

Regular article

**Paleolithic public goods games:  
Why human culture and cooperation did not evolve in one step**

Benoît Dubreuil  
Postdoctoral fellow  
Philosophy Department  
Université du Québec à Montréal

Correspondence:  
1409 boulevard Pie-IX  
Montréal (QC)  
CANADA, H1V 2C2  
514-525-6968  
[benoit.dubreuil@umontreal.ca](mailto:benoit.dubreuil@umontreal.ca)

**Abstract**

It is widely agreed that humans have specific abilities for cooperation and culture that evolved since their split with their last common ancestor with chimpanzees. Many uncertainties remain, however, about the exact moment in the human lineage when these abilities evolved. This article argues that cooperation and culture did not evolve in one step in the human lineage and that the capacity to stick to long-term and risky cooperative arrangements evolved before properly modern culture. I present evidence that *Homo heidelbergensis* became increasingly able to secure contributions from others in two demanding *Paleolithic public good games* (PPGGs): cooperative feeding and cooperative breeding. I argue that the temptation to defect is high in these PPGGs and that the evolution of human cooperation in *Homo heidelbergensis* is best explained by the emergence of modern-like abilities for inhibitory control and goal maintenance. These executive functions are localized in the prefrontal cortex and allow humans to stick to social norms in the face of competing motivations. This scenario is consistent with data on brain evolution that indicate that the largest growth of the prefrontal cortex in human evolution occurred in *Homo heidelbergensis* and was followed by relative stasis in this part of the brain. One implication of this argument is that subsequent behavioral innovations, including the evolution of symbolism, art, and properly cumulative culture in modern *Homo sapiens*, are unlikely to be related to a reorganization of the prefrontal cortex, despite frequent claims to the contrary in the literature on the evolution of human culture and cognition.

**Keywords:** cooperation; imitation; culture; social norms; public goods game; prefrontal cortex; inhibition; human evolution; Mid-Pleistocene; hunting; cooking; life history; *Homo heidelbergensis*; Neanderthal; *Homo sapiens*.

## 1. Introduction

There has been in recent years an impressive renewal of the literature on cooperation and culture. Several breakthroughs have been made, thanks to collaboration among philosophers, economists, psychologists, anthropologists, primatologists, and neuroscientists, all sharing the goal of expanding our knowledge of the forms that cooperation takes across cultures and across species, as well as our knowledge of its cognitive and neural underpinnings (Henrich et al. 2004; Gintis et al. 2005; Richerson and Boyd 2005; Fehr and Camerer 2007; Henrich and Henrich 2007, Heath 2008). Much of this research has been conducted by scholars of a naturalistic bent, who approach human culture and cooperation as the product of the evolutionary history of our species. These scholars have proposed frameworks that link culture and cooperation to various social dispositions, such as “social and cultural learning” (Henrich and McElreath 2003: 124), “conformism with moralistic punishment” (Richerson and Boyd (2005: 204-206), “imitation” (Alvard 2003: 136-139) or “imitation with conformist bias” (Heath 2008: 217). They have also proposed different models to explain how these dispositions could have been selected in the human lineage: kin selection, direct, indirect or strong reciprocity, costly signaling or group selection (Gintis et al. 2005; Richerson and Boyd 2005: 191-236; Henrich and Henrich 2007: 35-74)

Despite this widespread adherence to the evolutionary program, however, very few attempts have been made to link the rapidly growing literature on cooperation and culture directly with what we know of extinct hominins and their evolution. Paleoanthropology has remained for the most part a minor player in the recent literature on cooperation. As a consequence, we know more about how human-like forms of cooperation *could* have been selected for than we do about *when* they actually evolved in the human lineage. Granted, students of human cooperation cannot

be blamed for this failure of integration. Paleoanthropologists rarely agree on detailed evolutionary scenarios to offer to other disciplines. The interpretation of the most important artifacts and fossils remains frequently contentious, and the lack of data prevents testing competing hypotheses. But the difficulty of reaching a consensus on the details of human evolution should not put a stop to integrative approaches. Although we still have no clear picture of the life and behavior of extinct hominins, paleoanthropology can already constrain hypotheses about the evolution of cooperation and culture in some useful ways.

This article focuses on a specific population of large-brained hominins, generally regrouped under the label *Homo heidelbergensis*, which lived in Africa and Europe between about 700 kyr and 300 kyr and which is thought to be the common ancestor of *Homo sapiens* and Neanderthal (Rightmire 2004). My objective is to show that, although there is no evidence of the most definitive traits of properly human culture in this period of human evolution (e.g. symbolism, art, cumulative culture), *Homo heidelbergensis* was able to stick to very demanding cooperative arrangements in connection with feeding and breeding. The fact that such behaviors appear in our evolution much before art or symbolism, I contend, implies that human culture and cooperation did not evolve in one step. Consequently, understanding their evolution implies integrating more specific data about the evolution of the brain and behavior in extinct hominins.

I begin by presenting three groups of cognitive and neural mechanisms (affects, executive functions, perspective-taking) supporting cooperation and culture in modern humans (2). Identifying such mechanisms is a first step toward moving beyond general phenomena such as “imitation”, “conformism”, and “social learning”, on which most discussions of the evolution of human cooperation have been focused, but which cannot be easily mapped on to properly cognitive mechanisms realized in brain structures. I then present evidence that *Homo heidelbergensis* engaged in riskier and longer-term public good games than earlier hominins in

the domains of feeding and breeding. I argue that this change was made possible by the presence of a modern-like capacity on the part of individuals to assess the risks of cooperation and to stick to cooperative arrangements (3). I then relate the behavioral transition in *Homo heidelbergensis* to the evolution of the brain. Inhibitory control and goal-maintenance are cognitive abilities that are realized in the dorsal part of the prefrontal cortex, and I present evidence that this part of the human brain is most likely to have taken its modern form along with the evolution of *Homo heidelbergensis* (4). I conclude by sketching one important implication of my argument, which is that subsequent behavioral innovations, including the one associated with the evolution of symbolism, art, and properly cumulative culture in modern *Homo sapiens*, are unlikely to be related to a reorganization of the executive functions realized in the prefrontal cortex, despite frequent claims to the contrary (5).

## **2. The cognitive foundations of specifically human cooperation**

Cooperation and culture are not specific to humans, but there is no question that they take forms in humans that are unknown in other primates. For instance, we cooperate in everyday life with people we barely know, and we are often willing to jeopardize some of our core interests in long-term cooperative ventures with our kin and friends. It is true that this trust is sometime misplaced and that others sometimes deceive us, but cooperativeness is usually rewarding in the long run. It helps us as individuals to realize goals that are meaningful to us (raising children, succeeding in our professional life) and it helps us as a species to survive and to succeed.

Cooperative and cultural behaviors in modern humans are realized by cognitive mechanisms that are sometimes specific to humans and sometime shared with nonhuman primates. A study of the evolution of cooperation and culture must begin with the identification

of behaviors and cognitive mechanisms that are likely to have evolved in the human lineage since our split with our last common ancestor with chimpanzees. This is not the place for a complete examination of the cognitive foundations of cooperation and culture in humans and nonhuman primates, but I want to highlight three types of mechanisms for which the case for human specificity is rather strong and to which we can refer securely in our evolutionary reconstructions. I will argue that human cooperation and culture has a specific affective basis (2.1) and that it depends crucially on executive functions for the control of behavior (2.2) and on higher perspective-taking abilities for complex institution building (2.3). In the rest of the article, I will argue that a change in executive functions, and most particularly in inhibitory control and goal-maintenance, best explains the evolution of cooperation in *Homo heidelbergensis*.

## **2.1 The role of affects**

Monkeys and apes share many affects and motivations with humans. There is no question that they empathize with their conspecifics, or that they can be helpful in various circumstances (Cheney and Seyfarth 2007; de Waal 2006; Warneken et al. 2007). It is pretty clear however that nonhuman primates lack some of the motivations underlying human cooperation. One of them is the interest in sharing the attention and the emotional states of others that humans develop in the first year of their life (Tomasello et al. 2005). Not only is this interest essential for normal speech development; it is the cornerstone of cultural learning in humans (Tomasello 2007). Sharing attention with others is instrumental in learning social coordination and social norms. Teaching children to respect social norms, for instance, typically implies sharing attention with them on their actions and their consequences. Punishment of norm violations makes sense as long as both agents (the punisher and the punished) share attention on the norm that has been violated.

There is certainly a point in the human lineage when our ancestors evolved new social motivations, but when? The first step in answering this question is to decide what kind of alteration of behavior might have accompanied this transformation of human affects. Students of human evolution usually explain major transitions in the human lineage by reference to cognitive changes only (they refer to “greater or more fluid intelligence”), but affective evolution is a serious alternative that must be considered when looking for explanations of specific behavioral changes. A second step is to determine what kind of neurological changes might have accompanied the evolution of human affects. Basic emotions and motivations are realized in subcortical structures. Such internal changes would be impossible to detect in the endocasts of extinct hominins. But complex social motivations and emotions also depend on connections between subcortical and cortical structures, especially in the ventral, medial, and orbitofrontal part of the prefrontal cortex, in which social events and complex goals are represented and ascribed value (Fehr and Camerer 2007, Krueger et al. 2009). Although data are still fragmentary, the study of endocasts can potentially provide information about the shape, the size (in both relative and absolute terms), and the gyrification of these regions of the prefrontal cortex, a question to which I come back below (section 4).

## **2.2 The control of behavior**

Human cooperation relies on specific social motivations, but also on general executive functions like inhibition, planning, and working memory. These functions play a central role in cooperation and norm following because they allow us to stick to abstract goals by resisting the temptation of engaging in more immediately attractive courses of action. Psychologists use various tasks to test executive functions. One of them is the “less is more task,” which is used to

test inhibitory control (Carlson et al. 2005). In this task, a subject is presented a large and a small food reward, and he must learn that he must choose the small reward in order to receive the large one. To succeed in the task, the subject must learn to inhibit a prepotent response in order to select the smaller reward. Apes, just like three-year-old children, typically fail in this task. This suggests a greater capacity for inhibitory control in human adults. This is not to say that apes have no inhibitory control at all. Boysen and Berntson (1995), for instance, presented the task to number-trained chimpanzees. They have shown that presenting Arabic numerals instead of real rewards improved significantly the performance of apes. Many other factors impact on apes' success in this task and success is higher when the food is less visible and the disparity between the two choices is smaller (Vlaming et al. 2006). Another interesting finding among apes is that differences in performance between individuals are significant. Some apes learn the task pretty rapidly while others do not (Uher and Call 2008).

In sum, nonhuman primates have some capacity for inhibitory control, but there is still an impressive cognitive gap between them and humans. All normal human adults succeed in the “less is more” task after a few trials, even when the reward is salient. This flexible and powerful inhibitory control is necessary to secure everyday participation in long-term and often risky cooperative projects. To be sure, long-term and risky cooperation can be mutually beneficial, but only if our partners have the capacity to resist the temptation to make defection. Think of founding a family or of starting a business. How many opportunities for defection are there before the venture really becomes rewarding?

As for affective evolution, there was certainly a point in our lineage when our ancestors evolved human-like executive functions. Here again, the question is how such a change would have impacted on hominin behavior and what kind of neural rewiring might have accompanied it. We know that the prefrontal cortex plays a central role in executive functions. The dorsolateral

cortex, more particularly, one of the latest maturing parts of the prefrontal cortex in children, is associated with inhibitory control and goal maintenance in all kind of social tasks (Sanfey et al. 2003; van t'Hout 2006; Knoch et al. 2006). I explain in sections 4 why I think that a change in this part of the brain can be parsimoniously linked to the behavioral evolution found in *Homo heidelbergensis*.

### **2.3 The role of perspective taking**

Nonhuman primates have been shown to have some ability to represent to themselves the goals of others (Call et al. 2000; Hare et al. 2000, 2001, 2006). They can distinguish, for instance, an experimenter who is unable to give a reward from one who is unwilling (Call et al. 2004). They can also infer what would be the most rational actions for a conspecific given a certain context (Wood and Hauser 2008). Getting an explicit and stable representation of others' perspectives, however, is probably beyond their reach (Kaminsky et al. 2008). Cheney and Seyfarth (2007: 154-155) illustrate the limitations of baboons' perspective-taking abilities with the following anecdote from their fieldwork in Botswana:

When baboons cross from one island to another at the peak of the flood, they typically choose the shortest and shallowest route. If the flood is large, however, they are often forced to wade or swim for hundreds of meters. Young infants are carried ventrally and can be completely submerged for several minutes. Several years before we began our study, we were told, Sylvia's [a female baboon's] baby had drowned on a long crossing. [...] [Sylvia] acted as if she believed that, as long as *her* head was above water, everyone else's head must be above water too.

In humans, representing the intentions of others activates a wide range of brain areas. One of them is the medial prefrontal cortex (MPFC), which, as mentioned above, is involved in the representation of social events and abstract goals. Another is the superior temporal sulcus (STS),

associated with the representation of goal-directed actions. More complex tasks of perspective taking, such as the explicit ascription of a false belief, also activate another area of the brain that has come under close scrutiny in recent years: the temporoparietal junction (TPJ), the region at the junction between the temporal and parietal cortices.

The exact role of the TPJ in perspective taking is still controversial. Two broad views exist in the literature. For some, the TPJ is a region that processes high-level domain-general computations in tasks requiring a reorientation of attention in response to salient stimuli (see Decety and Lamm 2007; Mitchell 2007). For others, the TPJ is the locus of a mechanism that selectively processes mental states (see Saxe and Kanwisher 2003; Saxe and Powell 2006). Although this debate is unlikely to be settled soon, two remarks are relevant for the rest of my discussion. The first is that there is little doubt that the TPJ broadly construed is activated in high-level cognitive tasks that go beyond the ascription of mental states. Visual perspective taking, autobiographic memory, prospection, and navigation all activate the TPJ (Aichhorn et al. 2006; Abraham et al. 2008; Spreng et al. 2008). These tasks commonly involve a capacity to shift attention or to look at things from different viewpoints. The second remark is that, even if the TPJ can reliably be associated with different tasks involving attention shifting, there still can be a region within the TPJ that selectively processes mental states (Schotz et al. 2009).

I have argued elsewhere that a change in the high-level attentional and social-cognitive mechanisms realized in the TPJ explains well the behavioral transition associated with the emergence of *Homo sapiens* and especially the evolution of a symbolic and stylistic element in material culture (Dubreuil 2008; Henshilwood et al. 2009). The argument, put briefly, is that engaging in artistic and symbolic behaviors implies the attentional capacity to contrast different perspectives on objects and actions, that is, to understand how things can look from someone else's perspective or how appearance can differ from reality. I explain in section 5 why

data on cranial evolution favor this hypothesis, rather than the more common view that links the emergence of arts, symbolism, and cumulative culture in modern *Homo sapiens* to a reorganization of the executive functions realized in the prefrontal cortex (Mithen 1996; Noble and Davidson 1996; Deacon 1997; Coolidge and Wynn 2001; Cela-Conde et al. 2004; Amati and Shallice 2006; Noack 2006, 2007; Ardila 2008).

### **3. Public goods games in *Homo heidelbergensis***

I have presented in the previous section three kinds of cognitive and affective mechanisms underlying human-specific forms of cooperation. These mechanisms evolved in the human lineage and their transformation certainly has impacted on hominin behavior. In this section and the following, I argue that the behavioral transition associated with *Homo heidelbergensis* can be advantageously explained, at the cognitive level, by a change in the executive functions realized in the prefrontal cortex. To make my point, I summarize the most significant behavioral changes associated with *Homo heidelbergensis*. My objective is to show that groups of *Homo heidelbergensis* became increasingly able to secure investment in costly public goods. Game theorists use the concept of “public goods games” (PGG) to describe interactions in which players have a collective interest in the investment in a common pool, but no incentive to contribute personally to it. Lighthouses, clean air or fundamental research are kinds of public goods. They are beneficial to a large number of people, but individuals rarely have personal incentives to contribute to them. They rather have an interest to free ride and to take advantage of others’ contributions.

I present below evidence that *Homo heidelbergensis* became able to cooperate in an unprecedented manner in two Paleolithic public goods games (PPGG): the game of cooperative

feeding and that of cooperative breeding. My hypothesis is that securing contribution in these PPGG required cognitive abilities for inhibition and goal-maintenance equivalent to that of modern humans, and that these abilities most likely evolved along with Mid-Pleistocene encephalization process.

### **3.1. PPGG(1): Cooperative feeding**

Modern foragers' subsistence strategy and diet are directly determined by their capacity to cooperate. There are at least two reasons for this. The first is that some forms of foraging are intrinsically hard to perform alone. They can be dangerous (large-game hunting), involve mobility over great distances (difficult for mothers, young children, or injured individuals) or require some division of labor (as when a part of the group has to stay at a base camp while another forages). The second reason is that some subsistence strategies provide a highly irregular energy intake. This is the case with large-game hunting. The probability of killing a large prey every day is pretty low, but an average hunter can expect to kill at least a few in a year. If all hunters pool their takes, they can achieve a more regular energy intake. Switching to a more efficient subsistence strategy thus becomes possible and, indeed, meat sharing is ubiquitous among modern hunter-gatherers (Gurven 2004; Kaplan and Gurven 2005).

Food sharing can easily be understood as a PPGG. In principle, everybody has an incentive to consume the public good, but no incentive to contribute to it. Contribution among modern foragers is secured by agents' ability to stick to cooperative arrangements in the face of competing motivations. Hunters, for instance, have to face the fear of large preys and resist the temptation of defection during hunting. They also have to resist the temptation of keeping a larger part of their take for themselves or their kin, a temptation that can be rather strong in times

of food shortage. Anthropologist Kristen Hawkes (1993) has argued that males' contribution to the public good was principally motivated by the desire to attract attention and to gain mating opportunities, but some crucial facts make this interpretation unlikely. For instance, there is the fact that hunters are unsatisfied with those who contribute less or the fact that they often free ride on rules of sharing when they have the opportunity to do so (Gurven and Hill 2009). This is not to say that competition for prestige among hunters does not exist or is not important, but that it is better understood as a side effect of the presence of the norm of sharing in the first place.

Although hunting and meat eating is clearly present in apes, animal food does not play a fundamental role in apes' diet. Meat sharing among apes is also rare and generally done under pressure and harassment (Gilby 2006). Modern humans' specificity is not that meat always plays a central role in feeding, but that it can play a central role. Quechua agriculturalists from Highland Peru consume about 5% of their daily calories in animal food, while this share goes up to 96% among traditional Inuits (Leonard 2002). Most human groups lie between these two extremes. What is striking is the flexibility of human behavior and the capacity to adopt radically different subsistence strategies, including some based on highly cooperative food sharing.

It is widely accepted today that Plio-Pleistocene hominins (including early members of the genus *Homo* and probably also *Paranthropus*) were eating meat from small and medium-sized preys. The main evidence for this comes from butchery marks on animal bones found at hominin sites. There is unfortunately no consensus on the place of meat in the diet of early members of the genus *Homo*. One view is that *Homo habilis* and *Homo ergaster* were marginal scavengers, accessing carcasses only after felids and hyaenids. Another view is that they were more active scavengers, confronting other carnivores. The balance of the evidence suggest that early members of the genus *Homo*, and especially early *Homo erectus* after 1.9 myr, had access to carcasses with significant amounts of meat and were active rather than passive scavengers (for

a review of the debate and evidence, see Domínguez-Rodrigo 2002; Domínguez-Rodrigo and Pickering 2003, Plummer 2005). This suggests a more versatile diet and possibly enhanced feeding cooperation, but there is no evidence of a switch to a diet primarily based on meat and extensive sharing (Ungar et al. 2006).

The case of later hominins differs in some important respects. The discovery of a wooden spear dated at 125 kyr between the ribs of a Straight-tusked Elephant (*Hesperoloxodon antiquus*) in Lehringen in Germany provides evidence that early Neanderthals were large-game hunters. The finding of three well-preserved wooden spears in Schöningen dated at 400 kyr suggests that this was also the case with *Homo heidelbergensis*, their alleged ancestor (Thieme 1997; Dennell 1997). Another way to reconstruct the diet of extinct humans is to measure the proportion of stable isotope  $\delta^{13}$  and  $\delta^{15}\text{N}$  in the collagen extracted from ancient bones. Such analyses are difficult to conduct on older specimens, but have been done successfully on Neanderthals. They confirm that Neanderthals were getting the overwhelming majority of their dietary protein from animal sources and behaved as top-level carnivores, hunting mainly medium-sized to large herbivores (Richards et al. 2000). The capacity of both modern humans and Neanderthals to switch to a subsistence strategy based primarily on animal food suggests that this form of flexibility was also present in their Mid-Pleistocene common ancestor 700-300 kyr ago. When a behavioral pattern is shared within one clade, it is more parsimonious to assume that it is produced by the same proximate mechanisms.

Another important change in Mid-Pleistocene hominins is linked with the appearance of the controlled use of fire in hearths, an innovation that was probably concomitant with the emergence of *Homo heidelbergensis* (James 1989; Goren-Inbar et al. 2004). Some evidence of burnt animal bones has been found at Plio-Pleistocene sites (e.g. Swartkrans in South Africa), but there is no indication that hominins prior to the Mid-Pleistocene were able to keep a fire burning

for several hours. The controlled use of fire is also a form of PPGG. Cooking makes meat easier to masticate and facilitates the digestion of various plants (Wrangham and Conklin-Brittain 2003), and fire is a useful protection against predators, but keeping a fire burning for several hours requires a significant amount of work. Everyone has an interest in seeing the fire fueled with sufficient firewood, but also no personal incentive to fuel it. Humans can find cooperative solutions to such dilemmas, because they can represent complex divisions of labor, ascribe value to long-term cooperative goals, and resist the temptation of free riding.

My point here is not that the diet of early members of the genus *Homo* was identical to that of apes or australopithecines. The increasingly frequent evidence of tool use and butchery during the Plio-Pleistocene (between about 2.5 myr and 1.5 myr ago), as well as dental evolution in *Homo habilis* and early *Homo erectus*, suggests increased dietary versatility and a capacity to adapt to changing and unpredictable environments (Ungar et al. 2006). But the presence of cooking and large-game hunting in *Homo heidelbergensis* implies the capacity to switch to a mode of subsistence that is only possible given extensive resource and risk pooling.

### **3.2. PPGG2: Cooperative breeding**

The transformation of *Homo heidelbergensis*' subsistence strategy was accompanied by another change in human social life that was certainly just as meaningful. The change concerns the domain of reproduction and breeding broadly construed, and its significance can be illustrated by comparing the structure of life history in humans with that found in apes. Humans have an exceptionally long lifespan, but also an extended period of juvenile dependence. Hillard Kaplan and his colleagues (Kaplan et al. 2000; Kaplan and Robson 2002; Kaplan and Gurven 2005) have estimated that, for the first 20 years of their lives, humans consume more than they produce.

Chimpanzees, on the other hand, become self-sufficient around five years of age and remain so for the rest of their lives, investing modestly in their offspring during their adult life. The contrast with modern humans is striking. While chimpanzee mothers usually care for one dependent child at a time, human mothers must often care for three or four (Chapais 2008: 164). On the whole, therefore, the modern human life history implies huge transfers between generations. Most of the transfers go to children, although significant amounts are also allocated to the elderly and to debilitated individuals.

There are different ways in which cooperative breeding can be construed as a PPGG. The most obvious is to say that, at the level of natural selection, cooperative breeding is advantageous to parents (and to kin, more generally), because prolonged infancy has (presumably) an impact on cognition and behavior that enhances fitness. Kin thus have an interest in prolonged infancy, but also an incentive not to invest personally in it. But cooperative breeding can be described as a public good at another level. If intergenerational transfers and prolonged infancy contribute to raising healthy and cooperative individuals, it can be construed as a PGG at the level of the group itself. At the evolutionary level, this implies that cooperative breeding and modern life history could have been selected by group selection (Driscoll in press). At the psychological level, which is the focus of this article, it is reasonable to suggest that cooperative breeding is understood as a PGG in this sense by foragers themselves, who enforce norms prescribing investment in children and directing the flow of goods and services within the group to the advantage of families with more children (Gurven 2004). It is also reasonable to suggest that modern life history could evolve in our lineage only once hominins became able to secure intergenerational transfers, that is, once individuals became able to represent and ascribe value to long-term cooperative goals, as well as to resist the temptation of defection on a daily basis.

We do not exactly know when modern life history evolved in our lineage. Nevertheless, different lines of evidence suggest that life history in early members of the genus *Homo* was closer to the pattern found in apes, and that a modern-like pattern evolved in *Homo heidelbergensis* (for a detailed review, see Robson and Wood 2008). One line of evidence comes from the study of dental development. Although inferences on this basis must be drawn carefully, the overall evidence suggests that dental development in *Homo heidelbergensis* and Neanderthal was relatively close to the modern pattern (Ramirez-Rozzi and Bermudez de Castro 2004; Macchiarelli et al. 2006; Guatelli-Steinberg 2009). By contrast, dental growth in Plio-Pleistocene hominins was closer to the ape pattern, suggesting a similar organization of life history (Dean et al. 2001).

A second line of evidence comes from body size and brain mass. In primates, larger body size and brain mass are generally correlated with a slower life history. It is thus reasonable to take brain and body expansion in the human lineage as indirect evidence of a slower life history (Robson and Wood 2008: 401). The first important change occurred in Plio-Pleistocene hominins, when early *Homo ergaster/erectus* evolved for the first time modern-like body proportions. Nevertheless, it was only with *Homo heidelbergensis*, one million years later, that both body size and body mass entered the range of modern *Homo sapiens*, further suggesting the evolution of modern-like life history at this point in the human lineage.

Human infants grow more slowly than ape infants, but this is not the only problem that they create for foraging groups. For the first months and years of their life, human infants also find themselves in a complete state of dependence and vulnerability. Human babies cannot even hold their head steady for several months, while baby chimps can cling to their mothers a few days after their birth. Caring for defenseless babies is costly for humans. It becomes even more costly if the group opts for a subsistence strategy requiring great mobility, as was almost certainly

the case among *Homo heidelbergensis*. In consequence, evidence in favor of increased neonate dependence would strengthen the inference about the presence of cooperative breeding.

One way to find such evidence is to consider the evolution of brain size in conjunction with that of the birth canal. During the Pleistocene, delivering more vulnerable neonates was probably the price to pay for evolving bigger brains. Human babies have to pass through the birth canal, which imposes constraints on the maximum size of the brain at birth. Early delivery partly solves the problem, but it produces relatively less mature newborns (Rosenberg and Trevathan 1996). The other part of the solution is the evolution of a new birth mechanism. Human babies have such large brains that they must operate a series of rotations to pass through the birth canal. This is what makes giving birth so dangerous for human mothers and fetuses. It also explains why delivery generally takes a cooperative form in modern humans (Trevathan and Rosenberg 2001).

Although we have a fairly good idea of the evolution of brain size, the evolution of the birth canal must be inferred on the basis of a handful of incomplete pelvic bones. The reconstruction of a female pelvis from Gona dated at 1.2 myr suggests that the size of the birth canal in *Homo erectus* was evolving to accommodate larger-brained babies and might have imposed a constraint on encephalization (Simpson et al. 2008). The presence of the modern birth mechanism in *Homo heidelbergensis* and Neanderthal is still debated, because the presence of the characteristic twisted opening of the modern human pelvis is difficult to assess on available fossils (for different interpretations, see Rosenberg et Trevathan 2001 and Weaver and Hublin 2009). Nevertheless, a number of different reasons, taken together, support the idea that these species faced obstetrical difficulties similar to modern *Homo sapiens* and gave birth to similarly immature neonates. Indeed, the rare fossils available suggest that the size of the birth canal in *Homo heidelbergensis* and Neanderthal was similar to what is found in modern humans (Arsuaga

et al. 1999; Weaver and Hublin 2009) and that brain growth rate in juveniles was also similar (Ponce de León et al. 2008).

As for cooperative feeding, the evidence presented in this section does not imply that cooperative breeding evolved suddenly in *Homo heidelbergensis*. *Homo erectus*'s feeding and breeding pattern, for instance, were probably already quite different from that of australopiths and earlier hominins. But different lines of evidence support the idea that modern-like life history evolved during the Mid-Pleistocene, and was more or less similar in Neanderthals, *Homo heidelbergensis*, and *Homo sapiens*. As for cooperative feeding, the transformation of life history would not have been possible if Mid-Pleistocene hominins had not been able to secure contributions to the PPGG of cooperative breeding. The similarity of behavior within one clade suggests that the behavior is made possible by the same cognitive mechanisms, which, I suggest, is the capacity to represent, ascribe value, and stick to abstract goals while ignoring distracting motivations.

#### **4. Brain evolution and the case for a change in the PFC**

Paleoanthropological evidence points toward a major reorganization of social life during the Mid-Pleistocene. I have argued that the kind of PPGG in which *Homo heidelbergensis* begin implies modern-like capacities for representing and ascribing value to abstract goals, as well as for inhibitory control and goal-maintenance. This suggests that hominins became capable of securing contribution in risky and long term cooperative projects much before the appearance of behaviors generally presented as the Pinnacle of human cultural creativity (e.g. art, symbolism, cumulative culture). I now want to argue that what we know of brain evolution also supports the link between *Homo heidelbergensis*' cooperative abilities and a reorganization of executive

functions realized in the prefrontal cortex (PFC). In the next section, I will show that this argument also support the idea that subsequent behavioral transitions in the human lineage—and especially the one associated with the evolution of art, symbolism, and cumulative culture in *Homo sapiens*—was not caused by a reorganization of the PFC, as often proposed.

There are serious and well-known limitations to the reconstruction of brain evolution. The functional organization of the brain cannot be read in fossils. Endocasts provide no information on the internal structure of the brain, and what we know of the outer layer of the cortex is drawn from a handful of specimens. Our conclusions must thus remain relatively modest. Consequently, I will not claim that there has been a single reorganization of the PFC in the human lineage and that it happened in *Homo heidelbergensis*. I will rather contend that, if there is only one point in our lineage where such reorganization happened, it was in all likelihood there. By contrast, if there were many phases of reorganization, this one was most probably centered on the dorsolateral areas of the prefrontal cortex (DLPFC). Why the DLPFC? I mentioned in section 2 that the prefrontal cortex is involved in the representation of complex goals, values, social events and emotions, as well as in executive functions such inhibitory control and goal-maintenance. Properly executive functions are generally associated with the DLPFC, while the ventromedial prefrontal cortex (VMPFC) and orbitofrontal cortex (OFC) are more closely link to the integration of representations of goals and events with affective values (Ardila 2008).

There are different reasons to think that the functions associated with the DLPFC evolved more recently than those connected with the VMPFC and OFC in the human lineage. One reason is that the DLPFC contributes to the realization of long-term goals, but it cannot have this function if long-term goals are not represented and ascribed value in the first place. A second reason is that the capacity for inhibitory control and goal-maintenance is one of the latest to develop in infancy, much after children are able to represent complex social norms, emotions and

goals. Although ontogeny does not always recapitulate phylogeny, it provides a useful heuristic for identifying evolutionarily more recent mechanisms. A third reason is that a convincing argument could be made that Plio-Pleistocene hominins were capable of collaborating for the realization of future goals, an ability that allowed them to engage in group defense, passive or active scavenging, and the transportation of stone tool and carcasses over some kilometers (Gärdenfors and Osvath forthcoming). By contrast, there is no evidence that Plio-Pleistocene hominins engaged in more risky or long-term cooperative ventures—such as those described in section 3 for *Homo heidelbergensis*—that require the lasting capacity to resist the temptation for defection.

But there are other reasons to think that the PFC was reorganized along with the evolution of *Homo heidelbergensis*. Some of them come from paleoneurology. Our brain is about three times as large as expected for a primate of our size, and we have a fairly good idea of the most important phases of encephalization in the human lineage. The first phase of expansion is associated with Plio-Pleistocene hominins and with the emergence of the genus *Homo*. In early members of the genus *Homo*, average brain size departs from the average of 300-500 cm<sup>3</sup>, found in australopithecines, and reaches an average of 600-900 cm<sup>3</sup> (McHenry and Coffin 2000). The second phase occurs during the Mid-Pleistocene, especially in *Homo heidelbergensis*, whose brain size slowly reaches the modern range of 1100-1400 cm<sup>3</sup> (Rightmire 2004).

The cognitive implications of encephalization are far from clear. On the one hand, it is reasonable to assume that the expansion of the brain was under positive selective pressure, given the enormous metabolic costs of a larger brain (Aiello and Wells 2002). On the other hand, we do not know if cognitive changes should be related to *relative* or *absolute* brain growth. The problem is simple. There is a general correlation in primates between body and brain size and this correlation is not obviously related to cognitive differences. Hominins may have grown larger

brains simply because they were growing larger bodies. This is why paleoanthropologists often prefer to discuss *relative* rather than *absolute* brain growth in the human lineage and pay more attention to hominins' encephalization quotient (EQ), which expresses a ratio of brain mass to body mass, rather than to brain size properly.

Relative encephalization provides a slightly different picture than absolute encephalization. Plio-Pleistocene encephalization, more particularly, is less significant when considered in relative terms. The reason for this is that larger-brained Plio-Pleistocene hominins (*Homo ergaster/erectus*) also have larger bodies. The encephalization quotient, estimated between 2.5 and 3 for australopithecines and paranthropus, increases modestly to 3.1-3.6 with *Homo habilis*, *Homo rudolfensis*, *Homo ergaster* (McHenry and Coffin 2000: 127). These estimates also face serious uncertainties because of the limited sample of fossils, the difficulty of assessing body size for most of them, and the high degree of variation in size found in early members of the genus *Homo*. If one adds to these problems the general difficulty of reconstructing the behavior of various Plio-Pleistocene hominin populations, it becomes almost impossible to identify a correlation between behavior and relative and/or absolute cortical expansion in early members of the genus *Homo*.

But the case of *Homo heidelbergensis* is easier to assess. The first reason for this is that encephalization in *Homo heidelbergensis* is significant in both relative and absolute terms. Absolute brain size in this group ranges between 1100-1400 cm<sup>3</sup> and, despite the persistent difficulty of estimating body size for many specimens, EQ enters the range of variation found in Neanderthals and *Homo sapiens* (5-6.5) (Rightmire 2004). The second reason is that encephalization in *Homo heidelbergensis* can be more securely linked with behavioral changes, because there is no evidence that this taxon coexisted with other taxa, while at least three hominin

taxa coexisted in Africa during the Plio-Pleistocene (*Homo habilis*, *Homo erectus*, *Paranthropus*).

My suggestion is that the behavioral changes in *Homo heidelbergensis* were linked, at a minimum, with a functional reorganization of the PFC. But I want to make clear what evidence makes the suggestion plausible. On the one hand, there is no indication that encephalization benefited the frontal lobe more than other regions of the neocortex. Despite the dramatic enlargement of the frontal lobe during human evolution, its overall place in the human brain is still comparable in proportion to what is found in apes (Semendeferi et al. 2002). The frontal lobe benefited from encephalization, but so did the temporal, parietal and occipital lobes.

Besides size, some structural differences have been documented between the frontal lobe of humans and nonhuman primates, but these differences are for the most part related to size and are likely to have evolved along with encephalization. Rilling (2006: 73), for instance, argues that the human PFC is proportionally larger than that of apes because the non-prefrontal parts of the frontal lobe (the primary motor and premotor cortices) did not benefit equally from encephalization. Similarly, Semendeferi and colleagues (2001: 232) argue that the frontopolar cortex, the most anterior part of the PFC, associated with complex planning, benefited more from encephalization than other areas. Other distinctive features of the human frontal lobe include a higher level of cortical folding (gyrification) and a higher proportion of white matter, two features that suggests increased connectivity and functional differentiation and that probably also evolved along with encephalization (Rilling 2006: 72; Schoenemann et al. 2005; 2006).

The argument in favor of a functional reorganization of the PFC in *Homo heidelbergensis* is thus supported by different lines of evidence: the evolution of new public goods, the presence of the most important phase of encephalization in human evolution, and the fact that the most specific features of the human prefrontal cortex are related to size. I do not claim, however, that

there was no reorganization of the PFC earlier in human evolution. As mentioned above, an argument can be made that Plio-Pleistocene hominins were already cooperating about future goals on an unprecedented scale (Gärdenfors and Osvath forthcoming). This capacity could be realistically linked to mechanisms realized in the VMPFC and OFC and dedicated to the integration of affective value and abstract social goals.

## **5. Implications for *Homo sapiens***

The argument proposed in the previous sections has important implications for the evolution of behavior and cognition in *Homo sapiens*. If *Homo heidelbergensis* had a modern-like capacity for representing abstract goals and sticking to them in the face of competing motivations, and if this capacity is explained by a modern-like functional organization of the PFC, then subsequent cognitive and behavioural changes in the human lineage are unlikely to be related to a change in this area of the brain. This goes against several accounts that have related the evolution of art, symbolic, and cumulative culture to the expansion and reorganization of the PFC (Mithen 1996; Noble and Davidson 1996; Deacon 1997; Coolidge and Wynn 2001; Cela-Conde et al. 2004; Amati and Shallice 2006; Noack 2006, 2007; Ardila 2008). It is impossible to definitively rule out hypotheses about the evolution of the brain, but I will propose in this section two additional lines of evidence to add weight to my interpretation.

The first is that the evolution of the cranium in modern *Homo sapiens* was not related to a distinctive transformation of the size and shape of the PFC. Externally, the frontal bone of *Homo sapiens* does exhibit important specific features. It is, for instance, more vertically oriented in *Homo sapiens* than in Neanderthals or *Homo heidelbergensis* (Guipert and Mafart 2005). But things are different when one considers the internal shape of the frontal bone. In the inner profile

of the frontal bone is surprisingly stable in *Homo sapiens*, *Homo heidelbergensis*, and Neanderthal (Bookstein et al. 1999). By contrast to *Homo heidelbergensis*, *Homo sapiens*' frontal lobe is generally wider, but this widening is also present in Neanderthal and can be linked to a general allometric trend connected with encephalization (Bruner 2004). In sum, behavioral innovations associated in modern *Homo sapiens* do not coincide with any specific transformation of the PFC. It is obviously impossible to rule out the possibility of a functional change that would have been unrelated to changes in shape and size. But the stability of the frontal lobe adds plausibility to the hypothesis defended above and according to which a modern-like functional organization of the PFC was in place in *Homo heidelbergensis*.

The relative stability of the PFC during the last 500 kyr can be contrasted with changes in other brain areas. One of the most distinctive features of *Homo sapiens*' cranium morphology is its overall more globular structure. This globularization of *Homo sapiens*' cranium occurred between 300-100 kyr and has been associated with the relative enlargement of the temporal and/or parietal lobes (Lieberman et al. 2002; Bruner et al. 2003; Bruner 2004, 2007; Lieberman 2008). Paleoneurological reconstructions are currently insufficient to identify the precise regions that benefited from globularization. It is not unreasonable, however, to link this change with a functional reorganization of the higher association areas of the temporal and parietal areas (including the crucial region of the TPJ, discussed in section 2.3). Evidence in favor of this hypothesis comes from the functional organization of the temporal and parietal cortices. Comparative neuropsychological studies of humans and nonhuman primates indicate a displacement, in the course of human evolution, of the ventral and dorsal streams of working memory. In modern humans, the ventral stream, associated with object recognition (the “what” stream), is located more inferiorly in the temporal cortex than in nonhuman primates, while the dorsal stream, associated with spatial perception (the “where” stream), has been displaced more

superiorly in the parietal cortex (Ungerleider et al. 1998). The displacement of these streams coincides with the expansion of the late-maturing higher-association areas of the temporal and parietal cortices located in between.

I am perfectly aware that there is no consensus among archaeologists on the moment of appearance of the modern cranium and of properly “modern behaviours,” including the earliest evidence of symbolism, art, and cumulative culture (for a complete review of the various interpretation, see the contributions to Mellars et al. 2007). My point is simply that, if there is a coincidence between the biological and behavioral modernization of *Homo sapiens* in Africa between 300 kyr and 100 kyr, as an increasing number of students of human evolution tend to think, the neurological correlates of this evolution are not likely to be found in the PFC, as generally argued, but in the higher association areas of the temporoparietal cortex.

The temporoparietal cortex is certainly involved in many complex cognitive tasks. It plays a central role in attention shifting, perspective taking, episodic memory, and theory of mind (as mentioned in section 2.3), as well as in complex categorization and semantic processing (that is where Wernicke’s area is located). Although there is little doubt that these areas underwent functional and structural changes during human evolution, and although paleoneurology suggests that a change in these areas was concomitant with the evolution of modern *Homo sapiens*, the discussion remains quite open regarding the exact functional and neuronal changes that might have led to the evolution of the modern mind. This discussion will have to give a central role to the archaeological reconstruction of behavior.

I have argued elsewhere (Dubreuil 2008; Henshilwood and Dubreuil 2009) that a change in the attentional abilities underlying perspective taking and high-level theory of mind best explains the behavioral changes associated with modern *Homo sapiens*, including the evolution of symbolic and artistic components in material culture. It might be useful to emphasize that the

debate sketched above (section 2.3) about the more specific organization of the TPJ has no real incidence on my argument at this point. It would have an impact only if one could provide some reason to think that some populations of archaic humans (*Homo heidelbergensis* or Neanderthal) had sufficient attentional flexibility to engage in prospective thinking, autobiographic memory, or visual spatial perspective, but not to process false beliefs (or the opposite). At this point, I see no reason to think this is the case.

## **6. Conclusion**

A biologically informed view on human cooperation can only be reached by integrating data from various behavioral and brain sciences. This article is a modest attempt to link contemporary research on the evolution of cooperation and culture with what we know of extinct hominins' brains and behavior. As human cooperation and culture are specific in many ways, and as distinct behavioral patterns have existed in our ancestors, the reconstruction of the evolution of cooperation and culture in the human lineage is a real scientific challenge. Despite the serious difficulties facing the study of extinct hominins' brains and behavior, I have tried to show in the case of *Homo heidelbergensis* that the space of plausible evolutionary hypotheses can be constrained in some significant and useful ways. This is a necessary step in the interdisciplinary study of the evolution of human cooperation and culture. Speculation about how specifically human cooperation and culture might have been selected for in our evolutionary history can only be useful when regimented by Paleoanthropological frameworks linking ecological, morphological and behavioral data.

The explanation proposed in this article entails two corrections to influential accounts of the evolution of human cooperation and culture. The first is that the human mind did not evolve

in a single step, as accounts that focus on general phenomena such as “imitation”, “conformism”, or “cultural learning” seem to imply (Richerson and Boyd 2005; Henrich and Henrich 2007; Heath 2008). *Homo heidelbergensis*’ capacity to secure cooperation in the feeding and breeding public goods games implies not only that it could represent long-term goals and values, but also that it was able to stick to cooperative arrangements in the face of competing motivations. At the same time, the absence of evidence in favor of symbolic, art, or cumulative culture suggests that its mind was not entirely modern and that its capacity for cooperation and norm following did not translate into open-ended cultural creativity.

The second point is that emphasis on the executive functions of the PFC in influential accounts of the evolution of culture in modern *Homo sapiens* is probably misplaced (Mithen 1996; Noble and Davidson 1996; Deacon 1997; Coolidge and Wynn 2001; Cela-Conde et al. 2004; Amati and Shallice 2006; Noack 2006, 2007; Ardila 2008). *Homo heidelbergensis*’ evident capacity for cooperation, in conjunction with what we know of the evolution of the brain, suggests a modern-like organization of the PFC much before any evidence of symbolism, art, and cumulative culture. By contrast, paleoneurological evidence suggests that the temporoparietal areas changed significantly along with the evolution of the cranium, which is noteworthy given the implication of these regions in complex categorization and semantic tasks, attention shifting, perspective taking, episodic memory, and theory of mind.

## References

Abraham, A., M. Werning, et al. (2008). Minds, persons, and space: An fMRI investigation into the relational complexity of higher-order intentionality. *Consciousness and Cognition*, 17: 438–450.

- Aichhorn, M., J. Perner, et al. (2006). Do visual perspective tasks need theory of mind? *NeuroImage*, 30: 1059-1068.
- Aiello, L. C. and J. C. K. Wells (2002). Energetics and the evolution of the genus Homo. *Annual Review of Anthropology* 31: 323-338.
- Alvard, M. (2003). The Adaptive Nature of Culture. *Evolutionary Anthropology*, 12(136-149).
- Amati, D. and T. Shallice (2007). On the emergence of modern humans. *Cognition*, 103: 358-385.
- Ardila, A. (2008). On the evolutionary origins of executive functions. *Brain and Cognition*, 68(1): 92-99.
- Arsuaga, J.-L., C. Lorenzo, et al. (1999). A complete human pelvis from the Middle Pleistocene of Spain. *Nature*, 399: 255–258.
- Bookstein, F. L., K. Schafer, et al. (1999). Comparing Frontal Cranial Profiles in Archaic and Modern Homo by Morphometric Analysis. *The Anatomical Record (New Anatomist)*, 257: 217-224.
- Boysen, S. T. and G. G. Berntson (1995). Responses to quantity: Perceptual versus cognitive mechanisms in chimpanzees (*Pan troglodytes*). *Journal of Experimental Psychology: Animal Behavior Processes*, 21: 82–86.
- Bruner, E. (2004). Geometric morphometrics and paleoneurology: brain shape evolution in the genus Homo. *Journal Human Evolution*, 47: 279-303.
- Bruner, E. (2007). Cranial shape and size variation in human evolution: structural and functional perspectives. *Child's Nervous System*, 23: 1357-1365.
- Bruner, E., M. G, et al. (2003). Encephalization and allometric trajectories in the genus Homo: Evidence from the Neandertal and modern lineages. *Proceedings of the National Academy of Science*, 100: 15335-15340.

- Call, J., B. Agnetta, et al. (2000). Social cues that chimpanzees do and do not use to find hidden objects. *Animal Cognition*, 3: 23-34.
- Call, J., B. H. Hare, et al. (2004). 'Unwilling' versus 'Unable': Chimpanzees' Understanding of Human Intentional Action? *Developmental Science*, 7: 488-498.
- Carlson, S. M., A. C. Davis, et al. (2005). Less is More: Executive function and symbolic representation in preschool children. *Psychological Science*, 16: 609-616.
- Cela-Conde, C. J., G. Marty, et al. (2004). Activation of the prefrontal cortex in the human visual aesthetic perception. *Proceeding of the National Academy of Sciences*, 101(16): 6321-6325.
- Chapais, B. (2008). *Primeval kinship : how pair-bonding gave birth to human society*. Cambridge, MA: Harvard University Press.
- Cheney, D. L. and R. M. Seyfarth (2007). *Baboon metaphysics : the evolution of a social mind*. Chicago: University of Chicago Press.
- Coolidge, F. L. and T. Wynn (2001). Executive functions of the frontal lobes and the evolutionary ascendancy of Homo sapiens. *Cambridge Archaeological Journal*, 11: 255-260.
- de Waal, F. B. M. (2006). *Primates and philosophers : how morality evolved*. Princeton, N.J.: Princeton University Press.
- Deacon, T. W. (1997). *The symbolic species : the co-evolution of language and the brain*. New York: W.W. Norton.
- Decety, J. and C. Lamm (2007). The Role of the Right Temporoparietal Junction in Social Interaction: How Low-Level Computational Processes Contribute to Meta-Cognition. *Neuroscientist*, 13: 580-593.
- Dennell, R. (1997). The World's Oldest Spears. *Nature*, 385: 767-768.

- Domínguez-Rodrigo, M. (2002). Hunting and Scavenging by early humans: the state of the debate. *Journal of World Prehistory*, 16: 1–54.
- Domínguez-Rodrigo, M. and T. R. Pickering (2003). Early hominid hunting and scavenging: A zooarchaeological review. *Evolutionary Anthropology*, 12 275–282.
- Dubreuil, B. (2008). *What do modern behaviors in Homo sapiens mean for the evolution of language?* The Evolution of Language. Proceedings of the 7th International Conference (Evolang 7), Barcelona, World Scientific.
- Fehr, E. and C. F. Camerer (2007). Social neuroeconomics: the neural circuitry of social preferences. *Trends in Cognitive Sciences*, 11(10): 419-427.
- Gärdenfors, P. and M. Osvath (forthcoming). Prospection as a cognitive precursor to symbolic communication. In *Evolution of Language: Biolinguistic Approaches*. R. Larson, V. Deprez and H. Yamakido (eds). Cambridge: Cambridge University Press.
- Gilby, I. C. (2006). Meat sharing among the Gombe chimpanzees: harassment and reciprocal exchange. *Animal Behaviour*, 71: 953–963.
- Gintis, H., S. Bowles, et al. (2005). *Moral Sentiments and Material Interests. The foundations of Cooperation in Economic Life*. Cambridge, MA: MIT Press.
- Goren-Inbar, N., N. Alperson, et al. (2004). Evidence of hominin control of fire at Gesher Benot Ya'aqov, Israel. *Science*, 304: 725–727.
- Guatelli-Steinberg, D. (2009). Recent Studies of Dental Development in Neandertals: Implications for Neandertal Life Histories. *Evolutionary Anthropology*, 18: 9–20.
- Guipert, G. and B. Mafart (2005). Evolution de l'os frontal d'*Homo heidelbergensis* et *Homo neanderthalensis* et comparaison avec l'homme moderne. *Anthropologie*, 43(2-3): 159-167.

- Gurven, M. (2004). To give or to give not: An evolutionary ecology of human food transfers. *Behavioral and Brain Sciences*, 27: 543–583.
- Gurven, M. and K. Hill (2009). Why do men hunt? A re-evaluation of "Man the Hunter" and the sexual division of labor. *Current Anthropology*, 50(1): 51-74.
- Hare, B., J. Call, et al. (2000). Chimpanzees know what conspecifics do and do not see. *Animal Behaviour*, 59: 771-785.
- Hare, B., J. Call, et al. (2001). Do chimpanzees know what conspecifics know and do not know? *Animal Behaviour*, 61: 139-151.
- Hare, B., J. Call, et al. (2006). Chimpanzees deceive a human competitor by hiding. *Cognition* 101: 495-514.
- Hawkes, K. (1993). Why hunter-gatherers work: An ancient version of the problem of public goods. *Current Anthropology*, 34(4): 341-361.
- Heath, J. (2008). *Following the Rule: Practical reasoning and deontic constraint*. Oxford: Oxford University Press.
- Henrich, J., R. Boyd, et al. (2004). *Foundations of human sociality: economic experiments and ethnographic evidence from fifteen small-scale societies*. Oxford: Oxford University Press.
- Henrich, J. and R. McElreath (2003). The Evolution of Cultural Evolution. *Evolutionary Anthropology*, 12(3): 123-135.
- Henrich, N. and J. P. Henrich (2007). *Why humans cooperate : a cultural and evolutionary explanation*. Oxford: Oxford University Press.
- Henshilwood, C. S. and B. Dubreuil (2009). Reading the artifacts: Gleaning language skills from the Middle Stone Age in southern Africa. In *The Cradle of Language, Volume 2: African perspectives*. R. Botha and C. Knight (eds). Oxford: Oxford University Press: 41-61.

- James, S. (1989). Hominid use of fire in the Lower and Middle Pleistocene: a review of the evidence. *Current Anthropology*, 30: 1–26.
- Kaminski, J., J. Call, et al. (2008). Chimpanzees know what others know but not what they believe. *Cognition*, 109(2): 224-234.
- Kaplan, H. S., K. R. Hill, et al. (2000). A Theory of Human Life History Evolution: Diet, Intelligence, and Longevity. *Evolutionary Anthropology*, 9: 156-185.
- Kaplan, H. S. and A. J. Robson (2002). The emergence of humans: The coevolution of intelligence and longevity with intergenerational transfers. *Proceedings of the National Academy of Sciences*, 99(15): 10221-10226.
- Knoch, D., A. Pascual-Leone, et al. (2006). Diminishing Reciprocal Fairness by Disrupting the Right Prefrontal Cortex. *Science*, 314(5800): 829-832.
- Krueger, F., A. K. Barbey, et al. (2009). The medial prefrontal cortex mediates social event knowledge. *Trends in Cognitive Sciences*, 13(3): 103-109.
- Leonard, W. R. (2002). Food for thought: dietary change was a driving force in human evolution. *Scientific American*: 106-115.
- Lieberman, D. E. (2008). Speculations about the selective basis for modern human craniofacial form. *Evolutionary Anthropology*, 17(1): 55-68.
- Lieberman, D. E., B. M. McBratney, et al. (2002). The evolution and development of cranial form in *Homo sapiens*. *Proceedings of the National Academy of Science*, 99: 1134–1139.
- Macchiarelli, R., L. Bondioli, et al. (2006). How Neanderthal molar teeth grew. *Nature*, 444: 748-751.
- McHenry, H. M. and K. Coffing (2000). *Australopithecus* to *Homo*: Transformations in Body and Mind. *Annual Review Anthropology*, 29: 125–146.

- Mellars, P., K. Boyle, et al. (2007). *Rethinking the Human Revolution: New Behavioural and Biological and Perspectives on the Origins and Dispersal of Modern Humans*. Cambridge: MacDonald Institute of Archaeology.
- Mitchell, J. P. (2007). Activity in right temporo-parietal junction is not selective for theory-of-mind. *Cerebral Cortex*, 18: 262-271.
- Mithen, S. (1996). *The Prehistory of the Mind*. London: Thames & Hudson.
- Noack, R. A. (2006). The Frontal Feedback Model of the Evolution of the Human Mind: Part 1, The “Pre”-human Brain and the Perception–Action Cycle. *Journal of Mind and Behavior*, 27(3-4): 215–242.
- Noack, R. A. (2007). The Frontal Feedback Model of the Evolution of the Human Mind: Part 2, The Human Brain and the Frontal Feedback System. *The Journal of Mind and Behavior*, 28(3-4): 233–264.
- Noble, W. and I. Davidson (1996). *Human Evolution, Language and Mind*. Cambridge: Cambridge University Press.
- Plummer, T. W. (2005). Discord after Discard. Reconstructing Aspects of Oldowan Hominin Behavior. In *African Archaeology. A Critical Introduction*. A. Stahl (eds). Oxford: Blackwell Guides to Archaeology: 55-92.
- Ponce de Leon, M. S., L. Golovanova, et al. (2008). Neanderthal brain size at birth provides insights into the evolution of human life history. *Proceeding of the National Academy of Sciences*, 105(37): 13764-13768.
- Ramirez Rozzi, F. and J.-M. Bermudez de Castro (2004). Surprisingly rapid growth in Neanderthals. *Nature*, 428: 936-939.

- Richards, M. P., P. B. Pettitt, et al. (2000). Neanderthal diet at Vindija and Neanderthal predation: The evidence from stable isotopes. *Proceedings of the National Academy of Sciences*, 97: 7663-7666.
- Richerson, P. J. and R. Boyd (2005). *Not by genes alone*. Chicago, IL: University of Chicago Press.
- Rightmire, G. P. (2004). Brain size and encephalization in Early to Mid-Pleistocene Homo. *American Journal of Physical Anthropology*, 124: 109-123.
- Rilling, J. K. (2006). Human and nonhuman primate brains: are they allometrically scaled versions of the same design? *Evolutionary Anthropology*, 15: 65–77.
- Robson, S. L. and B. Wood (2008). Hominin life history: reconstruction and evolution. *Journal of Anatomy*, 212: 394-425.
- Rosenberg, K. R. and W. Trevathan (1996). Bipedalism and human birth: the obstetrical dilemma revisited. *Evolutionary Anthropology*, 4: 161–168.
- Rosenberg, K. R. and W. R. Trevathan (2001). The Evolution of Human Birth. *Scientific American*, 285: 60-65.
- Sanfey, A. G., J. K. Rilling, et al. (2003). The neural basis of economic decisionmaking in the Ultimatum game. *Science* 300: 1755-1758.
- Saxe, R. and N. Kanwisher (2003). People thinking about thinking people: the role of the temporoparietal junction in theory of mind. *NeuroImage*, 19: 1835-1842.
- Saxe, R. and L. J. Powell (2006). It's the thought that counts: Specific brain regions for one component of theory of mind. *Psychological Science*, 17(692-699).
- Schoenemann, P. T. (2006). Evolution of the Size and Functional Areas of the Human Brain. *Annual Review of Anthropology*, 35: 379-406.

- Schoenemann, P. T., M. J. Sheehan, et al. (2005). Prefrontal white matter volume is disproportionately larger in humans than in other primates. *Nature Neuroscience*, 8: 242-252.
- Scholz, J., C. Triantafyllou, et al. (2009). Distinct Regions of Right Temporo-Parietal Junction Are Selective for Theory of Mind and Exogenous Attention. *PLoS ONE*, 4(3): e4869.
- Semendeferi, K., E. Armstrong, et al. (2001). Prefrontal Cortex in Humans and Apes: A Comparative Study of Area 10. *American Journal of Physical Anthropology*, 114: 224-241.
- Semendeferi, K., A. Lu, et al. (2002). Humans and great apes share a large frontal cortex. *Nature Neuroscience*, 5(3): 272-276.
- Simpson, S. W., J. Quade, et al. (2008). A Female Homo erectus Pelvis from Gona, Ethiopia. *Science*, 322(5904): 1089-1092.
- Spreng, R. N., R. A. Mar, et al. (2009). The Common Neural Basis of Autobiographical Memory, Prospection, Navigation, Theory of Mind, and the Default Mode: A Quantitative Meta-analysis. *Journal of Cognitive Neuroscience*, 21(3): 489-510.
- Thieme, H. (1997). Lower Paleolithic Hunting Spears. *Nature*, 385: 807-810.
- Tomasello, M. (2007). If they're so good at grammar, then why don't they talk? Hints from apes' and humans' use of gestures. *Language Learning and Development*, 3(2): 133-156.
- Tomasello, M., M. Carpenter, et al. (2005). Understanding and sharing intentions: the origins of cultural cognition. *Behavioral and Brain Sciences*, 28: 675-735.
- Uher, J. and J. Call (2008). How the Great Apes (Pan troglodytes, Pongo pygmaeus, Pan paniscus, Gorilla gorilla) Perform on the Reversed Reward Contingency Task II: Transfer to New Quantities, Long-Term Retention, and the Impact of Quantity Ratios. *Journal of Comparative Psychology*, 122(2): 204-212.

- Ungar, P. S., F. E. Grine, et al. (2006). Diet in Early Homo: A Review of the Evidence and a New Model of Adaptive Versatility. *Annual Review of Anthropology*, 35: 209–228.
- Ungerleider, L. G., S. M. Courtney, et al. (1998). A Neural System for Human Visual Working Memory. *Proceedings of the National Academy of Sciences*, 95: 883-890.
- van 't Wout, M., R. S. Kahn, et al. (2006). Affective state and decision-making in the ultimatum game. *Experimental Brain Research*, 169(4): 564-568.
- Vlamings, P. H. J. M., J. Uher, et al. (2006). How the Great Apes (Pan troglodytes, Pongo pygmaeus, Pan paniscus, and Gorilla gorilla) Perform on the Reversed Contingency Task: The Effects of Food Quantity and Food Visibility. *Journal of Experimental Psychology: Animal Behavior Processes* 32(1): 60–70.
- Warneken, F., B. Hare, et al. (2007). Spontaneous Altruism by Chimpanzees and Young Children. *PLoS Biology* 5(7): 1414-1420.
- Weaver, T. D. and J.-J. Hublin (2009). Neandertal birth canal shape and the evolution of human childbirth. *Proceeding of the National Academy of Sciences*, 106: 8151-8156.
- Wood, J. N. and M. D. Hauser (2008). Action comprehension in non-human primates: motor simulation or inferential reasoning? *Trends in Cognitive Sciences*, 12(12): 461-465.
- Wrangham, R. and N. Conklin-Brittain (2003). Cooking as a biological trait. *Comparative Biochemistry and Physiology - Part A: Molecular & Integrative Physiology*, 136(1): 35-46.