10th Anniversary: Revisiting the Agenda

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Chairs: ***Fred H. Gage,*** *Salk Institute &* ***Pascal Gagneux,*** *UC San Diego*

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ABSTRACTS

Comparative Cognition in Primates

Tetsuro Matsuzawa, Kyoto University

Humans are a member of the order PRIMATES that has 447 species in the recent categorization. Among them, the hominoid family consists of 4 genera: humans, chimpanzees, gorillas, and orangutans. I have compared the cognitive function in humans and chimpanzees, who share a common ancestor 5-7 million years ago. Our laboratory study is known as the Ai-project, and our field study has been carried out in Bossou-Nimba, Guinea-Conakry, West Africa. Humans and chimpanzees are similar at early developmental stages, however, there remain several crucial differences. In comparison to humans, chimpanzees exhibit poor social-referencing abilities and rarely engage in general imitation and active teaching. Young chimpanzees possess exceptional working-memory capacities superior to those of human adults. However, the chimpanzees' ability to learn the meaning of symbols is relatively poor. Human neonates are characterized by the stable supine-posture that enables face-to-face communication via facial expressions, vocal exchange, gestures, and object manipulation. Based on parallel efforts in the field and laboratory, I present possible evolutionary and ontogenetic explanations for aspects of cognition that are uniquely human. The proposed "The Cognitive Tradeoff hypothesis", postulates the existence of a tradeoff between language and memory.
For more information, see Chimpanzee Ai Publications (specifically the Evolution of the brain and social behavior in chimpanzees).

Behavior & Ecology

James Moore, UC San Diego

The Matrix of Comparative Anthropogeny (MOCA, https://carta.anthropogeny.org/moca) lists 72 topics under the domains of Behavior and Ecology, but this greatly underestimates the role of behavior and ecology in hominin evolution. For example, the genetical, physiological and anatomical traits underlying bipedalism all probably owe their evolution to a behavioral change in an ancestor that created selection pressures favoring bipedal locomotion. Much of our understanding of behavior has relied on the phenotypic gambit – the assumption that we can safely ignore the genetic and physiological bases of behaviors and focus on the fitness consequences of phenotypes (their "function"). Doing so has been productive, but explicitly ignoring three of "Tinbergen's four questions" can be problematic: in addition to analysis of adaptive function, full understanding requires knowledge of proximate causation, evolutionary history, and ontogenetic development. In the next 10 years, I expect that a more integrated approach, as illustrated by recent work on the self-domestication hypothesis, will yield insights into the exact sense in which human behaviors have "evolved."

Paleoanthropology & Comparative Anatomy

William Kimbel, Arizona State University

That humans and chimpanzees shared a most recent common ancestor during the late Miocene of Africa is supported by both molecular and fossil evidence, and is beyond serious doubt. Likewise, there is no question that over the course of human evolution, virtually every anatomical/behavioral system (cognitive, reproductive, locomotor, dietary, social, technological) has been substantially refashioned relative to potential ancestral conditions, with dramatic consequences for our life-history. Much less certain are critical details concerning the extent of past taxonomic diversity, the phylogenetic relationships among our extinct ancestors and relatives, and the origin and environmental contexts of major adaptations. Yet each of these issues is an essential link in a chain of arguments from which we forge causal explanations about the past. While significant gaps in fossil and archaeological records account for much of the uncertainty, the mismatch between the scope of many of our key questions and the resolution of the data we bring to bear on them suggests greater modesty about our claims to understanding the past is warranted (e.g., the role of "climate change" in human evolution). Field work targeting under-sampled spans of time and space marks one path forward, but increased introspection about how our research strategies are constructed is a necessary adjunct to the agenda for paleoanthropology.

Nutrition and Paleodiet

Margaret Schoeninger, UC San Diego

Over the last 10 years, the fascination for identifying the 'Natural Human Diet' has expanded beyond anything imagined by Eaton and Konner who authored the first paper on Paleolithic Nutrition. The publication of Paleodiet and Paleonutrition cookbooks has exploded, almost exponentially although the science underlying these diets is not always very convincing. Over the same period, we have seen another explosion in the scientific literature on the diets of some fossil members of our lineage based on dental microwear analyses, stable isotope analyses, and microfossils and DNA in dental calculus. Around 2 million years ago some of our fossil relatives consumed diets unlike anything observed in living primates (e.g., sedges), others began to eat meat, and still others maintained the more general primate diet of leafy plants, fruits, seeds, nuts, and insects. Based on our knowledge of the diets of living nonhuman primates, of extant non-agriculturist humans, and of prehistoric humans, we know that living humans can eat virtually everything and that what cannot be eaten, we often feed to animals that we subsequently consume or we co-opt these animals to provide us with blood or milk for consumption. Yet, these sources show that the highly processed and heavily starch-based diet ingested most commonly across living humans today has existed for only 15,000 years at the very most. The extraordinary dietary flexibility of humans must be considered in order to understand the evolution and appearance of our species, *Homo sapiens*.

Comparative Genomics

Evan Eichler, University of Washington

Huxley and Darwin were among the first to appreciate the close evolutionary relationship of humans and other African great apes but also to ponder what genetic changes might make us human. Initial comparisons of human and chimpanzee genes, however, showed little difference (>99% identical) despite the numerous adaptations that must have occurred on various ape lineages. Most comparative genetic studies over the last two decades have emphasized subtle regulatory differences as underlying most human-chimp differences. Recent studies of more complex regions of our genome have revealed hotspots of rapid and dramatic evolutionary change. Embedded within these regions are hundreds of new duplicate genes several of which appear to be important in unique human-specific neuroanatomical adaptations including the expansion of the neocortex and increase in synaptic connectivity. These same regions have increased ape susceptibility to neurodevelopmental disease (eg. autism, intellectual disability and epilepsy) suggesting that human-specific genes and increased disease burden are linked.

Ancient DNA of Humans and Their Pathogens

Anne Stone, Arizona State University

Advances in method of ancient DNA analysis over the past ten years have transformed our views of human interactions and migrations as well as of the evolutionary dynamics of several of our pathogens. We now know that admixture among archaic and modern humans was common and that human populations have been quite dynamic, both in terms of migrations and admixture and in terms of rapid allele changes that enable environmental adaptation. Questions that remain include what was the role of selection after admixture between archaic and modern humans, how has climate change affected human diversity in the past, can we understand selective pressures on complex traits over time, and what was the diversity and structure of ancient African populations? Ancient DNA has also presented surprises about the emergence of some human pathogens; for example, Y. pestis, the causative agent of plague, has affected humans for much longer than expected, while M. tuberculosis, causing TB, appears to have jumped into humans more recently than previously thought. What may be impossible to know are how these population dynamics (for both humans and pathogens) played out in environments, such as the tropics, where DNA preservation is poor. In addition, some pathogens, such as single stranded RNA viruses may not preserve in any (or most) environments because of their rapid degradation after death. Insights from other ancient biomolecules, including proteins, and additional methodological improvements may overcome some of these obstacles.

Human Population Genetics and Origins

Sarah Tishkoff, University of Pennsylvania

Africa is thought to be the ancestral homeland of all modern human populations. It is also a region of tremendous cultural, linguistic, climatic, and genetic diversity. Despite the important role that African populations have played in human history, they remain one of the most under-represented groups in human genomics studies. A comprehensive knowledge of patterns of variation in African genomes is critical for a deeper understanding of human population history in Africa and the genetic basis of adaptation during human evolutionary history. Identification of functionally important genetic variants that impact human adaptation remains a challenge, particularly for complex traits influenced by multiple genes. Skin pigmentation is a classic example of a complex adaptive trait in humans. However, little is known about the genetic basis of skin pigmentation, particularly in Africa. To alleviate this disparity, we have measured skin pigmentation in a broad range of ethnically diverse Africans and have looked for associations with genomic variants. We observe a wide range of skin pigmentation in Africans and we identify novel variants associated with skin color including a previously uncharacterized gene that plays a critical role in production of pigment in melanocytes. These genes show signatures of natural selection and in many cases, the ancestral variant is associated with light pigmentation. Further, most variants originated before the origin of modern humans in Africa. These data shed light on the genetic basis of skin pigmentation in humans and exemplify how natural selection has shaped the human genome.

Comparative Medicine

Ajit Varki, UC San Diego

Long-term studies of disease incidence and pathophysiology in captive non-human primates have shed much light on human ailments. Much less attention has been paid to disease states that appear distinctly human and are not explained by anatomical differences. Ongoing comparative biomedical studies of humans and other living hominids (particularly chimpanzees, and the other "great apes") have revealed many surprising examples of such disease differences. Conversely, there appear to be some conditions apparently uncommon in humans, but prominent in other hominids. Examples of apparent differences include heart disease, carcinomas, chronic viral infections, autoimmune diseases, neurodegenerative conditions and female reproductive diseases. Given the close genetic similarity of all these species, it is worth continuing to investigate these differences, with the goal of better understanding the pathological processes involved, for the benefit of both humans and other hominids. Studies of ancient DNA may also tell us more about the unusual human disease propensities. This talk will present a brief summary of available information on this topic, mentioning

genetic and molecular explanations to date, and their relevance to anthropogeny. While mechanistic explanations remain unclear in most instances, major ethical and practical issues are also going to limit further understanding of disease differences between humans and our closest living evolutionary cousins.

Mental Disease
Daniel Geschwind, UCLA

One model of neuropsychiatric disease is that risk for these illnesses is heavily intertwined with human brain evolution and therefore, at least partially, a consequence of factors that underlie distinct human cognition and behavior. We know that many of aspects of human cognition and behavior, as well as brain structure are highly heritable, while also subject to major environmental effects, and include factors that may also predispose to common human disorders. Advances in understanding the genetic contributions to neuropsychiatric diseases now permit us to begin to understand how disease risk relates to other human phenotypes and human brain evolution. One particular salient example is the positive correlation between genetic risk for autism spectrum disorder (ASD) and educational attainment (EA), versus an inverse correlation between EA and schizophrenia (SCZ), despite a significant correlation between ASD and SCZ. These findings raise many questions and provide a roadmap for understanding how specific aspects of disease risk overlap, which aspects of brain function they represent, and further, how natural selection may have acted and continues to act on these processes. It has been more than 40 years since the seminal work of King and Wilson highlighted gene regulation rather than protein coding genes as a major source of human evolution. But, it is only recently that we have had the tools, such as the ability to measure gene expression networks across species and genome wide maps of regulatory elements, to study gene regulation. Some of our studies suggest that derived, human-specific gene expression networks may preferentially impact human disease, especially risk for Alzheimer's disease. More recently, we have started to integrate genetic risk data with the emerging maps of gene regulation to study human specific aspects of gene expression and gene regulation. These analyses indicate that human specific aspects of gene regulation, such as genes regulated by human specific enhancers, are indeed enriched in mutations or common genetic variants that increase risk for ASD and allied neurodevelopmental disorders. This provides strong evidence that genetic elements underlying human brain evolution are particularly susceptible to disruption in disease. With the advent of in vitro systems that permit study of brain development we anticipate that the multitude of specific hypotheses that emerge from these genome-wide studies can be directly studied, and models of the specific mechanisms of human cortical expansion and the relationship to psychiatric illness can be directly tested.

Life History
Kristen Hawkes, University of Utah

Humans evolved long before farming and herding began about 10,000 years ago. Where people now depend on wild foods, their practices are an "experimental opportunity" to discover how foraging for a living actually works: the problems and solutions, and especially how those vary by sex, age, and local socioecology. Of course, regional non-foraging political systems, trade with non-foraging neighbors, and recent technology - like motor vehicles and fire arms - commonly alter daily tradeoffs. But even where people are part-time foragers, their experienced assessment of opportunities can be an empirical window into the ancient tradeoffs and constraints that drove the evolution of our lineage. Differences in foraging strategies by sex and age are robust across socioecologies. Men usually specialize in foods taken unpredictably, in large packages, with portions widely claimed by many. Women specialize in foods more reliably acquired and consumed by their own families. Unlike our closest living evolutionary cousins, the great apes (or other mammals generally), humans never acquire all they eat or eat all they acquire. This economic interdependence is closely tied to our distinctive life history. Careful demographies of foraging as well as other traditional populations find age structures like those of state societies. The post-menopausal longevity, later maturation and earlier weaning that distinguish humans are crucial clues to what happened in the evolution of our lineage - now promising to help explain our pair bonding habit, big brains, and distinctively cooperative social appetites.

Parenting and Child Development

Alyssa Crittenden, University of Nevada, Las Vegas

Our species is characterized by extraordinary biological success. We have successfully populated all corners of the planet, calling a wide array of habitats in wildly different ecosystems 'home'. This remarkable success is not only a consequence of our distinct life history characteristics, but is intricately tied to our ability to cooperate with one another. The evolution of human motherhood tells a different story from that of our closest living relatives, the great apes. We have a comparatively long stage of dependence, yet begin to reproduce earlier, and human mothers wean their infants before they are nutritionally independent. This allows them to resume ovulation sooner and have subsequent offspring more rapidly, effectively shortening the interbirth interval (IBI). This shortened IBI allows women to give birth to new infants while simultaneously providing care for existing children, leading to greater reproductive success than their ape counterparts. Because human children are very energetically expensive, it begs the question – how did early hominin mothers do it? The answer is that they did it with help. They relied on assistance extending far beyond the pair bond, or even nuclear families, and were assisted by members of their social group of all ages, including from children. Given that children have a relatively long time to learn how to be a functional adult, social learning further highlights the utility of cooperative ties because adaptive information can accrue over many generations. Children can effectively assist in the care and maintenance of themselves as well as other children – making them an integral part of the human cooperative breeding matrix. In order to understand the history of our species, as it relates to family formation and child development, we must first consider how the distinct reproductive challenges faced by our ancestors were associated with the larger social contexts in which they evolved.

Comparative Brain Anatomy

Katerina Semendeferi, UC San Diego & **Jon Kaas,** Vanderbilt University

The focus will be on what we now know and what we want to know about the functional organization of the human brain and especially human neocortex. We know that humans have the largest brain and more neocortex of all primates, and likely the most neurons in neocortex, which constitutes 80% of our brain. This large cortex is divided into more areas (the organs of cortex) than in any other primate (about 200 per hemisphere), with greater functional and anatomical specializations than any other mammal. We have more extensive developmental and adult plasticity of neocortex and neocortical systems than in other mammals, including systems for memory, that allow us to learn and master specific spoken and written languages, retain vast amounts of cultural information, and recognize thousands of individuals, as well as perhaps, species of birds or kinds of cars. We need to know more fully how human cortex is divided into areas, more precisely what defines each area, how areas are divided into two or more classes of functional modules, how areas interact cortically and subcortically within functional networks, and how networks interact. Importantly, we need to know from comparative studies, how the human brain evolved from ancestors with less complex brains, and how the complexity of human brain emerges and varies in pre and post-natal development.

Language

David Perlmutter, UC San Diego

Combinatoriality in the evolution of human language. What is the question to ask about the evolution of human language? We know for certain that there is no way to reconstruct an original language or protolanguage by tracing contemporary languages back in time. There have been a number of proposals about how human language originated. Here we focus on how language came to have the form it has, concentrating on *phonology*, the combinatorial system that combines meaningless speech sounds into meaningful words. While the earliest stages of the phonologies of *spoken languages* evolved too long ago to be reconstructed, we can learn much from the *sign languages* that have evolved much more recently among deaf people and in communities with a significant deaf population. The key concept is the contrast between gestures and signs. While gestures vary in all kinds of ways, Stokoe (1960) showed that the signs of American Sign Language (ASL) consist of smaller parts (handshape, movement, and location) that combine to yield different signs. Like spoken languages, ASL and other mature sign languages have combinatorial phonological systems. With a relatively small inventory of handshapes, movements, and locations, many different combinations are

possible, yielding a large number of signs. Do sign languages have combinatorial phonological systems from the outset? Sandler *et al.* (2011) studied a newly developing sign language used by deaf and many hearing people in a Bedouin community in the Negev desert in southern Israel. They argue convincingly that it does not have a combinatorial phonological system like mature sign languages. These Bedouins communicate with gestures, not combinatorial signs. This is evidence of the viability of gestures for communication, at least in a small community whose members all know each other and share knowledge of their surroundings. New sign languages may begin as such gestural systems, evolving into sign language over time. What would cause a gestural system to evolve into a sign language? First a combinatorial phonology yields more consistent and uniform articulation in the community, facilitating comprehension of others' signing. With gestures, nothing would constrain variation and hence difficulty understanding others. Second, combinatorial phonology makes possible a vast expansion of the vocabulary. The relation between a sign's meaning and its form can be arbitrary, like the relation between words' sounds and their meanings in spoken languages. This enables combinatorial sign languages to have signs for any meaning. These two advantages of combinatorial sign languages like ASL over gestural communication are precisely what did *not* result from attempts to teach ASL to chimpanzees. First, the chimpanzees' "signing" was judges by ASL signers to be "erratic" – as opposed to the more consistent and relatively uniform signing of human signers. This is explained if the chimpanzees had not learned ASL's combinatorial phonology that shapes human signing. Second, while a combinatorial phonology makes possible a vast increase in the size of the vocabulary, the chimpanzees' vocabulary was tiny. This is explained if they had not learned any signs at all, but only a small number of gestures. We conclude that chimpanzees do not have the combinatorial abilities needed to learn a human language. Phonology is only one of several combinatorial systems in human language. Morphology combines meaningful parts of words into complex words, syntax combines words into phrases and phrases into sentences, semantics combines word meanings into the meanings of phrases and sentences. All take advantage of humans' combinatorial abilities. Chimpanzees' failure to master ASL phonology is due, we claim, to their not having those abilities. It is our combinatorial abilities that make human language possible. We are a combinatorial species.

Computational Neuroscience

Terry Sejnowski, Salk Institute

Ten years, ago we simulated small network models of the cortex and other parts of the brain and demonstrated that they could account for basic aspects of perception, working memory and decision making. However, these were toy models compared to real brain circuits, and many aspects of cognition, such as language, remained a mystery. Two revolutions have occurred in the last decade that are rapidly opening up a new era. In neuroscience, new optogenetic tools have made it possible to record from thousands of neurons simultaneous in several brain regions and selectively manipulate different types of neurons. Seeing the brain through the lens of neural populations has opened up a new dynamical perspective on cognitive function. The second revolution is based on deep learning in layered neural networks, based loosely on the architecture of the cortex, that can recognize speech, objects in images, translate between languages and, with the addition of a basal ganglia model, play Go at superhuman levels. This may lead to a better understanding of how language could have evolved from the previously existing cortical architecture in nonhuman primates.

Cultural Evolution and Dual Inheritance

Joseph Henrich, Harvard University

To seat humans within the natural world while recognizing our peculiar attributes, evolutionary researchers have increasingly recognized that humans—from our anatomy and physiology to our psychology and behavior—are the product of at least two distinct, but intertwined, inheritance systems, one based on genes and another on culture. To understand the emergence of our cultural inheritance system, much research now demonstrates how natural selection has shaped our attention, memory and motivation to improve our capacities for cultural learning, which infants, children and adults use to acquire everything from food preferences and word choice to tool making and social norms. However, filtered by these learning abilities, an accumulating body of adaptive information about processing food (e.g., cooking), making tools and communicating widely has shaped our species' genetic evolution,

expanding our brains, shrinking our guts, freeing out tongues and domesticating our sociality. In this talk, I'll explore the centrality of culture-gene coevolution for understanding human evolution, genetic variation, anatomy and psychology.

Morality and Cooperation

Patricia S. Churchland, UC San Diego

Morality is a social behavior seen in mammals, including humans, that depends on an interlocking brain organization shaped by four factors: (1) caring (rooted in attachment to kin and kith, and the pain of isolation), (2) recognition of others' psychological states (goals, feelings, needs); (3) learning social practices that emerges from the interactions of the reward system, hippocampus, and cortex (4) problem-solving in a social context (figuring out what modifications to a social practices serve stability and prosperity). Between species, the importance of these factors can vary. Social benefits are accompanied by social demands; we have to get along, but not put up with too much. Hence impulse control -- being aggressive or compassionate or indulgent at the right time -- is hugely advantageous. In hominins, the greatly expanded prefrontal cortex probably aided self-control, as well as problem-solving skills in both social and nonsocial domains, and augmented by the capacity for language. For most of our 300,000 years on the planet, hominin groups were small and moral practices were part of the shared tradition, encapsulated in habits as well as in songs, stories, and rituals. With the advent of agriculture about 10,000 years ago and the formation of much larger groups of humans, writing of laws became a tool to ensure everyone knew what was expected. Outstanding questions include how to foster cooperation when groups are very large and national self-interest is strong.