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HUMAN UNIQUENESS: A GENERAL THEORY

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ABSTRACT

The extensive, persistent ecological dominance of humans is unprecedented. We display a highly derived social adaptation involving uniquely extensive cooperation among nonclose kin. Further, humans possess adaptive capabilities, including language, high cognitive function, and technological virtuosity not previously seen on this planet. Moreover, this suite of properties emerged and was refined very rapidly on a geological time scale. These diverse features of humans present what is referred to as the "human uniqueness problem." A theoretical interpretation of these phenomena is one of the largest remaining challenges to the scientific enterprise. While many interpretations have been proposed—several containing important individual insights—none has yet proven robust or complete.

A straightforward resolution of the human uniqueness problem is proposed. It is argued that coalitional enforcement *is necessary and sufficient to allow extensive nonkin cooperation, leading to all major elements of human uniqueness. Coalitional enforcement arose uniquely in humans when the animals that founded the* Homo *clade acquired the ability to kill or injure conspecifics from a substantial distance. This resulted from the evolution of hominid virtuosity at accurate, high-momentum throwing and clubbing, previously supposed to be adaptations for hunting, predator defense or individual aggression. No previous animal could reliably kill or injure conspecifics remotely. This ability dramatically reduced the* individual *cost of punishing noncooperative behavior by allowing these costs to be distributed among multiple cooperators. The capacity for coalitional enforcement drove the evolution of a cooperative social adaptation stably and autocatalytically from the origin of incipient* Homo *about 2 million years ago through to the present moment—including socially supported, ultimately spectacular, refinements in weaponry and social monitoring, with attendant increases in efficiency of coalitional enforcement and thus in the extent of human cooperation. Its details rendered this evolutionary process very rapid.*

This theory is believed to be robust and relatively complete. For example, coalitional enforcement is necessary and sufficient to allow for the evolution of language in an ape. Further, given the likely functional organization of the ancestral vertebrate mind, the coalitional enforcement hypothesis predicts, in addition to genetic information, the emergence of a second stream of design information in Homo, *susceptible to Darwinian selection. A novel source of design information has long been suspected on empirical and intuitive grounds to be responsible for the uniquely high level of human adaptive sophistication. The unprecedented cognitive power of human minds is also predicted by these implications of the theory. Lastly, the "cognitive explosion" associated with the relatively recent appearance of behaviorally modern humans is predicted by the theory, as is the increasing size of human political units.*

The coalitional enforcement hypothesis and its immediate implications now enable the formerly elusive unification of diverse fields of study, including human biology, psychology, linguistics, paleontology, archaeology, anthropology, history, and economics.

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[Excerpts from Diana Jean Schemo's story "Lynch-Mob Justice Grows in Caracas" in the May 13, 1996 issue of the *New York Times*. It describes a killing in El Encanto, a poor suburb of Caracas, Venezuela, in which the formal state police presence is minimal.]

. . . when three strangers attacked some residents on their way to work, stripping them of money, tools and even clothes, the response was swift and deadly.

"I don't know if we all thought the same thing . . ." said Giovanni, 29, a father of two.

He was among the five residents forced to the ground by the attackers, who slashed their arms and backs with scissors [and] battered them with a rifle . . . Eventually, Giovanni yanked the rifle away and, finding that it was not real, screamed for help. Neighbors came running.

Two of the muggers escaped, but a third, Jose Hortensio Figueira Reyes, 31, was marooned at the center of a growing mob of local residents, who rained blows, kicks and stones on him until he was dead.

"We didn't decide to kill him," said a 36-year-old carpenter named Ruffino . . . "It was something that just happened. But afterward everybody said, 'At least this way they won't mess with us again'."

"For two months they [the muggers] were holding up four or five people a day," said Ruffino the carpenter.

Said Giovanni, the victim who fought back, "This was like the sixth time that they had ambushed people going to work. People got tired of it." . . .

The police investigating the [killing] in El Encanto received . . . a statement with 150 signatures claiming responsibility.

"I don't feel there can be any judgment," Ruffino said, "because it was the entire community, not one person. When they screamed for help I ran, and many others did too. First there were 50 people, and then more than 200."

"Everyone agreed that it was well we did it," [Giovanni] said. "The feeling of people was, 'Let's unite'."

MATURE CONTEMPORARY HUMANS are highly adept at deceptive manipulation, and these behaviors exert significant effects on various aspects of human social organization. However, such deception can persist only as a contingent, minority strategy in the context of a larger cooperative social adaptation. As incomplete and ambivalent as human cooperation commonly is, it is nonetheless far more extensive than among any other large animals. It is the ultimate source of human ecological dominance. I focus here on this characteristic and fundamental cooperation in humans.

In spite of their ecological power and capacity to enhance the fitness of cooperating animals, highly cooperative social adaptations are nonetheless rare, creating the superficial appearance of a paradox. Ground-breaking earlier investigation has substantially clarified the background to this putative contradiction (Haldane 1932; Hamilton 1964; Maynard Smith 1964; Williams 1966; Trivers 1971; Dawkins 1976; Wilson 1978; Symons 1979; Axelrod 1984; Betzig 1986; Alexander 1987; Daly and Wilson 1988; Barkow et al. 1992). Below, I briefly review the context to the present work that these seminal studies provide.

Many cases of animal cooperation involve closely related individuals. These are interpretable as a straightforward extension of the same simple evolutionary logic that lies behind cooperation among the cells of a multicellular organism; that is, alleles and allelic combinations that produce cooperation preferentially among entities likely to share such alleles by recent common descent can have a substantial selective advantage (Hamilton 1964; Maynard Smith 1964). These are referred to as inclusive fitness effects, and such behaviors are said to be kin- selected. Humans show numerous, apparently kin-selected cooperative behaviors (see, for example, Daly and Wilson 1988). Moreover, relatedness-based family units have presumably been a characteristic of hominids throughout their evolutionary history. These behaviors are not unique to humans, however, and they will be of only secondary concern here.

Cooperation between animals that are *not* closely related presents a more complex problem. I will argue below that all major elements of human uniqueness follow directly from our unprecedented levels of nonkin cooperation. Thus, solving the human uniqueness problem is equivalent to solving the problem of cooperation between nonclose kin.

Cooperation between two unrelated animals can produce significant mutual benefit. Commonly such cooperation involves investment, in the sense that the cooperating parties must pay some individual *cost* in return for the individual *benefit* that arises from a cooperative act. When the benefits exceed these costs, cooperation is potentially adaptive. But when such cooperative adaptations arise, they frequently create a new niche that is even more favorable to individuals than cooperation; it is occupied by those who gain the benefits of cooperation while evading its attendant costs. This niche has long been recognized from diverse theoretical points of view, and its occupants are variously referred to as "social parasites," "free riders," "defectors," or "cheaters," depending on local intellectual context.

As a result of individuals who occupy the social parasite niche, the cost/benefit ratio for cooperators is increased and the adaptive advantage of cooperation is reduced, frequently to the point where the cooperative behavior is individually maladaptive. As predicted by these considerations, nonhuman animals show extremely limited cooperation between nonclose kin (reviewed in Taylor and McGuire 1988; Dugatkin 1997).

Mathematical modeling studies suggest a formal solution to the social parasite problem (Maynard Smith 1983; Axelrod 1988; Boyd and Richerson 1992; Clutton-Brock and Parker 1995; Gachter and Fehr 1997, and references therein). Specifically, if a cooperating individual can impose a net cost (punishment) on a parasite that exceeds the net benefits of parasitism, then the parasitic strategy ceases to be adaptive and cooperation can evolve. However, the fundamental difficulty with such models is that punishment itself can be costly to the punishing cooperator (see Maynard Smith 1982). When the costs of imposing punishment exceed the benefits of avoiding social parasitism, punishment and attendant cooperation cannot evolve.

I argue below that this "cost-of-punishment problem" has represented the insurmountable barrier to highly cooperative adaptations in all large animals before the origin of *Homo*. I further argue that the antecedents of the *Homo* lineage solved the cost-of-punishment problem—initially inadvertently—for the first time in history by developing the ability to kill or injure conspecifics at a distance by using projectile and clubbing weapons. The ability for remote killing/injury permitted a collection of self-interested individuals to effectively and simultaneously attack another conspecific individual. This capability, in turn, supported the emergence of cooperative punishment—at a greatly reduced *individual* cost—in the context of what I will refer to as **coalitional enforcement**.

Although the capacity for remote killing, injury is necessary for fully developed coalitional enforcement, it is not sufficient. Also required are cognitive and behavioral devices that control and permit cooperative punishment in response to parasitic behavior. I will refer to these collectively as social monitoring devices. I will argue that the acquisition of the capacity for remote killing/injury in early *Homo* produced—immediately and in a straightforward way—very strong selection for improved social monitoring, and thus effective coalitional enforcement.

The emergence of coalitional enforcement is expected to have initiated an autocatalytic process in which nonkin cooperation (in addition to its many other adaptive consequences) supported continuous improvements in weapon performance and social monitoring. This, in turn, improved the efficiency of coalitional enforcement, leading to successive and continuous increases in cooperation. It is my hypothesis that this has been the central process in the evolution of *Homo*, beginning some 2 million years ago and continuing through to the present moment.

The capacity for coalitional enforcement creates a unique situation in which cooperation among nonrelatives can consistently promote the inclusive fitness interests of *individual* animals. Note that many behaviors shaped by this process will be superficially similar to those expected on theoretically uncertain group-selection models (critiqued in Williams 1966). This misleading fit between the predictions of group-selection models and behaviors produced by enforcement administered by coalitions of self-interested individuals may explain the persistent intuitive attractiveness of group- selection models for human evolution {also see section 3C; section cross-references will be enclosed in curved brackets throughout}.

INTRODUCTION

In this article, sections 1 to 4 contain a primarily analytical development of the coalitional enforcement hypothesis and its most direct implications, followed by Sections 5 to 8, which review a sample of the extensive empirical evidence that supports the theory. Before proceeding, it is important to be aware of several points.

First, the scope and potential generality of the theory are large. An adequate sampling of the supporting empirical evidence requires a wide range across many traditional disciplinary boundaries, which obviously carries the inescapable risk of controversies—many trivial, but a few that are potentially substantive. Moreover, because of the massive materials that bear upon the theory, it has frequently been necessary to reference the secondary (review) literature rather than the primary literature. These references have been carefully chosen to provide interested readers with convenient points of entry to the corresponding primary literatures.

Second, in order to cover the broad scope of the theory in a short format, this paper must be relatively terse and dense; high attention to detail is required to fully appreciate its message.

Third, the theory proposed provides a substantially new perspective on the available evidence. Under these circumstances, some elements of evidence and local, empirical generality that were previously thought to be of marginal significance (or even irrelevant) become centrally important, and vice versa. Further, this new perspective sometimes suggests different interpretations of individual elements of evidence than are currently popular. For specialists in some of the relevant areas—such as history, paleontology, archaeology and anthropology—such alternative interpretations may sometimes be initially jarring. This initial reaction should not be allowed to obscure the possibility of new insight. It will be necessary for specialists who wish to confront this work seriously to take the time to understand the totality of the theory, rather than merely reacting to the isolated cases of interpretation of empirical evidence that are at variance with older, more local perspectives.

Fourth, though many elements of available empirical evidence provide compelling support for the coalitional enforcement hypothesis, this evidence was originally collected within traditional theoretical frameworks. Such evidence is inevitably less than optimal for a test of new theory. It will therefore require the future efforts of many scholars to fully test and refine the coalitional enforcement hypothesis for human uniqueness.

1. DERIVATION OF THE THEORY

1A. COOPERATION AND COST OF PUNISHMENT

There are several largely independent ways in which the theory of coalitional enforcement can be derived. One relatively direct derivation follows. For simplicity this discussion is restricted to a specific subset of cooperative behaviors involving pairs of conspecific but unrelated individuals.

First, in some cooperative behaviors, only cooperators can receive the benefits of the behavior. I will refer to these as *primary mutualistic* behaviors. Mating in many animals is based on primary mutualism.

More commonly, however, it is not only possible for two animals to cooperate and generate a mutual benefit, but also for an animal to pursue an alternative, parasitic strategy in which some or all of the benefits of cooperation are obtained without paying some or all of the cost (*investment*) necessary to produce the benefit. Under these conditions, it can be in the interest of a cooperating individual to inflict an additional cost (*punishment*) on a parasitic individual in order to forestall parasitic behavior. Reciprocally, it can be in the interest of the parasitic individual to inflict additional cost (*extortion*) on the cooperating individual in order to forestall punishment or withholding of cooperation. For simplicity, the costs of punishment *to* each party are assumed to be generally similar. Thus, for example, the cost *to the cooperator* of administering an individual act of punishment will generally be roughly the same as the cost *to the parasite* of experiencing that act.

In the second class of cooperative behaviors, the *net benefit* to the cooperator (defined as the *gross benefit* minus the *investment cost* of the cooperative interaction) exceeds the investment cost itself. Under these circumstances, the cost of punishment that the cooperator is willing to incur will exceed the cost of extortion the parasite is willing to incur.

A simple quantitative example illustrates this. Suppose a cooperative behavior requires the investment of 2 units of cost by each cooperator and generates 5 units of benefit to each cooperator, or 5 units of benefit to a parasite and none to the parasitized cooperator (the *sucker* in game theory nomenclature). Under these conditions, the cooperator will be willing to incur additional cost in the form of punishment up to incrementally less than 3 units, leaving a small residual net benefit. In contrast, the potential parasite will be willing to incur no more than incrementally less than 2 units of cost in extortion. Under these conditions, parasitism is a less fit strategy than cooperation, and thus cooperation can potentially evolve. I will refer to the resulting cooperative behaviors as *secondary mutualism.*

In the third class of cooperative behaviors, the net benefit is less than the investment cost. Under these circumstances, the cost of extortion that the parasite is willing to incur will exceed the cost of punishment the potential cooperator is willing to incur.

Again, a simple quantitative example will illustrate this. Suppose a cooperative behavior requires the investment of 4 units of cost by each cooperator to generate 5 units of benefit to each cooperator or 5 units of benefit exclusively to the parasite. Under these conditions the cooperator will be willing to invest up to incrementally less than 1 unit of cost in punishment, but the parasite will be willing to invest up to incrementally less than 4 units of cost in extortion. Under these conditions the cooperative behavior cannot evolve. Such behaviors are thus, in practice, altruistic.

The only cooperative behaviors among nonkin that can evolve are those that are frequently mutualistic. Behaviors that are consistently altruistic, of course, cannot evolve. There are two crucial implications in this context. First, many potentially cooperative behaviors will involve a modest return on a relatively large investment—as in the case in the preceding example. I will refer to these as *low-return* cooperative behaviors. These will not evolve within groups of nonkin under the above conditions.

Second, it is likely that many, if not most, cooperative behaviors in a highly developed social adaptation will be low-return cooperative behaviors. Thus, for animals constrained to behave as described in the model above, the cost/benefit structure of cooperation must be such that a highly developed social adaptation involving groups of nonkin will be inaccessible.

1B. COST OF PUNISHMENT AND THE ORIGIN OF *Homo*

Low-return cooperative behaviors can become mutualistic if the cost/benefit logic of cooperation and punishment can be changed. There is apparently only one straightforward way to do this. Implicit in the treatment above is the assumption that the cost of a punishment event is borne exclusively by a single cooperator. This is likely to be the case for nonhuman animals {1D}. However, if the cost of punishment can be distributed among multiple cooperators, this cost to individual cooperators can be reduced.

I will argue in detail below that such an ability arose uniquely at the origin of *Homo* as a result of the development—initially for other purposes—of efficient throwing and clubbing {2; 5A}. Early species of *Homo* could thereby reliably kill or injure conspecifics at some distance away. This ability for killing or injuring remotely in turn allows a coalition of animals to cooperatively punish parasitic behavior at low individual cost—a capacity apparently not possessed by any other animal in history. Below and in the following subsection {1C}, I develop the formal theoretical framework for this solution to the cost-of-punishment problem.

Before continuing, it is important to recognize the context in which the solution arose. Judging from the common properties of chimps, bonobos and humans, their last common ancestor most likely lived in relatively small, stable groups in which animals recognized one another as distinct individuals {2}. These ancestral groups are thought to be the products of kin-selected behavior and natural selection for primary and secondary mutualism. The cost/benefit logic of punishment is expected to evolve in such animals on the basis of some assessment of the *aggregate future costs* of parasitism at the hand of each potential punishment target.

In such a social environment, the aggregate future cost of parasitic behavior to any individual is generally the same, whether punishment is individually or cooperatively administered. However, the individual cost of punishment is profoundly affected by whether punishment is individually or cooperatively dispersed.

As a simple quantitative example, consider the cooperative behavior described in section

1A, in which the cost to cooperators was 4 units and the benefit to cooperators or to a parasite was 5 units. When punishment is individually administered, the sustainable cost of punishment (about 1 unit) is much less than the sustainable cost of extortion (about 4 units), and the behavior cannot evolve. But if five cooperators can distribute the cost of punishment among themselves, the cost to cooperative individuals can remain below 1 unit, while the cost to the parasitic individual can exceed 4 units.

Under these changed conditions of cost/benefit, formerly altruistic behaviors can arise as mutualistic strategies. I will refer to cooperative behaviors of this form as *tertiary mutualism,* and to such cooperative punishment as *coalitional enforcement.* Coalitional enforcement behavior can be individually adaptive and, under conditions permitting it, should evolve. As long as cooperators engaging in coalitional enforcement are in a substantial majority, parasites will be driven to or near extinction.

Coalitional enforcement in the example described above is itself a primary mutualistic behavior. That is, under these specific circumstances, the benefit of the cooperative behavior (punishment) can be had by *any* of the cooperating individuals, but only if *all* cooperating individuals punish. This may represent the rudimentary form of the behavior. Once initially established, however, coalitional enforcement is expected to expand to punishing not only parasites, but also cooperators who refuse to punish {see subsection 1C for details}. Under these circumstances, it will be a robust and stable strategy.

Note that a converse strategy of *coalitional extortion,* where coalitions extort contributions from other individuals without corresponding reciprocity, is also possible. There are fundamental differences between coalitional enforcement and coalitional extortion though. Coalitional enforcement is self-sustaining. In contrast, local populations in which coalitional extortion is a common strategy are dynamically unstable. Coalitional extortion is highly fit only when the frequency of cooperators—i.e. parasitic targets—is high enough to support parasitism, but low enough to prevent coalitional enforcement from driving the extortion to extinction. Coalitional extortion under these conditions will lead to increasing frequencies of parasites and declining frequencies of cooperators until the fitness of the parasites is reduced below that of individuals in other populations where coalitional enforcement is the dominant strategy. Thus, coalitional extortion is expected to evolve only as a contingent, minority strategy—as it is, in fact, in contemporary humans.

1C. LANCHESTER'S LAW AND COALITIONAL ENFORCEMENT

More detailed treatment demonstrates that the adaptive opportunity presented by coalitional enforcement is substantially greater than may be immediately apparent from the preceding section. I propose that *Lanchester's Square Law,* which describes attrition during contemporary mechanized warfare (Lanchester 1916; reviewed in Lepingwell 1987), is also applicable to conflict with simple weaponry such as thrown projectiles and clubs. If so, the cost/risk to individual cooperative punishers decreases as an *exponential* function of the effective ratio of punishers to target.

This effect arises as follows. First, increasing the relative number of punishers decreases the time required to disable or kill the target(s), thereby terminating the conflict. Second and simultaneously, when the relative number of punishers is increased, the risk of return or defensive fire from the target(s) is perforce distributed among more punishers.

The following simple quantitative examples illustrate this. In one-on-one conflict, each party will generally have about an equal chance of being disabled or killed, thus terminating the conflict. In contrast, with ten effective punishers and one target, the target will almost certainly be killed or disabled (with a nearly 100% probability) in about one-tenth the time required in a one-on-one conflict. Moreover, the risk of return fire from the single target is distributed among ten punishers. Conflict duration is reduced tenfold *and* defensive fire from the target is distributed among ten punishers, producing a net one-hundredfold effect. The probability that any individual punisher is killed or disabled by return fire from the target is thus reduced to less than 1% with a ten-to-one punisher-to-target ratio. Analogously, with a 100-to-1 punisher to target ratio, the risk of disability or death to any individual punisher is less than one in 10,000 per episode.

These properties of projectile weapon punishment have the following crucial, interrelated implications. First, there will be strong selection for punishing cooperators to induce nonpunishing cooperators to punish, thereby producing the exponential reduction in individual risk.

Second, as a result of these exponentially declining risks, there will be only relatively weak selection for cooperators to resist punishing. Thus, nonpunishing cooperators will be a minor rather than a major impediment to the emergence of coalitional enforcement and tertiary mutualism. These two implications, collectively, indicate that the emergence of the capacity for remote killing/injury of conspecifics is the key to the solution not only of the cost-of-punishment problem itself, but also of the crucial subsidiary problem of why extensive punishing of nonpunishers arose uniquely in humans. [See Maynard Smith (1983), Axelrod (1988) and Boyd and Richerson (1992) for general, formal discussions of the background to this subsidiary theoretical problem.]

Third, there will be strong selection for punishing cooperators to improve coordination of punishment episodes in order to maximize exponentially reduced individual risk. Improved social monitoring permits this.

Fourth, as a result of decreased punishment costs, the number and consistency of tertiary mutualistic behaviors will tend to increase as an exponential function of social monitoring efficiency and projectile weapon range.

In summary, I propose that coalitional enforcement has been an inaccessible adaptation for all animals before the emergence of humans. The capacity to use clubbing and projectile weapons to kill or injure remotely, developed in the immediate ancestors of *Homo*, created the first animals in terrestrial history to which efficient coalitional enforcement—and large scale tertiary mutualism—was accessible. Moreover, in view of Lanchester's Square Law, once coalitional enforcement supported by projectile weaponry and the resulting expanded cooperation emerge, they are expected to be very rapidly refined and expanded. Further, ongoing selection for improvements in weaponry is expected, with corresponding increases in efficiency of coalitional enforcement and, thus, cooperation throughout the some 2-million-year history of the *Homo* clade.

1D. ENFORCEMENT IN NONHUMAN ANIMALS

To see that the above treatment accurately reflects the enforcement problem in nonhuman animals, consider punishment as it actually occurs. Individual acts of punishment take diverse forms, including the denial of future access to a resource (such as food), inflicting injury or death on a juvenile relative of the target individual, or inflicting injury or death directly on the target individual. However, even in cases where the primary sanction is not injury or death to the target individual, this sanction will generally require a threat of such injury or death. For example, threats will generally be required to repulse the target individual's advances toward a resource. In turn, for threats of injury or death to be credible they must be generally realistic (Dawkins and Krebs 1978; Grafen 1990; Zahavi and Zahavi 1997, and references therein).

Thus, all capacity to punish is limited by the *actual* capacity of the punishing animal to deliver injury or death to the target animal. This constraint is severe for nonhuman animals, for the simple reason that their strategies for injuring and killing are proximal; in order to kill or injure a conspecific, any nonhuman animal, no matter how individually formidable, must inevitably engage in a struggle at close quarters with an animal of very similar capability. Such proximal strategies produce only very limited capacities for more than one animal to participate in killing or injuring another conspecific animal. Under these conditions, the individual costs of punishment are inescapably great, and the credibility of threat is correspondingly limited.

2. EMERGENCE OF COALITIONAL ENFORCEMENT

Many details of the origin of coalitional enforcement in incipient *Homo* will likely never be known. A number of constraints on and features of this emergence can be reasonably inferred, however. First, the hominid population immediately ancestral to incipient *Homo* had morphological properties consistent with the requirements of the coalitional enforcement hypothesis. Specifically, this ancestral australopithecine lineage was no doubt significantly more bipedal than the last common ancestors of chimps and humans. Under these circumstances, redesign of the skeleton to support improved throwing and clubbing was sustainable {see 5A}.

Second, under these circumstances, simple selection for improved ability to knock down inaccessible fruit or to defend against predators, for example, is expected to have led to improved projectile and clubbing weapon capability. By hypothesis, this capability improved to the point that it allowed injury or death to be reliably inflicted on a conspecific from a significant distance, in at least the one local australopithecine population ancestral to *Homo*.

Third, available evidence indicates that chimps are capable of strategic cooperative violence against conspecifics to the very limited extent sustained by their largely proximal killing strategies (reviewed in de Waal 1982, 1989; Harcourt and de Waal 1992). Thus, this capacity was likely present in the last common ancestors of chimps and humans, and therefore in the australopithicine population immediately ancestral to *Homo*. Under these circumstances, rudimentary coalitional enforcement is expected to have emerged in incipient *Homo* as merely an expansion of this pre-existing capability permitted by improved clubbing and throwing.

Fourth, much of nonhuman ape cooperation, including cooperative violence, is likely to represent kin-selected behavior (reviewed in Harcourt and de Waal 1992; Wrangham and Peterson 1996). Thus, rudimentary coalitional enforcement in incipient *Homo* likely had the initial effect of merely extending such cooperative behaviors to progressively lower levels of kinship. Under these conditions of emergence, coalitional enforcement is expected and coalitional extortion {1B} would have remained a marginal, contingent strategy.

Fifth, collectively these circumstances are expected to have supported the emergence and rapid refinement of coalitional enforcement and tertiary mutualism {1B, 1C}. On the coalitional enforcement hypothesis, this emergence was the decisive event in the divergence of the australopithecine and *Homo* lineages and, based on current evidence, likely occurred 2.0 to 2.5 million years ago.

3. ALTERNATIVES TO THE THEORY

3A. INDIVIDUAL AGGRESSION, AMBUSH AND REVENGE

The capacity for remote injury or killing uniquely confers on humans not only the capacity for coalitional violence but also for successful blind ambush. This capacity is unlikely to be responsible for any significant larger human novelty, however. The reason is that individual ambushers are highly vulnerable to reciprocal ambush (revenge) at the hands of the target, or close kin of the target.

This is a specific case of the general point that the use of projectile and clubbing weapons in one-on-one combat is expected to be subject to the same selective constraints as individual aggression mediated by tooth and claw. Such behaviors are risky and costly, and animals are expected to use them only in those relatively rare cases when the adaptive benefits outweigh the formidable costs.

Beyond this, coalitional enforcement itself is expected to curtail weapon use for one-on-one aggression, compared to such behaviors in nonhuman animals. Specifically, coalitional killing of unusually aggressive individuals can be adaptive to individual coalition members {5B}. Thus, using weapons for one-on-one aggression will frequently backfire in the context of a small, stable coalition whose members can kill remotely and cooperatively. Therefore, somewhat paradoxically, the availability of reliable remote killing capabilities should reduce rather than increase individual aggressive behavior. Consistent with this view, contemporary humans are unique among top predators in being relatively placid in their dealings with unrelated conspecific nonmates under a wide variety of circumstances.

Lastly, while the capacity for revenge constrains the importance of one-on-one ambush, it has no such effect on coalitional enforcement. Specifically, subsequent attempts at revenge by a target of coalitional enforcement can be as cost- effectively punished cooperatively as any other parasitic act.

3B. THE HUNTING HYPOTHESIS

It has been suggested by others that early evolution of human cooperation was driven by the adaptive advantages of meat sharing (reviewed in Tooby and DeVore 1987). On this view, human weapon use arose primarily as part of a hunting or scavenging adaptation. While hunting/scavenging appears to have had at least some adaptive importance to early hominids, this hypothesis is flawed as a fundamental theory of human uniqueness.

First, meat sharing among nonkin is a specific case of cooperation for which the cost-of-punishment problem must be solved before it can be a sustainable adaptation {1A}. Hunting hypotheses to date either ignore this problem, or simply stipulate that it has been solved in some unspecified way.

Second, earlier hypotheses on hunting fail to explain why the other social carnivores of the African savanna did not also develop elaborately cooperative social adaptations. [Note that the limited social cooperation, including cooperative hunting/scavenging, in nonhuman savanna carnivores appears to reflect kin-selected and primary mutualistic behaviors.]

With these considerations in mind, it is important to interpret human hunting/scavenging, especially the highly cooperative hunting of recent modern humans, in the context of the coalitional enforcement hypothesis. On the basis of the discussion in subsection 1C, it is now possible to propose a more sophisticated version of the hunting hypothesis to explain human uniqueness. Specifically, human uniqueness might be supposed to result ultimately from the capacity of remote weaponry to allow individual risk in cooperative hunting/scavenging to be reduced as an *exponential* function of the number of hunters, while individual return is potentially reduced as a *linear* function of this number.

While this effect is no doubt significant, it is important to note that this new version of the hunting hypothesis still fails, not only as a general theory of human uniqueness, but even as a theory of hunting/scavenging involving cooperation of nonclose kin. Specifically, it is unable to account for the sustainable distribution of the risks and products of cooperative hunting/scavenging among nonkin, much less the broad, extensive tertiary mutualism of humans in general {see, for example, 4–7}.

In contrast, the coalitional enforcement hypothesis accounts for all of these behaviors, including modern hunting. On this hypothesis, highly cooperative human hunting/scavenging reflects a sustainable constellation of tertiary mutualistic behaviors. That is, coalitional enforcement solves the cost-of-punishment problem, so that both participation in still occasionally risky hunts, and the systematic distribution of kills, are sustainable adaptations.

It remains a problem for future investigation to establish in detail the importance of hunting/scavenging to early *Homo.* Though the current view that hunting/scavenging were adaptively significant behaviors seems plausible, the coalitional enforcement hypothesis does not require it. Indeed, it would have been formally possible for the use of weapons to sustain the long evolution of the human social adaptation in the complete absence of carnivory.

It is noteworthy that modern hunter/gatherers, living at latitudes similar to those of early *Homo,* frequently derive only a small portion of their total food value from hunting/scavenging (Kelly 1995). It is also noteworthy that one effect of improved weaponry during recent human evolution has frequently been a *reduction* in dependence on hunting {see 6D}. This is an unexpected consequence of any simple version of the hunting hypothesis, but predictable from the coalitional enforcement hypothesis.

3C. THE WARFARE HYPOTHESIS

Darwin (1871) originally proposed that *inter*-group warfare was the basis of human uniqueness. This hypothesis has been repeatedly revived and refined since that time. The various restatements of this hypothesis can be considered equivalent to the following: When humans within a group cooperate, they are able to compete successfully in warfare with other human groups that are less cooperative. Thus, it can be inferred that surviving humans are descended from those who were members of such cooperative groups. More general statements of the hypothesis are broader, and invoke all forms of intergroup competition, including warfare.

But such models are flawed as explanations of human uniqueness. First, they are all group selection models. They posit that human groups win competitions based on previously existing differences among the cooperative behaviors of their members, and that this selection is sufficiently strong to sustain cooperative behaviors that are nonetheless individually disadvantageous *within* the group. [Recall that parasitic strategies commonly have higher individual fitness in the absence of coalitional enforcement {1A; 1B}.] While such models are not inherently inconceivable, an extensive body of evidence since Williams's (1966) seminal work indicates that the circumstances under which they will apply are very limited.

More specifically, in order for such models to be credible, the following crucial question must be answered: Can selection at a simpler organizational level produce the same effect? Or, equivalently, is there a more direct selective route to the same outcome? If the answer to this question is yes, group selection effects are very likely to be either secondary or irrelevant. A central point of the hypothesis presented here is that coalitional enforcement apparently provides precisely such a more direct route to human cooperation. Thus, group selection effects, including those invoked in the warfare hypothesis, are most unlikely to be of primary importance.

This can be visualized intuitively as follows: Under group selection models, human cooperative behaviors must arise within groups, even though they are often individually maladaptive in that context. These groups must then come into sufficiently intense competition with other groups so that these *intra*group disadvantages are offset by the rewards of winning such competitions. Moreover, such intergroup competition must recur sufficiently often to offset the persistent subversion of cooperation as a result of its intragroup individual disadvantages.

In contrast, on the coalitional enforcement hypothesis *intragroup* (intracoalition) cooperation emerges automatically and is stably maintained by the individual, self-interested enforcement actions of coalition members. The fitness of individual coalition members is thus enhanced as a consequence of diverse cooperative behaviors—including, among many others, the capacity to wage effective warfare when the occasion arises.

Further, the most sophisticated recent formulations of the warfare hypothesis suggest that their uniqueness results from humans having achieved unprecedented "ecological dominance," such that the primary "hostile force of nature" for humans was other humans (Alexander 1990). This is proposed to lead to runaway group selection. Alexander's contributions in this area are many and formidably important; however, this particular suggestion is unlikely to be correct as a primary theory of human uniqueness for the following reasons.

On the one hand, this suggestion is arguably credible for very recent modern humans, but notably not for most of the history of the *Homo* clade. Specifically, there is no evidence that *Homo habilis* or *Homo erectus/ergaster* was more ecologically dominant than any other member of the diverse savanna carnivore guild or, for that matter, various large herbivores like elephants.

On the other hand, this formulation is implicitly circular: on this view, humans are ecologically dominant because they cooperate, but the proposed selection for cooperation requires prior unique ecological dominance.

The empirical record is also illuminating here. Intergroup warfare is expected to leave one unique paleontological artifact—sites involving multiple individuals killed simultaneously with human weapons. While such sites are found in the very recent record (the last 10,000–40,000 years or so), they are unknown throughout the 2-million-year history of the *Homo* lineage before this time (Keeley 1996). This chronology is exactly what would be expected on the coalitional enforcement hypothesis {see 6 for details}, but not on the warfare hypothesis for human uniqueness.

Finally, once coalitional enforcement arises, a subset of resulting cooperative behaviors—those supporting intergroup competition—yield secondary group selection effects that reenforce the primary effects of coalitional enforcement. These secondary effects are apparently entirely dependent on the previous existence of coalitional enforcement, however. There is no reason whatsoever to suppose that such group effects alone are sufficient as primary selection for human social behavior.

3D. OTHER HYPOTHESES

Models for human uniqueness have been proposed that are sometimes referred to as "combinatorial hypotheses." These models assume that humans possess a unique *combination* of adaptations that are shared individually with various other animals. For example, human uniqueness might result from some combination of social ancestry, bipedality (permitting provisioning and transport) and carnivory on such a view. The number and diversity of such models is enormous, and I will not attempt to critique them individually here.

There are two general problems, however. First, in spite of their diversity, no individual combinatorial hypothesis has garnered wide empirical support, and most are equally plausible (or implausible). Second, most are highly local in application. For example, some account with at least superficial plausibility for the origin of *Homo* but not for the rise of, say, Bronze Age Kingdoms or vice versa.

In contrast, the hypothesis developed here is unitary. I will argue that all the major nonstochastic evolutionary events of the *Homo* lineage, from its origin through the present moment, have a single primary cause—the rise and ongoing refinement of coalitional enforcement with its diverse supporting "technologies" and adaptive consequences.

4. LANGUAGE AND EXTRAGENETIC INFORMATION

4A. CONTEXT

In addition to its theoretical coherence, the coalitional enforcement hypothesis for human uniqueness is attractive on empirical grounds. Elements of this observational support are reviewed in sections 5 to 8 below. Many of these phenomena in turn are dependent on a very basic implication of the coalitional enforcement hypothesis. Specifically, the hypothesis provides a straightforward explanation of the origin of human communication—including language—and the associated emergence of a novel stream of design information supporting the unique sophistication of diverse human adaptations. This implication of the theory is reviewed here.

4B. HISTORY OF ANALYSIS OF LANGUAGE AND CULTURE

The recognition that humans have, in some sense, a "cultural heritage" acquired from other humans and contributing to adaptation is ancient. Moreover, Darwinian approaches to "cultural" evolution have been pursued in every generation since Darwin (Richards 1987; Degler 1991). Exploration of such approaches by biologically oriented investigators has continued through the present (see, for example, Dawkins 1976; Alexander 1979; Cavalli-Sforza and Feldman 1981; Lumsden and Wilson 1981; Boyd and Richerson 1985; Williams 1988; Durham 1991; Boyer 1994; Dennett 1995; Sperber 1996, and references therein). Further, several strong "evolutionist" traditions have long existed within anthropology and archaeology (Arens 1986; Johnson and Earle 1987; Tainter 1988; Pauketat 1994; Marcus and Flannery 1996; Maschner 1996), and are found in psychology and economics as well (Simon 1981).

This enormous body of ground-breaking work has made it increasingly clear that Darwinian processes are somehow involved in human evolution, not only in the genetic domain but also in an additional "cultural" domain. Most of the details of this process have remained obscure and contentious, however. For example, the precise way in which such a domain might have arisen and might function has remained unclear. Moreover, the reasons why such a novel informational domain might be unique to humans, at least quantitatively, has remained unknown. As a result, in spite of the importance of this general insight, its applications to date have been muddled, and it has had an astonishingly limited impact on the understanding of human behavior and evolution.

Much of the confusion in this area, in turn, results ultimately from the fact that insight has been almost entirely *empirical* or observational in origin. A credible *theoretical* framework that accounts for and predicts these phenomena has not been available, and no earlier treatment is based on a plausible theory of human cooperation {1} or of the origin of human language {4c}.

The coalitional enforcement hypothesis provides this previously missing theoretical framework. Its implications, in turn, allow various formerly isolated elements of insight from the large body of earlier seminal work to be unified in a coherent, straightforward theory of human evolution controlled by two partially independent streams of design information.

4C. LANGUAGE

It has been clear since Darwin that human linguistic competence has the complex, coherent structure expected of a highly derived adaptation to functions that include support of information exchange. Further, it has been obvious that such exchange implies a long history of unusually cooperative social adaptation. In spite of this, there has been isolated resistance to adaptationist interpretations of human language through to the present. This resistance has been possible, in part, because of the absence of a credible theory that explains the context and logic of language evolution. The coalitional enforcement hypothesis appears to provide this.

Animals are expected to engage in systematic hostile manipulation of one another in pursuit of relative (genetic) inclusive fitness advantage. As a result, honest signals are expected only under limited circumstances. In nonhuman animals these can include threat and kin-based cooperation. Put anthropomorphically, because nonhuman animals are free to lie to one another, the information provided by one animal to an unrelated conspecific is commonly unreliable, and there is no selection for adaptation to generalized exchange of such information. As predicted by these theoretical considerations, most animals are observed to show only highly limited honest signaling among nonkin (Dawkins and Krebs 1978; Grafen 1990; Zahavi and Zahavi 1997, and references therein).

In contrast to nonhuman animals, under appropriate circumstances contemporary humans exchange extravagant amounts of relatively reliable information with unrelated conspecifics. The coalitional enforcement hypothesis predicts this uniquely human behavior as follows: coalitional enforcement allows low-cost, cooperative punishment {1B, 1C} of dishonest communication within coalitions. This has the effect of substantially reducing the net benefit of many acts of hostile manipulation, while leaving undisturbed the adaptive opportunities for mutualistic exchange of reliable information in this specific context.

Once the human cooperation problem is solved by the emergence of coalitional enforcement, evolution of language with its various well-known properties will follow. [See Jackendoff 1994, Pinker 1994 and Deacon 1997 for reviews of the currently recognized fundamental properties of human language.] In particular, extensive genetic adaptation to language production and perception is expected and observed. Moreover, given limitations on amounts of available genetic information, extensive combinatorial cooperation among elements of "learned" information, and between genetic and "learned" information in the creation of contemporary language, is expected and observed. {See 4E–F for a discussion of this "learning" and cooperation in the context of the coalitional enforcement hypothesis.}

Note that the coalitional enforcement hypothesis predicts the emergence of expanded information exchange, using all applicable sensory modalities and combinations thereof. Thus, the hypothesis predicts emergence not only of language, but also of expanded "nonlinguistic" communication (such as gestural communication) in the *Homo* clade. Also note that the episodic, contingent use of language for "dishonest" purposes in contemporary humans is secondary. This parasitic use of language is dependent on the fundamental presumption of honesty in communication, and is frequently punished by other coalition members.

4D. HUMAN ADAPTATION AND EXTRAGENETIC INFORMATION

The specific element of human uniqueness most directly responsible for ecological dominance is intellectual/technological virtuosity—some recent claims to the contrary notwithstanding (critiqued in Gross and Levitt 1994). The human capacity to understand and manipulate the world is far greater than that of any other animal. This capacity is so extensive that it can be viewed as a qualitatively new adaptation. In the words of a thoughtful discussion of this issue, humans are the first animal to occupy the "cognitive niche" (Tooby and DeVore 1987). The question has remained as to why this is uniquely true of humans. I argue that human intellectual/technological virtuosity is a direct consequence of coalitional enforcement.

It is first necessary to define more precisely the problem to be solved. The products of human intellectual/technological virtuosity show a striking analogy to those of genetically controlled adaptive design in nonhuman organisms. For example, humans use technological products such as aircraft and weaponry, in part, to solve the same adaptive problems solved by genetically determined devices of wing, tooth and claw in nonhuman animals.

It is widely recognized that Darwinian selection is probably the only possible source of this adaptive design in human artifacts. Confusion has arisen in trying to understand in detail how this general insight actually applies, however. The most common mistake is to assume that conventional Darwinian processes operating on genetic information produce human minds whose properties somehow include generation of the novel, complex adaptive design reflected in human material artifacts sui generis.

Such explanations pervade not only the social sciences but even some subareas of the neurosciences. They are apparently incoherent, however. And conspicuously, they fail to explain human uniqueness. If building such minds by the action of Darwinian selection on genetic information were somehow possible, this adaptation would presumably be recurrent. Instead, it is unique to humans.

Before turning to a possible resolution of this confusion, two additional properties of human technological innovation must be recalled. First, its scale has recently become massive with the emergence of behaviorally modern humans about 40,000 years ago. Second, the speed of modern human innovation is unprecedented and sometimes appears to exceed rates achievable by the action of Darwinian selection on genetic information.

In view of these considerations, the theoretical challenge presented by human intellectual/technological virtuosity would be well-met if the following were true. First, if there emerged uniquely and stably in early *Homo* a new informational domain, partially or largely independent of genetic information. Second, if information in this domain is susceptible in some fashion to Darwinian processes, thus representing a novel source of adaptive design that controls, among other things, the properties of the artifacts of *Homo*. Third, if transmission and selection of information in this domain operates such that novel adaptive design can sometimes be generated on time scales of less than a single human generation. Fourth, if the information content of this domain grew very much larger relatively abruptly with the emergence of behaviorally modern humans.

I argue that coalitional enforcement is necessary and sufficient to support the emergence of a novel informational domain that has *all* of these properties. First, the emergence of large scale mutualistic information exchange—including linguistically supported communication—between nonclose kin is allowed by coalitional enforcement {4C}. This creates information (hereafter referred to as *extragenetic* information) that is stored in memory and can be transmitted indefinitely and independently of small kinship groups. Any elements that also produce adaptive design in hominids that transmit extragenetic information will be selectively favored {see 4E–F for details}.

Second, it has long been recognized that Darwinian theories of cultural evolution require that the underlying design information be replicated with sufficient fidelity on the one hand, while undergoing sufficient variation on the other, to support Darwinian processes. However, it has remained unclear as to how such capacities might have arisen or how they might currently function. I will argue below that these properties emerge with compelling simplicity in the specific context of enforcing coalitions, given one robust theory of how animal minds work {4E–F}.

Third, transmission of and selection operating on extragenetic information is at least partially independent of biological reproduction of the organism {4E–F}. Thus, novel adaptations produced by Darwinian processes acting on this information can arise on time scales of less than a single generation.

Fourth, as a straightforward consequence of coalitional enforcement, the amount and quality of available extragenetic information is expected to undergo an abrupt, rapid growth at a specific point in the evolutionary history of hominids. Thus, the well-documented but formerly poorly understood "cognitive explosion" associated with the recent origin of behaviorally modern humans emerges as a direct prediction of the theory. {See section 6 for details.}

4E. EXTRAGENETIC INFORMATION: FIRST ORDER REFINEMENTS

In this and the following two subsections, selected elements of the theory of extragenetic information outlined immediately above are developed in more detail. This discussion is designed to make the economy and high plausibility of the theory more clear and to increase the accessibility of later sections. [For simplicity, the phrase "by hypothesis" will be omitted throughout the lists in subsections 4E–F.]

First, extragenetic information consists exclusively of information encoded in long-lived neural structures capable of influencing behavior, however indirectly, and capable of transmission to other hominids, often but not always with linguistic support.

Second, I argue that we are now in a position to clarify significantly the vexing problem of how and why replication-with-variation and selection in the domain of "cultural" (extragenetic) design information originated and operates. It is useful to begin with the following two definitions.

On the one hand, analogously to the genetic domain, there is *direct selection* on elements of extragenetic information as a result of their phenotypic effects on the viability and fecundity of individual hominids holding and potentially transmitting this information. On the other hand, extragenetic information is stored mentally, so elements of such information can interact with one another. Thus, direct selection can create both genetic and extragenetic devices that operate on other elements of extragenetic information, and thereby impose *indirect selection* affecting the survival and transmissibility of this information. [I will use "genetic" and "extragenetic" devices henceforth as shorthand for informational, behavioral, morphological or material devices whose design is controlled or substantially influenced by genetic or extragenetic information, respectively.] Note that such selection is "indirect" only from the perspective of the hominids who transmit the information. From a perspective internal to the extragenetic informational domain, this selection is direct.

Indirect selection in the extragenetic domain is a compelling theoretical requirement. Specifically, selective loads are apparently near maximum in animal populations, and large numbers of additional deaths or reductions in fertility as a result of selection on extragenetic information are not expected to be sustainable. However, relatively small numbers of additional deaths shaping genetic and extragenetic devices that, in turn, impose indirect selection on extragenetic information could well be sustainable. Under such conditions the extragenetic domain can apparently become quite large {6, 8}.

The postulate of indirect selection on extragenetic information emerges not only directly from the coalitional enforcement hypothesis, but also indirectly and independently from a powerful class of theories of how minds work—as will be discussed immediately below. This insight is of the most fundamental importance, and few of the arguments throughout the remainder of the paper can be fully appreciated without a firm grasp of its significance.

This insight indicates that our confidence in the postulate of indirect selection should be very high. Moreover, it provides the first coherent, robust explanation for the evolutionary origin of replication, variation and selection *within* the extragenetic domain. This insight leads directly to a clear formal explanation of the unique cognitive power of human minds.

The powerful class of theories of mind mentioned above proposes that mental functions, including at least some of those subjectively experienced as perception and cognition, result from the operation of managed, internal Darwinian systems (see, for example, Jerne 1967; Edelman 1987; Changeux and Deheane 1989; also see Plotkin 1993 for a recent review). In simplified overview, such systems function by generating multiple alternative information structures and by competitively choosing among them on the basis of fit, congruence or interaction with other information structures—all within an individual animal.

In the case of perception, for example, members of sets of internal information structures representing possible organizations of salient features of the external environment are competitively tested for quality of congruence with incoming sensory data. Partially divergent copies of the "best fit" from one round are then regenerated and retested competitively in a second round, and so on. A rapid (unconscious) series of such rounds ultimately produces what we experience subjectively as "recognizing" our immediate physical environment. Thus, "recognition" here ultimately results from selection on members of arrays of competing percepts based on other mental information—in this case, sensory information.

When managed internal Darwinian processing culminates in an output structure, its salient features can be stored in long-term memory for future retrieval and use. Such uses include as a starting point (a "primitive") for future rounds of Darwinian processing or, alternatively, as a structure to control selection during such processing. On this theory of minds, the use of such primitives at the beginning of analysis of novel situations is responsible for what we subjectively experience as analogical thought.

This class of theories provides a robust alternative to many trivial or formally magical explanations for mental events. A theory of this form appears likely to be fundamentally correct—though, as yet, mechanistic detail remains largely unclear. For readers not familiar with such theories of mind, it is most illuminating to consider the analogy between such systems and the vertebrate immune system, as originally pointed out by Jerne (1967; reviewed in Plotkin 1993). Both systems apparently generate complex mature repertoires—of antibodies or of mental information structures—on the basis of managed internal Darwinian processes.

Once the honest communication problem is solved by the coalitional enforcement hypothesis {4C}, this theory of minds predicts, in a straightforward fashion, the emergence of a domain with all the relevant properties of the extragenetic domain described above. Most generally, the minds of contemporary vertebrates are the products of hundreds of millions of years of selection for the machinery supporting managed Darwinian information processing and the use of the products of such processing to control and organize behavior. Solution of the cooperation problem and the consequent emergence of large scale information exchange in incipient *Homo* does not create an operationally new kind of mind. Rather, characteristically powerful human minds emerge under these conditions as a result of joining highly derived, but formerly relatively isolated, vertebrate minds into extended serial processing arrays with the emergence of hominid cooperation.

Because individual vertebrate minds are inherently Darwinian processing devices, these newly emergent, multigenerationally persistent serial arrays in *Homo* inevitably process information in a managed Darwinian fashion. Under these conditions, the information transmitted across generations of hominids in coalitions will, perforce, be subject to direct and indirect selection.

Understanding the power of this intersection of the coalitional enforcement hypothesis with theories of mind can be improved by inspection from the somewhat different perspective that follows. All animal minds—including those of the hominids immediately ancestral to incipient *Homo* and of contemporary humans—consist of genetically designed systems for managed internal Darwinian processing of mental information structures. For nonhuman animals, the resulting mature mental information structures generally perish with the individual animal, analogously to its mature antibody repertoire—only the genetic design information for the hardware supporting the system itself is under conventional Darwinian selection and is transmitted genetically to offspring, analogously to the design information for immune system hardware.

With the emergence and refinement of large scale tertiary mutualistic exchange of information between nonclose kin, however, the mature products of these separate Darwinian processing systems (minds) can be transmitted to other minds indefinitely. Thus, such mature information structures are now potentially immortal. Moreover, such structures inevitably undergo new rounds of internal Darwinian processing in each new mind to which they are transmitted. In the course of routine internal Darwinian processing, each new mind will generate potentially novel variants of the transmitted information structure and subject these variants to selection against this mind's partially idiosyncratic informational repertoire.

Many rounds of such transmission and refinement will produce potentially vast improvements in congruence between such structures and salient elements of the physical environment, as well as internally among such information structures themselves. On the coalitional enforcement hypothesis, this effect is the source of the unique power of human minds.

A secondary implication of these considerations will also be important later {6}. Specifically, the achievable quality of extragenetic information structures will ultimately be dependent on the number of independent rounds of refinement, and thus on the effective size and temporal persistence of cooperative hominid coalitions. Indeed, since refined information structures can be used subsequently as primitives or to impose indirect selection, these coalition-size and persistence effects are likely to be exponential or quasi-exponential.

It is important to emphasize again two crucial points. First, the cooperative information processing and exchange described immediately above is expected to be a sustainable adaptation *only* in the context of enforcing—and, thus, cooperative—coalitions. Second, long-term memory apparently involves structural changes in neural connections (see Gazzaniga 1997, and references therein). Thus, extragenetic information is expected to contribute to the structural design of mature human brains fully as much as does genetic design information.

4F. EXTRAGENETIC INFORMATION: SECOND ORDER REFINEMENTS

First, it is crucial to recognize that selection on extragenetic information is expected to occur largely or exclusively in the context of hominid coalitions. Among other implications, indirect selection will reflect the coercive power of these coalitions {also see 7B}. More formally, extragenetic information structures representing both adaptive cooperative opportunities and the likely consequences of coalitional enforcement actions will be subject to high instantaneous levels of direct selection. These structures, in turn, will impose indirect selection on extragenetic information during managed Darwinian processing that leads to specific behaviors. Moreover, there will be strong direct selection for genetic and extragenetic devices sustaining transmission to and reception among coalition members of such extragenetic representations of the cooperative/coercive environment {4G}.

Second, the sum of all extragenetic information held by the members of a hominid coalition is defined to be the coalition's *extragenetic information pool.* An individual's *extragenotype*—all extragenetic information currently held by an individual—is created by sampling this pool. Individual hominids contribute to the pool to the extent that elements of their extragenotypes are effectively communicated to other coalition members. Elements of such extragenetic information pools are expected to become increasingly coadapted with time—generally analogously to coadaptation of alleles within a local gene pool.

Third, emergence and refinement of coalitional enforcement supports adaptive individual specialization—an example of tertiary mutualism. Thus, individual extragenotypes within cooperative hominid coalitions can contain some distinct elements. Under these conditions each member of a hominid coalition has some access to some of the adaptive benefits of extragenetic information held by other coalition members. Therefore, the size of extragenetic information pools will generally increase with increasing size of cooperative coalitions. This increase in the pool size and the related effect of coalition size on the quality of extragenetic information discussed above {4E} become crucially important in behaviorally modern humans {6}.

Fourth, extragenetic information includes information supporting what we subjectively experience as conscious beliefs about the world. However, it also includes far larger amounts of information that we are not always explicitly aware of. For example, the superiority of the human capacity to draw elementary causal inferences from routine daily experience apparently results from extragenetic design information acquired during early childhood development. More generally, most managed Darwinian processing of extragenetic information {4E} is expected to be done without conscious awareness. This is crucial. The quantity and nature of extragenetic information is expected to be largely inaccessible to assessment by introspection. Understanding must be approached in other ways, such as examination of the effects of extragenetic information on behavior.

Fifth, in a related point, extragenetic design information ultimately came to support an enormous array of adaptive cognitive, behavioral and material devices in *Homo.* Such devices are quite complex, and expected to commonly involve pleiotropic/combinatorial contributions from multiple elements of extragenetic information acquired serially in an extended process of accretion of design. Moreover, complex devices designed in this way are frequently opaque to direct "reverse engineering." [Recall that reverse engineering of developmental or physiological devices designed by genetic information is also extremely difficult, for precisely analogous reasons.]

Speculation about human minds/brains has been a deeply confused and contentious endeavor for at least the last 3000 years or so (see, for example, Searle 1984; Dennett 1995). On the theory proposed here, much of this confusion results from failure to distinguish between relatively *simple* replicating extragenetic design information itself and its tremendously *complex, diverse* phenotypic consequences. Among these consequences are no doubt processes we subjectively experience as characteristically human levels of "rational thought," "intentionality," "moral judgment" and "consciousness."

4G. EXTRAGENETIC INFORMATION: CONCRETE EXAMPLES

The preceding subsections are necessarily somewhat formal and abstract. It is therefore helpful before proceeding to enrich one's intuitive grasp of these important issues by considering specific examples of how these processes are expected to work.

Taking a young adult hominid coalition member as an example, consider his (or her) behavior as a potential *target* for coalitional enforcement. He has acquired during his development, from parents and peers, an extensive body of extragenetic information, including a "picture" of (extragenetic information structures representing) the enforcement/reward structure of his coalition. This picture controls (imposes indirect selection on the mental information controlling) his daily behavior. To the extent that this picture is accurate, he will reap the benefits of tertiary mutualism and avoid punishment at the hands of other coalition members. Under these circumstances he is relatively likely to survive and reproduce both his genetic and his extragenetic design information.

In contrast, if his picture overestimates the coercive threat from his coalition, he will sometimes be parasitized by other members of his coalition, and his fitness will be reduced. Among other consequences, he may experience "pain" or "displeasure" as a result of relative deprivation. These subjective experiences reflect the functioning of genetic and extragenetic devices that impose indirect selection on mental information—including extragenetic information. His picture of the coercive capabilities of his coalition may therefore change as a result of this indirect selection. Moreover, his persistence and contribution of extragenetic information to his coalition's pool will be threatened by the consequences of his being exploited, and his extragenetic informational repertoire will thereby also be vulnerable to direct selection.

Conversely, if his picture underestimates the coercive threat of his coalition, he will sometimes attempt parasitic behavior toward other coalition members that provoke painful and potentially lethal retaliatory enforcement actions. Analogously to the case above, the extragenetic information supporting this "unrealistic" picture will be highly vulnerable to both direct and indirect selection.

Now consider the behavior of this young hominid as a *participant* in coalitional enforcement actions. In the context of expected effects already described {1B, C}, direct and indirect selection on his extragenetic informational repertoire will result in his tendency to acquire and use the most effective weaponry and social monitoring devices available, and to exploit these optimally in pursuit of self-interest. Self-interest includes punishing parasitic behavior in other coalition members; for example, if he enters an enforcement action with inferior weaponry, he is more likely to sustain painful injury or death than if he enters with superior weaponry.

Given the costs of selection on extragenetic information, we expect the design of genetic and extragenetic devices that support the refinement of this information at the lowest attainable cost. For example, humans are expected to be highly adapted to observing (i.e., testing representational information structures against) both cooperation and punishment events affecting other coalition members. Such testing would allow the young hominid of our example to refine his picture of his coalitional environment rapidly and at relatively low cost.

In this context it is most striking to consider patterns in entertainment. For example, most of the highest-grossing films of the contemporary era and many of the best-selling novels and most-watched television programs apparently cater to predicted enforcement "voyeurism." A central thread in these plots is that "good guys" generally inflict violent punishment—often using state-of-the-art or even "futuristic" weaponry and technique—on "bad guys." Another large class of such entertainment products explores acts or lives of self-sacrifice, kindness or altruism, and apparently caters to and/or seeks to manipulate the predicted cooperation voyeurism.

4H. REPRISE

The following three general implications of the theory of extragenetic information developed in this section are important to have clearly in mind.

First, the theory predicts that individual hominids—including contemporary humans—will be highly adapted both to maximal exploitation of the coalitional enforcement tools available to them, and to accurate assessment of the resulting enforcement environments in which they live. Thus, for example, when a fundamentally new weapon technology permits substantial expansion of enforcement efficiency, the theory predicts that a corresponding increase in social cooperation will follow rapidly—within one or a few human generations. This is a robust, testable prediction of the theory, and I return to it in detail in section 6.

Second, one of the primary objections to Darwinian theories of human cultural evolution has been the observation that a significant fraction of human behaviors have no apparent direct adaptive relationship to the physical environment. However, if the coercive human coalition is itself a major element of the selective environment, and if coalitions sometimes impose "arbitrary" constraints (designed by extragenetic information) on their members, these formerly mysterious behaviors become fully interpretable on a Darwinian hypothesis. {See subsection 6E for discussion of a major source of such "arbitrary" constraints.}

Third, even the most elementary capacities of human minds are, by hypothesis, dependent on and limited by extragenetic design information. In turn, the quantity and quality of this information is absolutely limited by the effective size and temporal persistence of the coalitions in which we develop {4E–F}. Thus, when humans develop in small or historically unstable coalitions, their minds are limited; on the other hand, minds that develop in the context of larger, more stable coalitions are potentially correspondingly more powerful. Though this conclusion tends to be obscured by our universal individual intellectual conceit, it nonetheless appears to be an inescapable implication of the coalitional enforcement hypothesis. Full understanding of elements of the discussion of human history to follow {6} requires that this implication of the theory be clearly grasped.

5. SELECTED EMPIRICAL EVIDENCE

5A. HOMINID PALEONTOLOGY

In this and the following sections {6 and 7}, selected examples of the extensive empirical support for the coalitional enforcement hypothesis will be reviewed. One of the most compelling of these is the capacity of the theory to account parsimoniously for the complex set of events reflected in the hominid fossil record.

The coalitional enforcement hypothesis explicitly predicts that initial adaptations to improved weapon competence—throwing and clubbing—should emerge very rapidly and simultaneously with adaptations to increased social cooperation and to the generation and use of extragenetic information. The fossil record strongly supports this prediction.

The significance of the fossil record is more easily appreciated in light of contemporary human anatomy. The coalitional enforcement hypothesis predicts that contemporary humans are the products of some 2 million years of selection for competence in the use of projectile and clubbing weapons. Humans should thus have unique skills reflecting this history, and we do. Anyone who has watched an American baseball game is implicitly aware of this. Humans can throw a 90 mile-per-hour fastball (projectile) with remarkable accuracy, and hit such a fastball on the fly with a bat (club). As predicted, this virtuosity is unique to humans among all known lineages, living or extinct. Although other primates can throw and club, they do so with much less force, much less control, or both (see, for example, Goodall 1964; Plooij 1978).

Moreover, the extent of this virtuosity is probably even greater than it appears on the basis of humans living in contemporary complex civilizations. As Barbara Isaac (1987) has documented, there is good reason to believe that humans in less complex societies who practice intensively from an early age can throw simple projectiles with spectacular accuracy, momentum and frequency.

As expected, this virtuosity is supported by skeletal adaptations. For example, while the contemporary human hand has clearly been redesigned under selection for diverse adaptive capabilities, among these are certainly throwing and clubbing (compare Napier 1962 with Marzke 1983, 1997). Further, the contemporary human lower skeleton—legs and supporting structures—has clearly been redesigned for increased efficiency of bipedal locomotion (Klein 1989; Aiello and Dean 1990); however, this was likely not the sole relevant adaptive priority.

Specifically, Fifer (1987) has pointed out that some details of human leg structure strongly suggest that throwing was also an important adaptive priority. These properties include the details of the locking apparatus of the knee, and the relative massiveness of human legs in comparison to legs thought to be adapted exclusively to bipedal locomotion, such as in the ostrich. These and related properties allow the contemporary human posterior skeleton to act as an effective "launching platform" for accurate, high-momentum throwing. Note that these same properties also support more effective clubbing.

Analyses of hominid skeletal adaptations to throwing/clubbing have been widely underappreciated by paleontologists and physical anthropologists because there was no theoretical framework suggesting that these activities were important. That has now changed, and more extensive specialist attention to this issue is definitely warranted.

Contemporary human virtuosity in throwing has long been recognized empirically (Darlington 1975; Calvin 1983; Fifer 1987; Isaac 1987). Its theoretical significance has remained obscure, however. The coalitional enforcement hypothesis predicts the observed unique relationship between this virtuosity and the development of a social adaptation involving extensive cooperation between nonclose relatives, with its diverse, dramatic consequences {1}.

With these considerations in mind, I turn to the illuminating fossil record of *Homo* and its immediate ancestors. First, the hands of the australopithecines who immediately preceded ancestral *Homo* underwent changes from the presumptive last common ancestor with chimps (Aiello and Dean 1990; Susman 1994; Marzke 1997). These are interpretable as limited adaptation to the use of clubbing and projectile weapons—again, possibly for improved predator defense. However, these adaptations are significantly short of those in the contemporary human hand.

Second, by hypothesis, these capabilities improved sufficiently to support rudimentary coalitional enforcement in at least the local australopithecine population immediately ancestral to incipient *Homo*.

Third, with the origin of *Homo*, dramatic skeletal redesign followed. The details of these changes represent strong evidence for the coalitional enforcement hypothesis. Within less than several hundred thousand years of the emergence of incipient *Homo*, massively redesigned animals classified as *Homo ergaster/erectus* dominate the fossil record. These animals have essentially modern postcranial skeletons, with the implication that they could likely throw and club with skill approaching that of contemporary humans (reviewed in Walker 1993). Simultaneously, these animals also display substantially increased cranial volume, and are thought to have had an extended childhood (secondary altriciality) (reviewed in Walker 1993; Leakey and Lewin 1992; Tattersall 1995; Walker and Shipman 1996; Stanley 1996).

These latter two properties would be expected to be produced by genetic adaptation to substantially increased social cooperation and to the use of extragenetic information. Specifically, expanded cranial volume reflects, in large part, genetic adaptation to the receipt, use and transmission of extragenetic information in contemporary humans, and it seems likely to have had the same function in early *Homo*. Moreover, secondary altriciality extends the childhood period of efficient social learning, thus supporting the transmission of larger amounts of extragenetic information in contemporary humans and, again, it seems likely to have had the same function in early *Homo*. Further, this extended juvenile dependence is sustainable in contemporary humans only because of our substantially increased levels of social cooperation that allows for reliable support of vulnerable juveniles and, again, this seems certain to have been true in early *Homo* as well.

Fourth, the fossil record of the animals between the australopithecines and the extensively redesigned *Homo ergaster/erectus* is generally consistent with the expectations of the coalitional enforcement hypothesis. This record is as yet too fragmentary to be decisively informative, however (Tattersal 1995; Stanley 1996). Nonetheless, it is noteworthy that these incompletely understood transitional animals apparently left large numbers of stones (manuports) in their tool assemblages that could be used as thrown projectiles but are poor substrates for stone tool manufacture (Isaac 1984; Potts 1988). This suggests, as the coalitional enforcement hypothesis predicts, that these animals made systematic use of high-momentum thrown projectiles for the first time in history.

In summary, the contemporary human skeleton has been extensively redesigned to support both throwing and clubbing, and the use of extragenetic information. Further, elongated human juvenile development requires substantially expanded social cooperation. This suite of adaptations arises simultaneously and relatively rapidly in incipient and early *Homo*, precisely as the coalitional enforcement hypothesis predicts.

5B. DIRECT EVIDENCE FOR ENFORCEMENT ACTIONS

The theory predicts that the most important impact of weapons on human evolution was through coalitional enforcement. If this is the case, serious injury and death at the hands of fellow coalition members should have been relatively common throughout the history of the species. This possibility has received limited specialist attention because of the absence of a theoretical motivation for investigation. Motivation is now clear, and future intensive study of this issue will be of great interest.

In spite of this limitation, several currently available sets of observations are noteworthy. First, the cranial vault underwent a remarkable thickening, apparently precisely at the origin of *Homo* (Klein 1989). This is consistent with the predicted new selection for resistance to weapon injury at this time. [Activity-level effects are not in themselves necessarily sufficient to account for this massive thickening in early *Homo* (Lieberman 1997).] Second, the pattern of damage to some Lower and Middle Paleolithic adult hominid fossils is interpretable in various ways, including that they may have resulted from defensive wounds occurring during intraspecific violence (Trinkaus 1986). In view of the lack of evidence for organized intergroup warfare in premodern humans (Keeley 1996), these observations are consistent with the coalitional enforcement hypothesis.

Assessment is somewhat easier for the more abundant younger prehistoric materials. Significant fractions of skeletal remains from recent prehistoric sites show signs of death by homicide under conditions suggesting intragroup violence. For example, executions by clubbing and projectile weapons are strongly suggested by several burials at Cahokia in the American Midwest (around 1200 AD; Pauketat 1994). Moreover, orderly prehistoric graveyard burials of homicide victims are widely observed (see, for example, Walker 1989; Close and Wendorf 1990). These are consistent with intragroup violence, although other interpretations are also possible.

Extensive and relatively straightforward data are available from the historical era. These clearly indicate that death at the hands of members of one's own coalition (band, tribe, chiefdom or state) is quantitatively important. Two examples are illustrative. First, Lee's (1979) study of the !Kung San indicates a rate of intraband homicide of about 30/100,000 person-years, or about 1% per generation. [In contrast, the San historically experienced much lower levels of extraband homicide (Lee 1979).] Moreover, a significant fraction of these deaths can be described as coalitional enforcement. For example, in several cases, unusually aggressive individuals were killed by arrows launched by a group of fellow band members.

Second, Scully (1997a,b) found that killing of citizens by their own states (secondary coalitions; see subsection 6B) was extensive. For example, in the 20th century at least 170 million (and possibly as many as 360 million) people have been killed by their own governments, as opposed to the 42 million who died in the massive wars of the century.

The magnitude of this effect can be better appreciated by summarizing Lee's (1979) and Scully's (1997a,b) data as follows: the fraction of modern humans killed at the hands of their own coalitions ranges from about 1% for the !Kung San to 8.9% (13th Century), 4.7% (17th Century), 3.7% (19th Century) and 7.3% (20th Century) for citizens of state-level civilizations. Moreover, such fractions can be much higher on a local, episodic basis. For example, approximately one-third of all Cambodians were killed between 1975 and 1979 during the Khmer Rouge era (Scully 1997a).

Notice that death at the hands of members of one's own coalition is much more likely than death in other ways—including by disease or in war—to be "directionally selective" with respect to social behavior. That is, the probability of such death is likely to be contingent on earlier social cooperation/parasitism.

In summary, although mortality data are fragmentary, they nonetheless support, or in some cases are consistent with, the prediction of the coalitional enforcement hypothesis that death at the hands of one's own coalition is relatively common. In particular, the fraction of modern humans killed by members of their own coalitions is large enough to represent a very strong source of selection when iterated over the some 100,000 generations since the origin of *Homo*. On the coalitional enforcement hypothesis, the directional component of this selection is central to the evolution of human uniqueness.

5C. SIZE OF HUMAN COALITIONS

To support evaluation of the additional evidence to be discussed below, a quantitative treatment of human coalition size is necessary. The theory predicts that coalition size should increase during the early stages of the emergence of *Homo*. Larger coalitions substantially decrease the individual cost of coalitional enforcement and allow additional opportunities for tertiary mutualism {1A–1C; 4E–F}. However, this tendency to increased coalition size is expected to be limited ultimately.

Specifically, with the emergence of rudimentary coalitional enforcement, there will be strong selection for individuals to monitor not only their own interactions with other coalition members, but also the interactions between all other pairs of coalition members {1C; 4F,G}. This substantially increases individual fitness by allowing extensive coordination among punishers, thus producing the exponential risk reduction discussed in 1C. Moreover, it allows an individual to punish without first being individually parasitized.

As a result, the individual cognitive burden of coalitional enforcement increases as a quasi-exponential function of coalition size. [The precise relationship is equivalent to the number of unique pairs (p) that can be formed from a coalition of size n, which is given by the relation $p = n!/2[(n-2)!]$, which reduces to $n(n-1)/2$. This function has a continuously increasing slope.] Coalition size is therefore expected to increase with time, but only to the point where further increase in the cognitive burden of monitoring becomes unsustainable, given physiological, anatomical and developmental constraints on brain development. {See section 6 for discussion of the emergence of the large organizational units seen in contemporary humans.}

Once this size limit is closely approached, continued refinement of the social adaptation is expected to occur, but to produce increasing numbers and efficiency of tertiary mutualistic behaviors rather than further increases in coalition size. I will refer to such coalitions as *primary coalitions.*

It is not obvious a priori what this size limit might be. However, in pursuit of a different theory for the origin of human social behavior, Dunbar and collaborators have carried out an important series of empirical investigations that suggest that this number is of the order of 150 individuals (see Dunbar 1997 for a recent review of this work). [Note that this number generally refers to the *effective* size of the group of individuals with which a focal individual might cooperate over time—for example, through a seasonal round—rather than the size of a routine daily aggregate.]

In summary, on the coalitional enforcement hypothesis, the evolution of a highly derived adaptation to extensive cooperation within primary coalitions was the central process of evolutionary change during the some 2 million years between the emergence of *Homo* and the emergence of behaviorally modern humans about 40,000 years ago. Various genetically designed novelties of modern humans, such as language competence and brain enlargement/remodeling, all evolved in this context and, by hypothesis, were dependent effects of coalitional enforcement.

5D. EARLY HOMINID WEAPONS

Formally, enforcement in a coalition of about 150 individuals requires weapons that can kill/injure from a range of some 20 to 30 meters, allowing a potential perimeter of fire of perhaps 130 to 190 meters. Moreover, in the context of *multiple* individuals participating in coalitional enforcement, a relatively low probability of inflicting disabling injury or death per individual projectile throw is sufficient. [For computational and heuristic simplicity, I will assume throughout that enforcement risk is being equally distributed. Of course, this is unlikely in practice and the theory does not require it. Rather, the theory merely requires that risk be sufficiently broadly distributed to permit sustainable coalitional enforcement.]

These requirements are well within the capabilities of early hominid weapons. For example, a 400-gram stone manuport (about the mass of an American baseball) thrown from 20 meters (about the distance from the pitcher's mound to home on a baseball diamond) by an experienced hominid would have a significant probability of inflicting serious injury. Further, a well-thrown simple wooden spear would likely allow a kill probability per throw adequate for coalitional enforcement out to ranges of some 30 meters.

6. EMERGENCE OF BEHAVIORALLY MODERN HUMANS

6A. CONTEXT

The material record of behaviorally modern humans (the last 40,000 years or so) is substantially more extensive than for the preceding history of *Homo*. From this detailed record emerges some of the most persuasive support for the coalitional enforcement hypothesis.

One of the most important observations of contemporary paleontology and archaeology is the human "cognitive explosion" that begins with the Upper Paleolithic Revolution at about 40,000–50,000 years ago and extends through to the present (reviewed Roebroeks et al. 1988; Trinkaus 1989; Mellars and Stringer 1989; Mellars 1990; Leakey and Lewin 1992; Stringer and Gamble 1993; Wenke 1990; Gamble 1993; Roberts 1993; Sofer 1994; Tattersal 1995). This is associated with relatively abrupt emergence in the record of extensive material exchange, art, material symbolism and increasingly complex functional technologies, and the ongoing refinement of all these.

Conspicuously, it is widely recognized that the fossil record shows no evidence for a human genetic revolution corresponding to this behavioral revolution. On the one hand, anatomically relatively modern humans existed for at least 50,000–70,000 years before the Upper Paleolithic Revolution. On the other hand, subtle change in the human skeleton—especially reduced robustness—has been more or less continuous through the present (Mellars and Stringer 1989; Mellars 1990; Sofer 1994; Tattersall 1995). [Anatomically modern humans before the Upper Paleolithic Revolution are conventionally designated *early moderns* and those after are termed *late moderns* or *behaviorally modern humans.*]

The theoretical problem presented by these remarkable features of hominid history is incompletely or implausibly resolved by previously proposed models for the origin of human uniqueness. In contrast, the coalitional enforcement hypothesis directly predicts these features—including their abruptness—as well as diverse additional details of the behaviorally modern human record, as discussed in detail below {6C–E}.

Before proceeding, it is important to understand the constraints the theory imposes. Specifically, the extent of human coalitional cooperation at all levels is expected to be *strictly* determined by the properties of coalitional enforcement. Thus, factors that affect coalitional enforcement—weaponry performance and social monitoring efficiency—will constitute an aggregate *independent variable* by which the extent and scope of human cooperation, up to and including the contemporary state, will be strictly limited {1; 4E–G}. Moreover, increases in social complexity are expected to ensue rapidly when this constraint is elevated by improvements in weaponry and monitoring {4E–G}.

There are other potential independent variables here, including human population density and ecological carrying capacity, of course. However, the cooperative adaptations characteristic of behaviorally modern humans—by hypothesis, allowed and limited by coalitional enforcement—dramatically alter both ecological carrying capacity and the effects of population density. Therefore, coalitional enforcement efficiency is expected to be the single most important independent variable.

The theory explicitly predicts that the level of modern human coalitional cooperation (social complexity) in nonmarginal habitats should correlate robustly in space and time with the weaponry and social monitoring technologies supporting coalitional enforcement. There is apparently no cogent theoretical alternative to this relationship. It is essential that this critical point is grasped if the remainder of this paper is to be understood.

6B. TRANSITION TO MODERNITY: THEORY

The theory specifically predicts the following evolutionary sequence. Based on considerations above {1, 5C}, we expect emergence of early human social organization in which individuals are highly adapted to life within extensively cooperative primary coalitions of modest size. The relationship among different primary coalitions is generally expected to be formally similar to the relationship between individuals in a relatively nonsocial animal species.

Members of two different primary coalitions are expected to show only the limited cooperation consistent with kin-selected behavior and primary and secondary mutualism. They will engage in no tertiary mutualism. While such modest cooperation would likely have had significant effects—for example, in the form of mate exchange—it is much less than the level of cooperation often seen between members of different primary coalitions in contemporary humans.

From this level of organization, in turn, the coalitional enforcement hypothesis predicts the emergence of extensive cooperation *between* members of different primary coalitions. During the ongoing refinement of the human cooperative adaptation at the level of primary coalitions—from perhaps 2 million to some 40,000 years ago—several factors, including reduced individual enforcement cost and increased hunting/scavenging efficiency, would have continuously selected for improvement in projectile weaponry. As long as such improvements did not dramatically extend the effective range of projectile weapons they would have had only the effect of increasing the level of cooperation *within* primary coalitions.

In early modern humans, however, who by hypothesis were already highly adapted to coalitional enforcement, a critical range threshold exists. At the point where projectile weapon range becomes great enough that the members of multiple primary coalitions can share equally in the cost of punishment of a parasitic act by an "outlaw" primary coalition, tertiary mutualism between primary coalitions will emerge.

Analogously to the case of enforcement *within* primary coalitions—recall especially Lanchester's Square Law {1C}—there will then be strong selection for rapid refinement of this capability once it emerges. The resulting adaptations will include further improvements in projectile weapon technologies and social monitoring strategies operating among primary coalitions. These adaptations are expected to be largely controlled by extragenetic information in the expanded, high quality pools of these enlarged coalitions {4E–G}.

Because of the relative difficulty of monitoring at the levels of secondary coalitions {5C}, human cooperation on a day-to-day basis is expected to remain primarily focused on the primary coalition—as it arguably does through to the present moment. Nonetheless, the adaptive advantages of even limited tertiary mutualism among members of different primary coalitions are expected to be crucial. Collectively, these effects should produce an explosive refinement of tertiary mutualism among members of different primary coalitions.

Thus, on the coalitional enforcement hypothesis, tertiary mutualism among members of different primary coalitions, with its diverse consequences, is the behaviorally modern human social adaptation. The dramatically rapid rise and ongoing refinement of this adaption is likewise predicted by the theory.

I will refer to the resulting social unit in which members of different primary coalitions engage in tertiary mutualism as a *secondary coalition.* Some of the extensive empirical support for this view of the origin and nature of behaviorally modern humans is reviewed in the remainder of this section.

6C. WEAPONRY AND THE TRANSITION TO MODERNITY

In view of the above considerations, the coalitional enforcement hypothesis predicts that weaponry range and performance should correlate extensively with the degree of social cooperation among behaviorally modern humans. A remarkably robust correlation is in fact observed, and elements of this evidence are reviewed in this and the following subsection. The correlation between novel social monitoring devices and behaviorally modern human cooperation is discussed in subsection 6E.

The elements of evidence have been selected for their importance or clarity, and are not selected arbitrarily to support the coalitional enforcement hypothesis. With the ambiguous exception of early Mesoamerica discussed below {6D}, I am unaware of any significant evidentiary contradiction of the predicted correlation between weaponry performance and social complexity throughout the paleontological, archaeological and historical records.

Recall again that a major adaptive consequence of increasing secondary coalition size in behaviorally modern humans is expected to be the increased size and quality of extragenetic information pools that support corresponding increases in adaptive sophistication {4E–F}. This effect is crucially important to the following discussion.

The theory predicts that the initial emergence of behaviorally modern humans should correlate with the development of projectile weapons of significantly increased range. The development of "light bolt technology" fulfills this prediction well, and correlates with the advent of behavioral modernity; these weapons ultimately accompanied the earliest behaviorally modern humans as they spread across the globe (see especially Gamble 1993; see also Marks 1993; Sofer 1994; Shea 1997, 1998; Knecht 1997).

Light bolts are shafts that carry small, sharp, hafted points (Knecht 1997). Such points can have great penetrating power without high projectile mass (Ellis 1997). The effective range of such weapons is significantly increased over that of Lower and Middle Paleolithic projectiles for two related reasons. On the one hand, lighter bolts can simply be thrown farther. On the other hand, an individual can carry a number of light bolts, in contrast with only one or very few heavier Middle Paleolithic spears that would be carried. [See Thieme 1997 and Dennell 1997 for an example of such heavy spears, and Shea 1997; 1998 for reviews of these issues.] This supports greater effective range in coalitional enforcement actions by allowing a lower probability of kill or injury per individual throw.

The effective range of hand-thrown light bolts is estimated to be of the order of 60 meters (Knecht 1997; Hutchings and Bruchert 1997, and references therein). This corresponds to a potential perimeter of fire of about 380 meters—sufficient to support cooperative punishment by at least two primary coalitions {5C}. Thus, this range was apparently sufficient to cross the threshold for the emergence of secondary coalitions. By hypothesis, the enhanced extragenetic information pools supported by these initial larger coalitions allowed the development of early complex technologies in permissive local ecosystems. These included the further improvements in weapon technology discussed immediately below. By hypothesis, this transition was the crucial, rate-limiting step in the initiation of the Upper Paleolithic Revolution.

Further, the development of the atlatl/throwing stick (spear-thrower) in one or more of these early secondary coalitions produced a substantial increase in light-bolt projectile range. There is no evidence for this technology in or before the late Middle Paleolithic assemblages immediately preceding the Upper Paleolithic Revolution in Europe, but it is well represented immediately thereafter (Knecht 1997). Thus, the correlation between the advent of the light bolt/atlatl technology and the mature Upper Paleolithic is quite precise. The atlatl extends the range of light bolt projectiles by some two-to-threefold, thus attaining effective ranges of the order of 100 to 150 meters (Hutchings and Bruchert 1997). This corresponds to a potential perimeter of fire from 630 to 940 meters.

The light bolt/atlatl technology is predicted to have substantially increased the potential efficiency and scope of coalitional enforcement, resulting in increased secondary coalition sizes and enlarged, enhanced extragenetic information pools. As expected, substantial additional technological innovation is associated with the resulting mature Upper Paleolithic. Among the various consequences of this was the penetration of a greatly expanded range of local niches and, ultimately, the first developments of plant and animal domestication supporting a number of local horticulturalist adaptations (Rindos 1984; Muller 1986; Johnson and Earle 1987; Heiser 1990; Wenke 1990; MacNeish 1992; Seemon 1992; Gopher 1994; Levy 1995).

6D. ADVANCED WEAPONRY AND HIGH SOCIAL COMPLEXITY

Bow-and-arrow technology was developed one or more times by atlatl-possessing modern human coalitions in Eurasia or North Africa, and was apparently subsequently dispersed throughout Eurasia, Africa and, ultimately, the Western Hemisphere (Rausing 1967; Blitz 1988; Farmer 1994). The bow significantly extends light-bolt projectile range. Well-made simple (self) bows can project light bolts (arrows) to ranges of 200 to 250 meters (see, for example, Pope 1923). This corresponds to a potential perimeter of fire of some 1250 to 1570 meters.

This maximal range may be relatively unimportant in hunting (see Hutchings and Bruchert 1997 for a recent discussion). It is profoundly important to coalitional enforcement, however, where a relatively low individual probability-per-shot of inflicting injury or death is adequate. Moreover, the bow allows further reduction in bolt mass, with a corresponding increase in the number of bolts that can be carried. This makes the weapon tactically and strategically much more versatile than the atlatl in coalitional enforcement actions.

The theory thus predicts that the bow should substantially improve the efficiency of coalitional enforcement, and thus cooperation within and the size of secondary coalitions, with ensuing adaptive consequences. An extensive body of archaeological evidence supports this prediction remarkably well.

Note here that cooperation does not imply equality a priori. Where specialization becomes great, as it does in large secondary coalitions, differential access to enforcement and social monitoring technologies is probably inevitable. Under these conditions the conflicts of interest that characterize all cooperation between nonclose kin will produce significant inequality. Thus, the consistent observations of anthropology and archaeology, that complex human societies are "ranked" societies, is consistent with the coalitional enforcement hypothesis (see Wenke 1990; Pauketat 1994; Marcus and Flannery 1996 for recent reviews). To the extent that such adaptations avoid extreme coalitional extortion {1B}, they can be adaptively stable.

I begin first with the North American record because it is simplest. The bow was apparently introduced only after the development of *horticultural* adaptations that involved small-scale cultivation of plants by small groups (Blitz 1988; Seemon 1992; Shott 1993, and references below). Moreover, the emergence of intensive *agricultural* adaptations—involving cultivation strategies requiring cooperation within large groups—in this region was relatively recent, and remains are thus overlaid with only limited amounts of well-understood, historically deposited material.

The development of the Mississippian adaptation in the North American Southeast and the Anasazi Pueblo adaptation in the Southwest are particularly illuminating (Muller 1986; Wymer 1992; Seeman 1992; Shott 1993; Pauketat 1994; Pauketat and Emerson 1997; Vivian 1990; Matson 1991; Sebastian 1992, and references therein). Each of these more complex societies was preceded by an extensive period—more than 1000 years in the Southwestern case—of a relatively simple horticultural adaptation in which atlatl-using populations grew various crops, including maize. [These correspond to the early Basketmakers of the Southwest and the Adena/Hopewell/Late Woodland cultures of the Southeast.]

At around 500 to 600 AD in the Southwest and 650 to 800 AD in the Southeast, the bow was acquired, apparently from external sources (Blitz 1988). Within a very brief period in each case—of the order of several generations—a social adaptation based on intensive, large-field cultivation of maize and other Mesoamerican cultigens arose, supporting increased settlement size and density. Within about 200 years in each case, the spectacular flowerings of the Mississippian and Anasazi Pueblo cultures, respectively, were consolidated. Each was comprised of networks of interacting large, sedentary settlements, extensive long-range material exchange, and elaborate public architecture and ceremonialism. Each extended over large areas and encompassed at least tens of thousands of people.

These event sequences strongly support the prediction that introduction of the bow was the limiting step in the emergence of these extensive cooperative social adaptations. Conspicuously, the presence of a domesticate, maize, which would have permitted agricultural intensification, was not sufficient. This is paradoxical on conventional cultural materialist interpretations of human social complexity (Johnson and Earle 1987). In contrast, it is predicted by the coalitional enforcement hypothesis. Further, the effect of a substantially new hunting technology, the bow, was apparently rapid development of sedentary, agricultural adaptations. This effect is paradoxical on the hypothesis that the primary effect of early weapons was on hunting. It is predicted by the coalitional enforcement hypothesis.

Second, while agricultural intensification is a common source of material support for large secondary coalitions, it is not the only possibility. Under opportune local ecological circumstances, relatively complex societies can be supported by a ready supply of food from the wild. There are several North American examples of apparently precise correlation between acquisition of the bow and dramatic increase in social complexity in such contexts, as predicted (Reeves 1990; Maschner 1991; Lambert and Walker 1991).

The Calusa of southwestern Florida, who developed a complex chiefdom in the absence of agriculture, provide a particularly compelling example of this (Widmer 1988; Marquardt 1992). They and their immediate antecedents lived in a rich coastal estuarine environment with an unusually high productivity. They thus had an entirely different subsistence adaptation than the Late Woodland horticulturalists immediately to the north. Moreover, the ancestors of the Calusa had lived in this estuarine environment for the previous 1,000 years or so without an obvious increase in social complexity.

As expected, in view of their geographical locations, the ancestors of the Calusa acquired the bow at or near the same time as the neighboring Late Woodland ancestors of the Mississippians (Blitz 1988). The Calusa developed their agriculture-independent complex chiefdom rapidly after the introduction of the bow, and in apparent synchrony with the development of an agriculture-dependent complex chiefdom by the neighboring Mississippians. This striking phenomenon is poorly explained by other theories of the evolution of social complexity, but is predicted by the coalitional enforcement hypothesis.

Third, it is illuminating to compare the Old and New World records, because the bow apparently became widespread before plant domestication and the development of horticultural adaptations in the Old World, rather than afterwards as in the New World (Farmer 1994; Knecht 1997; Bar-Yosef 1998, and references therein). I restrict discussion to the details of the well-developed record from the Levant. The abrupt development of the relatively elaborate preagricultural sedentary Natufian adaptation about 11,000 BC apparently correlated with the acquisition of the bow by this population (Solecki and Solecki 1970; Valla 1995; Bar-Yosef 1998). This population, in turn, only subsequently domesticated several grains and initiated the Southwestern Asian Agricultural Revolution over the ensuing several thousand years (Bar-Yosef 1998).

Thus, the chronological relationships between transition to sedentary population aggregates and the domestication of plants was largely or entirely reversed in North America and the Levant. In contrast, the acquisition of a fundamentally new projectile weapon technology—the bow—and the adoption of sedentary, complex social adaptations in these two independent cases correlate well. These correlations and failures of correlation are those expected on the coalitional enforcement hypothesis. It is noteworthy here that, on the coalitional enforcement hypothesis, the chain of events initiated by the precocious acquisition of the bow in Eurasia is likely to have been ultimately responsible for the contemporary global ascendancy of Eurasian cultures. [See McNeill (1976, 1982) and Diamond (1997) for reviews of contemporary Eurasian cultural ascendancy.]

Fourth, it is currently widely thought that the bow did not come to Mesoamerica until after the initial intensive agricultural adaptations of the Olmec, Zapotec and other cultures (Coe 1994; Marcus and Flannery 1996). While the theory does not rigorously exclude the possibility that some other sufficiently advanced weapon technology—such as, some refinement of the atlatl—might support such developments, the robust correlation between acquisition of the bow and increased settlement size and stability elsewhere suggests that this should be reinvestigated.

Several observations are provocative in this context. For example, a presumptive stone shaft-straightener used in arrow manufacture was deposited in the record at about the time of the first large Olmec settlements (Coe and Diehl 1980, p 237). This suggests that the bow may have been introduced at this time—much earlier than now assumed.

Moreover, in the Oaxaca valley there is a provocative correlation between the *disappearance* of stone atlatl dart points and the appearance of early sedentary settlements (Marcus and Flannery 1996). Given their hunting patterns, these sedentary Oaxaca Zapotec were obviously not without projectile weaponry (Marcus and Flannery 1996). Thus, the important possibility exists that they acquired the bow and initially used hardwood or other projectile points that would be difficult to identify in the archaeological record. Future investigation of these issues will be of great interest.

More generally, while the correlation between acquisition of the bow and increased social complexity has long been suspected on empirical grounds (Blitz 1988; Lambert and Walker 1991; Shott 1993), its theoretical significance has remained unclear. The coalitional enforcement hypothesis predicts this relationship in a straightforward fashion.

In closing, I note briefly that the robust correlation between weapon performance and social complexity predicted by the coalitional enforcement hypothesis continues as expected through to the present (Johnson and Earle 1987; Wenke 1990; McNeill 1991; Lechtman 1993; Roberts 1993; Gies and Gies 1994; Davies 1996; Scarre and Fagan 1997). There is a striking correlation between the acquisition of cast bronze weaponry and the rise of "Bronze Age" kingdoms throughout Eurasia and, independently, the rise of the Inca kingdom in the Andes. Further, the rise of Mediterranean region "Iron Age" empires correlates well with the advent of forged iron weaponry, with its lower cost and improved availability over bronze. Moreover, the rise of the high-population-density modern European state and the ensuing industrial and scientific revolutions correlates with the simultaneous introduction of efficient cast iron technology and gun powder-powered projectile weaponry (guns and artillery) into Europe. Lastly, the contemporary development of aircraft and rocket weaponry, with its planetary range, correlates precisely with the unprecedented, ongoing development of massive international political/economic coalitions.

6E. SOCIAL MONITORING AND MODERNITY

The independent variable on which behaviorally modern human social complexity is predicted to be dependent is a composite. It consists not only of projectile weapon performance, but also of the properties of social monitoring that regulate coalitional enforcement {1; 6A}. The theory thus predicts a correlation between novel social monitoring devices and increased secondary coalition size, and extensive correlation is observed. [As above, although only a few specific cases can be explicitly mentioned here, these cases are not chosen with deliberate bias. Specifically, I am aware of no compelling evidence that contradicts the predictions of the coalitional enforcement hypothesis in this connection.]

An empirically robust yet theoretically obscure observation of contemporary archaeology and ethnography is the correlation between the emergence of large human political structures and of various other elements of fully modern human behavior, including elaborate public ceremonialism and construction of spectacular monumental architecture (Johnson and Earle 1987; Wenke 1990; Roberts 1993). The coalitional enforcement hypothesis accounts for these observations directly.

Before reviewing specific cases, it is important to appreciate the nature of the monitoring problem in secondary coalitions. The capacity of individual modern human cognitive/affective devices for monitoring cooperation or parasitism is expected to be largely saturated by the demands of enforcement at the level of primary coalitions {5c}. Thus, in order for extensive cooperation at the level of secondary coalitions to emerge, specialized monitoring strategies that do not place extravagant additional demands on individual minds are probably required. Moreover, these strategies would likely come to depend for their design on the enhanced extragenetic information pools of the enlarged (secondary) coalitions themselves.

Consistent with this last expectation, the emergence of such cooperative adaptations would be commonly associated with only limited genetic displacement (see, for example, Droessler 1981; Bar-Yosef 1998; reviewed in Cavalli-Sforza et al. 1994). Under these conditions, a variety of local adaptations are predicted to be idiosyncratic in superficial detail, but to share a common underlying logic shaped by commonalities between late modern human gene pools and the universal selective constraints on extragenetic design information that supports secondary coalitional cooperation.

With these general considerations in mind, a few specific cases and observations will be considered. First, an efficient strategy to monitor secondary coalitional cooperation with little additional cognitive demand is to require public (easily monitored) investment of large amounts of effort and resources in infrastructure; these structures function in tertiary mutualism within secondary coalitions. Such investment in infrastructure is "upfront," and requiring it substantially alters the cost/benefit structure of subsequent cooperation. Any future attempt at parasitic behavior carries the severe risk of forfeiture of this large investment.

Large public works projects, such as roads and irrigation systems, are universally associated with complex chiefdoms and states (Johnson and Earle 1987; Wenke 1990); such projects arguably fulfill this requirement. These structures also have mundane function, however, and their causal origin is complex. In contrast, truly monumental architecture, such as temples and tombs that have no overtly practical function, and yet within and around which the exchanges and interactions of secondary coalitional cooperation are organized, is more telling. These structures apparently have a purely social function and, by hypothesis, a monitoring function. The cross-culturally universal building of superficially nonfunctional, arbitrary monumental structures by large secondary coalitions has the properties expected, if they are produced by extragenetic information adapted to solving the monitoring problems of these coalitions.

In this context, it is striking that massive increases in arbitrary monumental architecture and extensive expansion of trade networks (an element of secondary coalitional cooperation) correlate well in a number of different archaeological records. The Hopewell and Mississippian cultures of North American Southeast prehistory are robust examples (Muller 1986; Smith 1990; Clay 1992; Pauketat and Emerson 1997, and references therein). The central role of massive cathedrals in the expanding long-range commerce of 12th and 13th century Europe is likewise striking (Branner 1969; Fischer 1996).

Second, another strategy to monitor secondary coalitional cooperation with little additional cognitive burden is to require public (easily monitored) demonstration of competence at elaborate, arbitrary ritual. This requirement has two implications. On the one hand, as with monumental architecture, a substantial upfront investment of time and memory is required. Moreover, public rituals are generally designed to elicit (demonstrate) and reenforce learned emotional response to cooperation at the level of secondary coalitions. [See LeDoux (1996) for a discussion of learned emotional responses.]

Thus, elaborate public ceremonialism has the properties expected if it is produced by extragenetic information adapted to solving the enforcement problems of large secondary coalitions. The level or amount of ceremonial behavior in behaviorally modern humans correlates robustly and cross-culturally with the size of political structures (secondary coalitions). In contrast, high levels of primary coalitional cooperation occur in modern humans in the nearly complete absence of public ceremonial behavior (see, for example, Johnson and Earle 1987, and references therein).

Social systems that involve cyclical (e.g., seasonal) dispersal in small groups (families and primary coalitions) and later reaggregation in larger groups (secondary coalitions) are especially illuminating. Elaborate public ceremonialism is generally restricted to the transient periods of reaggregation in secondary coalitions under these conditions, as the coalitional enforcement hypothesis predicts.

Third, relatively recent adaptive technological changes that depend on written language and printing have allowed the expansion of monitoring based on bureaucratic record keeping and the use of "money." Such strategies are efficient and become sustainable when coalition sizes grow large. In many contexts, in contemporary states these strategies have largely replaced those dependent on individual investment in public ceremonialism or monumental architecture. In this connection, it will be of interest to see the future effects on social monitoring of the revolution in electronic observation and information exchange and processing that is currently underway.

In summary, some of the most (superficially) bizarre, arbitrary behaviors of modern humans—including elaborate public ceremonialism and construction of extensive monumental architecture—have precisely the properties expected if they are adaptive responses to the special monitoring problems posed by expanding cooperation at the level of large secondary coalitions.

6F. PALEONTOLOGY OF INFORMATION SHARING

The coalitional enforcement hypothesis predicts that the abrupt emergence of complex, behaviorally modern human social organizations resulted from the transition to and refinement of cooperation at the level of secondary coalitions. One of the most important adaptive consequences of this development, in turn, is expected to have been the generation, refinement and mutualistic exchange of correspondingly enlarged amounts of extragenetic information. The archaeological record provides strong support for this prediction.

First, although we cannot directly measure levels of exchange of extragenetic information among prehistoric populations, we can measure them indirectly through material exchange recorded in preserved artifact distributions. These records clearly indicate that earlier populations, including archaic and early modern humans, carried out only very limited and localized exchange (Roebroeks et al. 1988; Mellars and Stringer 1989; Mellars 1990; Wenke 1990; Roberts 1993; Stringer and Gamble 1993; Sofer 1994; Tattersall 1995). In contrast, behaviorally modern humans episodically set up large exchange networks, often continental in scope (Muller 1986; Pauketat and Emerson 1997).

It is quite striking that this pattern of exchange networks begins precisely with the earliest mature Upper Paleolithic adaptation (Western Eurasian Aurignacian) and its associated weaponry innovations {6C}. Moreover, nominally nonfunctional objects (such as pendant adornments or religious artifacts) are among the most widely exchanged materials, beginning with the Aurignacian (White 1993). Among other implications, this suggests that something other than these items—for example, information—was the functional objective of exchange.

Second, the extensive material exchange networks associated with behaviorally modern humans are usually or always characterized by extensive dissemination of specific *styles* of elaborate public ceremonial behavior and monumental architecture (see, for example, Muller 1986; Pauketat and Emerson 1997). This observation has two crucial implications. On the one hand, it corroborates the claim that extragenetic information is among the items being exchanged. On the other hand, as elaborate public ceremonial behavior and monumental architecture correlate robustly with large secondary coalitions in the ethnographic record {6E}, it indicates that the expanded information exchange in prehistoric modern humans also occurred in the context of such coalitions, as the theory predicts.

6G. MODERNITY: ALTERNATIVE EXPLANATIONS

The Upper Paleolithic Revolution and the emergence of behavioral modernity are such dramatic and important events that much attention has been devoted to trying to account for them. One class of theories now widely discussed among biologically oriented investigators invokes a genetic change in the early modern population, resulting in behavioral modernity. It has been suggested that such changes affect intellectual function more generally, or language ability more specifically, and presumably would require some more or less subtle remodeling of the central nervous system (see, for example, Lieberman 1991; Bickerton 1995; Mithen 1996; Noble and Davidson 1996).

Although it is currently unclear how plausible these theories are, they are arbitrary and unnecessary on the coalitional enforcement hypothesis. Specifically, all known elements of brain redesign in *Homo* are predicted by this hypothesis to be dependent effects of adaptation to coalitional enforcement and its consequences, rather than one or more of them being primary causes of human uniqueness. It is useful to note that available empirical evidence is more consistent with the coalitional enforcement hypothesis than with these alternative theories.

First, the late Middle Paleolithic Chatelperronian adaptation among Neanderthals in southwestern Europe is provocative in this context. It is identified through a lithic technology that appears to involve substantial borrowing by European Neanderthals from a recently immigrated late modern population (Mellars and Stringer 1989; Leakey and Lewin 1992; Stringer and Gamble 1993; Tattersall 1995).

These two populations would apparently have been separate for some 400,000 to 500,000 years at the time of contact (Krings et al. 1997). Yet, if this interpretation of the Chatelperronian culture is correct, both populations were nonetheless highly adapted to the acquisition and use of extragenetic information. This is poignant support for the prediction that human adaptation to acquisition and use of extragenetic information is ancient and derived as predicted by the coalitional enforcement hypothesis, rather than being recently acquired with the advent of behaviorally modern humans.

Second, recent studies of fossil indicators of early human language capability indicate that language is likely to have arisen early in the history of *Homo*, as the coalitional enforcement hypothesis predicts (Kay et al. 1998). These observations provide no support for the proposal that fundamental language abilities are very recent, though late refinements in the subtleties of linguistic execution remains possible (see, for example, Lieberman 1991).

In overview, on the coalitional enforcement hypothesis, there is currently no substantive reason to believe that the ultimate hegemony of the modern human clade was anything but an historical accident resulting from serendipitous local development of light bolt technology. Had this technology been developed in a Neanderthal population instead, our lineage might now be extinct, and descendants of the Neanderthals might have walked on the moon.

6H. CONCLUDING REMARKS

Evidence reviewed here and in section 5 indicates that the coalitional enforcement hypothesis is a robust, general theory capable of accounting for most of the major events throughout the history of the *Homo* lineage. The specific examples described in this section indicate that the theory accounts in a straightforward way for the relatively abrupt emergence of behavioral modernity and the ensuing—and continuing—dramatic expansions of human social cooperation. To my knowledge, no other currently available theory provides a comparably direct, parsimonious explanation of these remarkable events.

7. ADDITIONAL IMPLICATIONS OF THE THEORY

7A. THE SELF-DOMESTICATION EFFECT

Modern human social behavior is remarkable not only in its detail, but also in the rapid rate at which this highly derived adaptation evolved. The coalitional enforcement hypothesis predicts this. With the emergence of coalitional enforcement in incipient *Homo*, a new, intense, directional source of selective pressure was created.

First, coalitional enforcement permits extension of cooperation beyond the limits of close kinship. Thus, cooperative punishers are frequently not deterred by countervailing direct inclusive fitness interests. They punish exclusively on the basis of the target's parasitic behavior, with obvious selective consequences.

Second, tertiary mutualism sustained by coalitional enforcement is a substantial adaptive advantage to coalition members. Moreover, members of established coalitions will generally choose new members, where choice exists, on the basis of the ability of these new members to contribute substantial service. In contrast, not only will noncooperative individuals be excluded or punished, but also less valuable or less competent individuals will often be excluded or undersupported, again with obvious selective consequences.

Third, increasing tertiary mutualism, in turn, increases the capacity of coalition members to reciprocally shield one another from competing selective environmental forces. Selective pressure from the external environment is frequently independent of or even directly antagonistic to the selective pressure applied by coalition members. This shielding can greatly increase the effectiveness of the directional selection described above.

On the coalitional enforcement hypothesis, modern humans are the descendants of some 100,000 generations of individuals who both imposed such selection *on* other hominids and survived such selection *by* other hominids.

This conclusion has two important implications. First, modern humans are self-domesticated animals—an insight suspected on empirical grounds since Darwin (1871). Contemporary human uniqueness arising from coalitional enforcement can be productively viewed as the result of selective breeding at the hands of unrelated members of the coalitions in which our ancestors lived for the last 2 million years or so.

Second, because of the intense, directional nature of this process, the rapid rate of evolutionary change in the *Homo* lineage is to be expected.

It is also likely that the highly derived genetic and extragenetic devices adapted to hominid self-domestication subsequently supported the uniquely broad and extensive domestication of other organisms by modern humans, leading to horticultural and agricultural adaptations. Note especially how extensively similar domestication and self-domestication are in operational detail.

7B. HUMAN SOCIAL PSYCHOLOGY

Various features of human social, ethical and economic behavior have not found easy or straightforward evolutionary explanation. The coalitional enforcement hypothesis apparently resolves much of this earlier confusion, as illustrated in several examples below.

First, in seminal studies it was pointed out that human ethical psychology likely reflects the requirements of human social cooperation (see especially Darwin 1871; Waddington 1960; Williams 1966; Trivers 1971; Alexander 1989). However, the details of the selective environment that produces such psychological adaptations, the nature of the design information that supports them, and the reasons they are unique to humans have all remained quite unclear. The coalitional enforcement hypothesis provides a direct resolution of these issues. For example, moral outrage and guilt, and their tendency to be restricted to circumstances involving groups of well-acquainted nonkin—that is, potentially enforcing coalitions—are predicted. These genetic and extragenetic devices are proximate mechanisms designed to support participation *in* and avoiding becoming a target *of* coalitional enforcement, respectively.

Second, modern humans appear to develop detailed "theories of mind" of very specific content that apply to other humans (Leslie 1994; Premack and Premack 1994). Similarly, modern humans appear to have a well-developed capacity to detect "cheaters" in social transactions (Cosmides and Tooby 1992). As with human social psychology more generally, this important empirical work has yet to produce a compelling theoretical account of the evolutionary origin of these capacities. For example, is has remained unclear precisely why such adaptations are unique to humans. These cognitive adaptations and their uniqueness to humans are predicted as adaptations supporting the social monitoring required for coalitional enforcement.

Third, humans commonly show "unexpectedly" high cooperation in economic behavior (Frank 1988; Mansbridge 1990). This is predicted by the coalitional enforcement hypothesis. Specifically, modern human genetic and extragenetic information shaped by a long history of coalitional enforcement is expected to produce individuals designed to participate in the highly cooperative tertiary mutualism these studies observe.

7C. HUMAN REPRODUCTIVE BEHAVIOR

Human sexual, family and child-rearing behaviors and properties are unusual among mammals (Symons 1979; Fisher 1992; Ridley 1993; Buss 1994; Baker 1996, and references therein). These include nearly ubiquitous monogamy or mild polygyny, and hidden or occult ovulation in females. These behaviors are economically explained by coalitional enforcement, as outlined below.

Most generally, one of the central effects of coalitional enforcement in this context is expected to be reduced variation in reproductive success among coalition members. First of all, more specifically, monogamy—and related mating schemes, including mild polygyny—is apparently the only adaptively stable mating system under such circumstances. This results, in part, from the vulnerability of would-be hyperpolygynous males to punishment at the hands of coalitions of other males.

Second, overt ovulation displays could conceivably be exploited by females to attempt unusual reproductive success through solicitation of differential access to material resources provided by males. Lethal or damaging punishment of individual females who pursue such strategies by coalitions of competing females might account for the loss of overt ovulation display in modern humans. Alternatively, overt ovulation display may have become more costly than adaptive with the advent of coalitions of potentially sexually aggressive males permitted by the emergence of coalitional enforcement.

8. UNIVERSAL COALITIONAL ENFORCEMENT

In addition to the direct empirical support for the coalitional enforcement hypothesis {5–7}, a compelling reason to believe that the hypothesis is fundamentally correct and complete is that it appears to be general. Specifically, the logic of coalitional enforcement {1} should be universal. Thus, we expect coalitional enforcement to be required to support cooperation among distinct (not identical by recent descent) elements of replicating information with potential conflicts of interest *irrespective* of the level of organization in question.

If this proposal is correct, coalitional enforcement should be an essential, ancient property of the cooperative coalitions of genes making up the complex genomes of contemporary organisms. This appears to be the case. Coalitions of elements of genetic information that control cosuppression systems apparently have the capacity to actively control ("punish") other genetic elements adapted to parasitizing the genomes of sexual organisms (Bingham 1997).

Moreover, "divide-and-conquer" strategies can be effective in preventing development of large chromosomal segments adapted to parasitizing the remainder of the cooperative sexual genome (Hurst et al. 1996). The detailed properties of known meiotic drive systems strongly support this view. The coalitions of genes that produce and control meiotic recombination likely evolved, in part, in response to the adaptive requirement for such a divide-and-conquer enforcement strategy (Hurst et al. 1996).

As expected, these classes of enforcement systems appear to be ubiquitous and ancient in sexual organisms with complex genomes.

Lastly, enforcement is expected to be required in order to sustain cooperation within the extragenetic domain, and between genetic and extragenetic information. The indirect selection imposed on extragenetic information {4} by genetic and extragenetic devices is expected to include such enforcement activity.

9. CONCLUSION

The coalitional enforcement hypothesis provides a coherent, parsimonious explanation for human uniqueness. The theory is accessible to verification/falsification by properly designed empirical investigations in diverse areas, including hominid paleontology, archaeology, anthropology, ethnography, linguistics, economics, sociology, political science, cognitive science and psychology.

The contemporary social sciences and humanities have accumulated enormous, valuable bodies of descriptive information that have led to local, empirical generalizations.

However, in contrast to the physical and natural sciences, these disciplines have yet to produce a meaningful, coherent theoretical explanatory structure (critiqued in Tooby and Cosmides 1992). As a result, analytical theory in the humanities and social sciences is frequently trivially self-referential. Attempts to develop a cogent *causal* theory of human evolution, such as that proposed here, will be essential to substantive further progress in these disciplines. In addition to its theoretical importance, such progress may have significant practical implications, including the support of development of more sustainable and humane ethical, economic and political systems.

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