Chapter 2 Cooperation, Altruism, and Human Evolution: Introduction Part I

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There can be no doubt that *Homo sapiens* is an unusually cooperative species—in both senses of the adjective, because while all primates are social and thus at least minimally cooperative, *H. sapiens* is social in a very particular manner. Human beings will patiently endure long, uncomfortable back-of-the-cabin flights in hideously cramped aircraft or stand meekly in long, slow lines at soup kitchens: conditions that would undoubtedly provoke unbridled aggression in any other higher primate. This odd proclivity provokes the question of just what it is about us humans that permits or even obliges us to cooperate (most of the time) in this way, subjugating ourselves to the necessities of public order. Furthermore, whatever that factor may be, when did we acquire it? Answering questions such as these is vital in developing any comprehensive understanding of our species as a biological and social entity; despite the elusiveness not only of the answers but also of the very questions themselves the contributions to this book constitute an important if necessarily preliminary step in the direction of developing such an understanding.

In the quest to comprehend and reconstruct the history of our most singular behavioral attributes, we immediately encounter one enormous difficulty. This is, of course, the fact that *H. sapiens* processes information about the physical and social worlds in which we live in an entirely unique way: one that is without parallel, or even obvious precedent, in Nature, today or in the past. We alone are symbolic animals, disassembling our surroundings into a complex vocabulary of mental symbols which we can shuffle according to rules to provide alternative versions of the world we inhabit—both as it is and as it *might* be. Other animals live in the environment more or less as Nature presents it to them, reacting to its stimuli with varying degrees of sophistication and nuance. In stark contrast, we live to a remarkable extent in environments that we re-create in our heads. And although clearly grafted on to a preexisting substrate of purely intuitive intelligence that mediated some very complex behaviors indeed, including such impressive accomplishments as making stone tools and exchanging objects over long distances, the exceptional human cognitive

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capacity that permits us to operate in this way was apparently acquired very recently and quite abruptly (Tattersall, 2004, 2008).

Today, ours is the only hominid species on the planet; and although we tend not to reflect on the fact, our lonely state is actually highly unusual. For the fossil record tells us in no uncertain terms that, throughout the long history of our family, several different hominid species typically coexisted. Indeed, we have clear evidence that as recently as some 40,000 years ago, the world was occupied by at least four different hominid species, and the arrival and spread of fully symbolic *H. sapiens* is almost certainly implicated in the rapid departure from the scene of such contemporaneous relatives as *Homo neanderthalensis*, *Homo erectus*, and *Homo floresiensis*. Uncomfortable as it may be, this reality undoubtedly tells us a great deal about ourselves as a species that (presumably as a result of our cognitive singularity) is not only intolerant of competition but also in a position to impose that intolerance.

In terms of self-knowledge, the thought is sobering. And, as just hinted, on an epistemological level it also means we are faced with the problems of context that are familiar in any attempt to explain the unique. Numerous questions about the behavioral nature of *H. sapiens* are, at best, only partially answerable on a strictly comparative basis. Is our extreme form of cooperativeness solely a function of our special and unprecedented cognitive facility? Or is it part of the necessary and preexisting substrate upon which that facility is grounded? Is it the result of longterm burnishing, by natural selection, of a property that has thus been finely honed in our lineage over the eons? Or is it an emergent quality that was acquired in a single event, through the chance addition of an otherwise unremarkable ingredient to a preexisting cognitive base that had, up to that point, functioned on an entirely different level of complexity? Is it related to what we perceive as altruistic or more generally cooperative behaviors in other primate and mammalian species? Or is it something entirely independent of those behaviors, something truly new? Is what we perceive as altruism in other primates directly comparable to whatever it is that we understand as altruism in our own social context? Or is it a by-product—or perhaps a facet-of something else entirely that we misconstrue in anthropomorphic terms? Indeed, does the recent radical reorganization of our cognitive system disqualify many aspects of our behavior, or even all, from direct comparison with their presumed counterparts in nonsymbolic precursors? This last question, particularly, demands our serious attention from the very outset. For, as Robert Cloninger (Chapter 5, this volume) observes, human beings simply cannot have the "same affective experiences" as those they "imagine [other species] might be having."

Still, despite its obvious inherent limitations, the only avenue we have for answering questions such as those just raised is through looking not simply at ourselves in isolation, but also in the context of what is known of the behaviors of organisms closely related to us. It is certainly tempting to consider that, by comparing behavioral repertoires, we will be able to see which among our behaviors are primitive, inherited from a very remote ancestor, and which are derived and thus recently acquired. But while the procedure itself might seem straightforward, even among living forms, compartmentalizing observed behaviors and sorting them into neatly comparable categories turns out, alas, to be a difficult task indeed. To complicate matters further, it is far from evident that the same categorizations apply validly across ranges of species. Behaviors displayed both by individuals and by local populations of the same higher primate species often turn out to be wildly variable, and their expression highly dependent on ecological circumstances. Among our extinct relatives the same presumably applied, with the additional difficulty that those behaviors cannot be observed but have to be inferred, frequently from very tenuous evidence. All of this makes it doubly unfortunate that the creatures believed to be our closest living relatives, the chimpanzees and bonobos, are not only quite remote from us—both an entire highly diverse hominid family, and the apes' own largely unknown evolutionary histories, lie between us and them—but also live in ecological circumstances that are radically different not simply from our own but also from those inferred for our very early ancestors.

Traditionally, the great apes—specifically chimpanzees—have been considered the most appropriate behavioral "models" for very early human relatives. In a broad cognitive sense, this may be fairly accurate: in all probability we can justifiably assume that, as the cognitive scientist Daniel Povinelli has put it, hominid ancestors were, like today's great apes, "intelligent, thinking creatures who deftly attend[ed] to and learn[ed] about the regularities that unfold[ed] in the world around them. But ... they [did] not reason about unobservable things: they [had] no ideas about the 'mind,' no notion of 'causation'" (Povinelli, 2004:34). So far so good: the apes are not modern humans, and neither were our own ancient ancestors. But if we try to go beyond this, to identify specific past behaviors to which we can trace back modern equivalents, we find ourselves in highly speculative territory. For a start, living H. sapiens turns out to be even more variable and situational in its behavior patterns than the apes are. It is hard to establish behavioral norms in a species in which it is no problem at all to find examples to illustrate both poles of any pair of behavioral antitheses you can imagine—something that amply illustrates the assertion by Donna Hart and Bob Sussman in Chapter 3 that "we are ... what we learn to be." Far less than members of *any* other species, are we condemned by our evolutionary past to any particular behavioral propensity in the present.

Clearly, though, we could not be the creatures we have become in the absence of a long and accretionary evolutionary history that includes our common ancestor with the apes. In reconstructing that history we are, of course, bedeviled by the unfortunate fact that behaviors rarely if ever preserve directly. What is more, rather few behaviors are even reflected in proxy evidence from which they might be reliably inferred. Still, the handful of proxies available, for a rather narrow range of social/behavioral features, is all we have to go on; and among those few potential proxies, ecological pressures are almost certainly more reliable than strict phylogenetic propinquity as predictors of behavior. Closely related primates may show dramatic differences in social organization, whereas creatures of the same general sort appear more likely to respond, or to accommodate, in broadly similar ways to similar environmental pressures. And, as forms that are physically adapted to forest existences, the apes—even the fairly eurytopic chimpanzees—do not provide close environmental analogs to the early hominids.

Nonetheless, "ape models" have traditionally dominated views of early hominid behavior, and they have been particularly conducive to Peterson and Wrangham's (1997) "Demonic Males" version of the "Killer Ape" scenario of human evolution articulated in the 1940s and 1950s by Raymond Dart (e.g., 1957). Something in models of this kind seems to exert an innate appeal to the reductionist human storytelling mindset. But as Hart and Sussman cogently point out, in Chapter 3 and elsewhere (e.g., Hart and Sussman, 2005, 2009), early hominids were largely defenseless creatures of small stature and had body structures that would have made them not only less efficient terrestrially than we are but also less agile in the ancestral arboreal milieu than are chimpanzees. These attributes hardly suited them well to be predators in either setting; indeed, in many respects, these early relatives must have been the very antithesis of the predator. Subsisting on largely plant-based diets, and living mostly in a mosaic of forest-edges-to-woodland, they much better fit the profile of prey species, vulnerable to a large variety of terrestrial and semi-arboreal large cats and other carnivores. To close this largely circumstantial case, there is also substantial direct evidence from the fossil record that early hominids were heavily predated upon.

From this, Hart and Sussman draw several important conclusions about probable social organization among early hominids. They include the high likelihood that these creatures lived in large groups for protection (just as modern baboons and macaques do in comparable environments), and that, within those groups, individuals were highly social and cooperative. And it would almost certainly have been in social contexts of this kind that the groundwork was laid for the later extraordinary cooperativeness of *H. sapiens*. This is not to say that very early hominids would have exhibited anything like the extremely unusual form of extensive and nuanced cooperation (and its partial inverse, subtle, and often disguised and indirect antagonism) that we see in *H. sapiens* today. To be expressed in their modern form, both of these attributes—in many ways opposite ends of a single spectrum—almost certainly necessitate symbolic cognition. But the ultimate roots of the modern human brand of sociality—its requisite biological underpinnings—were nonetheless more than probably laid down in those very early times.

One unusual aspect of cooperation, not reported in humans alone, is altruism, whereby individuals act in ways that appear to be contrary to their own interests while benefiting someone else. Ignoring the fact that human beings often act in self-destructive ways while benefiting nobody, advocates of the notion that natural selection is in the business of fine-tuning all aspects of behavior have sought to find direct evolutionary advantage in apparently altruistic behaviors, most commonly discovering such advantage in benefits that accrue to (genetically similar) kin. In this way, individual "fitness" is extended to embrace the "inclusive fitness" of the kin group. Such "kin-selection" models require the assumption that larger evolutionary outcomes result virtually exclusively from the working of natural selection that is nowadays usually referred to as "darwinian," although Pievani (Chapter 4, this volume) intriguingly points out that, in the social context, Charles Darwin himself (1871) expanded his definition of natural selection beyond the individual level to include the "tribe"—which would invoke something akin (sorry) to what is usually

referred to today as "group selection:" an unfashionable mechanism that is often seen as entirely distinct, or sometimes even antithetical, to natural selection.

Pievani (Chapter 7, this volume) goes on to examine the history of study of altruism more closely, in the process demonstrating that evolutionary change has to be driven by much more than simply the promotion or elimination of particular genotypes at the individual level. His preference is for a "multi-level" view that sees larger scale evolutionary outcomes, including such social attributes as cooperativeness and altruism, as products of much more complex histories. At the finer end of the spectrum of influences, the multi-level approach takes into account the significant reality that organisms have economic lives as well as roles as replicators, and in the broader context it recognizes that individuals and populations belong to species that are parts of dynamic wider communities that in turn live and change in sometimes dramatically fluctuating environments. Pievani emphasizes that, in the long term, the success of the ephemeral individual is inextricably bound up with the success of the group—and ultimately, of course, of the entire species, for it is of little evolutionary advantage to be the most splendidly adapted member (whatever that might in practice mean) of a species that is being outcompeted into extinction.

Pievani thus advocates that we extricate ourselves from purely "adaptationist" views of the evolutionary process (or, more properly, processes). He urges us to acknowledge the fact that any innovation (behavioral, genetic, or physical) must come into existence spontaneously, without regard to its function, and that the "current usefulness" of an attribute should hence be seen as independent of its "historical origin." Once we have made this conceptual separation, we are relieved from the necessity of seeing such behavioral features as altruism as driven by inexorable generation-by-generation pressures.

Pievani emphasizes the ubiquity in documented evolutionary histories of "exaptation," whereby heritable novelties come into existence entirely independently of any use to which they might eventually be put (he mentions birds' feathers, which are essential for flight but that for many millions of years were not exploited in this way). The fixation of any novelty in a population may even be a random event, although it will presumably be facilitated if the characteristic in question is highly advantageous. In the case of altruism, however, we also have to bear in mind that this is not a discrete feature. All developmentally normal humans have big brains; all are bipedal; all have small canine teeth. These are all truly human characteristics and all are functionally discrete. But altruism is not. Not all individual human beings are equally altruistic—or even altruistic at all—and altruism is simply one potential expression of a much larger general capacity for cooperation. To the extent that it works, kin-selection theory only explains why natural selection has not eliminated the "altruistic" extreme of the spectrum of cooperative behaviors.

Pievani notes that, whatever it may otherwise be, evolution is not a matter of optimization: it does not strive toward the perfect but instead "tinkers with structural constraints." By the nature of the hereditary apparatus, the new must always come about by modification of the old, and thus there can be no wholesale elimination of the old to facilitate the adoption of the newer and better. Which is why, Pievani suggests, we show many "ambiguous and contradictory behaviors" of "former prey

and predators at the same time." Our socially cooperative comportments, and our erratic individual ones too, are functions of a long and complex historical inheritance that can only be understood in this light. In the specific context of human behavioral evolution, the scenario Pievani favors is that altruism and cooperativeness of the human kind had their origins in an earlier tendency toward reciprocity, a tendency that proved advantageous in early human groups exposed to the hazards of woodland environments. A succession of circumstances then followed in which this tendency became exaptively amplified in a series of stages.

This scenario coincides well with what we know about the pattern of other behavioral acquisitions among our precursors, and it also fits comfortably with the fact that we still perceive echoes of our untidy origins in our dealings with each other and with the world around us. Because, as already emphasized, the new is founded on the old and is thus inextricably entangled with it. Optimization, however desirable from an engineering perspective, is rarely if ever an option in evolution, which at any moment can capitalize only on the best of whatever is available. If we seek to regard any of our behaviors, whether cooperative or aggressive, as fine-tuned by evolution for a specific function and thus as innate within us, we will miss the most important aspect of our uniqueness—namely, our almost infinite capacity to respond to circumstances. Members of *H. sapiens* may share a deep longing to understand "the human condition" in which they participate, but this does not mean that we all share an obligate behavioral state. To return to Hart's and Sussman's pithy formulation, to a very considerable extent we learn as individuals to be who and what we are.

Cloninger (Chapter 5, this volume) looks in some detail at various aspects of human learning and at the epistemological problems that arise from the complex and additive nature of human cognition and the resulting behaviors. He puts forward an ingenious model whereby major variables of human learning and personality arise from the following three distinct cognitive systems: behavioral conditioning, semantic learning, and self-aware learning. In Cloninger's scenario, these systems arose sequentially in human evolution, much as Pievani's model might predict. They and their sub-components interact to produce personality, the attribute that defines each of us as an individual. Cloninger finds that one character dimension (selftranscendence, the ability to step outside oneself and to know when rules apply) is a key to the fully modern mind; but his approach emphasizes the role of multiple feedbacks in the ultimate determination of the individual psyche. And even though his model is ultimately a "modular" one, in terms of the gradual acquisition of a set of discrete components of self-awareness over the long history of mammalian evolution, it also draws attention to the remarkable extent to which individual personality is shaped by multiple influences, among which situational and thus environmentally mediated stimuli are prominent.

Although there is plenty of evidence that symbolic cognition and its correlates are of remarkably recent origin, it is nonetheless fully evident that this capacity of ours is founded upon a very long and accretionary evolutionary history. No part of what we are, and so greatly prize ourselves for being, could have been acquired in the absence of any aspect of that long history. Cloninger courageously sketches in an evolutionary sequence in which those acquisitions might have been made. He identifies "precursor functions for symbolism" in living great apes, and sees these as the underpinnings for advanced degrees of cooperation in early hominids. In early *Homo*, he finds proxy evidence for initial enhanced function of the terminal association areas; these only later expanded into the "proactive fronto-temporo-parietal circuit" that promotes "autobiographical memory and self-aware consciousness in modern *H. sapiens*." The details of any such scenario are bound to be argued; but Cloninger's notion is compelling that not only our own senses of self but also the ways in which we perceive and process information about the world around us are dependent on self-aware consciousness of the kind he describes, mediated by "the specific functional abilities that emerged in human ancestors."

Again, we arrive at the notion that there is something very peculiar about modern human beings. We cannot legitimately seek to understand other animals, even close relatives, as less complex versions of ourselves; neither can we regard our own species as simply a more sophisticated version of them. Yes, we do indeed have ape brains inside our heads; but the added ingredient that Cloninger has striven to identify in us has produced an entirely new cognitive edifice, a structure with emergent and unprecedented properties. And this means that, as he is careful to point out, we have to be very cautious with our terminology. Humans have "self-transcendence," while other primates do not. As a result, such terms as "altruism" or even "cooperation" (inevitably possessing anthropomorphic overtones) are words we should not apply lightly, or without implicit qualification, to other species. Our anthropoid relatives may have immediate goals; and may even be aware of them, but they clearly do not process information, or make plans, or harbor motivations, in the same sense that human beings do.

Modern human beings are cooperative; and they would certainly never have become so had the biological underpinnings not already been present – not just in the hominid ancestor, but in a succession of precursor species among which, on average, behaviors we can at some level call cooperative had become more complex over time. Still, a yawning cognitive gulf was crossed when symbolic reasoning was acquired, well within the tenure of our species as diagnosed anatomically (Tattersall 2004, 2008). Certainly, our close(ish) relative *Homo neanderthalensis* indulged in a variety of behaviors, ranging from burial of the dead to the hunting of fearsomely large animals, that clearly required an advanced degree of coordination among individuals. Cognitively and socially these were impressive hominids, quite possibly the most intellectually complex beings that had ever existed before cognitively modern *H. sapiens* came along. But their social cooperation was almost certainly not mediated by mental information-processing in the modern human style. And we should be careful not to be misled by the terminology we use into thinking it might have been.

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