What Makes Us Human? Answers from Evolutionary Anthropology

JAMES M. CALCAGNO AND AGUSTÍN FUENTES

With contributions by: Matt Cartmill, Kaye Brown, Katherine S. Pollard, Robert Sussman, Robert M. Seyfarth, Dorothy L. Cheney, Benjamin Campbell, Sarah Hrdy, Kristen Hawkes, Karen R. Rosenberg, Mary C. Stiner, Steven L. Kuhn, and Ken Weiss

Today, scholars from numerous and highly diverse fields are not only addressing the question of what makes us human, but also seeking input from other disciplines to inform their answers to this fundamental issue. However, for the most part, evolutionary anthropologists are not particularly prominent in this discussion, or at least not acknowledged to be. Why is this the case? One reason may be that although evolutionary anthropologists are uniquely positioned to provide valuable insight on this subject, the responses from any one of us are likely to be as different as the research specializations and intellectual experiences that we bring to the table. Indeed, one would anticipate that a paleoanthropologist would not only have different views than a primatologist, geneticist, or behavioral ecologist, but from other paleoanthropologists as well. Yet if asked by a theologian, psychologist, or political scientist, and perhaps most importantly, by any curious person outside the walls of academia, do we have a response that most evolutionary anthropologists could agree on as reflecting our contributions to the understanding of being and becoming human? Our introductory textbooks usually begin with this fundamental question, yet seldom produce a concise answer.

James M. Calcagno is Professor of Anthropology and Fellowship Office Director at Loyola University Chicago. His research interests in biological anthropology have ranged from mechanisms of dental reduction to captive primate behavior. In 2009 and 2011, he co-organized Wiley-Blackwell AAPA symposia directly relating to the question "What Makes Us Human?"
Email: jcalcag@luc.edu
Agustín Fuentes is Professor of Anthropology at University of Notre Dame. His current research includes cooperation and community in human evolution, ethnoprimatology and multispecies anthropology, evolutionary theory, and interdisciplinary approaches to human nature(s). Recent books include *Evolution of Human Behavior Biological Anthropology: Concepts and Connections*, and *Race, Monogamy, and Other Lies They Told You: Busting Myths About Human Nature*.
Email: afuentes@nd.edu

In this series of brief essays, we attempt to provide insight into the possibility of a coherent evolutionary anthropological answer to what makes us human. We recognize that this simple, basic question is actually tremendously complex. Yet if we continue to tout in our classrooms the importance of evolutionary anthropology in understanding humanity, it seems unwise to avoid direct attempts to answer the question of such great interest outside our discipline. Our individual research efforts are, by necessity, more narrowly focused, and may contribute a piece of insight toward the question but not answer it. We propose that evolutionary anthropologists should step outside our normative practice to take on this broad and societally relevant question. This forum is a start.

We have assembled 13 distinguished evolutionary anthropologists bold enough to respond to the question of what makes us human. Individual perspectives include archaeology, behavioral ecology, human genetics, neuroanthropology, paleoanthropology, and primatology. No instructions were provided other than to answer the question in 800 words or less. In addition, no one else knew who the other contributors were, to avoid any temptation to respond in ways that might anticipate another author's comments. Thus, individual essays were not expected to conform to others' views in any way and were written entirely independently of each other. Given that conflicting views were not only expected, but indeed welcomed, we conclude with our own commentary distilling any common ground reached in the 10 essays that follow. *A priori* we reserved the right to regard some specific points as better than others.

Although depth and breadth are laudable and needed when discussing any complex subject, we seek to produce a brief answer that almost everyone in the field could agree on as hitting key points, and from which curious outsiders to the field could easily consume and benefit. This may be an impossible task. If so, perhaps greater attention is needed regarding the effectiveness of our discipline in connecting with a much larger audience. We hope that you will read these essays with an open mind. We are interested to see whether or not you agree with our conclusions.

Being Human Means that "Being Human" Means Whatever We Say it Means

MATT CARTMILL AND KAYE BROWN

What makes us human? This question can be read in several ways. It might be an empirical question about what distinguishes humans, like "How do you know this is an emu?" This one is easy. We all know how to identify humans: (1) upright bipeds with (2) nimble hands, (3) big brains, (4) short faces, (5) weird pelage, (6) protruding fat depots, and so on. We like to stress traits 1–3 because we associate them with having power over nature, but the others would be equally useful in keying out a specimen.

We believe a different question is being asked in this symposium — namely, "Which of our peculiarities give humanity its unique importance and significance?" This question is not empirical. Since humans decide what words mean, we can draw the animal-human boundary as we wish, give it any meaning we wish, and change both whenever we like.

The meaning, markers, and justification of human status have fluctuated throughout Western history. Language has generally been viewed as a crucial marker — so crucial that linguists change their definitions of language whenever rudimentary linguistic capacities are discovered among nonhumans. Lately, conceptions of the defining human excellence

have been shifting toward our "prosociality." Psychologists now tell us that humans are innately disposed to sacrifice themselves to help others, and apes are not. In recent literature, this supposed human peculiarity has been predicated of everything from allomothering to projectile weapons, and hailed as the foundation of language, social norms, and morality. But this ignores 50 years of sociological research that indicates that it takes socialization — of the right kind — to overcome the innate selfishness of children. That contradiction needs to be addressed. The experiments supporting the prosociality idea also need more comparative depth. Many supposedly innate human traits proclaimed by experimenters have turned out to be peculiar to Western elites.

Two genuinely pan-human traits may explain many of the phenomena currently attributed to innate human prosociality. The first is our unique propensity for imitation. Humans are the only terrestrial mammals that imitate sounds, and the only animal that imitates the things we see. Language, art, dance, and every aspect of human socialization depend on this propensity. We suggest that preverbal imitation, beginning with mother-infant pairs, is the foundation of all social learning in humans. Cultural homogeneity arises first from imitation, not from some innate, prosocial tendency to internalize norms and values. Social norms and values are inculcated mainly through language, which requires the faculty of imitation. Therefore, we believe that imitation must precede normative behavior in ontogeny — and, we suggest, in hominin phylogeny as well.

The second is the human capacity for seeing things from the other fellow's perspective. Humans are so strongly disposed to understand the motivations of others that we are always seeing motivations where they do not exist. Although this disposition encourages anthropomorphism and

superstition, it gives us adaptively valuable insight into the intentions of our friends, enemies, predators, and prey. Both sadism and compassion are grounded in this faculty of projection. People may be the only animals that find it rewarding to share with and help their own and other species; but they are also the only animals that find it rewarding to inflict gratuitous pain. Being human means that as well.

Our capacity for projection may have direct neural correlates, but it also depends on language. Dunbar[1] argues that while many animals have "first-order intentionality" (reading their own thoughts) and a few have second-order intentionality ("theory of mind"), human brain structures allow us to achieve sixth-order intentionality in exceptional individuals, such as Shakespeare. Dunbar would have us think that in writing *Othello*, Shakespeare intended his audience to understand that Iago wants Othello to believe that Desdemona knows Cassio loves her. This, Dunbar says, is sixth-order intentionality, beyond which the human mind cannot go. We doubt this, because we went one level further two sentences back and could go further still. This sort of nested "intentionality" appears to us to be a byproduct of syntax (sentence embedding), not neocortex volume.

Some argue that humans are objectively important because of our huge biomass and ecological impact. However, these are not properties of our species, but of the co-evolving agricultural symbiosis of which *Homo sapiens* is the CEO and chief personnel officer. Without our domesticates and their huge biomass, *Homo* would still be a rare predatory primate. All we can boast of uniquely is that we are the ones who have to make the decisions that will preserve this symbiosis or bring it crashing down — and us along with it.

REFERENCE

1 Dunbar RIM. 2007. The social brain hypothesis and its relevance to social psychology. In: Forgas JP, Haselton MG, von Hippel W, editors. Evolution and the social mind. New York: Psychology Press. pp. 21–32.

Matt Cartmill's writings and ongoing research deal with primate origins and phylogeny, comparative cranial anatomy and evolution, systematics, locomotion, the history and philosophy of science, and the biological correlates of language, morality, and consciousness. His most recent book is *The Human Lineage* (with Fred H. Smith). He currently serves on the faculty of Boston University and the emeritus faculty of Duke University. Email: cartmill@bu.edu
Kaye Brown developed and administers the *BU Dialogues in Biological Anthropology*, a filmed conference that spotlights current debates in the field. She writes on topics in architectural gerontology, social movements, and physical anthropology, and annually develops the national student design competition for long-term care administered by AIAS. She serves currently on the faculty of Boston University. Email: kaybrown@bu.edu

The Genetics of Humanness

KATHERINE S. POLLARD

What makes us unique as a species? From a genetic perspective, the answer is "Not very much." Sequencing of the human and chimpanzee genomes allowed us to line up our DNA against that of our closest living relative on the tree of life and take stock. We found that the human and chimp genomes are nearly 99% identical and that each changed about the same amount since our common ancestor.[1] To put this difference in perspective, a mouse and a rat differ at about 17 out of every 100 bases.[2] Humans are not especially fast evolving. Instead, it appears that a few key changes in the right DNA sequences had big effects, modifying traits such as bone morphology, dietary repertoire, and disease susceptibility, all of which distinguish humans as a species. So where are these high impact mutations?

Because proteins are so important for cellular functions and the genes that encode them make up only a few percent of our genome, a logical guess is that human-specific mutations are clustered in our genes. Interestingly, this is not the case. A third of our proteins are perfectly identical to the chimp version, and the rate of DNA differences in genes is about half of the genome average. There are genes, especially in the immune, digestive, and reproductive systems, with mutations that likely contributed to uniquely human functions. However, these genes explain only a small part of what makes us human.

In contrast, there is mounting evidence that mutations in gene regulatory sequences affecting when our proteins are expressed play a major role in human-specific biology, as hypothesized several decades ago.[3] Studies in a variety of different organisms support the importance of regulatory mutations in the evolution of closely related species.[4] Similarly, many of the fastest evolving sequences in the human genome are outside of genes in regulatory DNA.[5] These uniquely human regulatory sequences, called Human Accelerated Regions (HARs), are located near and likely control a very important collection of genes, many of which are involved in development and human disease. Because many of the genes with HARs are transcription factors that control the expression of other genes,[5] it is easy to see how a relatively small number of mutations in regulatory sequences could alter the function of an entire network of genes and thereby influence a trait, such as pelvic morphology or brain size.

But individual mutated bases of DNA are not the whole story. During evolution, stretches of DNA can be copied, deleted, or rearranged in a species' genome. These structural variations can lead to destruction or change in the functions of the genes and regulatory sequences they contain. The consequences are often detrimental, but occasionally beneficial. For example, the loss of olfactory receptors in humans has been linked to adaptive changes in our sense of smell and bitter taste perception, suggesting that humans are in some ways degenerate apes. Uniquely human structural variations comprise several times more bases of our genome than do human-specific single-base mutations. These dynamic regions likely harbor much of what makes us genetically human.

As novel technologies enable us to study a wider range of molecular data, geneticists will be digging even deeper for what makes us human. Sequencing hundreds of living and extinct human genomes will help to pinpoint the genetic changes that make us modern humans, in contrast to those that distinguish hominins as a group from chimps and other primates. Another new direction involves studying epigenetic changes, including losses or gains of chemical marks on the genome and the associated proteins that affect gene expression without altering the DNA sequence itself.[6] Further expanding the concept of the genome, studies of human evolution may soon include analyses of DNA from all the microorganisms that live in and on our bodies. It will be interesting to see if any of these broader definitions alter the current view that, genetically, humans are not especially unique as a species.

Katherine Pollard is at the Gladstone Institutes, Institute for Human Genetics, and Division of Biostatistics at the University of California San Francisco. Dr. Pollard's lab develops statistical and computational methods for the analysis of genomic datasets. Her research focuses on genome evolution, particularly on identifying DNA sequences that differ significantly between or within species and their relationship to biomedical traits. Many of these sequences encode regulatory signals, structural sites, and RNA genes.
Email: kpollard@gladstone.ucsf.edu

REFERENCES

1 The Chimpanzee Sequencing and Analysis Consortium. 2005. Initial sequence of the chimpanzee genome and comparison with the human genome. Nature 437:69–87.

2 Rat Genome Sequencing Project Consortium. 2004. Genome sequence of the Brown Norway rat yields insights into mammalian evolution. Nature 428:493–521.

3 King MC, Wilson AC. 1975. Evolution at two levels in humans and chimpanzees. Science 188:107–116.

4 Prud'homme BP, Gompel N, Carroll SB. 2007. Emerging principles of regulatory evolution. Proc Natl Acad Sci USA 104:8605–8612.

5 Pollard KS, Salama SR, King B, et al. 2006. Forces shaping the fastest evolving regions in the human genome. PLoS Genet 2(10):e168.

6 Cain CE, Blekhman R, Marioni JC, et al. 2011. Gene expression differences among primates are associated with changes in a histone epigenetic modification. Genetics 187:1225–1234.

Why We Are Not Chimpanzees?

ROBERT SUSSMAN

What makes us human? We all would agree that chimpanzees differ from gorillas, both in their anatomy and their behavior. They have different behavioral repertoires, different ethograms. Just as chimpanzees differ in their nature from gorillas, so too do they differ from humans. In this light, humans have different natures from both chimpanzees and gorillas. Each of these "higher primates" has a unique nature.

In attempting to describe what makes us human, it is necessary to compare humans with nonhuman primates. Some comparisons of this sort are quite simple. Chimpanzees are knuckle-walkers, humans are bipedal; chimpanzees instinctively build nests, humans do not; chimpanzees are adept at locomoting in trees, humans are not. Other aspects of human and chimpanzee natures relate to differences in how the brain functions. These differences are more difficult to compare.

We don't understand how differences in the brains of chimpanzees and humans relate to complex behavioral differences. However, we do know there are profound behavioral differences; the structure and function of their brains differ. Each is unique, and this leads to unique behaviors. Chimpanzees and humans are "playing different games." Say, chimpanzees are playing checkers and humans are playing chess. Each has a different behavioral repertoire, a different set of rules. Given the rules of the game within which each species can operate, it can only make certain moves, perform certain behaviors; it has a unique ethogram.

Robert W. Sussman is Professor of Anthropology at Washington University in St. Louis. His recent books include *Man the Hunted* (with Donna Hart) and *Origins of Altruism and Cooperation* (edited with C. Robert Cloninger). He is past Editor of American Anthropologist and the Yearbook of Physical Anthropology, and Secretary of the Anthropology Section, A.A.A.S.
Email: rwsussma@artsci.wustl.edu

The totipotentiality of behaviors for each species differs. Although there might be some overlap in the behaviors of chimpanzees and humans, the total potential of their behavioral repertoire is different. They have different natures.

Can we operationalize these differences? Can we measure the different behavioral repertoires of different species? Can we describe and compare their different potentials? Each population of a species should have the potential to perform the total repertoire of the species, but the distribution of behaviors of any population might display only a statistical representation of the total repertoire. We should be able to compare the behavioral totipotentiality of different species and compare the repertoire of different populations within the same species. We must be careful in making our comparative ethograms, however, because similar behaviors might be different, depending on context, history, and such.

Back to the question of what makes us human: we can compare the behavioral totipotentiality of humans and chimpanzees. I believe there are three human behavioral traits not found in chimps or any other animal; they are unique and exemplify what it means to be human: symbolic behavior, language, and culture. Symbolic behavior is the ability to create alternative worlds, to ponder about the past and future, to imagine things that don't exist. Language is the unique communicative venue that enables humans to communicate not only in proximate contexts, but also about the past, the future, and things distant and imagined, allowing us to share and pass our symbols to future generations. Culture is the ability found only in humans for different populations to create their own shared symbolic worlds and pass them on. Although chimpanzees can pass on learned behavior, they cannot pass on shared and different world views.

The differences between chimpanzee populations across Africa are trivial compared to the differences between human populations, and these differences can be quantitatively compared. For example, chimpanzee kinship systems are essentially the same in all populations, whereas those of humans vary tremendously. In chimpanzees, kinship directly relates to familiarity, proximity, and direct day-to-day, relatively short-term interactions. Human kinship is a created symbolic system not restrained by time or place, living or dead, or necessarily by any biological relationships, and is extremely variable across Africa. It is the product of symbolism, language, and culture, the things that make us human.

How would we study the totipotentiality of human nature? By using paleontology, archaeology, history, and ethnography, we can try to outline the totipotentiality of human behavior through time and among living human cultures. All of these things are part of human nature; they are biologically and genetically possible. To say, for example, that humans are by nature aggressive is true but trivial; they are also by nature cooperative. We need to compare the distributions of behaviors within and between each culture or subculture, then to quantify and compare the distribution of behaviors. For example, we might find that homicide occurs in all cultures. However, we might also find that the norm, statistically, is that the homicide rate is always exceedingly low as compared to the rate of cooperative or altruistic behaviors. We would also find that homicide rates vary between and among cultures. Is this variation genetic or culturally determined? Homicidal behavior is part of human nature, but this is not useful in explaining homicide rates, which are culturally determined. Culture is the unique part of human nature; homicide is not.

Cognition, Communication, and Language

ROBERT M. SEYFARTH AND DOROTHY L. CHENEY

Although fully evolved language provides the most striking difference between modern human and nonhuman primates, in the domain of communication and cognition, two simpler, more basic features, both necessary precursors of language, are what make humans unique. Nonhuman primates have sophisticated perceptual systems almost identical to ours, but only a limited ability to represent one feature of their environment that they cannot see: the mental states of another. This skill is not completely absent: like very young children, monkeys and apes can recognize another individual's motives and, as a result, anticipate what that individual is likely to do next.[1,2] They can also engage in simple forms of shared attention and social referencing.[3] However, monkeys and apes appear unable to recognize what another individual knows. They also cannot perceive when another individual holds a false belief.

Monkeys' and apes' knowledge of their own thoughts is similarly limited. They seem incapable of the sort of "what if" introspection that allows deliberate planning and the weighing of alternative strategies. In contrast, one-year-old children are not only aware of their thoughts but highly

Robert Seyfarth and Dorothy Cheney are, respectively, Professor of Biology and Psychology at the University of Pennsylvania. For 11 years, they conducted field research on the social behavior and communication of vervet monkeys in Kenya, resulting in the publication of *How Monkeys See the World* (1990, University of Chicago Press). Between 1992 and 2008, they directed a field study of social behavior, communication, and cognition among baboons in the Okavango Delta of Botswana, resulting in the publication of *Baboon Metaphysics* (2007, University of Chicago Press). Email: seyfarth@psych.upenn.edu, cheney@sas.upenn.edu

motivated to share them with others. The lack of these traits — the lack of a fully developed "theory of mind" and the motivation to share information with others — distinguishes nonhuman primates from humans.

But there is another, even more basic difference in communication that sets monkeys and apes apart from us. In monkeys and apes, vocal production is highly constrained. Compared with humans, but like most other mammals, nonhuman primates have a relatively small repertoire of calls, each of which is used in a restricted set of social contexts. The acoustic features of calls are largely genetically fixed, with only limited modification during development. Differences from human speech — acoustically flexible, learned, and highly modifiable — are obvious.[4,5]

Monkeys and apes overcome some of these limitations with a rich sense of what linguists call pragmatics: they have an almost open-ended ability to learn sound-meaning pairs, recognize individual voices, and combine information about individuals' social positions, past interactions, and current motives when assessing the meaning of vocalizations. In their interpretation of the meaning of vocalizations, listeners combine discrete-valued entities in a structured, rule-governed, and open-ended manner.[6] Their discrete, compositional perception has interesting parallels with language; their restricted production has none.

The striking difference between production and comprehension is puzzling because producers are also perceivers: why should an individual that can deduce an almost limitless number of meanings from the calls of others be able to produce only a limited number of calls of its own? The difference may arise because call production depends on mechanisms

of phonation, which are largely innate and physiologically complex, whereas comprehension depends on mechanisms of learning, including classical and operant conditioning, which are considerably more malleable and widespread even among animals with very different brains. But this explanation offers no answer to two crucial questions: why has natural selection so rarely acted to favor flexible vocal production in mammals and what were the circumstances that made humans an exception? One speculation argues that the selective pressures imposed by an increasingly complex social environment favored the evolution of a full-blown theory of mind, and this, in turn, favored the evolution of increasingly complex communication that required flexible vocal production.[6] Whatever the outcome of such speculation, in the domains of cognition and communication, two features, more than any other, make us uniquely human: a limited theory of mind and inflexible vocal production.

REFERENCES

1 Cheney DL, Seyfarth RM. 2007. Baboon metaphysics. Chicago: University of Chicago Press.

2 Cheney DL, Seyfarth RM. 2012. The evolution of a cooperative social mind. In: Vonk J, Shackelford T, editors. Oxford handbook of comparative evolutionary psychology. Oxford: Oxford University Press. pp. 507–528.

3 Tomasello M, Carpenter M. 2007. Shared intentionality. Dev Sci 10:121–125.

4 Hammerschmidt K, Fischer J. 2008. Constraints in primate vocal production. In: Griebel U, Oller K, editors. The evolution of communicative creativity: from fixed signals to contextual flexibility. Cambridge: MIT Press. pp. 93–119.

5 Seyfarth RM, Cheney DL. 2010. Production, usage, and comprehension in animal vocalizations. Brain Lang 115:92–100.

6 Seyfarth RM, Cheney DL. 2012. Primate social cognition as a precursor to language. In: Gibson K, Tallerman M, editors. Oxford handbook of language evolution. Oxford: Oxford University Press. pp. 59–70.

A Neuroanthropological Perspective

BENJAMIN CAMPBELL

What makes us human? I argue it is a brain that has evolved under social pressure to make us self-aware individuals who define ourselves by what we share with a group of familiar others. While that group of familiar others originally extended no farther than a band or tribe, it has since grown until it now includes, to varying degrees, a global human population. And with that, the focus on what makes us human has shifted from being a member of one group as opposed to another to being a member of the same species as distinct from other species.

Humans are distinct from our closest relatives, the great apes, in having an extended life span, late maturation, and higher reproductive rates. At the center of these traits lies the human brain, roughly six times larger than expected based on body size and three times larger than the chimpanzee's. It is our large brains that take a long time to develop. At the same time, our brains allow us not only to be more economically productive as adults and capable of subsidizing, as a group, the energy demands of our slow-developing offspring, but to still reproduce at a higher rate than do any of the extant hominoids. In other words, the selective pressures that led to a larger brain centered on group interactions that continue throughout the life span.

It follows that species-specific features of the human brain are likely to be intertwined with social intelligence. In fact, the large size of the human brain is primarily a function of increased cortical area. Most of the cortex serves as association areas, integrating sensory inputs into larger and larger bits of information that can be used by the prefrontal cortex for decision-making. Hence the size of the human cortex means that many different features of other individuals and the environment can be used to discriminate social situations and help us to choose a response, allowing the complex social strategies with which we are familiar as humans.

Compared to social cognition, potential changes in social emotion over the course of human evolution have received much less attention. Recent findings indicating that the human amygdala, associated with emotional saliency, is larger than that of other hominoids, suggest possible species differences in emotion. Humans may be more, rather than less, emotionally sensitive to their social environment, giving the group a greater impact on our emotional life.

In this context, the insula, a small cortical region between the temporal and frontal lobes, is of particular interest because of its role in integrating emotion and bodily sensation. Via the thalamus, the posterior insula receives afferents through a network of unmyelinated fibers from different parts of the body, including muscles, gut, and skin. These sensations, continually updated, are integrated within the posterior insula to create an ongoing representation of the body. This information is relayed to the anterior insula, where it is integrated with emotional impulses from the amygdala to create an ongoing global emotional awareness of bodily homeostasis; that is, whether, right now, as a whole, things are within tolerable limits or not.

Craig[1] refers to such an awareness as the salient self, a term implying individual self-awareness. However, other findings indicate that in addition to integrating sensations from within the body, the insula integrates external social signals as well, including sound and touch. In the rhesus macaque, neurons within the insula respond to species-specific calls, but not other sounds.[2] Similarly, in humans, the insula responds to music and language, both learned practices that are often used to define group membership. These findings imply that the salient self is not simply an individual experience, but includes a larger learned social dimension. In other words, the sense of being okay is experienced as the state of both one's body and the larger social group.

Recent brain imaging studies have shown the insula is activated in the case of social exclusion, as well as social inequality. It appears that our brain anticipates group membership based on equality as the default condition, and when this expectation is violated the insula senses a threat to bodily well-being. Such a picture is entirely compatible with our evolutionary history as hunter-gatherers dependent on each other for survival.

In sum, humans are inherently group beings with shared practices and beliefs, a point that social anthropologists have insisted on for some time. Such a definition can only be deepened by pointing to the way in which shared practices and beliefs are generated by our brains as a consequence of our evolutionary past.

Benjamin Campbell is Associate Professor of Anthropology at University of Wisconsin-Milwaukee. His recent research focuses on neuroanthropology. His article "Male Embodiment and Vitality in Subsistence Societies" will appear in *Neuroanthropology*, edited by Greg Downey and Daniel Lende (MIT Press) this fall. He is also the co-editor (with Michael Crawford) of *Causes and Consequences of Human Migration* (Cambridge University Press) due out this fall. Email: campbelb@uwm.edu

REFERENCES

1 Craig AD. 2010. The sentient self. Brain Struct Funct 214: 563–577.

2 Remedios R, Logothetis NK, Kayser C. 2009. An auditory region in the primate insular cortex responding preferentially to vocal communication sounds. J Neurosci 29:1034–1045.

Comes the Child Before Man: Development's Role in Producing Selectable Variation

SARAH HRDY

A concatenation of events and adaptations led a line of bipedal, already clever, tool-crafting apes in the genus *Homo* to evolve even larger brains with special aptitudes for language and for transmitting elaborate information, including templates for socially approved ("moral") behavior. It is unlikely that such apes could have evolved had they not already been peculiarly "other-regarding." It is the emergence of this facet of human nature that intrigues me most.

Other apes can attribute mental states to someone else, as when subordinates recognize what a dominant can and cannot see. They have the requisite neurological equipment for newborns to imitate some facial expressions in a caretaker, as human newborns do. Under some circumstances, chimpanzees identify another's plight or need and help, sometimes in targeted ways. Bonobos and chimpanzees may share food with one another, albeit typically grudgingly or only after persistent solicitations. Profoundly self-serving, they rarely, if ever, spontaneously share and cooperate with others the way humans routinely do. Yet from an early age, human infants voluntarily proffer food to someone else, even selecting precisely the item a recipient is most likely to enjoy. Long before they can speak, human infants obsessively monitor intentions and are eager to learn what someone else thinks and feels, including what someone else thinks and feels about them, leading babies to express symptoms of pride or shame. When combined with impulses to share and help, these other-regarding aptitudes make cooperation toward shared goals possible.

Since Darwin, explanations for humankind's peculiarly other-regarding tendencies have focused on the need for "altruistic" cooperators to collaborate in hunting or lethal intergroup warfare. But if advantages from hunting or raiding were sufficient, why didn't the predatory or raiding ancestors of chimpanzees (with six million years at their disposal) evolve to be more cooperative as well? Why is coordinated helpfulness so rare?

Elsewhere in nature, communal nurture of young has been a precursor to higher forms of cooperation. Rudimentary forms of shared infant care are found across the primate order, albeit not among great apes, where highly possessive mothers restrict access. Yet bipedal apes in the climatically unpredictable savanna-woodlands habitats of Plio-Pleistocene Africa, burdened by the costliest young in mammaldom, could have ill afforded exclusive mothering. Alloparents as well as fathers must have helped care for and provision young (the "Cooperative Breeding Hypothesis").

Demographic, life-historical, and biogeographic implications of such unapelike child-rearing are becoming increasingly well understood. But there would also have been psychological corollaries. These include mothers who are acutely sensitive to cues of alloma-ternal support with levels of maternal commitment contingent on them; variable levels of male commitment sensitive not only to probabilities of paternity and mating options, but also to alternative sources of nurture; and offspring developing in social contexts where they needed chronically to monitor and respond to the mental states and intentions of others, resulting in a cognitively and emotionally different developmental outcome. Over generations, these novel ape phenotypes would have been subjected to quite novel social selection pressures, so that youngsters just a little better at monitoring the mental states of others, at appealing to and soliciting nurture from them, would be the best cared for, best fed, and most likely to survive.

This explanation for the initial emergence of more other-regarding impulses in a great ape avoids the need to invoke unique evolutionary processes or activities that may or may not have been relevant for widely dispersed foragers in Plio-Pleistocene Africa. Alloparental provisioning has evolved multiple times in multiple taxa as kinship or mutualistic benefits induced alloparents to bring back food for someone else's dependent young to a hive, den, or home base. As in most primates, ancestors of early hominins would have been susceptible to signals of need from altricial young, as well as buffeted by unpredictable rainfall and resources, conditions known to predispose vertebrates to evolve cooperative breeding.

I propose that cooperative breeding had begun co-evolving with slower maturation and larger brain sizes by 1.8 million years ago. For this model to work, both sexes, albeit at various life stages, had to be able to move between groups, gravitating away from adversity and toward opportunities where resources at issue included not only food, water, or mates, but opportunities to receive or strategically provide allomaternal assistance to kin. Although multi-local residence patterns are well documented in the ethnographic record, it is not yet known how far back in time such porous social boundaries go. Nevertheless, extrapolating from what developmental psychologists are learning about modern humans and collateral ape lines, if early hominins relied on multiple caregivers, other-regarding impulses and more integrated perspective-taking would logically follow. If so, long before the evolution of behaviorally modern humans capable of symbolic thought and language, and even before anatomically modern big-brained humans, emotionally modern hominins that already were psychologically different from other apes would have been questing for intersubjective engagement.

ACKNOWLEDGMENTS

Sarah Hrdy is an old-fashioned anthropologist whose most recent book, *Mothers and Others: The Evolutionary Origins of Mutual Understanding*, was awarded the 2012 J. I. Staley Prize for outstanding scholarship and writing that crosses sub-disciplinary boundaries "to add new dimensions to our understanding of the human species," which is exactly what she and this project are trying to do. She is Professor Emerita in the Department of Anthropology at the University of California, Davis, associate of the Peabody Museum of Archaeology and Ethnology, Cambridge, Massachusetts, and A. D. White Professor At Large at Cornell University, Ithaca, New York.
Email: sbh@citrona.com

Grandmothers and Their Consequences

KRISTEN HAWKES

Both what we share and don't share with our primate cousins make us human. Easy enough to start a list. At least since Darwin, most would rate moral sentiments as distinctively human. But our modern selves didn't emerge from ancestral apes in one step. When did populations along the way become human? Before our big modern brains, before language, and before pair bonds, our longer lives, later maturity, and earlier weaning could have evolved in an already smart and gregarious ancestor due to rearing help from grandmothers. Although cooperative hunting and lethal between-group aggression are often nominated as evolutionary foundations for human prosociality, neither distinguishes us from chimpanzees. Grandmothering does. Our grandmothering life history intensified selection on infant appetites and capacities for social engagement, the foundation of our moral faculties.

What could have led to these changes in hominin life history? Plio-Pleistocene climates posed great challenges as increased aridity and seasonality constricted the distribution of foods that ancestral ape youngsters could effectively handle. That left mothers two choices: follow the retreating foods and maintain the diets their weanlings could manage or subsidize them longer. Increased juvenile dependence would allow mothers to remain in habitats inhospitable to youngsters and move into new ones as well. Although extended juvenile neediness would seem to reduce a mother's reproductive success, it offered a novel fitness opportunity for older females with

Kristen Hawkes is Distinguished Professor of Anthropology at the University of Utah. Her studies of hunter-gatherer foraging strategies aim at improving hypotheses about human evolution. The importance of grandmothers' help provisioning youngsters drew her attention to the evolution of human longevity, prompting her continuing comparisons of human and chimpanzee aging.
Email: hawkes@anthro.utah.edu

declining fertility. This novel opportunity is central to the Grandmother Hypothesis: by provisioning grandchildren, elders would allow younger females to bear subsequent babies sooner without net losses in offspring survival. As more vigorous grandmothers left more descendants, rates of aging slowed. That raised longevity and the fraction of female years lived past the fertile ages. The reduction in adult mortality lowered the risk of dying before reproducing, favoring delayed maturity to net the benefits of further growth to larger adult size.

Our characteristic postmenopausal longevity has long been recognized as a major clue to the evolution of human life history. But when George Williams tackled it more than half a century ago, menopause was still thought to be uniquely human. He proposed that it evolved because other changes in our lineage made late births riskier and offspring more dependent. Subsequent evidence shows that women don't stop early. Female fertility ends at similar ages in humans and the other great apes. The human difference is not menopause, but our slower somatic aging. Other apes become frail during the fertile years and rarely outlive them. Not so humans. Among traditional hunter-gatherers, a girl lucky enough to survive childhood usually has more than a 70% chance of living beyond the childbearing years; and women are more economically productive after menopause than before it.

In these hunter-gatherer populations, the standing fraction of adult women beyond the childbearing ages is near a third, even though life expectancies at birth are less than 40 years. Life expectancies in that range contribute to another common mistake. The fact that the highest national life expectancy now almost doubles the global record of 1850 is widely cited as evidence that postmenopausal survival is an artifact of recent history. But life expectancies

at birth are not measures of longevity. Instead they are very sensitive to the short lives of dying babies and rise dramatically when infant and juvenile mortality decline.

Sarah Hrdy revealed a momentous implication of our grandmothering life history in developing her Cooperative Breeding Hypothesis. Hrdy does not privilege grandmothers as I do here, but her synthesis identifies far-reaching consequences of human mothers' reliance on others for successful childrearing. Great ape mothers focus on one infant at a time. But human mothers have overlapping dependents to juggle and must worry about the availability and disposition of helpers. As a result, human babies, unlike other ape infants, cannot count on their mother's full attention. Both mothers and grandmothers have investment alternatives; in high-mortality environments, their commitment can mean life or death. So grandmothering makes infant survival more subject to variation in infants' own abilities to engage caregivers. Human infants' sensitivity to that engagement leaves them (ironically?) more psychologically vulnerable to social approval.

The increased stakes for infants intensify the sociality that we share with other primates. Social bonds matter across the order, as demonstrated by long-term demographic and behavioral observations, experiments, and hormonal assays, both in the wild and captivity. Starting from ancestral ape sociality, grandmothering magnifies selection pressures for desires and capacities to engage mutual attention in earliest life. So the social virtues Darwin identified as distinctively human need not depend on the bigger brains and language that certainly distinguish us. Instead, our brains, language, and even pair bonds may depend on the prior evolution of strong appetites for shared intentions, with sensitivity to praise and blame selected in ancestral youngsters reared in environments with ancestral grandmothering.

How We Give Birth Contributes to the Rich Social Fabric that Underlies Human Society

KAREN R. ROSENBERG

In comparing humans with other primates, one should emphasize the continuities as much as the distinctions. It may be futile to seek a single, critical, and universal human characteristic to explain the essence of our uniqueness. Nevertheless, considering those factors in which we are distinct elucidates significant aspects of human adaptation. Arguments can be made for morphological adaptations, like bipedalism or encephalization, or cultural behaviors, like language, tool use, ritual, or art, that are unique to humans or more elaborated than in other primates. Hrdy and other authors argue that humans are "cooperative breeders," meaning that parents share the child-rearing efforts with other individuals in their social groups. These alloparents may be grandparents, older siblings, other close relatives, or nonrelatives, and have important implications for our social and emotional dynamics. Alloparental care is important during the long phase of juvenile development that humans begin as helpless but large-bodied infants. I focus here on two aspects of cooperation that are direct consequences of the human birth pattern: assistance during labor (and, more generally, support of mothers during pregnancy, childbirth, and lactation) and care of helpless newborns.

A striking example of reproductive cooperation is what Trevathan called "obligate midwifery" or birth assistance. Human birth is complicated in that infants rotate as they pass through the birth canal, a result of pelvic adaptations to the conflicting constraints of bipedalism and enceph-

alization that evolved in mosaic fashion over the last 6-4 million years, and the resulting position in which babies emerge, facing away from their mother. As a result, laboring women benefit from the presence of a birth attendant who increases the survival chances for both mother and infant by such acts as receiving the emerging baby, moving an umbilical cord from around a baby's neck or clearing its breathing passage, encouraging a mother to change positions to create a more spacious birth outlet or to alleviate shoulder dystocia (a birth obstruction that can result in injury such as paralysis of the infant's arm), or providing emotional support during a long, exhausting labor. Clinical research on doulas (birth attendants who provide emotional support to the mother rather than assist directly in the mechanics of birth) shows that attention to women's emotional and social needs during labor leads to shorter labors and fewer complications. In contrast to birth among other primates, which is generally solitary, human rotational birth may not have been able to evolve outside a social context in which women had physical as well as emotional assistance during birth. Rotational birth probably evolved in the early-middle Pleistocene and may have made possible dramatic encephalization in humans, making birth assistance a longstanding part of human adaptation.

Beyond this important direct help during childbirth that is so characteristic of humans, we support pregnant or lactating women. Piperata showed that during the postpartum period, when energetic demands are high, women receive help in the form of social support from members of the community and often do not continue their normal work. Assistance also takes the form of sharing work and providing food or child care.

Intensification of effort in support of the reproductive success of preg-

nant, birthing, and nursing mothers may be a critical aspect of our adaptation. It allows female members of our species to gestate large-bodied offspring, birth those large-brained, broad-shouldered babies, and care for and carry those large, helpless newborns outside the womb for extended periods. Montagu characterized human fetuses as "exterogestate," meaning that they continue to grow outside the womb at rapid fetal rates only because of our cultural ability to buffer helpless newborns from environmental stresses. Human babies have also evolved to demand this care, resulting in what Wolpoff[1:433] described as "the combination of physical altriciality and social precociality in which children who cannot jump off the ground with both feet can control and manipulate every adult they come in contact with," maximizing the adult attention they receive.

Beyond birth assistance, investment in infancy is also possible because humans help each other by sharing the high energy demands, intensive monitoring, and attentive care that benefit mothers and their babies so much. The relationships women form with one another as a result of this sharing of effort create intense emotional bonds that form one underpinning of the uniquely complex extended family and nonfamily social networks universal to humans. This web of social ties, and its elaboration in support of human reproduction and child rearing, are among the critical factors that shape the unique human adaptation and, despite our close genetic and behavioral ties to other primates, establish a pattern of social behavior that sets us apart from our primate relatives.

Karen R. Rosenberg is Professor and Chair of Anthropology at the University of Delaware. She is a biological anthropologist with interests in paleoanthropology, specifically in the origin of modern humans, with particular focus on East Asia and the evolution of the modern pattern of human childbirth and infant helplessness. Email: krr@udel.edu

REFERENCES

1 Wolpoff M. 1999. Paleoanthropology. Second edition. Boston: McGraw-Hill.

To Whom Does Culture Belong?

MARY C. STINER AND STEVEN L. KUHN

For millennia, scholars have viewed humans as members of the animal kingdom, sharing many characteristics with creatures as diverse as horseshoe crabs and bats. For at least as long, people have sought to identify the features that distinguish us humans from other organisms, features that make us utterly unique.

Complex "culture" and a linguistic mode of communication are two of the most obvious things that make humans human. Culture is about knowledge building, conservation, and transfer. Its most remarkable property is that it can be shared among individuals and across generations independently of genetic inheritance. While humans are uniquely cultured, they may not be the only creature that possesses a capacity for culture. In fact, there is considerable diversity of opinion among anthropologists as to whether culture as a cognitive and behavioral adaptation distinguishes humans from other animals absolutely or only by degree.

The question of whether we are alone in our possession of culture is also fundamental to understanding how this most typical of human characteristics came into being. To study evolutionary processes of any sort, we must identify where and how certain traits derived from earlier, simpler forms, and how they were amplified, altered or eliminated with time. Iso-

lating the modern human species categorically from all other animals, present and past, is common to many narratives of human evolution as well as religious accounts of human creation. As intuitively appealing as this practice may be, claims of absolute breaks with other life forms are impediments to learning how humans developed their remarkable facility for and dependence on culture.

At a genetic level, it is easy to see that a great deal of what makes us human is what also makes us mammals, vertebrates, or multicellular organisms. Nowhere is this more apparent than in our DNA, with more than 98% shared with chimpanzees and only somewhat less shared with chickens and mice. Any number of remarkable developments in how animal species interact with the physical world have resulted in whole new dimensions of existence. Several of these have evolved more than once in the history of life. Flight is one example that continues to instill wonder and confound evolutionary scientists. We know that the capacity for flight developed independently in birds and bats, both of which rely on modified forelimbs, while invertebrate insects took to the air using entirely different structures. Knowing this fails, however, to tell us how wings came into being in general or in each case. Today, we commonly appeal to preadaptations for flight that arose by chance, were favored by more proximate needs, and happened to potentiate rapid movement of a new kind. And then we try to find out what those characteristics would have been.

Cultural transmission of information and behavioral traditions is another remarkable development in the evolution of life. Should it be considered the singular possession of humans? Behavioral studies show that other social mammals and birds develop local knowledge traditions that are passed among individuals and across generations. It seems that the main barrier to calling these examples rudimentary culture is that the behav-

iors are transmitted by means other than human language. Yet humans share culture through both linguistic and nonlinguistic modes of communication. Body language, gesture, and simple performance are central to the transmission of many skills and physically embodied forms of cultural knowledge, such as dance and many crafts. Why should we admit these as channels for cultural transmission in humans but disallow them for other social organisms?

Virtually all scholars will agree that culture redefined the character of the evolutionary process in humans, allowing us to leap across adaptive thresholds quickly and efficiently. This viewpoint leaves two distinct questions for the next generation of social scientists. Just how unique is the capacity for culture among intelligent species, of which humans are but one? And how specialized are the various means for sharing elements of learned traditions with conspecifics? All modes of communication are tools for information transmission; there must be a point where imitation grades into ritualized gesture and ritualized gesture into recombinable structured elements. Modern human language is extraordinarily versatile, and there is nothing quite like it to be found in other animals. That experiments with nonhuman primates or cetaceans fail to elicit human language is hardly the point, however. Apes and dolphins should not be expected to emulate our modes of communication any more than dragonflies should be expected to fly like birds.

A central aim of anthropology is to understand the origins of humans and the complex behaviors that characterize us today. If this is our goal, the question of what species may possess something akin to culture must be more inclusive. Otherwise, we run the risk of shutting the door to understanding how humans "got" culture in the first place, ignoring the evolutionary substrate of our own unique cognitive evolution.

Mary C. Stiner is Professor of Archaeology in the School of Anthropology at the University of Arizona in Tucson, AZ. She conducts archaeological research on Paleolithic and early Neolithic sites across the Mediterranean region. Her interests include human evolution and paleoecology, ancient hunting practices, animal domestication, and early ornamental traditions.
Email: mstiner@email.arizona.edu
Steven L. Kuhn is Professor of Archaeology in the School of Anthropology at the University of Arizona. He explores changes in ecology, foraging adaptations, and land use of Pleistocene hominins through Paleolithic technologies. He has conducted field and laboratory studies in Italy, Israel, Turkey, Greece, Syria, Serbia, and the U.S.
Email: skuhn@email.arizona.edu

To Be or Not To Be (Human), Is that a Question?

KEN WEISS

What makes us human? This seems a perfectly reasonable, interesting question to ask but, even on superficial examination, it's really not meaningful at all. By the usual criterion that a scientific statement must be testable, it is not clear that answers to "What makes us human?" would qualify. Or is this a humanistic rather than scientific question? Think of it this way: Look in a mirror; what do you see? How do you know it's "human"? Let's consider what a scientifically meaningful answer might entail.

We couldn't simply agree to count anyone as human who is born to qualified "human" parents. That just bumps the question back a generation, and another generation, and another, until at some point in fossilized history we'd have gone back enough generations to question whether the parents still qualified as human. So that doesn't work.

One obvious, seemingly objective answer that quickly comes to mind is possession of "the human genome." However, I put that in quotes because there is no such thing! It's a Platonic ideal, a DNA sequence assembled from perhaps more (the truth is currently unclear) than one person, that's repeatedly updated and corrected. It's not even as intuitively obvious as a traditional type-specimen because, as a composite, no human (whatever that means!) ever had that sequence. It is strictly an arbitrarily agreed-on reference

sequence. Evan if from just a single person, any two instances, between people or within any person, differ from the reference by a few million nucleotides. So do we need a second, out-group reference such as "the chimpanzee" sequence (itself just a type-specimen) to give us an outer bound of humanness?

Even in the simplest comparisons, a random human and chimp sequence differ by tens of millions of nucleotides. But there is also substantial identity, varying in detail with each comparison one might use; that won't help define what's uniquely human, so it's not a terribly satisfying solution. And why pick on chimps? Why not, say, gorillas, giraffes, or growling Neandertals, since we have (a Platonic composite of) their sequences. Or were they also "human" and hence no out-group?

Clearly, something relevant to the question involves genes, but it is not so clear just what it is. Perhaps we should choose "the" gene for some chosen trait (another Platonic ideal)? Who decides which gene? When one nucleotide can be the difference between life and death by disease or failed embryological development, which should count? Surely we should include individuals who are not the Platonic ideal of human, perhaps lacking some typical trait, such as vision, hearing, limbs, or "normal" intelligence. But where is the line to be drawn?

Genome sequence analysis shows that each human (assuming we know in advance what that means!) carries a unique set of numerous genes that, because of mutation, are not functional, but that would otherwise seem to be necessary because, for example, if you inactivate it in a mouse, the mouse turns belly up. Other genes probably cover the inactivated genes' functions. Indeed, most traits are due to the interac-

tions of many different genes, each varying. Hence each instance of the trait is genetically different!

This complexity suggests that we should turn to traits rather than genes. Would they be tooth morphology, pelvic shape, or the position of the foramen magnum? Perhaps we'd prefer the traditional favorites of our hubris, language and intelligence. Is there a qualifying IQ or elocution cutoff we can use? We might just as well pick, say, armed warfare or religion as "making us human," except that would disqualify Quakers and atheists. Trait selection provides no easy answer.

Clearly, humans are something different from anything else, and yet, individually, no one of us is identical to anyone else. Indeed, our understanding of evolution depends on population thinking, and the answer to what makes us human is necessarily a collective one. However, that is ephemeral and less than crystal clear, because every instant the collection changes with new individuals (and unique genotypes) being born and others lost.

If a rhesus looks in a mirror, what does it see? Does it make its own species distinction? If only it could tell us how. Let's parse the question itself: "What" implies enumerable components, "makes" implies determinative causation, and "us" implies collective identity. Finally, "human" vaguely implies that we know the answer ahead of time, to which the other words relate, an inherently circular definition. So overall, this really isn't much of a scientific question, after all.

In the end, we can rest easy, however. Every answer to the question of what makes us human is elusive. Everyone will understand the question differently and can answer it without fear of contradiction. That, after all, is what makes us human!

Ken Weiss is Evan Pugh Professor of Anthropology and Genetics at Penn State University. His interests are in genetic variation and causal complexity, and the evolutionary processes that generate them. His research on these topics involves computer simulation, genome mapping, and experimental developmental genetics of craniofacial variation. Email: kenweiss@psu.edu

Reprise: What Does Make Us Human?

JAMES M. CALCAGNO AND AGUSTÍN FUENTES

As expected, ten different essays provided ten distinctive responses to the question, "What Makes Us Human?" Thus, it is not surprising that undergraduate students, when faced with the same question at the start of an introductory course in biological anthropology, have difficulty answering it at the end of the semester. Our ambitious (perhaps unrealistic) goal here is to provide a coherent response that is comprehensive enough that most, if not all of our panel of experts, find reasonable, and succinct enough to be easily digested by students first learning about anthropology and scholars in other disciplines with similar interests. We deeply appreciate the insightful comments of each of our contributors, making our attempt at this possible.

We begin with Dr. Weiss' essay, given that he poses a critical challenge to our stated goal, commenting that "even on superficial examination," it's not a meaningful question. His reasoning is important and well-taken. We should not view all humans as conforming to a "Platonic ideal," in search of the essence of humanity. Instead, we must account for individual variation over time and space, recognizing that the sum of being human is greater than the parts. At the same time, however, we respectfully disagree that the question lacks meaning, for the very reason he uses later: "Clearly, humans are something different from anything else…." We recognize that each individual is unique and that boundaries of humanity are blurred over time, but feel it is unwise for evolutionary anthropologists to respond to a question of such great human interest by implying "bad question, please move along." Indeed, our response to his query "Is this a humanistic rather than scientific question?" would be that it is both a humanistic and a scientific question, and exactly why an anthropological perspective is vital to the discussion.

Weiss's comment that there is "no such thing" as the human genome supports our original expectation of different perspectives emanating not only from major research specialties, but also within them, given Dr. Pollard's genetic viewpoint. Although Pollard clearly recognizes that "not very much" separates us from the chimpanzee genome, she also points out "that a few key changes in the right DNA sequences had big effects…all of which distinguish humans as a species." For Pollard, species' genomes are there to be assessed as real biological patterns, not as Platonic ideals. Although she cautions that a definition of "human" may not have nearly as much to do with genetics as was once thought, she notes that our current view that humans are not especially unique as a species genetically could change with novel technologies, which may provide more resolution to genomic and epigenomic differences between us and nonhumans.

As might be expected from a primatological perspective, Dr. Sussman emphasizes the fact that humans have "different ethograms" from nonhumans. While recognizing many similarities with our close relatives, he notes "profound behavioral differences," and that the totipotentiality of behaviors for each species differs. Most relevant and uniquely human in his comparison of behavioral totipotentiality are "symbolic behavior, language, and culture." Similarly, Drs. Seyfarth and Cheney contend that "fully evolved language provides the most striking difference between modern human and nonhuman primates." Specifically, they argue that two features of cognition and communication limit the other primates and make us unique: our full blown theory of mind and flexible vocal production.

Dr. Campbell's neuroanthropological perspective on cognition and communication is in harmony with the views of our primatologists, as he contends that we have "a brain that has evolved under social pressure to make us self-aware individuals." He points to neuroscience findings that our "sense of being okay is experienced as the state of both one's body and the larger social group." Similarly, Drs. Hrdy, Hawkes, and Rosenberg focus on social interaction and cooperation in their essays, each offering insight into what "made" us human. Hrdy emphasizes alloparental care more generally to explain why "humankind's peculiarly other-regarding tendencies have focused on the need for 'altruistic' cooperators to collaborate." Hawkes narrows the importance of alloparental care more specifically to grandmothers, noting that "our brains, language, and even pair bonds may depend on the prior evolution of strong appetites for shared intentions, with sensitivity to praise and blame selected in ancestral youngsters reared in environments with ancestral grandmothering." Rosenberg focuses on the "direct consequences of the human birth pattern" and acknowledges the unique human social ties and behaviors we have in support of childbirth and child rearing.

Hrdy makes a compelling conclusion that "long before the evolution of behaviorally modern humans capable of symbolic thought and language, and even before anatomically modern big-brained humans, emotionally modern hominins already psychologically different from other apes would have been questing for intersubjective engagement." Presumably such hominins would have had language "perception" abilities similar to those of humans, but lacked our language "production" skills, as noted by Seyfarth and Cheney. This further illustrates the impossibility of clearly demarcating human from nonhuman in an evolutionary sense, even though clear differences between humans and our closest relatives exist today. Thus, we are rightly reminded by Drs. Stiner and Kuhn that as intuitively appealing as it is to see ourselves as unique, "claims of absolute breaks

with other life forms are impediments to learning how humans developed their remarkable facility for and dependence on culture."

Finally, Drs. Cartmill and Brown return to a theme of Weiss, noting that "Which of our peculiarities give humanity its unique importance and significance?" is not an empirical question, but still an interesting one. They emphasize two key human universals: "our unique propensity for imitation" and "seeing things from the other fellow's perspective." Importantly, they also remind us that "we are the ones who have to make the decisions that will preserve this symbiosis or bring it crashing down — and us along with it."

So what do we as evolutionary anthropologists tell inquiring minds who seek an answer to "What makes us human?" We all certainly can agree that an evolutionary perspective is required. Yet ironically, an evolutionary perspective makes the question much more complicated, because at no point in time can we ever point to one generation of humans whose parents were nonhumans. We are connected to other species in many ways. Thus, great caution is urged when trying to distinguish us from all other species without recognizing the core continuities. However, there clearly is something distinctive about humans today as opposed to other living species. As Rosenberg stated, "considering those factors in which we are distinct elucidates significant aspects of the human adaptation." We propose that these essays, and our own views, point to two key factors that make us human.

First, humans are characterized by a fully developed theory of mind, with the ability for flexible language skills and the concomitant symbolic and global reality of culture. This is a common theme among essays emanating from diverse research perspectives within evolutionary anthropology (see Whiten and Erdal[1] for a similar and well-reasoned conclusion). Our language abilities, social interaction, symbolic behavior, and cultural variation all seem tied to our desire to understand the minds of others, for both cooperative and selfish reasons. It is this cultural and cognitive reality, lived simultaneously through social, linguistic, symbolic, and evolutionary contexts, that makes humans truly distinct from other beings on the planet. We are not "ignoring the evolutionary substrate of our own unique cognitive evolution," as Stiner and Kuhn warn against, but using comparisons with other species to understand differences in the "totipotentiality" of human behavior, as Sussman suggested. Nonhuman primates surely show signs of empathy, cooperation, and imitation,[2] which would be expected from an evolutionary perspective. However, no other species are so intensely motivated, both cooperatively and competitively, to reconstruct their entire environment and live their lives based on their concerns with the mind of others.

Second, and as the direct result of our first point, we are biocultural animals.[3,4] As Marks[5] recently elucidated, no other species has evolved as we have: human evolution is not simply a biological process, but truly a biocultural process. Our biology cannot be understood outside of the aforementioned cultural and cognitive reality, and culture cannot be fully understood without biology. Thus, our biology and culture are not just intertwined, but melded together, co-existent, inseparable. Evolution is about both continuities and discontinuities. Our biocultural nature is the core discontinuity that emerges in our evolutionary history (even though this discontinuity between living humans and nonhumans must have emerged in a continuous way over time). Our contributors demonstrate our biocultural nature eloquently in varied ways, and much of evolutionary anthropology makes this point, directly or otherwise.

These two human attributes have led to our being a hugely influential part of nature, and how we define ourselves can have great consequences for our entire planet. Are we masters of the universe or something more nuanced and complicated? Much of academia and the public at large want answers. Evolutionary anthropologists have a central toolkit to bring to bear on this topic. We have to be ready to participate in an open and engaged discussion, regardless of what we think of the particulars of the questions (or answers!). By thinking aloud with one another, and maybe even going beyond the boundaries of our intellectual comfort zones, we may be able to enrich our own research endeavors and contribute in meaningful and lasting ways to how people think, not only about becoming human, but about being human.

REFERENCES

1 Whiten A, Erdal D. 2012. The human socio-cognitive niche and its evolutionary origins. Phil Trans R Soc B 367:2119–2129.

2 de Waal FBM, Ferrari PF, editors. 2012. The primate mind: built to connect with other minds. Cambridge: Harvard University Press.

3 Calcagno JM. 2003. Keeping biological anthropology in anthropology, and anthropology in biology. Am Anthropol 105:6–15.

4 Fuentes A. 2012. Race, monogamy and other lies they told you: busting myths about human nature. Berkeley: University of California Press.

5 Marks J. 2012. The biological myth of human evolution. Contemp Soc Sci 7:139–157.