

The Emergence of Human Uniqueness: Characters Underlying Behavioral Modernity

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Although scientists are aware that humans share the same biological heritage as do all other organisms on the planet, the reliance of *Homo sapiens* on culture and cooperation has resulted in what can best be described as “a spectacular evolutionary anomaly.”^{1,11} The extra-somatic adaptations, technological dominance, and success of our species in colonizing every terrestrial habitat have no parallel.² Moreover, *Homo sapiens* accounts for about eight times as much biomass as do all other terrestrial wild vertebrates combined,³ an amount equivalent to the biomass of all 14,000+ species of ants,⁴ the most successful terrestrial invertebrates. Human societies are complex, with more specialized economic niches in the United States than the total number of mammalian species on the planet.⁵ While some might suggest that only post-industrial humans achieved stunning biological success, data suggest that humans living as hunter-gatherers would have attained a world population of more than 70 million individuals⁶ and a total biomass greater than that of any other large vertebrate on the planet if agriculture had not been repeatedly invented as they spread.

ing that produces cumulative cultural adaptation and social norms that regulate all aspects of life. These derived traits span physiological adaptations, behaviors, cognitive abilities, and evolved emotions not seen in our closest primate relatives.

Chimpanzees raised in human families do not acquire language or human culture; they learn only a few hundred vocabulary terms and no rules of grammar.^{10,11} In contrast, exposed human children do acquire some chimpanzee culture.¹¹ Chimpanzees also show little prosocial behavior in experiments that elicit extensive “other-regarding behavior” by humans.^{12,8} Chimpanzee females do not share food readily, even with their own infants,¹³ whereas food transfers to kin and nonkin are extensive in hunter-gatherer societies.¹⁴ Hunter-gatherers exhibit levels of cooperation-mediated task specialization that are not approached by any primate.¹⁵ We also know that human juveniles, but not chimpanzees, are dependent on adults for care and food provisioning until they reach full adult body size. Moreover hunter-gatherers have exceptionally long adult life spans, with baseline adult mortality being one-fifth that of wild chimpanzees.¹⁶ Finally, healthy human females show high fertility in early adulthood, followed by a precipitous decline to hormone mediated sterility long before other signs of physiological senescence.

In order to account for human uniqueness, we must focus on three research questions: What are the specific behavioral proclivities, cognitive capacities, and emotional mechanisms that set us apart? Why did this suite of traits evolve in humans and

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Identifying the causes of human uniqueness is one of the most exciting and philosophically profound issues of all scientific research. Despite this, only recently have theoretical and empirical advances allowed research to focus directly on human uniqueness. Although cultural and biological views of human behavior have been at odds for at least a half-century, recent research on culture-gene interaction has begun to converge on a paradigm that integrates not only areas of anthropology,^{7,8} but all the biological, social, and behavioral sciences.^{1,9}

Recent studies of life history, experimental economics, animal social learning, and cognitive and evolutionary psychology, combined with findings from biological anthropology, define a set of key traits in the emergence of human uniqueness. These include large brains, long adult life spans, protracted juvenile dependence, an obligate postreproductive period, prosocial emotions that promote extensive cooperation with nonkin, complex communication, and a reliance on social learn-



Figure 1. a) Matsigenka woven cotton gowns and b) gold nose pennants are examples of cultural transmission via peaceful interaction with tribes of a different language family. Only lowland Amazonian tribes historically located adjacent to more complex highland groups show these borrowed highland traits. Extensive horizontal cultural transmission requires both evolved social learning mechanisms and cooperative conventions that facilitate extensive interaction with distant nonkin groups. (Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.)

not in other animals? Why did they evolve when and where they did, not earlier, later, or in a different ecological context?

HUMAN UNIQUENESS: CULTURE AND COOPERATION

We suggest that two fundamental characteristics account for human uniqueness.

The first of these characteristics is extensive reliance on social learning, resulting in cumulative adaptive change in extrasomatically stored information. This system of informational evolution is the dominant force of adaptation in humans, but no other species. The proclivity for imitation in combination with guided modification and powerful transmission biases leads to special evolutionary trajectories of behavior unanticipated by standard behavioral biology. The capacity for high-fidelity social transmission has produced a complex symbolic communication system that allows transfer of information about events not directly observed (or observable) by either party.

The other characteristic is extraordinary cooperation between nonkin, including specialization, a regular flow of goods and services between individuals and groups (Fig. 1), and the formation of increasingly complex alliance networks. Human cultural conventions solve the problem of reliably and stably associating cooperating individuals with each other. A long natural history of within-group cooperation has led to cultural and biological co-evolution that produced emotional mechanisms facilitating cooperative behavior between kin and nonkin including morality, fairness, justice, anger, indignation, guilt, and the emergence of universal human traits such as ethnicity and religion.

HUMAN AND ANIMAL “CULTURE”

Culture is information (beliefs) stored in brains, institutions, and material goods that is transmitted socially and influences behavior. Because cultural variants, like genes, are units of information that influence their own transmission, their frequencies change through time and culture evolves. This means that both

genetic alleles and cultural variants interact with environment and each other to produce observed behavioral phenotypes. Important theoretical work on the cultural system of inheritance began in the 1970s with Cavalli-Sforza and Feldman,¹⁷ and was subsequently infused with formal population modeling by Boyd and Richerson.¹⁸ Because social learning mechanisms are shaped by genetic evolution, but also influence the relative advantage of alternative genotypes, genes and culture co-evolve. It has become clear that dual inheritance theory is requisite for a complete understanding of human behavior.^{1,8,9} Recently, studies of dual inheritance theory have undergone tremendous growth in sophistication and complexity as a greater understanding of the biological nature of culture has emerged.^{19,20}

Dozens of animal species are known to transmit behavioral patterns by social learning. These include tool use and food extraction techniques, as well as variety of social behaviors.^{21,22} Some biologists refer to these socially learned behaviors as animal “culture” and have classified different regional variant combinations of learned traits as differ-



Figure 2. An Ache man teaches his brother's stepson (genetically unrelated) how to butcher a deer. Human cultural transmission is strongly dependent on teaching as well as imitation, and requires the teacher to behave altruistically toward learners. The human willingness to teach nonkin as well as kin is probably related to life in cooperative breeding social units. Active teaching allows for the transmission of complex information, such as religious beliefs and social norms, not directly observable by imitators. (Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.)

ent "cultures."²³ The great apes, especially chimpanzees and orangutans, are notable in this regard, with over thirty different regional traditions distinguishing localized populations.^{24,25} However, other researchers argue that animal "traditions" should not be equated with human culture and point to important differences in mechanisms of social learning, the accumulation of

learned traits, and the content of what is transmitted as differentiating humans from other animals.^{10,26-28}

Cumulative Cultural Adaptation

Many animals acquire socially learned traditions, but none display increasingly complex behavioral patterns built on prior socially transmit-

ted behaviors, a phenomenon that Tomasello²⁹ has called the "ratchet effect." Research in experimental psychology is beginning to elucidate differences in learning mechanisms that may explain why only human social learning is cumulative.³⁰ For example, many animals transmit behaviors mainly through repeated exposure to a context that increases their chances of acquiring a behavior through individual learning. Indeed, only fifteen years ago Galef²⁷ suggested that all known cases of animal traditions could be explained by such "enhancement." In contrast, humans engage in imitation: learning by watching it done. Researchers were initially uncertain if other animals could learn by imitation, but evidence now shows that apes, marmosets, dolphins, rats, and many species of birds also learn through imitation.^{31,32}

Although learning by imitation is critical to cumulative culture, chimpanzees, too, learn by watching a model, yet do not have cumulative culture. Experiments suggest that chimpanzees are more inclined to emulation, or learning to get the desired result, rather than imitation, copying the precise means. For example, Horner and Whiten³³ conducted experiments showing that human children copy unrewarded actions presented by an adult model, whereas chimpanzees quickly eliminate actions that are superfluous to obtaining the reward. Further studies have shown that this is a consistent difference in human versus chimpanzee social learning.³⁴ Indeed, the human proclivity for "unrewarded imitation" is very rare in nature (see McGregor³⁵ for an example in pigeons). Furthermore, experiments show that children readily imitate altruistic and "other-regarding" behaviors as well,^{11:28-29} something never observed in apes. Children not only copy model actions precisely, but simultaneously incorporate an emotional reaction that to do things otherwise is "wrong."³⁶

Tomasello³⁴ concludes that human social learning includes an exceptional focus on actions rather than just goals. Nevertheless, chimpanzee "emulation" results in transmission of behavior with notable fidelity



Figure 3. Allowable forms of conflict and rights of signaling are extensively regulated by social norms in Ache society. a) Men can only engage in intratribal violence through regulated club-fight duels. b) Older men referee the duel and women kinsmen ensure that certain rules are followed that generally permit only nonlethal injury. c) When a death does occur, special body scarification, which others are not allowed to display, is applied to the killer after an extensive period of regulated food deprivation and other ritual purification. (Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.)

across a chain of individuals within a social group and between social groups that observe each other.³⁷ This allows some traditions to spread through space and time. However, follow-up experiments have shed additional light on critical differences between chimpanzees and humans. For example, chimpanzees imitate behaviors that provide immediate rewards but are reluctant to adopt subsequent new behaviors that can provide even higher rewards.³⁸

Careful analyses of social learning in humans and apes will almost certainly uncover other critical distinctions. For example, humans regularly engage in “teaching,” but none of the apes have been observed to do so.³⁹ Unlike other animals, humans teach not only offspring, but other adults and even nonkin (Fig. 2). Human imitation also includes multiple transmission biases, such as conformity bias, success and prestige bias, and similarity bias, which may be critical to explaining cumulative culture in our species.⁸

Theoretical modeling has also provided important insights into why cumulative culture is rare among nonhumans.²⁶ For example, Boyd and Richerson⁴⁰ demonstrated that the selection force on social learning depends on the amount of previously existing useful culture to copy. Copying is most favored in groups that already have many copiers who have already produced adaptive culture. If imitation capacity is mainly adaptive when present at a high frequency, how would it get started?

Social Norms, Ethnicity, and Language

Despite considerable research on cultural transmission mechanisms, less work has been done on the content of social transmission and whether humans show uniqueness in this realm. We propose that language and social norms are evolving informational systems not observed in other primates. Hill²⁸ proposed that human “culture” is conceptually distinct from animal traditions because it consists of three components universally present in all human societies: socially learned techniques and technologies; socially learned regulation of behavior (norms, conventions, rules, laws) achieved through third-party rewards and punishments; and symbolic and emotional reinforcement of, and signaling adherence to, a specific rule system (ritual, morality, religion, ethnicity).

The second and third components on this list have not been described in nonhuman animals. The transmission of these components may rely on unique cognitive adaptations for transmission by teaching.⁴¹ Members of human societies continuously negotiate conventions that limit within-group competition and promote within-group cooperation. The learning of such conventions may rely on teaching, as well as conformist and success-biased transmission, and may result in the spread of group-beneficial norms through a process of cultural group selec-

tion,^{42,43} something that is unknown for any other species.

The uniqueness of this cultural process is evident in hunter-gatherer societies, where socially learned norms regulate competition over valuable biological resources and promote cooperation. Indeed, all hunter-gatherer societies develop regulations²⁸ that control access to things such as mates, food patches, already-acquired foods, signaling opportunities, kin and allies, and political power. Such regulations also govern acceptable expression of conflict (Fig. 3), age-sex-structured behavioral patterns, and public health hazards. These regulations constrain the competitive game of life for ethnic in-group members. Cultural norms are reaffirmed and reinforced symbolically through ritual and, because interaction with others “playing by the same rules” is advantageous, ethnic signaling is universal in human societies (Fig. 4).^{44,45} When people become experts at playing the game of life by a specific set of rules, they internalize a commitment to those rules (morality) and react emotionally against any violations that threaten to bring change.

It has long been argued that language is what makes us human and sets us apart from other animals. But language appears to be a cognitive offshoot of social learning. Evolutionary linguists suggest that language consists of three central cognitive abilities that must be accounted for in order to explain why humans alone have language,



Figure 4. Yora tribesmen are distinguished by a variety of traits such as plucked eyebrows and body hair, a unique facial necklace, penis ties, and waist sashes, Urucu-latex painted hair with flaring straight bangs, perfume-smelling flowered armbands, and a belt of woven beads and monkey incisors. Neighboring Arawakan groups (Matsigenka and Piro) exhibit none of these traits. Ethnic markers are ubiquitous in human societies and probably are used to signal adherence to a common set of social norms in order to find willing social partners. (Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.)

These cognitive abilities are communicative intentions, capacity for reference, and production and interpretation of structured sequences.⁴⁶ The first of these may be derived from cooperative breeding, while the second and third components are part of the high-fidelity social learning mechanisms that humans apply to all cultural transmission.

Ultrasociality

We use terms like “hyper-cooperation” and “ultrasocial” to describe regular cooperation in social groups composed partially or completely of nonkin. Although wild chimpanzees sometimes cooperate with unrelated individuals,⁴⁷ humans provide extensive help to nonkin in ways that

seem unanticipated by the “selfish individual” perspective of evolutionary biology or the “rational self-regarding actor” paradigm of economics. Surprisingly, behavior often seems designed to promote group welfare. Hunter-gatherer societies show numerous cooperative institutions, from social status leveling^{48,49} and alloparental caretaking⁵⁰ to between-group exchange,⁵¹ cooperative food acquisition,¹⁵ and extensive, even generalized food redistribution.¹⁴ But not until the emergence of experimental economics did it become clear that the predicted Nash equilibrium behaviors, from economics, or evolutionary stable strategies, from biology, based on assumptions of self-interested actors, systematically failed to predict human behavior.

Recently, many carefully controlled experiments have demonstrated unexpected cooperation in numerous contexts.⁵² For example, despite mythology to the contrary, people frequently *cooperate* rather than defect in the one-shot *Prisoners Dilemma*.⁵³ They also expect others to cooperate if they have met or talked with them. Experimental subjects indicate that they prefer the cooperate-cooperate outcome over the defect-cooperate outcome that would provide them higher payoffs.⁵⁴ They make generous offers far above the predicted equilibrium in *Ultimatum* games and reject “unfair” offers despite a substantial loss of potential resources.⁵⁵ They divide resources with others in one-shot anonymous *Dictator* games, even though they have complete control over the division. They entrust large endowments to “dictators,” relying on them to split a stake fairly, in the *Trust* game.⁵⁶ Finally, contributions to *Public Goods* (in games and real life) are notably higher than the expected zero contribution predicted by formal rational actor models.⁵⁷ While the evolutionary interpretation of results from experimental economics is still strongly debated,^{58,59} the results indicate a clear behavioral distinction between humans and apes; for example chimpanzee “dictators” in captivity never pass food from one cage to another.

As multitudes of “cooperation” games were tested under ever more rigorous conditions, two things became clear. First, people did not cooperate simply because they failed to understand the games or because they were blindly playing “as if” some typical ancestral conditions rather than the experimental conditions applied to the situation.⁶⁰ Second, the proclivity to cooperate characterizes remote tribal peoples as well as those in nation-states, but the levels of cooperation vary with “cultural” factors.^{61,62}

More recent theoretical exploration has uncovered a universal “core dilemma of cooperation”—conditions that, when met, can lead to the evolution of altruistic cooperation in any species. Mathematical models derived from the Price equation⁶³ unite kin selection, reciprocal altruism, group selection, indirect reciprocity, and norm-based cooperation into a single framework and demonstrate that any mechanism that regularly associates acting altruistically with being the recipient of altruistic behavior can favor the evolution of cooperation.^{11:35–74,215–218} The models show that no form of cooperation is truly altruistic in the genetic sense. All cooperative mechanisms proposed either increase the direct fitness of the actor or can be explained by inclusive fitness effects. While kin selection and reciprocal altruism are the best-known examples of this, experimental research shows that significant levels of cooperation can also be achieved through reputational effects,⁶⁴ communication⁶⁵ by punishment of noncooperators,⁶⁶ and between-group competition.⁶⁷

THIRD-PARTY PUNISHMENT

Research on cooperation in humans was significantly advanced with the empirical demonstration of third-party punishment by a majority of subjects who observe uncooperative behavior.⁶⁸ This punishment is labeled “altruistic” because it consists of a penalty, applied at a cost by an observer, to an individual exhibiting uncooperative behavior when interacting with an unrelated third party. In conjunction with this,

a large number of experiments confirm that when noncooperators are punished for defection (free-riding), they subsequently behave cooperatively.⁶⁹ However, whether third-party punishment should be labeled “altruistic” and whether it can induce cooperation in societies without state-sponsored enforcement is still debatable. Several studies suggest that such punishment may be designed to enhance the reputation of the punisher in nonlaboratory settings.^{70,71} Other studies have suggested that retaliation may limit the ability of any punishment to produce collective good.^{72,73} This may be why, so far, empirical evidence for punishment of noncooperation is mixed in hunter-gatherer studies.^{74,75}

... the evolved taste for “fairness” in dyadic and small-scale interpersonal interaction appears to be directly related to evolved neural mechanisms^{84,85} that are also activated in the application of punishment by impartial judges in modern legal systems.⁸⁶ In short, humans may have evolved emotional machinery not present in apes that promotes nonkin cooperation.

Despite the debate over its ultimate causality, however, the observations of third-party punishment in experiments have led theorists to explore how cooperation might be achieved through such punishment.^{76–78} The observed high frequency of initial cooperation and willingness to punish has led to new terms to describe these traits. “Strong reciprocity”^{79:169} is defined as “a propen-

sity to reward those who behave cooperatively and to punish those who violate norms of acceptable behavior, even when reward and punishment cannot be justified in terms of self-regarding, outcome-oriented preferences.” Similarly, terms such as “other-regarding preference” and “prosociality” describe the proclivity to take into account the payoffs to other individuals as well as to ones self in cooperative dilemmas.

Third-party punishment, strong reciprocity, and pervasive prosocial tendencies appear to be derived features of the genus *Homo*, since chimpanzees, unlike humans, do not punish “unfairness” or the lack of other-regarding behavior by compatriots,^{80,81} and show only limited evidence of other-regarding behavior.^{12,82} Prosociality in humans as compared to other apes may be related to cognitive features of our species, such as greater cognitive ability in cooperative realms.⁸³ Most importantly, the evolved taste for “fairness” in dyadic and small-scale interpersonal interaction appears to be directly related to evolved neural mechanisms^{84,85} that are also activated in the application of punishment by impartial judges in modern legal systems.⁸⁶ In short, humans may have evolved emotional machinery not present in apes that promotes nonkin cooperation.

CRITICAL PRE-ADAPTATIONS

The suite of traits that has set humans apart from other animals must be explained by historical and ecological circumstances acting on prior evolved adaptations. For example, Richerson and Boyd⁸⁷ and Alvard⁷ have proposed that intrinsic characteristics of the genus *Homo*, such as advanced theory of mind⁸⁸ (the ability to understand that others have a different state of knowledge or belief), and extrinsic events such as increased climate variability in the Pleistocene might have combined to produce the evolution of cumulative cultural capacity in hominins. Following their lead, we outline a series of preadaptations that may help explain why later *Homo* evolved unique traits that chimpanzee, ele-

phant, and porpoise lineages did not. Other apes have large brains, regularly engage in social learning, and exhibit theory of mind. Moreover, those ape species also passed through the Pleistocene without evolving the combination of characters that make humans biological outliers. We must, therefore consider important preadaptations in the genus *Homo* that led to human uniqueness.

First, hominins are bipedal and, as a result, cover geographical ranges far larger than other apes do. Even hunter-gatherers living in tropical forests have daily home ranges that are two to three times those of chimpanzees, and lifetime home ranges more than two orders of magnitude greater.^{89–93} Thus, individual hominins faced more environmental variability than do chimpanzees. Theoretical models suggest that this would favor social learning capacity.⁹⁴ Second, bipedal hominins evolved exceptional manual dexterity because their hands were freed from locomotory constraints, and they could carry tools with little cost. This would have favored increased tool using and making behavior and probably increased selection pressure on imitative capacities as well.

Third, by at least 2 million years ago, hominins had begun to depend on high-quality, widely dispersed resources that were difficult to obtain. This shift of feeding niche had important life-history implications.⁹⁵ Juveniles could not fully feed themselves due to the complexity of the extractive niche, and this led to their provisioning by close kin. As large-package foods became common, the foods returned to the juvenile home base were probably “shared” by co-residents. This pattern would have provisioned children, but also allowed temporarily sick or injured adults to obtain food until recovery. Such a pattern, similar to that reported for other social carnivores, such as wild dogs,⁹⁶ might partially explain why hunter-gatherers experience early adult mortality at one-fifth the rate of wild chimpanzees,¹⁶ That pattern would favor a life history with later age at maturity and delayed onset of senescence.

COOPERATIVE BREEDING

Cooperative breeding is a pattern in which individuals other than genetic parents engage in behaviors that increase juvenile survival and/or the fertility and survival of reproductive adults. Anthropologists have borrowed terms such as “helpers-at-the-nest” to describe those who provision juveniles or each other’s families when constrained by infants. Ethnographic observation in hunter-gatherers suggests that our species was organized into extended-kin-group resource acquisition and consumption units that engaged in cooperative breeding.^{95,97,98} Recently, a full appreciation of the implications of cooperative breeding has tied this pattern to the evolution of prosocial

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behaviors and emotions, as well as many features of human life history.^{98,99} Empirical studies of cooperative breeding in humans have employed three methodologies: analyses of provisioning and food flows between individuals and families¹⁰⁰; statistical detection of kin impact on fitness components;^{91,101} and behavioral observation of allomaternal caretaking.⁵⁰ Although we pioneered the second method,⁹¹ we recognize that it has the greatest likelihood of incorrectly assessing the value of specific kin help. Regressions of child survival on the survival of specified kin during the same time period may produce false positives due to phenotypic correlation and false negatives due to substitutability of help and indirect pathways of impact.¹⁰² This means that all three methods should compliment each other for a full understanding of helping behavior in

human societies. Here we focus mainly on food provisioning.

Because energy harvest rates and the costs of accumulating dependent offspring do not follow the same age curve in hunter-gatherers,^{103,104} breeding pairs in human societies can expect to be net food producers at some ages and net consumers at other ages (Fig. 5). Most importantly, those who provide food to families in need during one period may not receive shares back from the same families when they later become net energy producers. Instead, conformity to food-sharing norms of “generalized reciprocity” within kin groups or residential bands frequently result in “need-based” food sharing with those having many dependents.¹⁰⁵

Data on net food production and transfers among the Ache hunter-gatherers of Paraguay and the Hiwi of Venezuela are instructive. Hill and Hurtado⁹⁸ showed in spot samples that ~30% of women and ~45% of men in these societies had no dependent offspring at any point in time. Nevertheless, adults often intentionally acquired more food than they consumed. The surplus was distributed according to the food-sharing conventions of each group. This resulted in approximately 1.3–1.4 adult “helpers” per breeding pair in each group. In the middle reproductive years, demographic and food production parameters imply that average families must be substantially dependent on outside provisioning to survive. This expectation was verified with data on actual families showing that more than half of the nuclear families in which the wife’s age was between 30 to 45 years experienced long-term net daily energy deficits in production.⁹⁸

Although some models have emphasized matrikin as the cooperative breeding unit in humans,¹⁰⁶ research on the Ache and Hiwi indicates that males are more important as provisioners, while grandmothers provide other types of support. Indeed, postreproductive Ache and Hiwi women contributed very little to meeting the food deficits of high-dependency families because older women were a small fraction of the population and not very productive relative to younger men.



Figure 5. Two Hiwi extended families with contrasting juvenile dependency loads. a) The first patrilocal extended family has an excess of adult male producers and acquired surplus food throughout our monitoring period in the 1980s. b) The second mixed-kin family experienced a net deficit of caloric production over several observation years. Extensive food flows within and between extended families regulated by sharing norms allow hunter-gatherers to feed families with high dependency loads during periods of life history in which more dependent children are being raised than can be fed by genetic parents. (Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.)

Whether these results are typical of other foraging societies and periods in hominin history remains an open question. But, contrary to popular views, we note that vertebrate prey makes up the most food energy and virtually all of the protein lipid in most modern foraging societies that have been well studied.^{95,107} Everything from archeological assemblages¹⁰⁸ to high-latitude colonization¹⁰⁹ to isotopic studies¹¹⁰ and tapeworm genetics¹¹¹ suggests that hominins were highly dependent on meat for a long time. In both our study populations, meat was the most important component of the diet (78% for Ache, 80% for Hiwi⁹⁵); young and unmarried men were the main surplus food providers, contributing 93–100% of the deficit for middle-aged families; and the numerical importance of male helpers was augmented by male-biased adult sex ratios due to infanticide and neglect.^{91,112}

The Ache and Hiwi data suggest that nuclear families in hunter-gatherer societies are not capable of producing sufficient resources to sustain typical fertility and child survivorship rates through the entire life span (Fig. 6). Instead, all breeding pairs experience runs of bad luck, ill health, and an unsupportable offspring dependency load in mid-life that is covered by food transfers from other adults.⁹⁸ Because resour-

ces are actively transported back for needy families and often saved preferentially for them when they are absent, long-term provisioning probably is not explained by “tolerated theft” or costly signaling.¹¹³ Instead, kin-biased group composition, pay-to-stay arrangements,¹¹⁴ benefits of group augmentation,⁹⁷ indirect reciprocity,¹¹³ between-group competition,⁶⁷ and cultural group selection^{42,43} may be required to explain generalized reciprocity within residential bands.

COOPERATIVE BREEDING AND LIFE-HISTORY COEVOLUTION

Many derived features of human life history coevolved with a cooperative socioeconomic system. Hunter-gatherer children are born helpless. They undergo a long period of brain growth and slow body growth that is associated with almost total dependency until they reach full adult body size. The adolescent growth spurt must be subsidized by helpers, since there is no sudden increase in the productive ability of juveniles or their parents during teen years.⁹⁵ Fertile females are able to invest more per unit time in reproduction because they are resource subsidized. These subsidies allow women to raise multiple juvenile offspring through long periods of overlapping dependency and obligatory parental

investment. Finally, the low adult mortality and long life span in humans allows for a postreproductive cohort that assists reproduction of the next generation.

In hunter-gatherer societies, female fertility is compressed in length, but amplified in height when scaled to our life span and compared to other apes. Hunter-gatherer women typically achieve early adult fertility rates of approximately 0.3 offspring per year, whereas ape fertility typically peaks around 0.2 offspring per year.⁹⁵ Wild chimpanzees show interbirth intervals after surviving offspring that are nearly twice as long (~70 months¹¹⁵), as typical hunter-gatherer interbirth intervals.⁹¹ However, despite higher initial fertility, human females begin a period of steep fertility decline sooner than chimpanzees do and well before the onset of significant senescence in other body functions.⁹¹ For example, healthy chimpanzee females maintain at least 50% of their maximum fertility rate for about 30 years.¹¹⁵ Whereas healthy Ju/hoansi and Ache women maintain fertility at 50% of their maximum rate for only about 20–25 years.⁹¹

Even though their fertility decline leads to hormonally mediated sterility (menopause), women continue to live for decades, engaging in indirect reproduction by helping their children and grandchildren to survive and reproduce.¹⁰¹ While such kin helping may be sufficient to explain

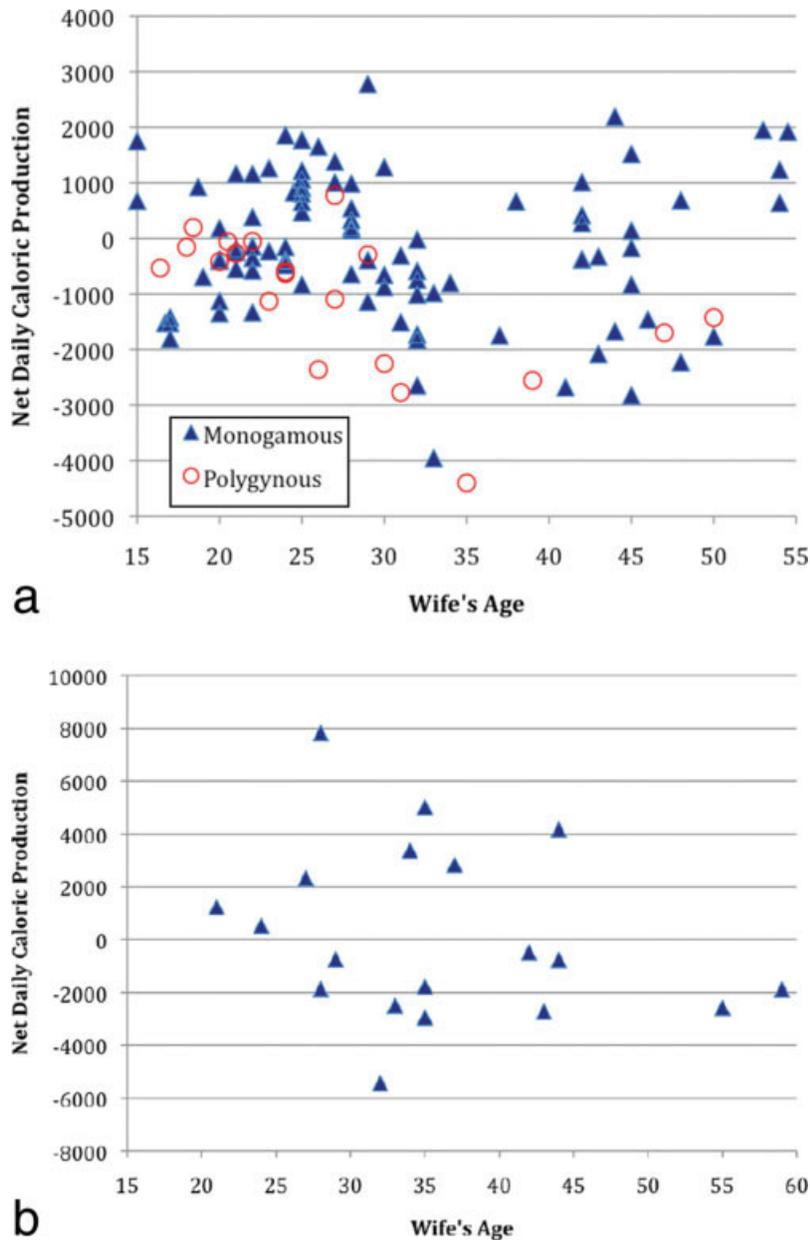


Figure 6. Net energetic production a) by age of all Ache nuclear families (triangles, monogamous; circles, polygynous) alive in 1970 (precontact) based on measured age-specific consumption and production (postcontact), and of all b) Hiwi nuclear families by age during one two-year observation period when all were completely dependent on foraging. Cooperative breeding is indicated because a fraction of families in both societies, mainly late middle age, were observed to require long-term energetic supplementation in order to raise their dependent offspring. (See Hill and Hurtado⁹⁸). (Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.)

the postreproductive life span in females,¹⁰⁶ the levels of genetic contribution by postreproductive women do not appear to be high enough to offset fitness losses due to fertility termination.^{91,116} Since increased reproductive span should have evolved with increased life span as it does in most organisms, no evolu-

tionary model supported by data currently explains menopause. One possibility, consistent with the Ache and Hiwi data we have summarized, is that menopause is favored because of the investment patterns of male helpers. Perhaps sons, who will be equally related to their own offspring or siblings, prefer to provision

younger females (wives) of high intrinsic fertility rather than older females (mothers) whose reproductive machinery has declined in efficiency due to senescence.¹¹⁷ This pattern would be further amplified if women receive subsidies from potential lovers. As a woman loses male provisioning, her reproductive output may drop low enough to favor termination of continued investment in her reproductive function. Hill and Hurtado⁹¹ have shown that a drop to one-sixth of peak fertility would favor menopause in Ache women if it diverted energy from their own reproduction to the statistically measured impact on the survival of grandchildren. Thus, menopause may be an adaptation to provisioning patterns and subsequently result in further provisioning (by postreproductives).

Implications of Cooperative Breeding

Hrdy⁹⁹ recognizes cooperative breeding as a critical trait in human evolution that can account for prosocial emotions and some life-history traits. Here we elaborate. Studies show that cooperative breeding species often develop task specialization, effective communication, amplified prosocial behavior, and facilitation of social learning. For example, cooperatively breeding callitrichids prefer to provision others as well as themselves in controlled experiments.¹¹⁸ Many cooperative breeders show incipient social norms, such as regulations about who can breed and what types of helping are required, which are backed by punishment from both breeders^{114,119} and nonbreeders.¹²⁰ Deceptive false-helping behavior probably indicates norm enforcement in other species.^{121,122} Active demonstration of behavior by altruistic models (teaching) is also mainly limited to cooperative breeding species.^{39,123}

Finally, cooperative breeding results in social clustering of individuals with a strong impetus to read each others' intentions to coordinate effectively in reaching shared goals. This may provide the "communicative intentions" necessary for the evolution of language. Not surprisingly, some species, such as honeybees,

known for their complex communication, are also cooperative breeders.

Thus, we suggest that cooperative breeding may explain the large gap in “shared intentionality”¹²⁴ and exceptional cooperative, but not competitive, social intelligence that distinguishes human and chimpanzee cognitive abilities.⁸⁷ Most importantly, these cognitive traits may provide an important cue as to why humans alone have cumulative cultural capacity. Apes have notable social learning skills, but they often view behavioral models as potential competitors rather than helpers, and try to deceive or manipulate them. Humans, on the other hand, imitate while presuming that the model intends to help them rather than to compete. This may explain why human children precisely imitate rather than simply emulate to reach a goal.³³ Children often assume that a “teacher” has their best interest at heart and intentionally demonstrates useful behavior. This may also explain why children readily imitate newly introduced behaviors despite already having learned other solutions to a problem, whereas chimpanzees do not.³⁴

BEHAVIORAL MODERNITY AND HUMAN UNIQUENESS

The perspective on human uniqueness discussed here may shed new light on the evolutionary dynamics of what is often termed behavioral modernity.^{125,126} Here we discuss evidence from the paleoanthropological record concerning emergence of the capacity for cumulative culture, creation of social norms, ethnicity, and extensive cooperation between nonkin facilitated by prosocial emotions, along with life-history shifts such as long juvenile period and long life span. This information is then used to present a hypothetical sequence of adaptation that may help organize future research.

Life History and Cooperative Breeding

Dental development and brain growth patterns increasingly suggest

that early *Homo* exhibited a life history closer to the faster juvenile growth of apes than to the slower growth rates of modern humans.^{127,128} If that is correct, the fast life history of early *Homo* implies that food sharing and care of debilitated individuals in the early Pleistocene were not sufficient to buffer periods of injury and illness that would have lowered adult mortality and extended the juvenile period to modern human levels. Available data may imply, however, that a human-like life history had emerged by the Middle Pleistocene if slow juvenile growth is shared by both Neanderthals and early *Homo sapiens*.^{128,129}

Provisioning of juveniles and slow life history is more likely in the context of home-base camps where food is shared among camp occupants.

However, some evidence suggests that Neanderthals did not have a slow life history like humans,¹³⁰ so the timing of life-history change remains uncertain. In any case, all interpretations of currently available data imply that emergence of a slow life history took place well after the shift to a hunted and extractive diet. This is indicated by gut size reduction,¹³¹ flake-tool use, and taphonomic assemblages.¹⁰³

Provisioning of juveniles and slow life history is more likely in the context of home-base camps where food is shared among camp occupants. In this light, Potts¹³² has argued that lithic accumulations once considered to be home bases for early *Homo* were most likely stone stockpiles used during the transportation of resources from the acquisition site to a consumption site. Not until the beginning of the Middle Pleistocene is it probable that accumulations of artifacts and animal bones in cave and shelter

locales,¹³³ as well as evidence of hearths with animal and plant food consumption, tool making, and other activities,¹³⁴ indicate residential camps to which humans repeatedly returned to share food and other resources.

Paleoanthropological data may eventually indicate the beginnings of provisioning of disabled adults as well, which is critical for the evolution of long life spans and the emergence of a postreproductive phase. Currently, however, the evidence for adult provisioning in the Early Pleistocene is unconvincing.¹³⁵ The large Middle Pleistocene Atapuerca assemblage appears strongly dominated by young individuals, with the likelihood that no postreproductives are represented.¹³⁶ There are more convincing suggestions of provisioning of the sedentary disabled and elderly by the initial Late Pleistocene. Of note is the Shanidar I individual, who had severe injuries that had healed,¹³⁷ perhaps indicating that some elderly individuals cared for juveniles and were provisioned by others who foraged.

Cumulative Culture and Nonkin Cooperation

Cumulative cultural capacity is indicated by traits that require multiple innovative steps and cannot feasibly be acquired through individual learning in a single generation. By these criteria, incipient cumulative cultural ability may have been present around the time that hominins occupied temperate latitudes.^{109,138} Even during interglacials, biologically subtropical humans would have needed fire and some kind of body coverings for survival, suggesting reliance on semi-complex socially transmitted innovations.¹³⁹ On the other hand, the monotony of Middle Pleistocene stone technology displays little cumulative cultural innovation for much of this period. An east-west division recognized in Early and Middle Pleistocene lithic industries, with bifaces common across much of Africa, India, and Western Eurasia, but rare elsewhere,¹⁴⁰ persisted for hundreds of millennia. Moreover,

morphological differences among Middle Pleistocene bifaces seem more attributable to lithic raw material and artifact life histories than protocultural traditions.¹⁴¹

Evidence of significant cumulative social transmission is more convincing in both Africa and Europe by the initial Late Pleistocene or slightly earlier.¹⁴² By that time, different technological traditions had emerged across limited geographical space. In Africa, these include distinctive changes in technological complexes, as at Still Bay to Howieson Port,^{143,144} that span at the scale of millennia or even less. Elsewhere, geographic differentiation in lithic technology industries includes the well-known Levallois Mousterian, Szeletian central European industries, and the North African Aterian.^{145,146} Most importantly, if Châtelperronian or some other post-Mousterian industry is a product of Neanderthals,¹²⁵ this implies that the cognitive machinery required to produce cumulative culture must have evolved before the human-Neanderthal split.

Ethnic signaling, indicating social norms and intergroup competition or segregation, is a ubiquitous feature of modern *Homo sapiens*, with group membership often signaled by personal adornment. The earliest potential evidence of ethnic signaling may be ground ochre and manganese dioxides found in sites from Europe, Africa, and India during the late Middle Pleistocene,^{147,148} although these materials also may have served other functions.^{148,149} Perforated shell beads are more direct markers of personal adornment, and appear considerably later than do pigments, in the early Upper Pleistocene at some South African and Near Eastern sites and by the mid-Late Pleistocene in Europe.^{125,150}

Cooperation between nonkin is probably indicated by large residential group size, and material sources transported over large distances. The transition to larger social groupings is clearly evident by OIS 3, including a shift toward central place foraging and increasingly distant resource forays among all hominins of western Eurasia at least.^{151,152}

A TEMPORAL SEQUENCE

In this paper we have suggested that cumulative cultural capacity and mechanisms that promote cooperation between nonkin are keys to the spectacular biological success of *Homo sapiens*. Here we present a possible chronological sequence of related adaptations that form a set of working hypotheses for future research:

A. Bipedality led to manipulative dexterity, low-cost transport, and larger home range. These traits favored more extensive tool use and greater selection for social learning capacities.

The transition to larger social groupings is clearly evident by OIS 3, including a shift toward central place foraging and increasingly distant resource forays among all hominins of western Eurasia at least.

Oldowan tools indicate abilities not present in other apes. Amplified home range was a critical preadaptation for the subsequent dietary shift to widely dispersed but nutrient-dense resources.

B. Dietary shift to a hunted and extracted diet created juvenile dependence on adult provisioning. This promoted kin-based cooperative breeding along with evolution of early prosocial emotions, enhanced theory of mind, shared intentionality, and more complex communication that facilitated task specialization and integration of the shared goals of cooperative breeders. The emergence of a home-base economic system allowed adults debilitated by illness and injury to recover, favoring later senescence and later sexual maturity.

C. Imitative capacity and shared intentionality interacted to produce cumulative cultural capacity. This relied on a pedagogical mode of interaction in which imitators pre-

sumed that models were motivated to help rather than compete with them. The emergence of cumulative culture was a slow process because high-fidelity social learning can only be strongly favored when there are already useful cultural traits to be copied. In order for cultural accumulation to take place, there must be a large population, frequent and close interaction between models and imitators, and long time periods to allow rare innovations to arise, spread, and stabilize without being lost through stochastic processes.

D. Cumulative cultural capacity and prosocial emotions led to language, social norms, ethnicity, and extensive nonkin cooperation. This allowed the emergence of social norms regulating mate exchange between kin groups and promoted intergroup peaceful interaction due to cross-cutting genetic interests, as well as the emergence of gifting and trading. Because of the increase in effective interacting group size, with members of multiple residential or social units becoming models for imitation, cultural accumulation sped up enormously. Cultural group selection became an important force in human history. Increased cooperative proclivities and reliance on social learning continued to coevolve to produce a uniquely cultural and cooperative species.

CONCLUSION

The last Interglacial/Glacial cycle was a critical period for the spread of uniquely human cultural components of cooperation. At the beginning of the Late Pleistocene, the archeological record paints a picture of most hominins living in small and widely dispersed social groups, with incipient or no ethnic and symbolic display, and still slowly changing artifact assemblages. At the end of this period, there is evidence of periodic large group size, intense and diverse personal adornment, representational and geometric art, and diverse, rapidly changing artifact assemblages. These uniquely human characteristics are observed within the single species *Homo sapiens* throughout the world by the end of the Pleistocene.¹⁵³

Humans of the late Pleistocene already represented an anomaly and had evolved the traits that would lead to dramatic biological success. They progressively achieved dominance on the planet through cultural adaptation and cooperation. Human ultrasociality has continued to expand, promoted by culturally transmitted institutions that regulate cooperation and competition. The signaling of adherence to specific social norms through ritual and ethnicity has provided the spice of modern cultural diversity. Most importantly, the coevolution of cultural capacity and nonkin cooperation have repeatedly created new physical, technological, and social environments for subsequent evolution. Thus, the evolution of human uniqueness did not cease with the global spread of anatomically modern humans but continued throughout the Pleistocene, into the Holocene, and in the present, with consequences for the earth's biota that we noted at the beginning of this essay.

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