

How Different Are Humans and “Great Apes”? A Matrix of Comparative Anthropogeny

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THE CHALLENGE OF COMPARATIVE ANTHROPOGENY

Comparisons of nonhuman hominids with humans are difficult, as so little is known about their phenotypic features (great ape phenomes), in contrast to what we know about humans (Varki et al., 1998). Ethical, fiscal, and practical issues also limit collection of further data about these species (Gagneux et al., 2005; McConkey and Varki, 2005), all of which are currently endangered in the wild. A Matrix of Comparative Anthropogeny (MOCA) has been established at the website of the Center for Academic Research and Training in Anthropogeny (CARTA), and attempts to collect existing information about human-specific differences from “great apes” currently scattered in the literature. Having such information in one location could lead to new insights and multidisciplinary interactions, and to ethically sound studies to explain differences and uniquely human specializations. It is for this reason that MOCA is called a matrix, ie, an arrangement of information from which something else originates, develops, or takes form. This approach could allow us to connect the dots between different human specializations, and shed light on how and in what sequence each difference came about.

OUR EVOLUTIONARY HERITAGE AND PRIMATE NATURE

Classification

Humans are one of approximately 400 primate species. Eighty million years of evolution have given rise to a staggering range of primate species, ranging in size like that

of a small rodent, to the several 100 pound gorilla silverbacks (Martin, 2012). The fossil record places human origins firmly in Africa, with ~4 million years of bipedal hominin evolution on that continent before the first hominin fossils appear outside Africa (Antón et al., 2014). Following initial waves of migration of members of the genus *Homo* out of Africa, there was a final migration of behaviorally modern *Homo sapiens* from Africa, a species that replaced all other extant members of the hominin clade, with limited interbreeding (Varki, 2013; Pääbo, 2015).

Common Phenotypic Features of Humans

Like most other primates, humans are usually born as singletons, have long lactation periods, and manifest a relatively slow development of the young. Like most nonhuman hominids, humans are also long-lived, and belong to complex social groups. Humans have the same number of bones and teeth as chimpanzees (with the exception of a missing baculum/penis bone in human males). Similarities in the organization of our brains are also obvious, such as the sharing of all major areas and a six-layered cortex. It is not uncommon for a human observer of wild chimpanzees to be reminded of human acquaintances through one of the ape subjects. But these individuals have and use no names, never sit around a fire, and they do not discuss the details of yesterday or plan for tomorrow.

Comparative Genomics

Our genomes have a very similar size (~3 billion base pairs for each parental haploid genome) to those of our closest relatives and even show similar packaging into

chromosomes (with the exception of a fused chromosome in humans, we have 23 pairs as compared to the 24 pairs found in great apes; Ventura et al., 2012). The total number of genes is also similar. Complete sequencing of the great ape genomes confirmed that these are very similar to our own (Prado-Martinez et al., 2013). At the level of alignable sequences we are ~99% identical. However, around 5% of the total DNA in the chimpanzee genome differs from that of humans, if one considers the DNA that is missing in either species but present in the other (Britten, 2002). With the discovery of novel functional elements in our genomes comes the realization that noncoding DNA differences probably play important roles in the regulation of gene expression (Capra et al., 2013). This supports the classical suggestion that regulatory changes likely explain much of the phenotypic differences between humans and our ape relatives (King and Wilson, 1975).

COMPARATIVE ANTHROPOGENY

What Is Anthropogeny?

Anthropogeny is a classic term encompassing the exploration of the origins of the human species (Hooper, 1839). It contrasts with traditional anthropology, which includes the much broader study of modern humans and their varied cultures and behaviors, as well as studies of other primates.

A Comprehensive Comparative Approach Is Needed

Given the lack of understanding of the factors that shaped the evolution of our species from ape-like ancestors over the last 6 million years or so, explaining the origin of the human phenomenon will critically rely on interactive insights gained from drastically different scientific domains: biological, social, medical, physical, and computational (see Fig. 9.1).

Limited Information Is Available on the Phenomes of Nonhuman Hominids

Compared with the vast store of information we have on humans, our knowledge of great ape phenomes is very limited (Fig. 9.2). All living great ape species are currently also endangered due to the rapid destruction or deterioration of their habitats (tropical forests in Africa and Southeast Asia), predation by human bush meat hunting, and emerging infectious diseases arising from ecological disturbances. In the best of all possible worlds there would be a concerted effort to more fully understand the phenomes of their captive counterparts, not only for the purposes of understanding human origins, but also for improving the care for these endangered populations (Gagneux et al., 2005). However, traditionally, only chimpanzees have been kept for research purposes, with very few

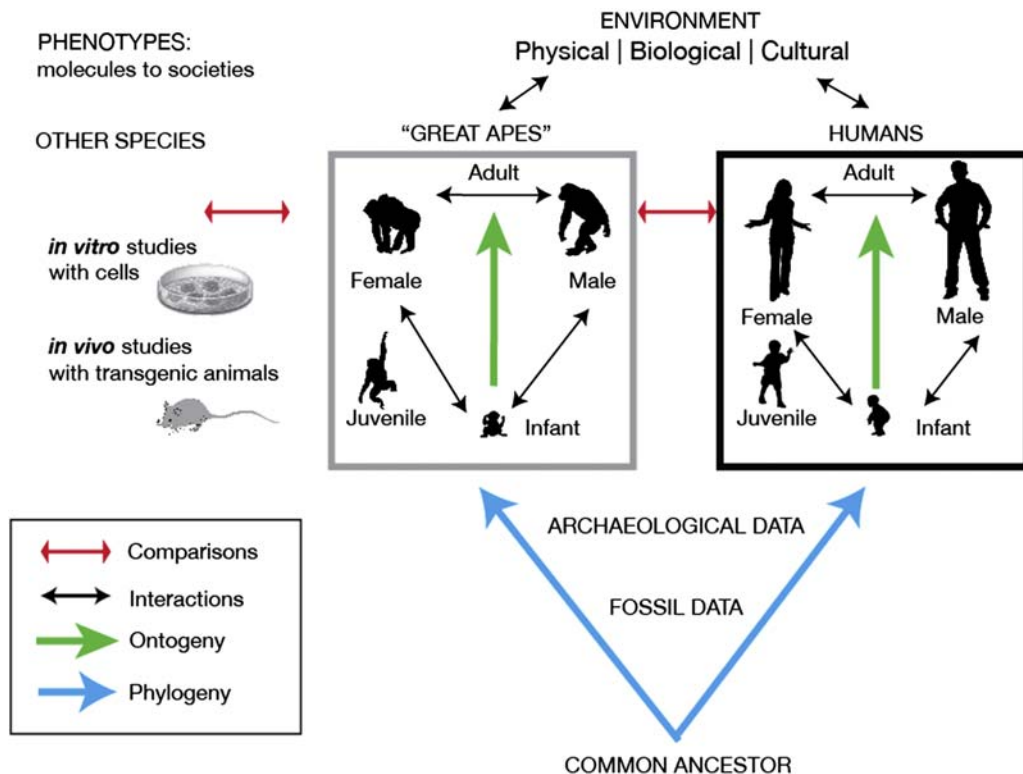


FIGURE 9.1 A systematic approach to Anthropogeny. Updated by P. Gagneux, from Varki, A., Nelson, D., 2007. Genomic differences between humans and chimpanzees. *Annual Review of Anthropology* 36, 191–209.

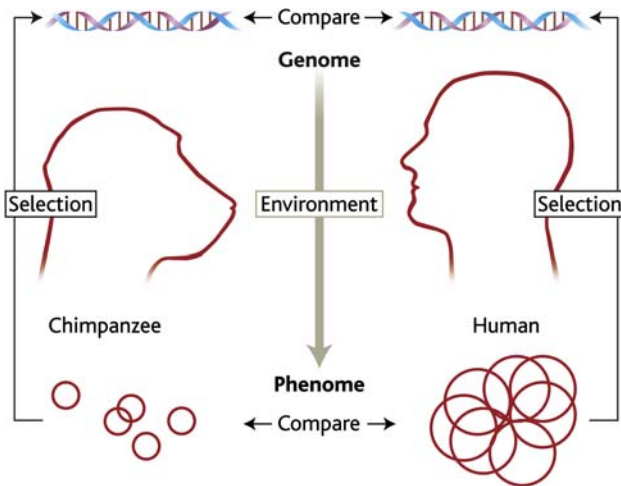


FIGURE 9.2 The need for more information about “great ape” phenomes. *Reproduced from McConkey, E.H., Varki, A., 2005. Genomics. Thoughts on the future of great ape research. Science 309, 1499–1501.*

bonobos, gorillas, or orangutans in captivity (mostly restricted to zoos). Research activities on captive great apes have also now all but ceased around the world with few notable exceptions: Japan, the United States, Gabon, and African ape sanctuaries. There are several dozen great ape research sites where great apes are studied in their natural environment, and most of these sites have ape populations that are completely habituated to the presence of human observers. These provide precious remaining research opportunities but unfortunately, also greatly increase the risk of predation and infectious disease to these populations (Kondgen et al., 2008).

Ethical and Practical Limitations on Further Acquisition of Information

The phylogenetic proximity and psychological similarity of great apes and humans have raised strong objections and prompted legislation prohibiting any invasive or destructive research on these species (Altevogt et al., 2011; de Waal, 2012). However, routine medical care of captive populations remaining in sanctuaries could generate urgently needed materials to enhance our knowledge of great ape basic biology (Gagneux et al., 2005). In practice, opportunities to collect more phenotypic information on these species remains limited, and the current situation of asymmetric phenotypic information is unlikely to ever change for the better.

Body, Mind, and Society of Humans Show Major Departures From Those of “Great Apes”

Humans differ from great ape species in external and internal anatomy, cognition, and social behavior in many

important ways. This, and a good dose of anthropocentrism, explain why our closest relatives the chimpanzees were traditionally grouped into the nonexistent taxonomic group that used to be called “pongids” or colloquially, the “great apes.” A systematic approach to human differences from these close evolutionary cousins is exemplified by MOCA.

MATRIX OF COMPARATIVE ANTHROGENY

Origins and Rationale

MOCA started as a simple list of features allegedly unique to humans kept by one of us (A.V.). With the establishment of CARTA came the opportunity to expand and correct this list, which has grown into over 500 items (topics) falling into 24 different domains (see section: [Organization Into Domains of Human Knowledge](#) in this chapter).

Goals

MOCA attempts to collect existing information currently scattered in the literature about human-specific differences from great apes (O’Bleness et al., 2012). Having such information in one location could lead to new insights and multidisciplinary interactions, and to ethically sound studies to explain differences, as well as uniquely human specializations. This is why MOCA is called a matrix. This approach will hopefully allow us to connect the dots among different human specializations and shed light on how and in what sequence these have evolved. Furthermore, it may allow us to connect different specializations and potentially discover which ones may have caused others. Importantly, such a chronology will be very helpful in ruling out certain scenarios due to inconsistencies in timing. By definition, MOCA will always be a work in progress.

Organization Into Domains of Human Knowledge

MOCA is organized into 24 different alphabetically sorted domains based on areas of scientific knowledge, and each topic is assigned to the domain it most closely relates to. Topics are cross-listed with other topics across all domains whenever warranted. For example the entry on “composition of milk” in the MOCA domain Biochemistry would be cross-listed with blood group antigens (Pathology), domestication (Behavior), duration of lactation (Development), parental investment (General Life History), sialic acid content of the brain (Neuroscience), difficulty in breastfeeding, and breast development without pregnancy/lactation (Reproductive Biology and Disease), and should further be cross-listed with microbiome (Ecology).

SELECTED EXAMPLES OF COMPARATIVE ANTHROPOGENY

Space does not allow a systematic and complete summary of the information currently in the MOCA resource. The following is a brief mention of just a few topics in each of the 24 domains.

Anatomy and Biomechanics

Among the striking human features are reduced fur, upright posture and ability for sustained running (Bramble and Lieberman, 2004), visible sclera (whites) of the eyes (Tomasello et al., 2007), and a larger and better opposable thumb (Tocheri et al., 2008). Great apes also appear to have much stronger skeletal muscles (Walker, 2009).

Behavior

Humans are an “invasive species” that occupy a wide range of habitats. Some other primate species use a fixed place as night shelter (eg, baboons). Humans build camps or villages and use sites (home bases) for prolonged periods of time. Places, individuals, and social groups have names. The use of fire allowed the transformation of materials (silcrete, pitch, compound adhesives), which opened numerous new possibilities uniquely to our species (Wadley et al., 2009). Cooking with fire profoundly affected the hominin lineage, by allowing access to much wider variety of food sources: plant tubers and seeds could be detoxified, and meat and plants rendered much more easily digestible (Wrangham et al., 1999). Fire also allowed an extension of human daily activity into the night (Wiessner, 2014) and the colonization of much colder ecosystems (Roebroeks and Villa, 2011). The use of fire and other controlled energy sources eventually launched the anthropocene, an epoch in which humans have been altering landscapes, climate, and the fate of countless animal species (Balter, 2013).

Cell Biology and Chemistry

The composition of milk is different between humans and other hominids. Like humans, great apes produce milk with a much higher number of free milk oligosaccharides than most mammals do (over 200 compared to 50) (Urashima et al., 2009). But humans appear to have longer oligosaccharides and lack the ability to produce the sialic acid Neu5Gc in their milk (and in the rest of their body) (Tao et al., 2011).

Cognition

Drastic differences in cognitive development include very early tendencies of shared attention in humans and rapid language acquisition by normal children learning thousands

of words by age three and often multiple languages. Human children exhibit profound interest in others’ minds and pronounced prosocial tendencies (Jaeggi et al., 2010). Social cognition also develops earlier in human children (Wobber et al., 2014), and could be related to cooperative breeding in our species (Hrdy, 2009).

Communication

Perhaps one of the most important human characteristics is our linguistic capacity. Whereas other primates clearly communicate, their communication system is not open-ended, ie, they do not have means to convey infinite meanings and information about events displaced in time and space (ie, displaced reference) (Penn et al., 2008). Symbols open up possibilities of defining identity and practicing magic. Language also allows sharing of minds by communication about events and concepts removed in time and space. Importantly, language also allows for gauging individual reputation, the existence of which profoundly affects the likelihood of altruistic acts, even when these are not mutualistic (Fehr, 2004). The origin of human language remains a very contested field of research. The role of gesture and music as launching systems for spoken language are worth investigating (Fay et al., 2014) and so are tantalizing connections between complex (Acheulian and Levallois) stone tool manufacture and the need and capacity for syntax (Stout and Chaminade, 2007; Stout et al., 2015).

Culture

The effective intergenerational transmission of information with language and theory of mind allows for rapid ratcheting of cultural innovations even across societies (Tennie et al., 2009). Such networks made possible trade of rare materials such as shells, pigments, and obsidian. All large human societies have institutions, which are involved in regulating the lives and interactions of society members. Such institutions can also contribute to high levels of social stress, as those individuals with the power to control the institutions can strongly interfere with the lives of large numbers of individuals in their societies. Key biological phenomena regulated by cultures include sexual and reproductive behaviors (Pemberton et al., 2012).

Dental Biology and Disease

Humans lack a pronounced sexual dimorphism in their canines (Plavcan, 2012). The much shortened face and jaw of humans contributes to the impaction of wisdom teeth. While humans and their hominin ancestors also have much thicker enamel than extant apes (Horvath et al., 2014), the overall size of human molars is much reduced, possibly due

to the long history of consuming cooked food and much reduced need for chewing (Wrangham et al., 1999).

Development

Human development, especially neurodevelopment is delayed even further, far beyond that seen in other primates. A high fetal rate of brain growth is maintained throughout gestation and continues in the first year of life (Leigh, 2004). Myelination (the insulation of nerve fibers) in humans is only complete in the third decade—in contrast to chimpanzees, where the process completes around age 10 (Miller et al., 2012).

Ecology

Humans occupy the highest trophic level in most environments. The use of technology such as fire, projectile weapons, hunting machines (nets, traps, snares), and animal skins for warmth and protection has allowed humans to colonize ecosystems around the world. Our species has also increasingly engaged in niche construction (Rendell et al., 2011; Creanza and Feldman, 2014). The ability to swim and to manufacture watercraft (rafts, floats, and boats) further supported the spread of our species.

Endocrinology

Chimpanzees may have higher levels of active thyroid hormone in their circulation (Gagneux et al., 2001). Evidence suggests potential changes in dehydroepiandrosterone (DHEA) metabolism (Blevins et al., 2013) and a unique adolescent growth spurt (Bogin, 1999), potentially mediated by hormones.

General Life History

Childhood, defined as a relative slowing in somatic growth but continued brain development, and the postreproductive survival of females appear to be uniquely human, among primates. Both phenomena contribute to the transfer of behavior, language, and culture between generations (Bogin, 2009) and are linked to the cooperative nature of human child rearing (Hrdy, 2009).

Genetics

While the vast majority of genes are shared between humans and other hominids, there are a few that only exist functionally in humans or in chimpanzees (O’Bleness et al., 2012). Many regulatory regions in the genome have also undergone changes unique to humans or to one of the other ape (hominid) lineages. Examples abound. Multiple changes have occurred in genes associated with sialic acid biology

(Varki, 2010). Human accelerated regions have been identified and include DNA coding for small regulatory RNA (Capra et al., 2013). Several of these functional genomic elements affect brain cortical development in utero (McLean et al., 2011; Charrier et al., 2012; Boyd et al., 2015; Reilly et al., 2015). Studies of gene expression patterns in a variety of tissues and individuals of varying ages are rapidly adding formidable amounts of data with high relevance for understanding human specific phenotypes, eg, brain gene expression, testes gene expression (Khaitovich et al., 2006; Somel et al., 2009).

Genomics

The levels of genetic diversity tend to be surprisingly high in most great ape populations, which despite their low numbers, maintain over twice the diversity found in humans. Notable exceptions are bonobo and mountain gorillas, which exhibit levels of genetic diversity lower than humans (Prado-Martinez et al., 2013). Unstable repeat elements in the genome of great apes have differentially expanded in chimpanzees and gorillas (Marques-Bonet et al., 2009). Recent families of transposable elements and endogenous retroviruses have differentially expanded and inserted in humans and chimpanzees (Magiorkinis et al., 2015). Most recently, evidence for differential and strong selection on the X chromosomes of great apes has been interpreted as resulting from lineage specific control of selfish (testis expressed, meiotic drive) elements on large tracts of the X chromosome (Nam et al., 2015).

Immunology

Several aspects of the human immune system have recently been modified by natural selection, possibly due to the unique pathogen regimes that humans encountered. Possibly related to this, humans have undergone biochemical changes with regard to certain molecules found on the surface of most of their cells as well as receptors on a variety of immune cells (Parham et al., 2012; Varki, 2010). Much research is currently focused on understanding how the microbiome of humans and their closest living relatives contributes to immune system maturation, and how humans came to carry much reduced microbial diversity (Moeller et al., 2014).

Medical Diseases

There are many differences in disease susceptibility between humans and other hominids. Examples include *falciparum* Malaria, Influenza A, frequency of progression of HIV infection to AIDS, and bacterial sexually transmitted infections (*chlamydia*, chancroid, syphilis, and gonorrhea) (Varki and Varki, 2015; Varki et al., 2011).

Mental Disease

Humans are prone to a range of mental diseases never so far diagnosed in any ape. These include early onset syndromes such as autism, but also later onset diseases such as bipolar disorder, schizophrenia, and Alzheimer's disease.

Neuroscience

Relative to body size, the human brain is three times larger than any ape brain. However some of the early claims of major regional allometric differences between human and other primate brains have not been substantiated (Semendeferi et al., 1997). But much new evidence has been found for differences in cellular architecture, the packing of mini columns in several cortical areas (Schenker et al., 2008), as well as in connectivity, such as the massively increased arcuate fasciculus connecting language areas in humans (Rilling et al., 2008). Comparing gene expression in different brain regions across species also revealed that micro RNAs are involved in shaping human-specific brain development (Somel et al., 2011). The emerging field of stem cell and induced pluripotent cell biology allows direct comparison of human and nonhominid cells in vitro. Derived neuronal cell lineages exhibit interesting differences in gene expression, motility, and branching patterns (Marchetto et al., 2013).

Nutrition

Hominin ancestors used their technical and cognitive skills to become top predators around 2 million years ago. While some great apes regularly hunt and consume a range of vertebrate prey, only humans habitually hunt and sometimes even cover much of their caloric intake with meat (at higher latitudes). The use of fire brought with it the invention of cooking. Cooking allows access to novel food as it detoxifies tubers and seeds, renders food much more digestible and easy to chew, and also permits the preserving of animal foods by smoking (Smith et al., 2015).

Organ Physiology

Heat dissipation through eccrine sweating, and the phenomenon of emotional lacrimation (crying) appear unusually pronounced in humans. Emotional blushing is a physiological reaction to social embarrassment and has never been described in nonhumans, and one of the most peculiar emotions of humans (Darwin, 1872). The reaction occurs in all humans but is more readily visible in individuals with light (melanin poor) skin.

Pathology

Cancers of epithelial origin (carcinomas) appear to be rare in nonhuman hominids but are among the most common killers

in our species (Varki and Varki, 2015). Also not been described in the great apes is Alzheimer's disease (Finch and Austad, 2014) or coronary thrombosis (Varki et al., 2009).

Pharmacology

Most human societies use mind-altering drugs. There are no reports of wild apes using such agents, even though wild chimpanzees have been shown to self-medicate by ingesting plants (Huffman, 2003). Psychedelic drugs can contain psychoactive chemicals that induce altered states of consciousness, including spiritual sensations (Sullivan and Hagen, 2002).

Reproductive Biology and Disease

While pair-bonding is very common in human societies, none of the other primates exhibit prolonged pair-bonding in the context of multimale, multifemale groups. A certain degree of confidence in paternity combined with personal names and kinship terms allows for paternal kinship networks spanning many social groups, allowing for the existence of clans and tribes (Chapais, 2013). The prolonged postreproductive survival of females allows grandmothers to help with the care of the young, and also to pass on much cultural information (Kim et al., 2014). Cultural transmission by the elderly might even have allowed selection for genetic variants that protect cognitive capacities late in life (Schwarz et al., 2015; Hawkes, 2015). Cooperative breeding is also strongly distinctive of humans, as compared to all the great apes (Hrady, 2009).

Skin Biology and Disease

Reduced hair, increased subcutaneous fat, and a great variation in skin, hair, and eye pigmentation are unusual human features (Jablonski, 2012; Kuzawa, 1998). Permanent breast development in adult human females is another obvious difference (Dixson, 2009).

Social Organization

For most of human prehistory, preagricultural humans lived in small groups but large social networks. Larger groups, even larger social networks, and complex hierarchies, arose among agrarian societies (Smail, 2008).

TOPIC TIMELINES AND RELATIONSHIPS

How are these and other uniquely human features functionally related to each other and which ones arose first along the lineage leading to humans? As an example, a rough sequence of major items based on current evidence would be as follows: facultative bipedality, changes in the hand anatomy, full striding/running bipedality, control of fire, cooking, home base use, much larger brains, burials,

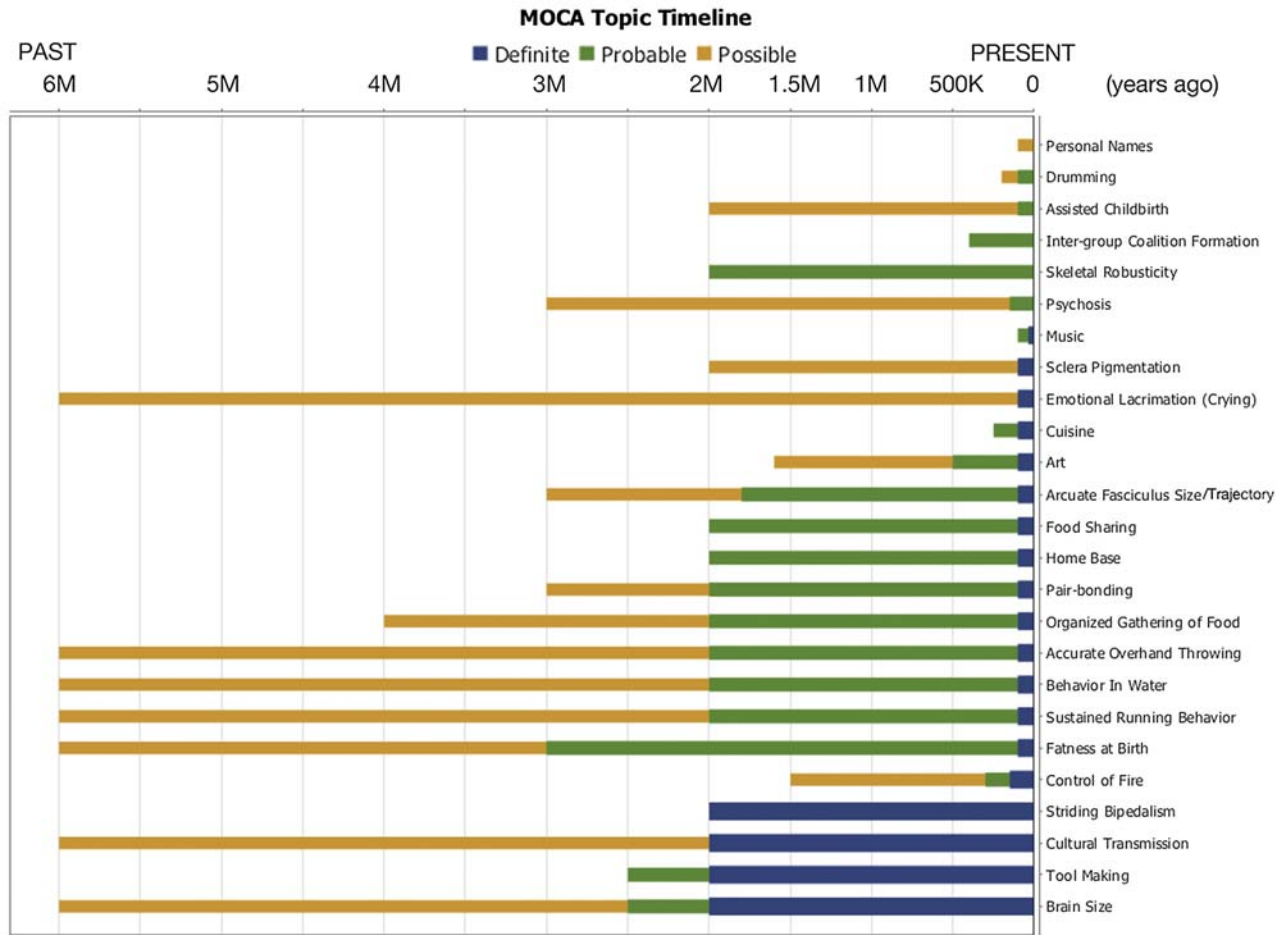


FIGURE 9.3 Example of timeline analysis derived from Matrix of Comparative Anthropogeny (MOCA) topic data.

symbolic capacity, and projectile weapons. There is a special problem with obtaining definitive time lines for various forms of cognitive behavior such as musicality and language, which do not easily leave fossil evidence. This is also true of more ephemeral materials like ropes and nets. But with most apparently human-unique features it is possible to assign three rough time points at which the emergence of the feature may have occurred: possible, probable, and definite. Shown in Fig. 9.3 is an example of a collection of such timelines for various prominent examples of uniquely human features, relative to the great apes. Someday, if such a diagram could contain definitive dating for the emergence of all of the items in MOCA, the story of human origins would essentially tell itself.

GENERATING NETWORKS OF RELATIONSHIPS AMONG MATRIX OF COMPARATIVE ANTHROPOGENY TOPICS

Volunteer writers of MOCA topic entries are encouraged to indicate relationships to other topics, designated at the same

three levels as above: possible, probable, and definitive. As such entries are completed it will be increasingly feasible to create complex networks of relationships between many uniquely human features. An early example of such a network is shown in Fig. 9.4. Connections arising from genetic and genomic topic entries will eventually emerge, bringing together the roles of nature and nurture in the origin and evolution of our species.

SYNTHESIS WITH EXISTING THEORIES OF HUMAN ORIGINS

There is no shortage of so-called “umbrella hypotheses,” which try to explain most, if not all, human features based on one underlying mechanism. Given the long time period during which hominins evolved from one or possibly a combination of some ancestral lineages giving rise to modern humans, this is extremely unlikely. On the other hand each of the theories may have something to contribute to understanding human origins. They can all now be reexamined in the context of MOCA Topics, Timelines, and Networks. Eventually, new theories and syntheses may emerge.

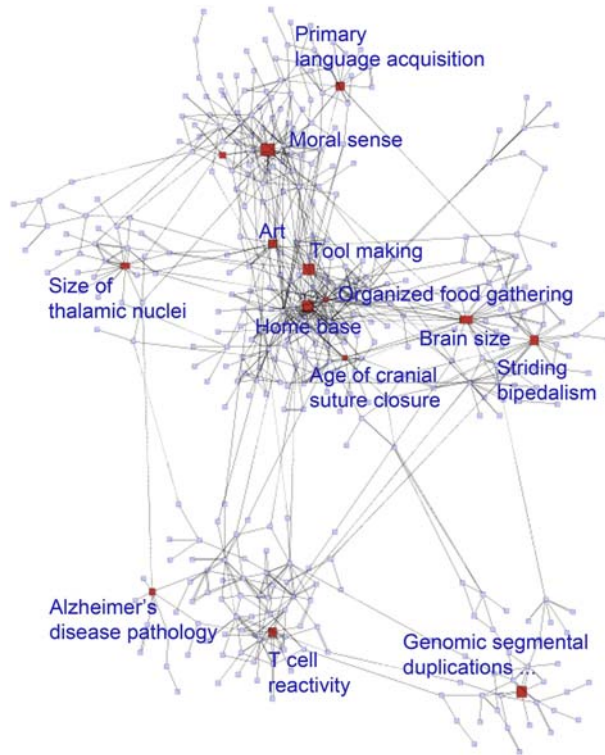


FIGURE 9.4 Example of a relational Matrix of Comparative Anthropogeny (MOCA) topics.

CAVEAT: ABSENCE OF EVIDENCE IN NONHUMAN PRIMATES IS NOT EVIDENCE FOR ABSENCE

Many aspects of claimed human uniqueness have been challenged in recent times. For example, symbolic communication is well documented in several species of nonhuman primates (vervets, guenons). Cultural phenomena have been well described in common chimpanzees, where different types of complex tool uses and foraging behaviors are clearly passed on intergenerationally, by observational learning (Tennie et al., 2009). By the same token, there is no evidence that chimpanzees are aware (have a meta-representation) of their own cultures (Gruber et al., 2015).

MOVING THE GOALPOSTS

With each discovery of a human-like behavior in a nonhuman primate, there is a tendency to redefine the human-like trait so as to exclude the new observation. One is then accused of “moving the goalposts” each time this happens. The problem may lie with where the goalposts were placed to begin with. We should be comparing the capabilities of the average adult human with that of the average great ape, not that of the most successful ape known with that of a four-year-old human. But then, one might be accused of being anthropocentric and promoting human exceptionalism. While there are indeed

many risks involved in pursuing such views, a balanced approach to anthropogeny inherently requires an emphasis on human uniqueness.

CONCLUSIONS AND FUTURE PROSPECTS

It is abundantly clear that the long list of attributes setting humans apart from their ape relatives did not arise overnight, nor were they driven by a single factor. Rather, these traits are the combinatorial outcome of over 6 million years of evolution, during which ancestral populations experienced successive and potentially conflicting selective pressures arising from climate, competition with other species, infectious disease, demographic collapse and recovery, founder events (bottle necks), and niche construction, whereby our ancestors set in place ecological and social-cultural niches which in turn exerted strong selection on past populations. While it is very informative to ponder the circumstances that could have exerted these combined effects on our species, the lack of any other species with symbolic, linguistic, and ratcheting culture makes for an immense challenge when attempting an evidence-based approach to anthropogeny. Humans are both “biologically cultural” with brain development requiring linguistic input and “culturally biological” as cultural practices such as cooking actively changed human biology. The evident animal nature of humans combined with these many human-unique attributes make for a striking paradox.

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