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The Stone Age Institute Press has been established to publish critical research into the archaeology of human origins. The Stone Age Institute is a federally-approved non-profit organization whose mission is investigating and understanding the origins and development of human technology and culture throughout the course of human evolution, and to disseminate information to the general public regarding science education, in particular about our evolutionary origins. The ultimate goal of these undertakings is to provide a better understanding of the human species and our place in nature.

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Kathy Schick and Nicholas Toth
Co-Directors, Stone Age Institute
Series Editors, Stone Age Institute Press Publication Series

STONE AGE INSTITUTE PUBLICATION SERIES
NUMBER 4
Series Editors Kathy Schick and Nicholas Toth

THE HUMAN BRAIN EVOLVING:

Paleoneurological Studies in Honor of Ralph L. Holloway

Editors

Douglas Broadfield
Florida Atlantic University

Michael Yuan
Columbia University

Kathy Schick
Stone Age Institute & Indiana University

Nicholas Toth
Stone Age Institute & Indiana University

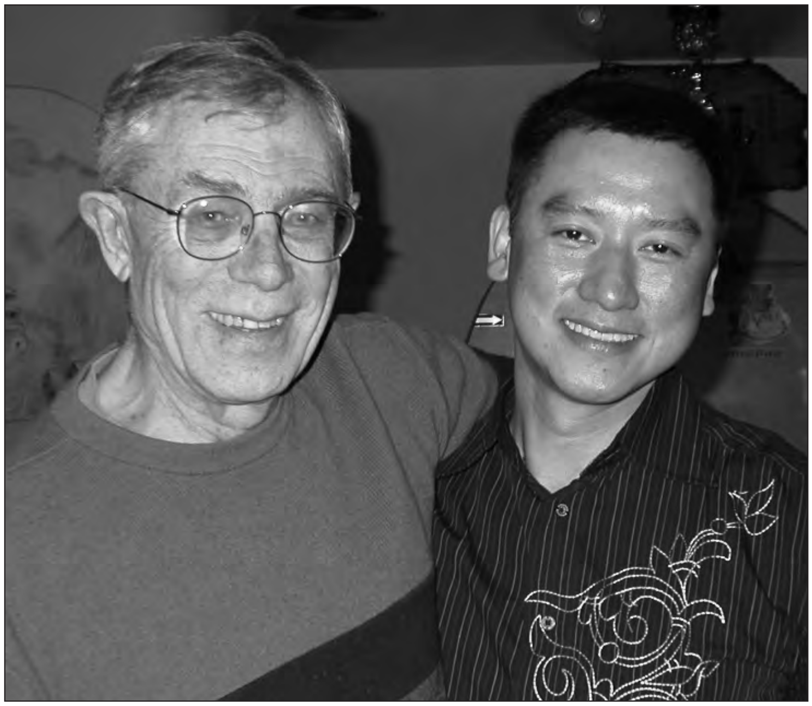
Stone Age Institute Press · www.stoneageinstitute.org
1392 W. Dittemore Road · Gosport, IN 47433

FRONT COVER CAPTIONS

Center: Portrait of Ralph L. Holloway.
Upper left: A modern human brain.
Upper right: Ralph measuring landmarks on an endocast ca. 1976.
Lower right: Homo habilis cranium KNM-ER-1813 from Koobi Fora, Kenya (photo by Holloway).
Lower left: Ralph with an endocast of the Flores "hobbit" cranium.

Published by the Stone Age Institute.
ISBN-10: 0-9792276-3-1
ISBN-13: 978-0-9792276-3-9

DEDICATION



To
Michael Sheng-Tien Yuan

Michael Sheng-Tien Yuan, D.D.S., M.A., M.S., Ph.D. was born in Taiwan (ROC) on November 17, 1959. In an earlier life before he chose orthodontics and anthropology as his careers, Michael was an internationally recognized actor, earning acclaim for his role in the Taiwanese motion picture *Jade Love* (1984), which received a number of Golden Horse Awards and was featured at film festivals around the globe. In 1988 after completing his dental degree at National Taiwan University and two years of compulsory military service, Michael moved to New York to work on his Master's in orthodontics from Columbia University. After completing his orthodontics degree Michael entered the Ph.D. program in Anthropology at Columbia. Shortly after entering the anthropology program Michael had his last brush with the acting bug when he was offered the lead in Ang Lee's first American film, *The Wedding Banquet* (1993). Michael turned down the offer, choosing instead to focus on his new career.

Michael was Ralph Holloway's student from the moment he entered the anthropology program. He worked closely with Ralph and Doug Broadfield on a number of endocast projects, bringing his ample artistic skills to the science of paleoneurology. Though his dissertation work was on dental development, Michael is most remembered in anthropology for his contributions to our understanding of human brain evolution. After completing his Ph.D. in 2000, Michael moved back to Columbia's College of Dental Medicine as an Assistant Professor of Clinical Dental Medicine. As with everything he did Michael threw himself entirely into his new profession, anatomist. He earned a third dental degree in 2003.

In his short tenure at Columbia, Michael became one of the most beloved instructors in not only the College of Medical Dentistry, but also Columbia's College of Physicians and Surgeons, earning three Teacher of the Year awards. He was promoted to Associate Professor in 2008. After Michael became ill he continued to teach from his hospital bed, sending the medical and dental students details of the various procedures he underwent, and relating them to the current anatomical region the students were learning. True to the way he lived, the dedication on his last teaching award summarizes our feelings for Michael: …in appreciation for his "wisdom, gentleness, and ability to … accept life's challenges and use them to grow."

Contributors

John M. Allman (cebus@caltech.edu) Division of Biology, California Institute of Technology, Pasadena, California, USA

Nicole Barger (nbarger@ucsd.edu) Department of Anthropology, University of California at San Diego, USA

Doug Broadfield (broadfie@fau.edu) Department of Anthropology, Florida Atlantic University, Boca Raton, Florida, USA

Emiliano Bruner (emiliano.bruner@cenieh.es) Centro Nacional de Investigación sobre la Evolución Humana, Burgos, Spain

Daniel P. Buxhoeveden (buxhoeve@gwm.sc.edu) Department of Psychology, University of South Carolina, Columbia, South Carolina, USA

Joseph M. Erwin (agingapes@gmail.com)Foundation for Comparative and Conservation Biology, Needmore, PA

Dominique Grimaud-Herve (dgherve@mnhn.fr) Département de Préhistoire, Muséum national d'Histoire naturelle, Paris, France

John W.K. Harris (jwharris@rci.rutgers.edu) (PhD, U California-Berkeley, 1978; Prof, SAS) Center for Human Evolutionary Studies, Department of Anthropology, Rutgers University, New Brunswick, New Jersey, USA

Patrick R. Hof (patrick.hof@mssm.edu) Department of Neuroscience, Mount Sinai School of Medicine, New York, NY

Ralph L. Holloway (rlh2@columbia.edu) Department of Anthropology, Columbia University, New York, New York, USA

Karin Isler (kisler@aim.uzh.ch) Anthropological Institute & Museum, University of Zürich-Irchel, Zürich

Jason A. Kaufman (kaufman@caltech.edu) Division of Biology, California Institute of Technology, Pasadena, California, USA

James E. King (kingj@U.Arizona.edu) *Emeritus*, Department of Psychology, University of Arizona, Tucson, Arizona, USA

David Lordkipanidze Georgian National Museum, Departement of Geology and Paleontology, Academy of Sciences of Georgia, Tbilissi, Georgia

Alan Mann (mann@Princeton.edu), Department of Anthropology, Princeton University, Princeton, New Jersey, USA

Robert D. Martin (rdmartin@fieldmuseum.org) Department of Anthropology, The Field Museum, Chicago, Illinois, USA

Janet Monge (jmonge@sas.upenn.edu), Department of Anthropology, University of Pennsylvania, Philadelphia, Pennsylvania, USA

Francine "Penny" Patterson The Gorilla Foundation, Woodside, California, USA

Mary Ann Raghanti (mraghant@kent.edu) Department of Anthropology and School of Biomedical Sciences, Kent State University, Kent, OH

James K. Rilling (jrillin@emory.edu) Department of Anthropology and Center for Behavioral Neuroscience, Emory University, Department of Psychiatry and Behavioral Sciences, Emory University School of Medicine and Division of Psychobiology, Yerkes National Primate Research Center, Atlanta, Georgia, USA

Duane M. Rumbaugh (drumbaug@aol.com) *Emeritus*, Language Research Center and Department of Psychology, Georgia State University, Atlanta, Georgia, USA

E. Sue Savage-Rumbaugh (suerumbaugh@gmail.com) Great Ape Trust, Des Moines, Iowa, USA

Natalie Schenker (nmschenker@ucsd.edu) Department of Anthropology, University of California at San Diego and Department of Anthropology, The George Washington University, Washington, D.C., USA

Kathy Schick (kaschick@indiana.edu) Stone Age Institute and Indiana University, Bloomington, Indiana, USA

P. Tom Schoenemann (toms@indiana.edu) Anthropology Department, Indiana University, Bloomington, Indiana and Stone Age Institute, USA

Katerina Semendeferi (ksemende@ucsd.edu) Department of Anthropology and Graduate Program in Neurosciences, University of California at San Diego, USA

Chet C. Sherwood (sherwood@gwu.edu) Department of Anthropology, The George Washington University, Washington, D.C.

Francys Subiaul (subiaul@aol.com) The George Washington University, Mind, Brain & Evolution Center, Department of Speech & Hearing Science, Washington, D.C., USA

Jared Taglialatela (jtaglial@kennesaw.edu, jtaglia@emory.edu) Department of Biology, Kennesaw State University and Yerkes National Primate Research Center, Emory University, Atlanta, Georgia, USA

Nicholas Toth (toth@indiana.edu) Stone Age Institute and Indiana University, Bloomington, Indiana, USA

J. Michael Tyszka (jmt@caltech.edu) Brain Imaging Center, California Institute of Technology, Pasadena, California, USA

Eric J. Vallender (eric_vallender@hms.harvard.edu) New England Primate Research Center, Harvard Medical School, Southborough, Massachusetts, USA.

Anne H. Weaver, Ph.D. (oneweaver@msn.com) Anthropology Department, University of New Mexico, Albuquerque, New Mexico, USA

THE HUMAN BRAIN EVOLVING: PALEONEUROLOGICAL STUDIES IN HONOR OF RALPH L. HOLLOWAY

EDITED BY
DOUGLAS BROADFIELD, MICHAEL YUAN, KATHY SCHICK AND NICHOLAS TOTH
STONE AGE INSTITUTE PRESS, 2010

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Preface

For those who work in the area of human brain evolution Charles Duell's, Commissioner of the United States Patent Office, 1899 mythical quip that "Everything that can be invented has been invented," seems abundantly appropriate to the nearly fifty year long career of Ralph L. Holloway, Jr. As each of us has struggled to introduce the field to a supposedly new idea, we each at some point have run headlong into a similar idea proposed by Ralph some ten, twenty, or forty years earlier. While this may seem dejecting, few researchers in the field have ever been made to feel this way by Ralph. Instead we and the field in general have been propelled forward by Ralph's boundless curiosity.

On April 27 – 28, 2007 researchers from Europe and the United States gathered at the Stone Age Institute and Indiana University to celebrate and pay tribute to Ralph Holloway's unparalleled contributions to the field of human brain evolution. Reflecting the diversity of Ralph's research, the symposium was an eclectic mix of the top minds in the field who over a two period synthesized ideas from the fossil record, state-of-the-art imaging, neuroscience, behavior and genetics, culminating in this festschrift, *The Human Brain Evolving: Paleoneurological Papers in Honor of Ralph L. Holloway*.

The content of the symposium ranged from the latest unpublished findings, modern revisions of previously proposed hypotheses of brain evolution, and new syntheses of current information. The papers presented in this volume represent in part many of the ideas presented at the symposium as well as reflections on the diverse discussions of the topics covered and the presentation of new data collected in response to conversations held at the symposium, making *The Human Brain Evolving: Papers in Honor of Ralph L. Holloway* unique in that a collection of such diverse topics in the field of human brain evolution have never been presented before in one place.

The symposium leading to this volume was the culmination of discussions that began back in the mid-1990s between one of our beloved colleagues to whom this book is dedicated, Michael Yuan, and Doug Broadfield. At that time Ralph discussed his retirement as eminent. Originally, Ralph had planned to retire from Columbia University around 2007, making the timing of the symposium apropos. The fruition of the symposium is due in large part to Kathy Schick and Nick Toth, co-directors of the Stone Age Institute, who not only threw the entire assets of the institute behind the planning and execution of the symposium, but also sacrificed their personal time and energy to put together what for many was a flawless and memorable weekend. In addition, the symposium was only possible through the generous support of not only the Stone Age Institute, but also the College of Arts and Sciences of Indian University, the Office of the Provost of Indiana University, the Indiana University Foundation, Carol Travis-Henikoff, Anthony Hess and Richard Foley. The conversations generated by the various talk were often sparked by the discussants, Bill Kimbel and Leslie Aiello, who managed to shed new light on the topics present through deft synthesis of the data and hypotheses. Finally, we are indebted to Mila Norman and Blaire Hensley-Marschand of the Stone Age Institute who worked behind the scenes to make sure no detail in pulling off the symposium was missed, and to Amy Sutkowski and Lawrence Buchanan for their help in the layout and design of this volume.

Often when a symposium is planned the organizers attempt to draw together a slate of experts in the field that often have a relationship with the honoree. In many ways a symposium of this nature is a reflective look back on the esteemed career of a beloved colleague by friends and former students. In determining the list of attendees it was necessary to pare a list of nearly one hundred individuals down to approximately twenty-five. While this unenviable task is often relegated to the organizers, we also solicited Ralph's input. The result was a menagerie of experts less chosen for their close personal relationship with Ralph and more simply because Ralph was fascinated by an individual's research. As a consequence of satisfying Ralph's unrivaled curiosity, the symposium was not just a meeting of minds, but also a meeting of firsts. It was one of the first symposia that brought together individuals from what before then were widely disparate fields such as paleoanthropology and molecular biology. It was also ironically the first time Ralph had ever met some of the participants in person. That someone would participate in a symposium for an individual they had never met is a genuine reflection of the admiration and respect scientists the world over have for Ralph Holloway.

Doug Broadfield
October 2010

Introduction

Douglas Broadfield, Kathy Schick and Nicholas Toth

The human brain is arguably the most important product of our evolution. How our early ancestors moved about the landscape looks to the question, when did hominins separate from the ancestor we share with chimpanzees, but it does not answer the question, when did our ancestors begin to think like us? It is assumed that the answer to this question is as simple as looking at the fossil record and recording the time when brain size increased above that of other apes. While early researchers such as Keith, Smith, and Broca among others assumed that human cognition is the result of brain size, more recent studies have done much to elucidate our understanding of human brain evolution.

For over a century researchers from all areas of science have weighed in on the evolution of the human brain usually drawing from their own knowledge in medicine, neuroscience, behavior or paleontology. In many ways the study of human brain evolution was viewed more as a hobby rather than a research career path. The result was a confusing oversimplified picture of brain evolution. However, this armchair approach to the subject all changed with Ralph Holloway's 1967 publication *The Evolution of the Human Brain* in the journal *General Systems*, albeit he did not know quite yet what to make of endocasts. In less than ten years, though, Holloway (with credit also going to Harry Jerison) had established a new field of study, *paleoneurology*, or the study of nervous system evolution.

From April 27-28, 2007 researchers from North America and Europe came together at Indiana University and the Stone Age Institute for *The Human Brain Evolving: Papers in Honor of Ralph L. Holloway* to celebrate the achievements of Ralph Holloway as well as to present the current status of the fledgling field of paleoneurology and to discuss its future. The result of the conference as demonstrated in the works presented here is that Holloway's seminal work has been responsible for turning paleoneurology into a dynamic field that cuts across all disciplines. The most noticeable characteristic of the works presented here is that they are not limited to a single line of study, say endocasts. Instead paleoneurology has evolved into a diverse field that draws data from every available technique, including genetics, behavior, the fossil record and imagining modalities. As a result, the chapters of this volume are loosely arranged into seven different topical themes.

The first set of papers looks at the theoretical concept of brain evolution. **Chapter 1** by Ralph Holloway is a retrospective originally published in *Annual Review of Anthropology* that sincerely captures the evolution of the field. What is most revealing in this chapter is that Holloway like others before him had difficulty early in his career accepting the validity of fossil endocasts as analytical tools. The reader will also learn about the principal themes of brain evolution first developed by him that still dominate the field today. **Chapter 2** by Robert Martin and Karin Isler is the result of 30 years of research on the Maternal Energy Hypothesis, an idea Martin first introduced in 1981 that examines the developmental strategies that go into the evolution of large brains. The Maternal Energy Hypothesis looks at mammalian brain evolution in general, but the concepts of the hypothesis are directly applicable to human brain evolution. The last chapter in this section, **Chapter 3** by Tom Schoenemann, takes a closer look at a specific problem in human brain evolution, the importance of brain size. Here Schoenemann argues that absolute increases in brain size observed in the fossil record likely resulted in concomitant alterations in cognition, spurring the development of features such as language.

The next section of papers looks at evidence that focus on the hard evidence for brain evolution, endocasts. **Chapter 4** by Ralph Holloway presents a new interpretation of the controversial LB1, *Homo floresiensis*, endocast. Here it is suggested that LB1 displays characters in the endocast that are similar to modern microcephalics while also possessing features that may be autapomorphic. The bottom line, though, according to Holloway is that the jury is still out on the status of LB1 until more specimens can be found. In **Chapter 5**, Dominique Grimaud-Herve and David Lordkipanidze take an in-depth look at a couple of possible ancestors to *H. floresiensis* in the Dmanisi fossils D 2280 and D 2282. Like LB1 these have been controversial for their taxonomic designations based on a unique suite of features absent in contemporaneous fossils. Based on the affinities observed in these endocasts to early members of *H. erectus* the authors conclude that D 2282 may be *H. ergaster* while D2282 is likely *H. erectus*. **Chapter 6** by Emiliano Bruner examines the evolution of the parietal cortex in later human groups, primarily Neanderthals and early modern humans. Through a morphometric analysis of endocasts, Bruner proposes that the parietal lobes of some late hominins increased allometrically with brain size, but that in modern humans the parietal lobes increased non-allometrically or are larger than what would be predicted for a hominin with our brain size. The final paper in this group, **Chapter 7**, by Anne Weaver takes a look at one of the most overlooked brain regions, the cerebellum. The cerebellum, an area dedicated to motor coordination and related tasks, is assumed to have changed little during the course of primate brain evolution. However, approximately 30,000 years ago the relative size of the cerebellum compared to the size of the cerebrum changed – the cerebellum became relatively large next to the cerebrum when compared to our most immediate ancestors. Weaver suggests that while the evolutionary reasons for the change are uncertain, the changes appear to occur around the time significant mutations in regulatory genes such as microcephalin and ASPM appear.

Anne Weaver's analysis of cerebellar evolution in *H. sapiens* is a beautiful introduction to the chapter that follows. **Chapter 8** on *Study of Human Brain Evolution at the Genetic Level* stands alone as a unique section on the genes important to brain development by two of the leading researchers in the field, Eric Vallender and Bruce Lahn. Several years ago Lahn's lab at the University of Chicago published several seminal papers on the importance of understanding evolution, including brain evolution, through the action of genes. Two of those genes ASPM and microcephalin according to Vallender and Lahn, may figure prominently in brain evolution, primarily the evolution of modern human brain size. In addition, Vallender and Lahn cautiously remind the reader that work in this area of paleoneurology is only in its infancy and that much of the heavy lifting is yet to be done.

The next section of the book focuses on a collection of papers that examine brain evolution through examination of the neurological and neurocytoarchitectural evidence derived through a variety of techniques as well as development. In **Chapter 9**, Katerina Semendeferi and her team look at the evidence for human brain reorganization by examining the brains of our closest living primate relatives, the apes. One of the most important outcomes of their studies is the conclusion that the human brain is the result of mosaic evolution, increasing disproportionately not only in more derived regions, but also in areas assumed to be conservative in function and development.

One research method that is just beginning to impact the field is the application of diffusion tensor imagining. Previously the only methods for deriving brain pathways and activity were invasive experiments and certain imaging techniques. Among the imaging techniques that can be used to view brain activity in real time are the two, Positron Emission Tomography (PET) and Functional Magnetic Resonance (fMRI), that can generally provide insight into the connectivity and functionality of various brain pathways. However, the biggest impediment to using these modalities to study brain evolution is figuring out how to get your subject, say a chimpanzee, to lie still in the machine and cooperatively follow your commands without moving too much. Today a new technique known as Diffusion Tensor Imaging (DTI) is permitting researchers the first opportunity to access brain regions once off limits with other techniques. **Chapter 10** by Jim Rilling and **Chapter 11** by Jason Kaufman et al. provide insight into the value and application of this revolutionary approach. Rilling uses *in vivo* images of macaque, chimpanzee and human brains to demonstrate the difference observed between these species with regard to brain activity and lateralization. Complementing Rilling, Kaufman et al. apply DTI to a preserved gorilla brain to reconstruct various fiber tract pathways. This methodological paper for the first time looks at the capacity to delve into the histology of the brain in valuable specimens that are often unavailable for sectioning, using DTI. It also provides important information on the current shortcomings of imaging techniques (see also Chapter 4), and the need for more research on the methodology of imaging techniques.

Chapter 12 examines an often-overlooked aspect of brain organization, minicolumns. Here Dan Buxhoeveden revives Pasko Rakic's seminal work in the 1970s that found that the brain is organized into minicolumns that are a product of how the brain develops its various neurocytarchitectural layers. Buxhoeveden hypothesizes that the development of minicolumns directly affects features such as brain size and organization. This echoes to a certain degree Vallender and Lahn's paper discussing the effects of genes on brain development and evolution, suggesting that the development of additional minicolumns that may affect brain size as well as the variability among minicolumn size and distribution are likely the result of mutational events. Along these specific lines, in **Chapter 13** Raghanti et al. examine the effects of neurotrasmitter systems in cognition. However, unlike minicolumns where some of the genetics that likely affect their development have been discerned, the evolutionary consequences of the genes behind neurotransmitters are far from being well understood. Few researchers have attempted to link neuromodularity to human brain evolution, but as Raghanti et al. demonstrate the differences in the function of the three neurotransmitters studied are so acute between humans and chimpanzees that they not only provide an explanation for cognitive differences between us and our closest living relative, but also a potential explanation for certain human neuropathologies such as schizophrenia.

In **Chapter 14**, Doug Broadfield investigates sex differences in the corpus callosum. In 1982 Holloway and Kitty de Lacoste published a seminal paper on sex differences in the corpus callosum of humans, finding that the corpus callosum of females was proportionally larger than males. This paper set off a firestorm, and for the second time in his career Holloway earned credit for establishing a new field in neuroscience, this being sex differences and the brain. As with other questions examined here it is understood that modern humans display a particular feature apparently unique to the species. As with the question of when did the brain enlarge, Holloway's work on the corpus callosum raised the issue of when sex differences appear in hominins. In this study Broadfield looks at the corpus callosum of chimpanzees to determine if sex differences are an ancient feature of brain evolution or a recent phenomenon. In this case it appears that human sex differences in the corpus callosum are unique, albeit apparently built on a trend that stretches back to the last common ancestor we shared with chimpanzees.

The next two papers in the volume may appear somewhat out of place among studies of neurotransmitters and endocasts, but as the reader with gather from these two papers, understanding development is imperative to understanding brain evolution. The first of these papers (**Chapter 15**) is by Janet Monge and Alan Mann, two researchers that have spent much of their careers studying issues of development. Here Monge and Mann provide new evidence that provides valuable insight into modern human development as well as early hominin development. By knowing how our early ancestors developed we can have a better idea of how brain growth proceeded as well as obtain reliable measurements of adult brain size from juvenile specimens. In the second paper related to dental development our late colleague Michael Yuan presents data that supplements and in some ways challenges the work of Mann and Monge. In **Chapter 16**, Yuan looks at perikymata counts in Asian populations to determine if the use of perikymata in determining age in modern human populations needs to be reexamined.

The last section of this volume looks at brain evolution through behavior. While there are countless studies on animal and primate cognition, most do not examine animal cognition through the lens of human brain evolution. Two papers look at human brain evolution through two behaviors that are central to human cognition, learning and language. **Chapter 17** by Francys Subiaul examines human brain evolution through imitation learning. Imitation is an important skill for many animals, especially primates. We learn most of the skills we acquire early in development through imitation. By looking at macaques, apes and humans Subiaul concludes that human imitation did not evolve singularly, but instead arose as a result of mosaic evolution acting on multiple brain regions over the course of millions of years through selective pressures arising from ecological, technological and sociological means. **Chapter 18** by Duane Rumbaugh, Sue Savage-Rumbaugh, James King, and Jared Tagialatela takes a look back at the Rumbaughs' work on language acquisition in chimpanzees and bonobos. They conclude that based on the capacity for apes to acquire language along with other expressions of intelligence they display human brain evolution did not proceed with the development of human brain structure *de novo*, but instead occurred via to co-option and exaptation of structures that exist with the ape brain. In this volume's final chapter (**Chapter 19**), Nicholas Toth and Kathy Schick review the prehistoric archaeological record and examine how it correlates with probable brain reorganization and speciation in the course of human evolution. They document the appearance of novel behaviors over the past several million years of evolution and assess their cognitive complexity.

Almost fifty years ago Ralph Holloway exploded out of Berkeley to take on a field that was transitioning from the assumption that brain evolution was a simple matter of evolving big brains to the realization that human brain evolution is an immensely complex problem. Relying on little more than infinite curiosity and an innate ability to synthesize presumptively disparate data, Ralph Holloway changed the face of Anthropology. Ralph's contributions are too numerous to count. He lent his knowledge of neuroscience to the fossil records to make endocasts relevant not just for what they reveal about brain size, but also for the features they possess and what they can tell us about the mosaic evolution of the brain. He also charted the course for others by telling anyone interested where they should be looking for answers (e.g., inside the brain, in behavior, through sex differences, through modern variation). The result of this lifetime of work is a vibrant field, producing this volume on a variety of topics all related to brain evolution. To paraphrase Isaac Newton, if we the editors, authors, and others in the field see a little further, it is because we stand on the shoulders of giants. Ralph Holloway is certainly one of those giants.