behind the cultural changes observed at the beginning of the Middle Stone Age (McBrearty and Brooks 2000). The reason behind this is that context-free language allows much more efficient teaching in all aspects of human life, thus it allows more complex artifacts to be made and more complex cultural traditions to emerge and spread. While the context-dependent early human language allowed hominids to occupy the niche of a big-game hunter; context-independent, probably fully syntactic language allowed *Homo sapiens* to invade others niches that were out of reach for other primates and to start a niche construction unparalleled in the history of earth.

Online Appendixes

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Notes

1. Prey size follows Bunn (1982), where the body weights of an individual in each size class, in pounds, are: 1 (<50); 2 (50–250); 3A (250–500); 3B (500–750); 4 (750–2000); 5 (2000–6000); 6 (>6000).
2. “Unbeatable” because the bite of Komodo dragons contains bacteria that quickly infect the wound, and even large-sized mammals (pigs and deer) will die in a matter of hours. In this light, active confrontation with Komodo dragons seems to be highly counterproductive, as even a small wound can result in the death of hunters.

References

- Alemseged Z (2003) An integrated approach to taphonomy and faunal change in the Shungura formation (Ethiopia) and its implication for hominid evolution. *Journal of Human Evolution* 44: 451–478.
- Antón S, Leonard WR, Robertson ML (2002) An ecomorphological model of the initial hominid dispersal from Africa. *Journal of Human Evolution* 43: 773–785.
- Arbib MA (2005) From monkey-like action recognition to human language: An evolutionarily framework for neurolinguistics. *Behavioral and Brain Sciences* 28: 105–167.
- Arbib MA, Liebal K, Pika S (2008) Primate vocalisation, gesture, and the evolution of human language. *Current Anthropology* 49: 1053–1076.
- Bickerton D (1990) *Language and Species*. Chicago: University of Chicago Press.

- Bickerton D (1995) *Language and Human Behaviour*. London: UCL Press.
- Bickerton D (2003) Symbol and structure: A comprehensive framework for language evolution. In: *Language Evolution: The State of the Art* (Christiansen M, Kirby S, eds), 77–93. Oxford: Oxford University Press.
- Bickerton D (2005) The origin of language in niche construction. http://de.dir.groups.yahoo.com/group/Wissenschaft_Kunst_und_Philosophie/message/3079?/1
- Binford LR (1981) *Bones: Ancient Men, Modern Myth*. New York: Academic Press.
- Binford LR (1986) Reply to Bunn and Kroll. *Current Anthropology* 27: 444–446.
- Binford LR (1988) Fact and fiction about the Zinjanthropus floor: Data, arguments and interpretations. *Current Anthropology* 29: 123–135.
- Blumenschine RJ (1985) Percussion marks, tooth marks, and the experimental determinations of the timing of hominid and carnivore access to long bones at FLK Zinjanthropus, Olduvai Gorge, Tanzania. *Journal of Human Evolution* 29: 21–51.
- Blumenschine RJ (1987) Characteristics of an early hominid scavenging niche. *Current Anthropology* 28: 383–407.
- Blumenschine RJ (1989) A landscape taphonomic model of the scale of prehistoric scavenging opportunities. *Journal of Human Evolution* 18: 345–371.
- Blumenschine RJ (1991) Hominid carnivory and foraging strategies, and the socio-economic function of early archaeological sites. *Philosophical Transactions of the Royal Society of London* 334: 211–221.
- Blumenschine RJ, Prassack KA, Kreger CD, Pante MC (2007) Carnivore tooth-marks, microbial bioerosion, and the invalidation of Dominguez-Rodrigo and Barba's (2006) test of Oldowan hominin scavenging behaviour. *Journal of Human Evolution* 53: 420–426.
- Bobe R, Behrensmeyer AK (2004) The expansion of grassland ecosystems in Africa in relation to mammalian evolution and the origin of the genus *Homo*. *Paleogeography, Paleoclimatology, Paleoecology* 207: 399–420.
- Bobe R, Behrensmeyer AK, Chapman RE (2002) Faunal change, environmental variability and late Pliocene hominin evolution. *Journal of Human Evolution* 42: 475–497.
- Boesch C (2002) Cooperative hunting roles among Tai chimpanzees. *Human Nature* 13: 27–46.
- Boesch C (2005) Joint cooperative hunting among wild chimpanzees: Taking natural observations seriously. *Behavioral and Brain Sciences* 28: 692–693.
- Bramble DM, Lieberman DE (2004) Endurance running and the evolution of *Homo*. *Nature* 432: 345–352.
- Brennan M (1990) *Word Formation in British Sign Language*. Stockholm, Sweden: University of Stockholm Press.
- Bunn HT (1981) Archaeological evidence of meat eating by Plio-Pleistocene hominids from Koobi Fora, Kenya. *Nature* 291: 574–577.
- Bunn HT (1982) *Meat-eating and Human Evolution: Studies of the Diet and Subsistence Patterns of Plio-Pleistocene Hominids*. Doctoral dissertation, University of California, Berkeley.
- Bunn HT (1983) Evidence on the diet and subsistence patterns of Plio-Pleistocene hominids at Koobi Fora, Kenya, and at Olduvai Gorge, Tanzania. In: *Animals and Archaeology: Hunters and Their Prey*, B.A.R. International Series, 163 (Clutton-Brock J, ed), 21–30. Oxford: British Archaeological Reports.
- Bunn HT (1991) A taphonomic perspective on the archaeology of human origins. *Annual Review of Anthropology* 20: 433–467.
- Bunn HT, Kroll EM (1986) Systematic butchery by Plio/Pleistocene hominids at Olduvai Gorge, Tanzania. *Current Anthropology* 27: 431–451.
- Bunn HT, Kroll EM (1988) A reply to Binford. *Current Anthropology* 29: 123–149.
- Burling R (2005) *The Talking Ape: How Language Evolved*. Oxford: Oxford University Press.
- Campbell R, Martin P, White T (1992) Forced choice recognition of sign in novice learners of British sign language. *Applied Linguistics* 13(2): 185–201.
- Capaldo SD (1997) Experimental determination of carcass processing by Plio-Pleistocene hominids and carnivores at FLK 22 (Zinjanthropus), Olduvai Gorge, Tanzania. *Journal of Human Evolution* 33: 555–597.
- Chomsky N (1986) *Knowledge of Language: Its Nature, Origin and Use*. New York: Praeger.
- Conard MJ, Prindiville, TJ (2000) Middle Palaeolithic hunting economies in the Rhineland. *International Journal of Osteoarchaeology* 10: 286–309.
- Corballis MC (2001) *From Hand to Mouth*. Princeton, NJ: Princeton University Press.
- Courchamp F, Macdonald DW (2001) Crucial importance of pack size in the African wild dog *Lycaon pictus*. *Animal Conservation* 4: 169–174.
- Creel S (1997) Cooperative hunting and group size: Assumptions and currencies. *Animal Behaviour* 54: 1319–1324.
- Creel S, Creel NM (1995) Communal hunting and pack size in African wild dog, *Lycaon pictus*. *Animal Behaviour* 50: 1325–1339.
- Darwin CR (1871) *The Descent of Man and Selection in Relation to Sex*. London: John Murray.
- Deacon T (1997) *The Symbolic Species*. London: Penguin Books.
- de Heinzelin J, Clark JD, White T, Hart W, Renne P, WoldeGabriel G, Beyene Y, Vrba E (1999) Environment and behavior of 2.5-million-year-old Bouri hominids. *Science* 284: 625–629.
- deMenocal PB (2004) African climate change and faunal evolution during the Pliocene-Pleistocene. *Earth and Planetary Science Letters* 220: 3–24.
- Dessalles J (1998) Altruism, status and the origin of relevance. In: *Approaches to the Evolution of Language* (Hurford JR, Studdert-Kenedy M, Knight C, eds), 130–147. Cambridge: Cambridge University Press.
- de Waal F (1982) *Chimpanzee Politics*. New York: Harper & Row.
- Dominguez-Rodrigo M (1997) Meat-eating by early hominids at the FLK 22 Zinjanthropus site, Olduvai Gorge, Tanzania: An experimental approach using cut mark data. *Journal of Human Evolution* 33: 669–690.
- Dominguez-Rodrigo M (2002) Hunting and scavenging by early humans: The state of the debate. *Journal of World Prehistory* 16: 1–54.
- Dominguez-Rodrigo M (2003) Bone surface modifications, power scavenging and the “display” model at early archaeological site: A critical review. *Journal of Human Evolution* 45: 411–415.
- Dominguez-Rodrigo M, Barba R (2006) New estimates of tooth mark and percussion mark frequencies at the FLK Zinj site: The carnivore-hominid-carnivore hypothesis falsified. *Journal of Human Evolution* 50: 170–194.
- Dominguez-Rodrigo M, Barba R (2007) Five more arguments to invalidate the passive scavenging version of the carnivore-hominid-carnivore model: A reply to Blumenschine et al. (2007a). *Journal of Human Evolution* 53: 427–433.
- Dominguez-Rodrigo M, Pickering TR, Semaw S, Rogers MJ (2005) Cut-marked bones from Pliocene archaeological sites at Gona, Afar, Ethiopia: Implications for the function of the world's oldest stone tools. *Journal of Human Evolution* 48: 109–121.
- Donald M (1998) Mimesis and the executive suite: Missing links in language evolution. In: *Approaches to the Evolution of Language* (Hurford JR, Studdert-Kenedy M, Knight C, eds), 44–67. Cambridge: Cambridge University Press.
- Dornhaus A, Chittka L (1999) Evolutionary origins of bee dances. *Nature* 401: 38.
- Dornhaus A, Chittka L (2004) Why do bees dance? *Behavioural Ecology and Sociobiology* 55: 395–401.
- Dunbar R (1998) Theory of mind and the evolution of language. In: *Approaches to the Evolution of Language* (Hurford JR, Studdert-Kenedy M, Knight C, eds), 92–110. Cambridge: Cambridge University Press.

- Engelard CP, Pickering TR, Dominguez-Rodrigo M, Barin CK (2004) Disentangling early stone age palimpsests: The functional independence of hominid- and carnivore-derived portions of archaeofaunas. *Journal of Human Evolution* 47: 343–357.
- Estes RD (1991) *The Behavior Guide to African Mammals*. Berkeley, CA: University of California Press.
- Fanshawe JH, Fitzgibbon CD (1993) Factors influencing the hunting success of an African wild dog pack. *Animal Behaviour* 45: 479–490.
- Fernandez MH, Vrba E (2006) Plio-Pleistocene climatic change in the Turkana basin (East Africa): Evidence from large mammal faunas. *Journal of Human Evolution* 50: 595–626.
- Fox M (2007) *Talking Hands: What Sign Language Reveals About the Mind*. New York: Simon & Schuster.
- Frobenius L (1981) *Afrikai Kultúrák*. Budapest: Gondolat.
- Funston PJ, Mills MGL, Biggs HC (2001) Factors affecting the hunting success of male and female lions in the Kruger National Park. *Journal of Zoology* 253: 419–431.
- Gardner RA, Gardner BT, Cantfort TE (1989) *Teaching Sign Language to Chimpanzees*. Albany, NY: State University of New York Press.
- Gaudzinski S, Roebroeks W (2000) Adults only: Reindeer hunting at the Middle Palaeolithic site Salzgitter Leberstedt, Northern Germany. *Journal of Human Evolution*: 38: 497–521.
- Gilby IC (2006) Meat sharing among the Gombe chimpanzees: Harassment and reciprocal exchange. *Animal Behaviour* 71: 953–963.
- Gilby IC, Eberly LE, Pintea L, Pusey AE (2006) Ecological and social influences on the hunting behaviour of wild chimpanzees, *Pan troglodytes schweinfurthii*. *Animal Behaviour* 72: 169–180.
- Gilby IC, Wrangham RW (2007) Risk-prone hunting by chimpanzees (*Pan troglodytes schweinfurthii*) increases during high diet quality. *Behavioral Ecology and Sociobiology* 61: 1771–1779.
- Givón T (2002) *Bio-Linguistics: The Santa Barbara Lectures*. Herndon VA: John Benjamins.
- Goodall J ([1971] 1996) *In the Shadow of Man*. Phoenix, AZ: Orion Books.
- Goodall J (1990) *Through a Window*. London: Penguin Books.
- Greenfield PM (1991) Language, tools and brain: The ontogeny and phylogeny of hierarchically organized sequential behaviour. *Behavioral and Brain Sciences* 14: 531–595.
- Haddingham E (1979) *Secrets of the Ice Age*. New York: Walker and Company.
- Hauser M, Chomsky N, Fitch WT (2002) The language faculty: What is it, who has it, and how did it evolve? *Science* 298: 1569–1579.
- Hauser M, Fitch T (2003) What are the uniquely human components of the language faculty? In: *Language Evolution: The State of the Art* (Christiansen M, Kirby S, eds), 158–181. Oxford: Oxford University Press.
- Hewes G (1973) Primate communication and the gestural origin of language. *Current Anthropology* 14: 5–25.
- Hoberg EP, Alkire NL, de Quieroz A, Jones A (2001) Out of Africa: Origins of the *Taenia* tapeworms in humans. *Proceedings of the Royal Society of London Series B* 268: 781–787.
- Hockett CF (1963) The problem of universals in language. In: *Universals of Language* (Greenberg JH, ed), 1–29. Cambridge, MA: MIT Press.
- Holloway RL (1995) Toward a synthetic theory of human brain evolution. In: *Origins of the Human Brain* (Changeoux JP, Chavallion J, eds), 42–54. Oxford: Clarendon Press.
- Holloway RL (1996) Evolution of the human brain. In: *Handbook of Human Symbolic Evolution* (Lock A, Peters C, eds), 74–116. New York: Oxford University Press.
- Hopper P, Traugott EC (1993) *Grammaticalization*. Cambridge: Cambridge University Press.
- Hughes JK, Haywood A, Mithen S, Sellwood BW, Valdes PJ (2007) Investigating early hominin dispersal rates: Developing a framework for climate data integration. *Journal of Human Evolution* 53: 465–474.
- Hurford J (2007) *The Origins of Meaning*. Oxford: Oxford University Press.
- Knight C (1998) Ritual/speech coevolution: A solution to the problem of deception. In: *Approaches to the Evolution of Language* (Hurford JR, Studdert-Kenedy M, Knight C, eds), 68–91. Cambridge: Cambridge University Press.
- Krause J, Lalueza-Fox C, Orlando L, Enard W, Hublin J, Burbano HA, Fortae J, Rasilla M, Bertanpetit J, Rosas A, Paabo S (2007) The derived FOXP2 variant of modern humans was shared with Neandertals. *Current Biology* 17: 1908–1912.
- Lachmann M, Számadó Sz, Bergstrom C (2001) Cost and conflict in animal signals and human language. *Proceedings of the National Academy of Sciences USA* 28: 13189–13194.
- Lee RB (1979) *The !Kung San*. Cambridge: Cambridge University Press.
- Lewin R (1998) *Principles of Human Evolution*. London: Blackwell Science.
- Lewis ME (1997) Carnevorian paleoguilds of Africa: Implications for hominid food procurement strategies. *Journal of Human Evolution* 32: 257–288.
- Liebal K, Pika S (2005) “Hands-on communication”: Use of gestures in apes and humans. *Proceedings of Interacting Bodies Conference 2005*, Lyons, France.
- Lieberman DE, Bramble DM, Raichlen DA, Shea JJ (2007) The evolution of endurance running: Reply to Pickering and Bunn (2007). *Journal of Human Evolution* 53: 439–442.
- Lombard M (2005) Evidence of hunting and hafting during the Middle Stone Age at Sibidu Cave, KwaZulu-Natal, South Africa: A multianalytical approach. *Journal of Human Evolution* 48: 279–300.
- Lupo KD, O’Connell JF (2002) Cut and tooth mark distributions on large animal bones: Ethnoarchaeological data from the Hazda and their implications for current ideas about human carnivory. *Journal of Archaeological Science* 29: 85–109.
- Marshall L (1976) *The !Kung of Nyae Nyae*. Cambridge: Cambridge University Press.
- Maynard Smith J, Harper DGC (1995) Animal signals: Models and terminology. *Journal of Theoretical Biology* 177: 305–311.
- Maynard Smith J, Szathmáry E (1995) *Major Transitions in Evolution*. Oxford: Freeman.
- McBrearty S, Brooks AS (2000) The revolution that wasn’t: A new interpretation of the origin of modern human behavior. *Journal of Human Evolution* 39: 453–563.
- McPherron SP, Alemseged Z, Marean CW, Wynn JG, Reed D, Geraads D, Bobe R, Bearat HA (2010) Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature* 466: 857–860.
- Michener CD (1974) *The Social Behaviour of Bees*. Cambridge, MA: Belknap Press of Harvard University Press.
- Miller G (2001) *The Mating Mind*. New York: Anchor Books.
- Mitani JC, Watts DP (1999) Demographic influences on the hunting behavior of chimpanzees. *American Journal of Physical Anthropology* 109: 439–454.
- Mitani JC, Watts DP (2001) Why do chimpanzees hunt and share meat? *Animal Behaviour* 61: 915–924.
- O’Connell JF, Hawkes K, Lupo KD, Blurton-Jones NG (2002) Male strategies and Plio-Pleistocene archaeology. *Journal of Human Evolution* 43: 831–872.
- O’Connell JF, Hawkes K, Lupo KD, Blurton-Jones NG (2003) Another reply to Dominguez-Rodrigo. *Journal of Human Evolution* 45: 417–419.
- O’Connell JF, Lupo KD (2002) Reply to Dominguez-Rodrigo. *Journal of Archaeological Science* 30: 387–390.
- Olsen S (1989) Solutré: A theoretical approach to the reconstruction of Upper Palaeolithic hunting strategies. *Journal of Human Evolution* 18: 295–327.

- Peters CR, Vogel JC (2005) Africa's wild C4 plant foods and possible early hominid diet. *Journal of Human Evolution* 48: 219–236.
- Pickering TR, Bunn HT (2007) The endurance running hypothesis and scavenging in Savanna woodlands. *Journal of Human Evolution* 53: 434–438.
- Pika S, Mitani J (2006) Referential gestural communication in wild chimpanzees (*Pan troglodytes*). *Current Biology* 16: 191–192.
- Pinker S (1994) *The Language Instinct*. London: Penguin Books.
- Pinker S, Bloom P (1990) Natural language and natural selection. *Behavioral and Brain Sciences* 13: 707–786.
- Pobiner BL, Rogers MJ, Monahan CM, Harris JWK (2008) New evidence for hominin carcass processing strategies at 1.5 Ma, Koobi Fora, Kenya. *Journal of Human Evolution* 55: 103–130.
- Pollick A, de Waal FBM (2007) Ape gestures and language evolution. *Proceedings of the National Academy of Sciences USA* 104: 8184–8189.
- Potts R, Shipman P (1981) Cutmarks made by stone tools on bones from Olduvai Gorge, Tanzania. *Nature* 291: 577–580.
- Power C (1998) Old wives' tales: The gossip hypothesis and the reliability of cheap signals. In: *Approaches to the Evolution of Language* (Hurford JR, Studdert-Kenedy M, Knight C, eds), 111–129. Cambridge: Cambridge University Press.
- Roche H, Delages A, Brugal JP, Feibel C, Kibunja M, Mourre V, Texier PJ (1999) Early hominid stone tool production and technical skill 2.34 MYR ago in west Turkana, Kenya. *Nature* 399: 57–60.
- Sallandre M, Cuxac C (2002) Iconicity in sign language: A theoretical and methodological point of view. In: *LNAI 2298, Proceedings of the International Gesture Workshop GW 2001* (Wachsmuth I, Sowa T, eds), 171–180. London: Springer-Verlag.
- Sandler W (2005) Sign language: An overview. In: *Encyclopedia of Language and Linguistics*, Vol. 11, 2nd ed (Brown K, ed), 328–338. Oxford: Elsevier.
- Selvaggio MM, Wilder J (2001) Identifying the involvement of multiple carnivore taxa with archaeological bone assemblages. *Journal of Archaeological Science* 28: 465–470.
- Semaw S (2000) The world's oldest stone artefacts from Gona, Ethiopia: Their implications for understanding stone technology and patterns of human evolution between 2.6–1.5 million years ago. *Journal of Archaeological Science* 27: 1197–1214.
- Semaw S, Renne P, Harris JWK, Feibel CS, Bernor RL, Fesseha N, Mowbray K (1997) 2.5-million-year-old stone tools from Gona, Ethiopia. *Nature* 385: 333–336.
- Semaw S, Rogers MJ, Quade J, Renne PR, Butler RF, Dominguez-Rodrigo M, Stout D, Hart WS, Pickering T, Simpson SW (2003) 2.6 million-year-old stone tools and associated bones from OGS-6 and OGS-7, Gona, Afar, Ethiopia. *Journal of Human Evolution* 45: 169–177.
- Senghas A, Kita S, Ozyurek A (2004) Children creating core properties of language: Evidence from an emerging sign language in Nicaragua. *Science* 305(5691): 1779–1782.
- Shipman P, Walker A (1989) The cost of becoming predator. *Journal of Human Evolution* 18: 373–392.
- Speth JD (1989) Early hominid hunting and scavenging: The role of meat as an energy source. *Journal of Human Evolution* 18: 329–343.
- Stander PE (1992) Cooperative hunting in lions: The role of the individual. *Behavioural Ecology and Sociobiology* 29: 445–454.
- Stanford CB (1999) *The Hunting Apes*. Princeton, NJ: Princeton University Press.
- Stiner MC (2002) Carnivory, coevolution, and the geographic spread of the genus *Homo*. *Journal of Archaeological Research* 10: 1–63.
- Számádó Sz, Szathmáry E (2006) Competing selective scenarios for the emergence of natural language. *Trends in Ecology and Evolution* 21(10): 555–561.
- Taub SF (2001) *Language from the Body: Iconicity and Metaphor in American Sign Language*. Cambridge: Cambridge University Press.
- Thieme H (1997) Lower Palaeolithic hunting spears from Germany. *Nature* 385: 807–810.
- Tobias PV (1995) The brain of the first hominids. In: *Origins of the Human Brain* (Changeoux JP, Chavallion J, eds), 61–83. Oxford: Clarendon Press.
- Tooby J (1987) Comment. *Current Anthropology* 28: 399–400.
- Turner A (2000) *The Big Cats and Their Fossil Relatives*. New York: Columbia University Press.
- Van der Merwe NJ, Tschauner H (1999) C4 plants and the development of human societies. In: *C4 Plant Biology* (Sage RF, Monson RK, eds), 509–549. London: Academic Press.
- Vrba ES (1985) African Bovidae: Evolutionary events since the Miocene. *Suid-Afrikaanse Tydskrif vir Wetenskap* 81: 263–266.
- Walker R, Hill K, Kaplan H, McMillan G (2002) Age-dependency in hunting ability among the Ache of Eastern Paraguay. *Journal of Human Evolution* 42: 639–657.
- Ward C (2002) Interpreting the posture and locomotion of *Australopithecus afarensis*: Where do we stand? *Yearbook of Physical Anthropology* 45: 185–215.
- Washburn SL, Lancaster C (1968) The evolution of hunting. In: *Man the Hunter* (Lee RB, DeVore I, eds), 293–303. Chicago: Aldine.
- Watts DP (2008) Scavenging by chimpanzees at Ngogo and the relevance of chimpanzee scavenging to early hominin behavioral ecology. *Journal of Human Evolution* 54: 125–133.
- Watts DP, Mitani JC (2002) Hunting behavior of chimpanzees at Ngogo, Kibale national park, Uganda. *International Journal of Primatology* 23: 1–28.
- Yeshurun R, Bar-Oz G, Weinstein-Evron M (2007) Modern hunting behavior in the early Middle Palaeolithic: Faunal remains from Misliya Cave, Mount Carmel, Israel. *Journal of Human Evolution* 53: 656–677.
- Zeevat H (2006) Grammaticalisation and evolution. In: *The Evolution of Language: Proceedings of the 6th International Conference* (Cangelosi A, Smith ADM, Smith K, eds), 372–378. Singapore: World Scientific.