THE CEREBELLUM AND COGNITIVE EVOLUTION IN PLIOCENE AND PLEISTOCENE HOMINIDS

BY

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To the Company of Scholars.

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ABSTRACT

In the course of hominid evolution, the both the cerebellum and the neocortex have expanded, but they have done so at different rates. Differences in relative cerebellar volume with respect to overall brain and body size among Pliocene and Pleistocene hominids correlate with archeological and skeletal indicators of cognitive evolution.

The cerebellum and the neocortex process information in different but complementary ways. The neocortex manipulates mental representations of objects, concepts, and events using data-rich “declarative” learning and memory processes. The cerebellum, on the other hand, uses “procedural,” rule-based and hierarchically organized functions to coordinate a continuum of sensory-motor and cognitive neural representations (Parkins 1997; Ullman in press).

The present study used integrated data from Magnetic Resonance Images of living human and non-human primate endocrania and three-dimensional virtual models of hominid endocasts. Reduced major axis and least squares regression were used to calculate actual/predicted cerebellar volume with respect to brain volume (“cerebellar quotient” = “CQ”) for a sample of living primates, including recent humans, and fossil hominids.

The evidence supports a three-stage model of hominid cerebellar evolution. In the first stage, brain mass expanded non-allometrically with respect to body mass (encephalization). CQ increased in parallel with encephalization, as *H.* habilis and *H. erectus* gradually developed a high level of technological competence, reflecting well-developed procedural cognitive processes and cultural mechanisms for disseminating technological information. In the second stage, represented by Middle Pleistocene, Late Archaic, and Early Modern *Homo sapiens*, absolute cerebellar volume increased only slightly, accompanied by a dramatic expansion of the neocortex, resulting in a marked decline in CQ. Neocortical expansion supported declarative knowledge with respect to the rich repertory of objects and activities and their mental representations. In the third stage, *after* the emergence of early anatomically modern humans, both brain and body mass were reduced, but absolute and relative cerebellar volume increased. Cerebellar algorithms for manipulating sensory-motor representations were extended to manipulation of conceptual representations as well. Computational efficiency was increased without an increase in overall brain mass.

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1 INTRODUCTION

Purpose

The research described below addresses the broad question of when the particular array of mental qualities characteristic of modern humans evolved. The study focuses on the specific problem of whether there are significant differences in relative cerebellar volume in Pliocene and Pleistocene hominids that can be related to archeological and skeletal evidence for mosaic developments in cognitive evolution.

Significance of Research

The results produced by the present research support an integrated, parsimonious model of human cognitive evolution incorporating the cerebellum as a major contributor to behavioral differences among Pliocene and Pleistocene hominds. In addition to its considerable explanatory power, the model described in the chapters following is capable of generating numerous testable hypotheses.

Role of the Cerebellum in Cognition

The cerebellum contributes to many cognitive functions. It is involved in working memory and regulates voluntary direction of attention (LaBar, Gitelman, Parrish and Mesulam 1999). It participates in cognitive control of language processes (Iidaka, Sadato, Yamada and Yonekura 2000; Price, Green and von Studnitz 1999; Schumacher, Lauber, Awh, Jonides, Smith and Koeppe 1996; Schlosser, Hutchinson, Joseffer, Rusinek, Saarimaki, Stevenson, Dewey and Brodie 1998; Silveri, Leggio and Molinari 1994). It also regulates higher order aspects of motor learning and memory (Ito 1990; Jenkins and Frackowiak 1997; Mushiake and Strick 1993).

The cerebellum and the neocortex represent and process information in fundamentally different, but complementary ways (Parkins 1997). Neurological functions in which the cerebellum participates are “procedural” (hierarchically organized and rule-based) rather than “declarative” (based on manipulations of individual mental representations of facts and events) (Ullman In press). Increasing cultural complexity in the Pliocene and Pleistocene required shifts in cognitive strategies that altered the functional balance between the neocortex and the cerebellum. Cerebellar changes in the context of other indicators of cognitive evolution can help to identify important phylogenetic turning points, the behavioral changes that accompanied them, and the selective forces that shaped them.

Results of the research described below suggest that cerebellar evolution in hominids occurred in three distinct stages, which parallel the conventional Lower, Middle and Upper Paleolithic stages of archeology. More fine-grained changes in cerebellar volume relative to overall brain size accompanied transitions within Stages Two and Three: from the Early to the Developed Acheulean; and from the Early to the Late Upper Paleolithic.

Research Hypotheses

Overview of Question

The research project was designed to evaluate evolutionary changes in volume of one clearly delimited region of the brain, the cerebellum. Most functional regions of the brain register ambiguously on fossil hominid endocasts. The cerebellum, occupying the posterior cranial fossa (PCF), is an exception. However, the cerebellum is not the only occupant of the PCF. Moreover, it protrudes supero-rostrally beyond the PCF through a hiatus in the tentorium cerebelli.

In order to evaluate cerebellar proportions in fossil hominids it was necessary to develop methods to relate cerebellar and PCF volumes and to determine whether this relationship is consistent from taxon to taxon; and to relate cerebellar volume to both brain volume and body mass.

Research Hypotheses

The specific objective of the research project was to examine the degree and timing of non-allometric changes in cerebellar volume in Pliocene and Pleistocene hominids. Comparisons of relative cerebellar volume were made among hominid groups, using the following hypothesis:

Cerebellar volume (CBLM) in hominids increases isometrically with respect to both body mass (BoMass) and brain mass (BrMass):

$$\mathbf{H_{01}:\quad CQ = k * EQ}$$

In order to test the central null hypotheses, cerebellar volume had to be estimated from measurements of posterior cranial fossa volume (PCF) in fossil hominids. This required the development of appropriate empirical regression models for estimation of cerebellar volume from PCF volume in living primates. Three secondary hypotheses were tested for the purpose of estimating cerebellum volume from PCF volume:

1. In modern humans, total posterior cranial fossa volume (PCF) is correlated with total cerebellar volume (CBLM):

$$\mathbf{H_{02} : \quad PCF_{human} = k * CBLM_{human}}$$

2. In modern apes, total PCF volume (PCFV) is correlated with total cerebellar volume (CBLM):

$$\mathbf{H_{03}: \quad PCF_{nonhuman} = k * CBLM_{nonhuman}}$$

3. The slopes of the Least Squares Regression lines for modern humans and non-human primates are equal:

$$\mathbf{H_{04}: \; PCF/CBLM_{nonhuman} = PCF/CBLM_{human}}$$

Model of Hominid Cognitive Evolution Incorporating Changes in Relative Cerebellar Volume

Results of the research (for details, see Chapter 12, “Data Analysis and Results”) provide evidence for refuting the main null hypothesis. Relative cerebellar volume varied among hominid groups, just as it does among non-human primates (e.g., MacLeod, Zilles, Schleicher and Gibson 2000; and Matano and Hirisaki 1996, 1997; Rilling and Insel 1998; Semendeferi and Damasio 2000). Changes in relative cerebellar volume are correlated with archeological and fossil skeletal evidence for increased motor and cognitive efficiency.

Cerebellar volumetric changes have interacted with neocortical reorganization and encephalization in response to historical environmental variability. Cognitive behavior in early hominids was contextually adaptive, not a directional trajectory aimed towards modern human morphology. Brain size, body size, and relative cerebellar volume each rose and fell to a different degree and at different rates from taxon to taxon, in response to shifting genetic and environmental contexts.

Description of Model

The model, which is described more detail in Chapter 14, “Summary and Conclusions” is briefly outlined below. The model is organized within a chronological and taxonomic framework loosely based on Wynn’s (1996) steps in cognitive evolution. Each step is characterized by increasing cultural complexity: more complex objects, larger sets of objects, and more complex action sequences related to manufacturing, using, and classifying such objects in a social context. As cultural elaboration continued, there was an increasing need for “*complexity management”*, a term introduced by Holloway (1967) to refer to “behavioral attributes related to efficiency and fineness of discrimination, and adaptive problem-solving ability, which includes factors such as memory storage, recall, attention-span, and delay of response,” (p. 5). The model described below extends Holloway’s definition in that it includes cognitive strategies for organizing experience based on computational logic.

The elements of the model include:

- the role of the cerebellum in storing and coordinating complex algorithms for procedural learning and memory (including manipulation of “cognitive” as opposed to “motor” engrams)
- increasing representational complexity with the proliferation of culturally generated objects and object sets

- non-allometric changes in relative cerebellar volume and neocortical volume over time in fossil hominids
- interaction among the following variables:
  - EQ (encephalization quotient = actual/predicted brain mass)
  - CQ (cerebellar quotient = actual/predicted cerebellar volume)
  - NetBrain (total brain mass – cerebellar volume)
  - TotalBrain (= total brain mass, including cerebellum)
  - Body Mass (BoMass)

Three Stages in Hominid Cerebellar and Cognitive Evolution

The proposed model recognizes three stages in hominid cerebellar evolution, comprising six phases related to changes in cognitive strategies and related behavior. For full references and discussion of the archeological and paleontological evidence summarized below, see Chapter 4 “Background Research and Literature Review – The Fossil Record” and Chapter 5 “Cognitive Evolution: Archaeological Evidence and Models.”

Stage I: Overall encephalization

In Stage I, overall encephalization is accompanied by a non-allometric increase in cerebellar volume, supporting new motor and cognitive behaviors that emerged in the Lower Paleolithic. Stage I comprises three phases.

Phase 1-I (6 mya – 2.5 mya) – earliest hominids

Characterized by:

- NetBrain expansion;
- drop in CQ compared to *Pan* (but cerebellar lateral lobes may have expanded at expense of vermis);

- neocortical reorganization, including parietal lobe expansion;
- enhanced cross-modal integration in posterior parietal “association areas” coordinated by cerebellar algorithms;
- behavioral repertory builds on cultural gestural systems and tool-making incipient in common *Pan*/hominid ancestor;
- conceptualization of simple object sets, one-to-one correspondences within object sets, incipient in common ancestor;
- unknown reliance on material culture or symbolic vocal communication.

Phase 1-II (2.5 mya – 1 mya) – early **Homo** ***(including early*** **Homo erectus*); Early Paleolithic/ Oldowan (Mode 1)***

Characterized by:

- Overall brain expansion – both CQ and EQ increase relative to earlier hominids;
- Consolidation of cultural dependency on tools;
- neocortical reorganization, including hemispheric lateralization (petalia, expansion of Broca’s area, lithic debris suggesting right-handedness);
- behavioral repertory for arbitrary, culturally transmitted gestures accompanied by arbitrary vocal utterances;
- increased complexity of objects, object-sets (material culture);
- increased ability to maintain one-to-one correspondences within large object-sets and even among object-sets (incipiently recursive behavior);
- procedural learning and memory functions of cerebellum expand as gestures, vocal signals, and object-manipulation become more complex.

Phase 1-III (1 mya – 300 kya) – **Homo erectus** *and Middle Pleistocene* **Homo***; Acheulean (Mode 2)*

Characterized by:

- Whole Brain expands, but so does Body Mass, with little or no net rise in EQ;
- Rise in CQ (cerebellum constitutes a larger proportion of the NetBrain);
- consolidation of hemispheric division of labor for spatial vs. linguistic functions (petalia; parietal asymmetry; Broca's area; upper limb asymmetry);
- highly sophisticated visuo-spatial skills;
- extended voluntary attention;
- elaboration of motor routines;
- hierarchical organization of objects and object-sets enables recursive manipulation of motor routines and related conceptual hierarchies;
- cerebellum expands to meet demands for procedural learning and memory and working memory
- cerebellum extrapolates from coordination of motor routine neural representations to conceptual neural representations;
- cerebellum coordinates neural representations for complex oro-facial movements and object representations for simple, rule-based language;
- increasing number of objects, object-sets and related neural representations results in encephalization towards the end of this phase.

Stage 2: Neocortical Expansion

In Stage 2 neocortical volume expansion relative to both body mass and cerebellar volume supported storage and processing of more and more neural representations. As the neural network expanded, a limit was reached in which any further increase in size would have compromised computational efficiency. Stage 2 comprises two phases.

Phase 2-I (300 kya – 35 kya) – Late Archaic **Homo***; Middle Paleolithic/ Mousterian (Mode 3)*

Characterized by:

- marked increase in EQ;
- marked decrease in CQ;
- clear evidence for hierarchical, recursive object-oriented behavior (e.g., prepared core techniques; consistent, if simple, pyrotechnology);
- Efficiency of neocortical computational network reaches critical point as more and more complex objects and object sets incorporated into cultural environment.

Phase 2-II (35 kya – 15 kya) – Early Modern **Homo sapiens***: Early Upper Paleolithic*

Characterized by:

- slight decrease in overall brain mass;
- slight increase in CQ;
- proliferation of "aesthetic" objects related to ritual behavior based on procedural memory as well as conceptual complexity;

- cerebellar functions support elaborate motor routines, increased complexity of hierarchically-organized objects (e.g.more frequent hafted tools);
- number of complex object-sets increases;
- individuals who have greater neuro-computational capacity have selective advantage;
- cerebellum improves neural computation by complex hierarchical organization of algorithms for manipulation of concepts and engrams;
- cerebellum facilitates greater manual precision.

Stage 3: Cerebellar Expansion

The cerebellum expanded as it extended its control functions from sensory-motor to cognitive processes. Computational efficiency was improved as the cerebellum subsumed individual neural representations into more easily manipulated hierarchical algorithms.

Phase 3-I (15 kya – present) – Recent Homo sapiens*: Late Upper Paleolithic – Present*

Characterized by:

- little or no increase in EQ;
- marked rise in CQ;
- manipulation of object-sets and concepts previously performed by neocortex as functions of declarative memory and learning now relegated to cerebellum; large object-set subsumed in more complex computational hierarchy;
- computational algorithms handled by cerebellum offer alternative cognitive strategy for recursive manipulation of highly complex, hierarchically organized

concepts and object-sets. These included formalized interpersonal categories such as kinship systems and political entities as well as material culture.

Summary

Cerebellar evolution played an important part in the emergence of the modern human cognitive repertory. Early hominids developed a high degree of technological competence, supported by increased neocortical and cerebellar capacity. Middle and Late Pleistocene hominids applied their technological competence, based on well-developed procedural cognitive processes, to produce a wide range of cultural artifacts. It is likely that they had extensive lexical repertories and syntactical mechanisms to express complex concepts, supported by well-developed neocortical declarative learning and memory functions. Modern human cognition and behavioral evolution emerged gradually as more, and more complex objects, object-sets, and their representations placed greater demands for efficiency on computational neuroanatomy. Cerebellar functions related to timing, ordering, and sequencing of motor representations were extended to manipulation of conceptual representations as well. More efficient, hierarchical organization of conceptual and lexical representations formed the basis for highly complex syntactical constructs and formal cognitive operations. Cognitive and neurological evolution involved reorganization of both the cerebellum and the neocortex, accompanied a functional interplay between these two important, complementary neurological structures.

2 INTRODUCTION TO BACKGROUND RESEARCH AND LITERATURE REVIEW

“. .. few branches of human biology are more bedeviled with half truths, selective omissions, and the forthright proclamation of unproved propositions than that which deals with brain size and, especially the relationship between brain size and function.” (Tobias 1971)

The brain is the centralized coordinating mechanism of a biologically based information processing system in vertebrates. An understanding of human cognitive evolution requires evidence from many disciplines (neuropsychology, developmental psychology, cognitive psychology, functional radiography, and human paleontology). Research conducted in recent decades has provided data to resolve long-standing debates about the nature of brain function and cognition. An emerging consensus in the neurosciences supports a “weak modularity” model reconciling the “unitary/generalist” versus “domain-specific” positions. “Innatists” and “environmentalists” are finding common ground in an “epigenetic” model, in which the cerebral cortical areas develop upon innate potentials activated by sensory-motor experience. Computational modeling based on parallel processing in neural networks has demonstrated how learning may take place in a complex biological system like the human brain.

Refined radiographic techniques suggest that the cerebellum may be a central player in human cognition, capable of integrating cortical and subcortical neural signals in a “weak modularity model;” contributing to cortical organization in an “epigenetic model;” and performing as a coordinator of neural signals in a neural network model.

The cerebellum mediates proprioceptive and sensory-motor signals as they are routed through the basal ganglia, thalamus, and cerebral cortex. It contributes to complex cognitive operations, including motor learning. Recent computer imaging studies have implicated the cerebellum in “higher” cognitive functions, including cognitive aspects of language production such as word searches. Models of cerebellar function suggest that the cerebellum plays an important role in timing and sequencing of neural signals, independent of their content. Many uniquely human cognitive operations, especially those involving language and fine manipulation, depend upon timing and sequencing of neural representations. Cerebellar connections extend to many parts of the cerebral cortex, notably those listed by Holloway (1996) as being key regions in the evolution of modern human cognition. The cerebellum participates in cortical functions involving these areas. It also appears to contribute cortical regional specialization via thalamic input during ontogeny (See Appendix, Table A-1 for a summary of studies confirming cerebellar connections with brain regions listed by Holloway.)

Neural and Cognitive Organization

Brain volume (even brain volume relative to body mass) is at best only gross holistic index of information processing capacity. It conveys little about specific cognitive functions. How cognitive function may be revealed by brain structure is still only partially understood, in spite of almost two centuries of committed inquiry. Deeply rooted polarities along a set of related axes permeate many levels of analysis across diverse disciplines, from cognitive psychometry to neuropsychology, developmental psychology, neuroanatomy and paleoneurology. The discussion that follows briefly outlines the issues and evidence contributed by these disciplines regarding the nature and evolution of human cognition.

Epistemology

How does mind arise from matter? This is the ultimate question driving cognitive inquiry. If we are to presume that we can understand human cognitive evolution, we must first address this important issue.

Can we know how mind arises from matter? Those who believe we can (including the author of the present work) generally adopt an optimistic reductionist viewpoint. Included among those who do not believe the mind is accessible to our understanding are “boggled skeptics,” who predict that “the human brain is more complicated than it is smart” (Churchland 1986, p. 315-316). For “principled skeptics,” on the other hand mental experience is not reducible to physical explanations, either because mental substance is distinct from physical substance (substance dualists), or because mind arises from nonphysical properties of the physical brain (property dualists.) Churchland also classifies among principled skeptics scholars who model cognition as a propositional, logic-like process which cannot be explained in terms of the architecture of the brain (e.g., Fodor 1983).

Models of Cognition

Whether the skeptics will be vindicated will depend upon whether a credible reductionist model of cognitive function can be generated. The historical dualistic model of mind as machine with a non-material executive overseer, employed by Descartes and his intellectual heirs, is not adequate to the task. The mind-as-computer model has greater potential as a starting point.

Two views of the mind-as-computer have shaped an intense controversy over recent decades. Systematists model the mind as a serial information processor. In a classic systematic model, the substrate of computation is not relevant to the nature of computation (i.e., sensory-motor information can be transmitted through any medium, from neurons to silicon pathways). In systematic models, representations are localized in a specific brain region.

Connectionists, on the other hand, model neurons as nodes that are organized in distributed networks. Representations activate distributed aggregations of neurons involving impressions from many sensory modalities and multiple exposures. Connectionist models map well onto neuroanatomy, which does in fact, comprise networks of interconnected neurons. Connectionist learning models have demonstrated complex behaviors, including face recognition and learning of regular and irregular verb forms (Elman, Bates, Johnson, Karmiloff-Smith, Parisi and Plunkett 1996). In connectionist models, parallel rather than serial computation is emphasized: many neural subunits are involved in simultaneous information processing.

Neither systematists nor connectionists address the issue that in living organisms, information processing based on complex neural structures has arisen over billions of years of evolutionary history. Neural mechanisms based on biochemical interactions (e.g. light sensitivity vs. olfactory sensitivity vs. tactile sensitivity) have accrued and interacted in specific environments. Nor is information in living organisms restricted to databases localized within a central processor. Rather, it is encoded in the structure of the organism itself, as a wing embodies historical information about effective functioning in previous generations of wing-bearers (Dennett 1996). Neural information is thus distributed throughout the structure of the organism as well as within the concentrated neural structure of the brain. Many authors oriented in a “Standard Social Sciences Model” (Tooby and Cosmides 1995) have proposed that cognition is also, or even primarily, distributed in the cultural environment, i.e., “exosomatically” (e.g., Hutchins 1995; Noble and Davidson 1996; Salomon 1993; Vygotsky 1978).

. The cerebellum is the quintessential embodiment of a distributed, plastic computational neural structure whose activity informs complex behavioral output, as described below.

Evidence

A wide range of evidence is called into play in testing models of neural structure and function. Clinical psychologists subject pathological and normal control subjects to behavioral and psychometric testing, with the classic “double blind” test as the gold standard; neurologists examine anatomical evidence derived from surgical, postmortem, and radiographic studies. Others, including linguists (e.g., Chomsky, Pinker), philosophers (e.g., Dennett, Searle), or behavioral psychologists (e.g., Donald), explore cognition in terms of its propositional or representational structure with minimal emphasis on the architecture which supports it. The emerging discipline of cognitive science occasionally produces researchers who attempt a more thorough integration of behavioral and anatomical evidence (e.g., Calvin and Bickerton 2000; Deacon 1997; Elman et al. 1996), but these attempts, reviewed in more detail below ("Scenarios for Cognitive Evolution", p. 107), are rare.

Historical attempts to develop integrated models of cognition have confronted several essential issues, which are outlined below:

Cognitive Structure

A longstanding tension between theories which emphasize an holistic view of brain organization and those which model the brain as an aggregate of diverse, specialized, and neurologically localized functional regions has characterized the neurological sciences for more than 150 years.

While neuropsychologists have focused on behavior, neurobiologists have looked at the gross anatomy and cytoarchitecture of the brain. Ultimately, the cognitive functions postulated by neuropsychologists must map onto functional biology. However, as the two disciplines have historically developed their own investigative techniques and taxonomies of cognition, this level of theoretical integration has not yet been achieved, although neural network modeling has made good progress in that direction.

The Psychological Perspective: Unitary Intelligence vs. Faculty Psychology

Unitary Intelligence ("g")

Early investigators (e.g., Burt 1909; Piaget 1952; Spearman 1904, 1927 Terman 1916; Yerkes 1917) viewed intelligence as a generalized capacity to process information, regardless of content. An extensive literature is devoted to the design of psychometric tests of Intelligence. Factor analysis was developed to isolate the common characteristic of a general intelligence factor, or "*g*" factor, from its specific manifestations. Such tests have historically been constructed to measure aspects of verbal, spatial and mathematico-logical abilities, as well as cultural knowledge. Supporters have claimed that these abilities are consistently correlated because they are manifestations of an underlying, quantifiable, "*g*" factor. A handful of investigators continue to pursue the unitary perspective, based on the psychometric methodology of Spearman and his followers (e.g., Bouchard 1993; Burt 1909; Eysenck 1993; Herrnstein and Murray 1994; Jensen 1998; Spearman 1904, 1927). Unitary models are intuitively appealing because they can account for the subjective experience of holistic consciousness, correlations between verbal, spatial and mathematical/logical test scores, and the apparently seamless way that individuals manifest cognitive behavior. It is noteworthy that high "*g*" faculties are those which are least amenable to connectionist models.

The psychometric approach in pursuit of a general intelligence factor has been strongly criticized for philosophical, methodological and statistical reasons. Gould's influential critique is typical (Gould 1996). Gould has argued that evaluations based on "*g*" commit both a philosophical error: reification of an undefinable quality; and a moral error: judging the worth of individuals based on an unequal distribution of an innate, variable, measurable (but, according to Gould, fallacious) quality. He has been especially critical of the application of factor analysis to the question of "*g*," stating that there is no substantiated causal relationship between different kinds of cognitive abilities which justifies accepting "g" as a central dynamic in cognitive performance.

The dispute over "*g*" is fueled by moral outrage against racial biases expressed in popular publications (e.g., Austin 1995; Gould 1996; Herrnstein and Murray 1994; Painter 1995). Political agendas, arguments *ad hominem* and oversimplifications obscure the more balanced, well supported, moderate (if somewhat vague) consensus that has emerged in the 1990s with respect to the contribution of "*g*" to human cognition. The majority of researchers agrees that humans vary with regard to their cognitive ability; that such ability is more or less correlated across cognitive tasks; and that it is to some degree heritable and to some extent quantifiable.

Biological support for "*g*" has been ambiguous. A number of studies have shown that brain volume (and cerebellar volume) are correlated with performance on tests of intelligence after adjustment for body size (Jensen 1998; Paradiso, Andreason, O'Leary, Arndt and Robinson 1997).

Aside from brain volume, other biological factors such as neural processing efficiency, neural density and connectivity, fluctuating hormonal levels, rate of glucose metabolism and other factors may contribute to overall cognitive function (Jensen 1995). Gall attempted to measure factors such as reaction time (Gall 1812/1968, cited in Jensen 1998) without success. However, experiments conducted with modern monitoring equipment have suggested that certain elementary cognitive tasks ("ECTs"), including reaction time in voluntary movement, may underlie cognitive efficiency across domains (Paradiso et al. 1997; Jensen 1998). Whether processing speed is a true measure of cognitive capacity is a matter of dispute (Richardson 2000; Thomas and Karmiloff-Smith 1998). However, processing speed may be an index of one or more other variables, including network interconnectivity or number of neurons involved in computation (itself a factor of brain volume or neuron density), that affects performance.

Speed of neocortical processing may be enhanced by cerebellar function. One hypothesis is that cerebellar volume, which is significantly correlated with the ability to retain already encoded information in the verbal domain, may account for the correlation between cerebellar volume and IQ (Paradiso et al. 1997).

One recent PET imaging study (Duncan, Seitz, Kolodny, Bor, Herzog, Ahmed, Newell and Emslie 2000) has established recruitment of one or both lateral frontal lobes and anterior cingulate gyrus correlated with high "*g*" tasks, but not in similarly structured low "*g*" tasks. Thus, a modular function localized in the lateral frontal lobes may subserve a wide range of cognitive demands in different subject domains. The psychometric test these researchers employed for verbal abilities involved analyzing sequences of alphabetical letters, and did not involve semantic, representational or syntactical qualities. Nor did they attempt a quantitative analysis of the area of cortex recruited by individuals with differing performance. This important study provides evidence for one possible common computational process underlying "*g*," and in doing so suggests that "*g*" itself is a modular function not necessarily related to the size of any cortical area or of the whole brain.

Faculty Psychology

A growing number of investigators have shifted their research from psychometrics to exploration of cognitive processes. They have argued that "intelligence" is not a singular phenomenon (e.g. Fodor 1983; Guilford, 1967; Thurstone 1938). Faculty psychology, the "view that many fundamentally different kinds of psychological mechanisms must be postulated in order to explain the facts of mental life," (Fodor 1983, p. 1) has a long history, beginning with Gall, whose misguided promulgation of phrenology should not obscure his seminal descriptions of functional localization (Gall 1812/ 1968).

The present resurgence of faculty psychology owes much to Noam Chomsky, whose work on linguistic function has been a model for most modular theories of brain function developed since the 1970s (e.g., Chomsky 1980). Distinct cognitive faculties have been designated as "modules" (Fodor 1983);

“intelligences” (Gardner 1993; 1999); “functions” (Luria 1973; 1980); “primary mental abilities” (Thurstone 1938); or “domains” (Karmiloff-Smith 1996).

Taxonomy and Organization of Cortical Functions

If, as the evidence suggests, cognition relies on hierarchically organized networks involving dispersed, but localized cortical regions, a number of questions arise. What is a cognitive function? How are functions organized? To what degree are functions heritable? How (and when) did functional specialization evolve? In addition, how does cortical organization relate to function?

Vertical vs. Horizontal Organization

Even the most committed proponents of generalized intelligence acknowledge the existence of specific mental functions. These may be seen as encapsulated modules (“vertically” organized), or as differentiated aspects of a generalized or centralized cognitive capacity (“horizontally” organized). Hierarchical models often include one or more inclusive levels of generalized Functions, or domain-general levels. The influential models of Piaget, for example, specify a generalized cognitive capacity that proceeds through definite “stages,” based upon interaction with the environment. Specific cognitive abilities emerge across the board when one stage is fully mastered (e.g., sensory-motor competency is seen as the necessary condition for linguistic, mathematical and spatial cognitive processes). Following Spearman (1927, cited in Fodor 1983), models that incorporate “*g*,” are generally hierarchical, with subsidiary mental abilities arising from, or dependent upon, general intelligence.

Fodor (1983) has pointed out that hierarchical models may vary in the degree to which they emphasize a vertical or horizontal relationship among cognitive functions. For Fodor, information from a set of encapsulated modules is utilized as input for a separate level of cognitive behavior involving “thought,” or a central processing facility. According to Fodor, one of Churchland’s “principled skeptics,” higher level cognition requires universal connectivity, which cannot be reduced to a consistent, stable architecture susceptible to analysis. Other researchers, many of them advocates of connectionist models, are more optimistic (e.g., Elman et al. 1996; Karmiloff-Smith 1996; Kosslyn and Koenig 1992).

Number and Nature of Cognitive Faculties

Although the exact number, function and organization of neural elements is a matter of ongoing inquiry, there is a strong consensus among cognitive neuroscientists that neural organization is in fact hierarchical. More restricted units (neurons, neural sub-networks) provide input to more inclusive subnetworks and networks (Kosslyn and Koenig 1992).

Gardner (1993; 1999, pp. 36-40) has advanced a set of criteria by which a domain (“intelligence”) can be recognized:

- “the potential of isolation by brain damage”;
- “evolutionary history and plausibility”;
- “an identifiable operation or set of core operations”;
- “susceptibility to encoding in a symbol system”;

- “a distinct developmental history . . . [and] definable set of expert and ‘end-state’ performances”;
- “existence of *idiot-savants*, prodigies, and other exceptional people”;
- “support from experimental psychological tasks”;
- “support from psychometric findings”

Gardener has not distinguished modules and domains, in the sense of Karmiloff-Smith or Fodor, nor has he elaborated upon the issue of neuroanatomical organization. However, modular underpinnings are to some degree implicit in Gardner’s criteria (e.g., isolation by brain damage).

Gardner’s proposed list of “intelligences” is concordant, if not entirely congruent, with domains recognized in a broad consensus of faculty psychologists. These may be hierarchically organized to include domains, which rely upon logical cognition (classifying, ordering, and quantifying); physical cognition (understanding and operating upon the properties of physical objects) (e.g., Spelke 1991); and language (e.g., Langer 1993).

Many of the Functions that are highly correlated with “*g*” appear to share in common subfunctions based on combinativity and praxis. These functions involve precisely timed, algorithmic sequencing to compose, decompose, and recompose representational elements into higher-order representations according to syntactical constraints (Corballis 1991).

3 BACKGROUND RESEARCH AND LITERATURE REVIEW: NEURAL ARCHITECTURE

Historical Perspective

To what degree does neural architecture predetermine function? How are neurological functions organized? These questions continue to be debated, even as a consensus emerges from a long historical debate regarding the relationship of cognitive structure and its neurological infrastructure.

In the mid-nineteenth century, medical opportunities for brain research permitted individuals such as Broca (1861), Gall (1812/ 1968), Wernicke (1874), Jackson (1875), and Harlow (1868) to observe the effects of localized brain injury on human behavior. Animal studies complemented and expanded information gained from observation of humans.

In their most extreme early forms, localizationist theories in neuroanatomy postulated distinct brain centers, or “organs” analogous to other physiological organs such as the kidney, heart, or liver, which performed specific identifiable cognitive functions (e.g., Gall (1812/ 1968), cited in Churchland 1986). Damage to a cortical center meant loss of the function it controlled. The famous case of Phineus Gage (Harlow 1868), and the often-cited pioneering work of Broca and Wernicke provided the impetus for localizationist research.

In holistic models, on the other hand, the cerebral cortex, if not the whole brain, is the generalized locus of a wide range of “higher” cognitive operations. Evidence for at least some generalized functions came from experiments by Marie Jean-Pierre Flourens, who found that the gradual ablation of the cerebral cortex in mammals degraded, but did not eliminate, many aspects of behavior (Flourens 1824). Flourens concluded that the all portions of the cerebral hemispheres were equipotent, and that higher mental functions depended upon the quantity of brain substance in the cerebral hemispheres, rather than its organization. Lashley (1949, 1950) conducted similar ablation experiments in rats and monkeys, and came to similar conclusions. Unable to find reliable associations of neocortical areas with behavior, he concluded that the clue to behavioral evolution lay either in the number of interconnections among nerve cells or in their biochemical characteristics.

During the late nineteenth and early twentieth centuries, evidence accrued to invalidate the extreme versions of both localizationist and holistic models. A degree of localization was suggested by study after study of patients with localized brain damage who lost some cognitive abilities but not others. In the 1970s, a body of dramatic evidence for localization was produced by series of psychoneurological tests performed with patients who had undergone therapeutic surgical separation of the cerebral hemispheres for treatment of epilepsy. These studies demonstrated that the cerebral hemispheres function asymmetrically in linguistic as well as non-verbal tasks (Gazzaniga 1967, 1970, 1983; Gazzaniga, Bogen and Sperry 1962; Levy-Agresti and Sperry 1968; 1983). Experiments with dichotic listening confirmed differential function of the hemispheres in both normal and commissurotomized individuals (Hiscock, Cole, Benthall, Carlson and Ricketts 2000; Shtyrov, Kujala, Lytinen, Kujala, Ilmoniemi and Naatenen

2000; Springer and Gazzaniga 1975; Springer, Sidtis, Wilson and Gazzaniga 1978).

Other research, however, suggested a degree of generalization in cortical organization. In many individuals, functions formerly performed by a damaged brain region might be assumed by another region (Azari and Seitz 2000). One extreme example of the plasticity of neural tissue is seen in therapeutic hemispherectomy. Children who undergo this procedure often achieve close-to-normal cognitive function, as the remaining hemisphere assumes the functions that would have been performed by the missing hemisphere (Verity, Strauss, Moyes, Wada, Dunn and Lapointe 1982)

The hypothesis of specificity was further undermined by experiments in which stimulation of various brain regions during surgery produced different effects, depending upon the timing or order or the stimulus (Sherrington 1906, cited in Churchland 1986). The accumulation of evidence from animal experimentation, human neurological patients, and electroencephalographic studies of normal and brain-damaged individuals confirmed that at least some cognitive functions resulted from the coordinated activity of multiple, dispersed, specialized brain regions. Modular models, first introduced by Jackson (1975) (Jackson 1875) and Luria (1973; 1980) were adopted to account for the distributed but specialized nature of cognition.

As long as the study of brain function was confined to non-human animal brains and “natural experiments” permitted by observing arbitrary human diseases and injuries, exploration of human neural organization was somewhat unsystematic. The development of electroencephalographic methods in the middle decades of the twentieth century, and then of sophisticated radiographic imaging and computational modeling since the 1980s, have permitted expanded opportunities for controlled, systematic, non-invasive observations of human brain function and organization.

Cortical Structural Organization

In most mammals, including humans, the cerebral cortex is a multilayered tapestry weaving together the topological sensory and motor interactions of the organism within its environment. In addition to its laminar structure, the neocortex is composed of groups of vertically organized columns of cells (processing units), that perform specific mental functions (cortical areas). Processing units have remained similar in size (approximately 110 neurons) throughout the course of mammalian evolution, although the number of cortical areas has increased as brain size has increased (Deacon 1990b Killackey 1995).

The cortical areas of macaques and marmosets, counted as distinct cytoarchitectural areas observed in nissl-stained sections, have been mapped. However, the number of cortical areas typical of a human brain is not known and may vary from individual to individual and from time to time within individuals. Over 100 distinct cortical areas have been identified in humans, as opposed to 52 cortical areas in the marmoset, and 70 in both the cat and macaque (Deacon 1990b; Killackey 1995; Levitt 1995; Passingham 1975). The increased number of neocortical areas in humans correlates with a dramatic increase in the volume of the neocortex relative to overall brain volume (Jolicoeur, Pirlot, Baron and Stephan 1984; Killackey 1995; Stephan 1972; Passingham 1975).

The earliest comprehensive scheme of cortical organization was formulated by Brodmann, based on histological distinctions among cortical regions (Brodmann 1909). Subsequent histological and electrophysiological mapping, along with lesion studies confirmed and refined the general outlines of Brodmann's scheme, and demonstrated that histological distinctions correspond in a general way with functional differentiation. Brodmann's scheme, somewhat modified, is still widely cited and will be used below, unless otherwise indicated.

Approximately 25 per cent of the human neocortex is occupied by "primary" sensory and motor cortices (Brodmann areas 3, 4, 17, 41, and 42). The supplementary cortical areas, which occupy approximately 75 per cent of cortical area in humans, process multiple types of input, and are defined by distinct, but interdigitated thalamic, cortical and subcortical connections.

It must be emphasized that, although a brain region may be active during a certain cognitive task, the exact role of that region in informing the behavior is often not known. In such a case, the most that can be said is that the region "contributes to" or is "involved in" the task. While a specific region may be necessary for the performance of a cognitive task, no single brain region is sufficient to support any complex cognitive behavior.

Interspecific Comparisons

Principal nuclear and interconnecting fiber patterns are homologous among primate species. However, both nuclear and cortical regions vary in volume and function from species to species (Holloway 1996; Krubitzer 1995). Major sulcal patterns generally conform to cortical functional areas identified by electrophysiological mapping experiments (Zilles, Armstrong, Moser, Schleicher and Stephan 1989). However, minor cortical folding is much more variable (Radinsky 1972; Welker 1990). Gyrification in anthropoids is at least in part an allometric function of brain volume (Jerison 1982) as well as neocortical volume (Zilles et al. 1989).

The relative volume of a given cortical area correlates with functional/behavioral specialization and continuing peripheral input (Jones, Panger and Woods 1997; Manger, Woods and Jones 1996; Mogilner, Grossman, Ribary, Joliot, Volkmann, Rapaport, Beasley and Llinás 1993; Seitz, Huang, Knorr, Tellmann, Herzog and Freund 1995).

Cortical mapping reflecting functional compensation has been reported for blind children and adults (Kujala, Alho and Naatanen 2000; Roder, Teder-Salejarvi, Sterr, Rosler, Hillyard and Neville 1999). Cortical reorganization has also been reported in humans and non-human primates who have lost sensory/motor function (Jones et al. 1997) or regained it through surgical intervention (e.g. Mogilner et al. 1993).

Thalamic input defines a primary (core) area, either ipsilaterally or contralaterally, or both. Subsequent ipsilateral cortico-cortical projections emanate in cascading fashion from the core area. Areas further removed from core areas (supplementary areas) tend to receive more diverse inputs. The term “association area,” which originally referred to cortical regions that were not "primary," has been replaced with terminology that reflects a much more complex cortical organization. Thus "core" areas receive primary sensory input; "root" areas receive secondary sensory input; and "belt" regions (association areas; convergence zones) integrate input from multiple modalities (Deacon 1997; Elman et al. 1996; Killackey 1995; Pandya, Seltzer and Barbas 1988). Compared to other mammals, including other hominoids, humans have proportionally more area devoted to supplementary cortex, and secondary areas are larger relative to their adjacent primary areas (Elman et al. 1996).

Input and Cortical Organization

Several lines of evidence indicate that cortical organization is at least partially input-driven:

- As described above, both cortical architecture and input to the primary sensory areas of the cortex are informed by the thalamus. For example, haptic and proprioceptive input is channeled to the sensory cortex via the dorsal thalamus, which receives topographically patterned input from the cerebellum and basal ganglia. Connections extend from primary cortical regions to adjacent and non-adjacent cortical areas, in networks, which store dispersed neural representations of the original stimuli. Secondary and tertiary "association areas" incorporate representations from multiple sensory modalities. Thalamic axons are guided by axons extending from the incipient neocortex (preplate) which acts as a template for subsequent cortical development. "Afferent specification" refers to the role of subcortical structures in targeting and specifying the function of neocortical areas during neurogenesis and cell migration (Killackey 1995).

- Neocortical transplants. Studies in which segments of neocortex have been transplanted in fetal rodents have shown that cortical neurons are pluripotent in early ontogeny but become functionally specialized as development proceeds (e.g., (O'Leary, 1989; O'Leary and Stanfield 1985; Stanfield and O'Leary 1985).
- Cortical reorganization in response to trauma, or sensory deprivation, or recovery of function.
- “Cortical exuberance” (Killackey 1995). Neocortical projection neurons extend processes to multiple target cortical areas. Some of the neural processes are elaborated (or eliminated) based on continued afferent input (or lack of input). Cortical exuberance is a mechanism akin to pruning by neuronal cell death. It has been observed in primates, as in all other vertebrate species.
- Cortical plasticity in early ontogeny (e.g. recovery of function after hemispherectomy (Verity et al. 1982) and cortical reorganization after other, less drastic instances of brain damage, even in adults.
- Individual variability in cortical organization (Kandel and Hawkins 1993; Kimura 1993).
- “Critical” or sensitive periods (Elman et al. 1996.) Human infants (like chinchillas and monkeys) are able to distinguish speech from non-speech sounds at birth. Gradually the categorical perception of all speech sounds is

lost to humans, until they are only able to perceive the phonetic range of their own native tongue(s) (Kuhl 1983; 1991). The babbling of human infants also moves from inclusive to exclusive, until the child is producing only the sounds present in its surrounding speech environment (Pettito 1987). Other domains show a similar pattern of generality followed by specifity as innate predispositions are honed by exposure to environmental stimuli.

“Epigenetic” Model

An “epigenetic” model reconciling cortical pluripotentiality in immature individuals with dedication of cortical neurons and localization of function in adults has been proposed by Elman et al. (1996). These authors have provided extensive evidence based on developmental studies that the cortical organization arises from two sources: (1) innate architectural biases and (2) input biases, which restrict the type of information available to a given set of neurons and how such information can be processed. In their connectionist model, parts of the cerebral cortex are pluripotent even after birth. They gradually develop the modular organization seen in maturity, informed by these innate biases and based upon interaction with the environment.

The Weak Modularity Model

In recent decades, cognitive science has recruited functional imaging studies and computer network modeling to provide support for faculty psychology models. PET, MRI, and fMRI studies have shown that in adult humans, complex cognitive functions recruit neurons from anatomically dispersed brain regions. An emerging consensus supports a “weak modularity” hypothesis (Kosslyn and

Koenig 1992). According to the weak modularity model cognition is characterized by the following attributes:

- plasticity
- biochemically mediated
- temporal synchronization
- parallel computational interactions among
- input-driven
- representational
- topographically mapped modules (which may be physically dispersed although unitary in function)
- consisting of computational units (single neurons)
- hierarchically organized into
- integrated cortical and subcortical networks
- which participate in a multiplicity of functions

Subcortical Structure and Function

Recent research utilizing functional imaging studies (fMRI, PET) is bringing much-needed insight into the issue of how brain morphology relates to behavior. Important contributions from both neurochemical studies and computational modeling justify optimism that a comprehensive, theoretically coherent model of brain function will be developed in the future. The present proliferation of studies focused on mapping of brain regions activated during cognitive tasks represents an important phase in developing such a model.

"Higher," characteristically human, mental Functions are not end-stage cortical appendages, layered onto the "lower" brain regions like frosting on a cake. Every "higher" Function depends upon an extensive network of subfunctions performed by both cortical and subcortical brain regions. Subcortical regions must have evolved in tandem with the cerebral cortex and play an essential role in language, thought, memory, planning, and complex motor learning (Holloway 1964; Noback and Moskowitz 1962).

For example, the important role of emotional valence informed by subcortical limbic structures such as the amygdala, the hippocampus, and the "non-dominant" right hemisphere in rational decision making has received both popular and scholarly attention (Damasio 1994; Goleman 1995; Markowitsch 1995). Other studies have documented the role of the hippocampus as a mediator of declarative memory and spatial cognition (McNaughton, Knierim and Wilson 1995); of the amygdala and basal ganglia for procedural memory (Markowitsch 1995); and of the thalamus in filtering stimuli for directed attention (Laberge 1995; Posner 1995). The boundaries between "purely motor," "purely sensory" and "purely cognitive" functions are conceptual artifacts (for example, phonemic representation of words, motor planning for vocal articulation, inaudible rehearsal of words, and word searches for verbal completion tasks belong to a functional continuum, from sensory-motor to cognitive. A similar example of sensory-motor/cognitive continuity involves proprioception, object shape, motor programs for tool use, knowledge of objects, memory of objects, verbal representation of objects (c. f., Klatzky, McCloskey, Doherty, Pellegrino and Smith 1987).

Relative Volume of Subcortical Structures

Interspecific differences have been documented among primates in the relative volumes of cortical and subcortical structures. Many of them have been based on a single, though extensive, sample of fixed, serially sectioned brains prepared by researchers at the Max-Planck-Institut für Hirnforschung, Neurobiologische Abeteiling in Frankfurt (e.g., Bauchot 1978, 1982; Bauchot and Stephan 1966; 1969; Jolicoeur et al. 1984; Matano and Hirasaki 1996; Passingham 1975; Radinsky 1975; Stephan 1972; 1988; Stephan, Bauchot and Andy 1970; Stephan, Frahm and Baron 1981; Stephan 1988).

Detailed quantitative studies of thalamic nuclei have been performed on small samples of serially sectioned non-human primate and modern human brains (Armstrong 1980; 1981; 1982; Browne and Simmons 1983; Gilissen and Zilles 1995; 1996 Gilissen, Iba-Zizen, Stievenart, Lopez, Trad, Cabanis and Zilles 1995; Zilles, Stephan and Schleicher 1982; Simmons 1990).

The Cerebellum: a Content-Independent Processor

The cerebellum is the only subcortical region that leaves an impression on the endocranium. Comprising an estimated 15,000,000 neurons (Altman and Bayer 1997), this large, ontogenetically distinct hindbrain structure has recently received intense scrutiny by neuroanatomists and paleoneurologists. Many imaging studies, in the context of connectionist models, suggest that the cerebellum contributes to domains dependent upon praxic functions, including ballistic functions, regardless of content (Corballis 1991). However, most theorists of cognitive function make only brief mention of the cerebellum as a participant in praxic aspects of cognition (e.g. Calvin and Bickerton 2000; Corballis 1991; Kosslyn and Koenig 1992). This appears to be the result of several dynamics:

1. Because of technical difficulties, cerebellar regional mapping in PET and MRI studies was not feasible (Fox, Raichle and Thach 1985).
2. The contribution of the cerebellum to cognitive functioning was not recognized. As recently as 1989, a pre-eminent cerebellar authority, stated unequivocally that the cerebellum was simply a movement coordinator (Eccles 1989).
3. The reiterated organization of the cerebellum has been interpreted to mean that its function is limited and relatively simple (hence, that it could not be an important contributor to “higher” cognition (Altman and Bayer 1997).
4. Cerebellar organization has changed little since it first appeared in lower vertebrates (Altman and Bayer 1997).
5. Allometric studies employed a very limited sample and statistical methodologies that suggested that the cerebellum was “progressive,” but less so than the neocortex (e.g. Passingham 1975).

Since the late 1980s, when technical advances in neuroimaging permitted the cerebellum to be included in functional studies (Fox et al. 1985), increasing attention has been directed to cerebellar function.

Cerebellar Structure and Function

Early researchers recognized the role of the cerebellum in control of ipsilateral musculature and coordination of movement (Crosby, Humphrey and Lauer 1962; Flourens 1824; Luciani 1891, cited in Glickstein and Voogd, 1995). Continued research confirms the role of the cerebellum in motor functions, including proprioceptive input for coordination of multi-joint movements (Haggard et al. 1994); classical conditioning (Daum et al., 1993); motor coordination and planning (Thach et al., 1992); initiation of complex or differentiated movements (Salmon & Butters, 1995); timing of movement (Raymond et al., 1996); motor learning and predictive control (Jenkins & Frackowiak, 1993); spatial event processing (Petrosini et al., 1996); and incremental acquisition of new visuo-motor skills (Doyon et al., 1997).

The importance of the cerebellum in supporting cognitive Functions has been explored in an accelerating proliferation of studies over past decade. Over 200 articles pertaining to the role of the cerebellum in cognition were published between January of 1997 and May 2000. (Selected articles especially salient with respect to the present study are summarized in the Appendix, Table A-4.)

Perusal of the cerebellar literature yields a set of interrelated observations:

- the cerebellum participates in a wide range of functions via its connections with diverse subcortical and cortical areas, including the basal ganglia; thalamus; posterior parietal cortex; premotor cortex; ocular cortex; and prefrontal cortex (including Broca's area).

- based on the stylized and stereotyped circuitry of the cerebellum a number of reviewers have advanced hypotheses attributing a master computational role to the cerebellum (i.e., it may perform similar operations on diverse types of input)
- temporal organization of cognitive processes, sequencing of information, and sensory-motor integration are the most consistently mentioned hypotheses proposed to explain the contribution of the cerebellum to cognitive functions
- cerebellar function is involved with sequencing or ordering data. “Cognitive” patterning is computationally analogous to sensory motor patterning. “Cognitive” and sensory-motor neural events may be structured similarly, but involve different somatic expressions, depending upon which cortical and subcortical regions are involved in the neural components recruited during the event.

Connectionist Models of Cerebellar Function

The cerebellum appears to contribute to efficient performance of difficult tasks in a general way to promote the smooth control of either thoughts or motor sequences (Paradiso et al., 1997). Such control systems would involve motor learning but might extend to mental learning or timing of complex motor functions as well (Bloedel, 1993; Ito, 1990, 1993). Leiner et al. (1993) contended that the cerebellum can improve the performance of *any* other parts of the brain to which it is reciprocally connected, whether sensory, limbic, motor or cortical association regions. As Gowlett (1996) has pointed out, natural selection would probably favor any such mechanism that could be generalized to a number of functions. The cerebellum governs timing and sequencing, and is active during activities requiring procedural memory rather than declarative knowledge (Daum et al., 1993). Neurological subfunctions enhanced by cerebellar evolution include regulation of changes in directed attention (Leiner et al., 1993); shape recognition (Gao et al., 1996); spatial event processing (Petrosini et al., 1996); procedural and working memory processes (Middleton & Strick, 1997); ballistic skills (Middleton & Strick, 1997); and language processing (Iidaka et al. 2000; Silveri et al. 1994; Schlosser et al. 1998; Silveri, Di Betta, Filippini, Leggio and Molinari 1998).

Connectionist methodology is especially useful for modeling cerebellar functions. A number of proposals have been advanced to model cerebellar function. In one such model, based on cerebellar analogues in fish, learned predictions about sensory input are generated and subtracted from actual sensory input, bringing unpredicted inputs into relief. Effective function depends upon precise timing and sequencing of pre- and post-synaptic events (Bell, Han, Sugawara and Grant 1997). The idea of comparing sensory feedback to internalized representations or dynamics is echoed in several of the models described by Ito (1993). In these models, the cerebellum acts as a “feedforward controller” acting in parallel with a “feedback controller” (the cerebral cortex). Sensory feedback is compared either to an internalized representation of movement dynamics or to actual “online” skeletomuscular feedback. The cerebral cortex and cerebellum appear be reciprocal systems for representation and information processing which function as a self-correcting adaptive control system (Parkins 1997) (Braitenberg, Heck and Sultan 1997).

Relative Cerebellar Volume

Several quantitative studies reporting the “progressive” expansion of the primate cerebellum have been published (Jolicoeur et al. 1984; Matano, Baron, Stephan and Frahm 1985a; Matano and Hirasaki 1996; Matano, Stephan and Baron 1985b; MacLeod, Zilles, Schleicher and Gibson 2000; Passingham 1975; Stephan et al. 1970; Stephan 1972; Stephan et al. 1981; Stephan 1988). Many early investigators reported the human cerebellum to be larger both absolutely and relative to overall brain volume than in other primates (Haines 1986; Leiner, Leiner and Dow 1986; 1989; 1991; 1993). These authors attributed this increase to a disproportionate rate of expansion of the lateral cerebellar lobes, including the dentate nucleus. However, their conclusions have been based on intuitive rather than lacked quantitative data and failed to consider allometry in their interpretation of dentate and lateral lobe expansion.

More recently, a number of studies have appeared, offering evidence that the human cerebellum is in fact *smaller* than would be expected for a primate of similar brain volume.

In one such study based on a series of anthropoid MRI scans, *Homo* is shown to have a smaller than expected relative cerebellar volume (Rilling and Insel 1998). The authors of this study have interpreted the data to indicate a “grade shift” between monkeys and apes. They suggest that both brain and cerebellum increased in volume, without a change in their allometric scaling, followed by a change in the scaling relationship at some point in hominid evolution, reducing relative cerebellar volume, perhaps as cerebellar expansion was outpaced by cerebral expansion. This interpretation is consistent with measurements with pilot study informing the present research (Weaver, n.d., unpublished data).

Similar results were obtained in another study using the same MRI sample (Semendeferi and Damasio 2000). These authors found that the human cerebellum is significantly smaller than expected for an ape brain of human size.

The results of the recent quantitative *in vivo* studies cited above regarding relative cerebellar volume contradict earlier studies based on fixed histological samples (Jolicoeur et al. 1984; Matano et al. 1985a; Matano et al. 1985b; Passingham 1975; Stephan 1972; 1988; Stephan et al. 1981; Stephan et al. 1970). It is unclear whether they contradict the findings of MacLeod et al. (2000), as the units of comparison may not be homologous.

Inconsistencies among published studies appear to be due to

(1) Small sample sizes. The number of primates from individual species is very small in all studies (in most cases only one individual is included), with the exceptions of the human samples of 10 measured by (Semendeferi and Damasio 2000) and 6 measured by (Rilling and Insel 1998);

(2) The weighting of the samples. The histological sample is heavily biased in favor of prosimians and monkeys, with few hominoids included;

(3) Statistical methodology. Analyses based on the histological sample employ “progression indices” using an empirically derived insectivore baseline.

The MRI analyses derive regression lines from their own samples of five anthropoid families (Rilling and Insel 1998) or five hominoid genera (Semendeferi and Damasio 2000); (MacLeod et al. 2000);

(4) unknown inter-rater measurement discrepancies between studies

(5) unknown measurement error due to inconsistent tissue shrinkage in the case of the histological studies and image-processing limitations in the case of the MRI studies.

If the histological sample is used in a least squares linear regression of cerebellar volume on brain volume for the anthropoid sample from the database of Stephan et al. (1981), then the human cerebellum falls below the predicted value. Excluding the human cerebellar volume from the regression derivation (using untransformed variables, and first subtracting cerebellar volume from overall brain volume) produces similar, if less marked results, but does not result in negative values for the predicted cerebellar volume in the smaller-brained individuals.

No matter which regression approach is used, if the regression equation is derived from anthropoid values alone, the results support the MRI studies (using anthropoid and hominoid baselines) and contradict the histological studies (using the insectivore baseline). Thus the discrepancies between the analyses based on the histological sample differ from those based on the MRI sample are at least in part artifacts of the statistical analysis rather measurement or sample inconsistencies. However, given the very small sample size and lack of intermediate data points, there is no way to reliably interpret the function relating cerebellar volume to brain volume for anthropoids in the histological database. The present research, which incorporates hominid cerebellar volumes and a larger human sample into the regression analysis, produces slightly different results from previous studies. In this more representative sample, modern human cerebellar volume falls well above a RMA regression line calculated for anthropoids. (See Chapter 11, “Data Analysis and Results”.)

The Dentate Nucleus

Leiner et al. (1986) observed that the dramatic enlargement of the lateral lobes of the human cerebellum occurred in parallel with enlargement of the parietal cerebral association cortex as well as certain areas of the frontal cortex. The cerebellar dentate nucleus in humans has become “quasicorticalized,” presumably to permit a more extensive dendritic network (Altman & Bayer, 1996) resulting in volumetric increase in the cerebellar lobes.

To the present author’s knowledge, only three quantitative analyses of the dentate nucleus have been published.

One study, based on the German histological sample described above, concluded that the dentate nucleus is indeed “progressive” and accounts for lateral lobe expansion in humans (Matano and Hirasaki 1996). A second study found that relative expansion of the dentate was localized in the ventral portion of the nucleus (Matano 2001). Another recent study, based on a more extensive sample, arrived at contrary results, concluding that the human dentate has the smallest ratio of dentate volume to cerebellar hemispheric volume of all the primates studied; but that the lateral cerebellar lobes have expanded disproportionately with respect to the vermis as well as with respect to the rest of the brain (Mcleod, 2000). Discrepancies in the results of these studies appear to be due to differences in the scale of magnification at which the samples were analyzed, differences in sample membership, and possible inter-observer error (C. E. MacLeod, personal communication, March, 2000).

Cerebellar functional asymmetries

The cerebellum is asymmetrically organized with respect to function. Cerebellar functional asymmetries correlate with contralateral hemspheric functional asymmetries for a number of verbal and nonverbal subfunctions. For example, the right cerebellar hemispheres are active during word selection and search (Desmond, Gabrieli and Glover 1998); sequential memory and language processing (Riva and Giorgi 2000); word and pattern encoding and retrieval of episodic memory (Iidaka et al. 2000) verbal fluency (Schlosser et al. 1998). Cerebellar involvement has been demonstrated in many other studies of verbal and cognitive function, but cerebellar asymmetries are not specifically addressed. (For a representative list and summary of studies documenting cerebellar involvement in cognition, see Appendix, Table A-4).

4 BACKGROUND RESEARCH AND LITERATURE REVIEW: COGNITIVE EVOLUTION - THE FOSSIL RECORD

The fossil record offers several important clues to phylogenetic cognitive reorganization in the form of both postcranial as well as endocranial evidence.

Postcranial Indicators of Cognitive Evolution

Vertebral Neuro-canal

Relative cross-sectional diameters of portions of the vertebral neuro-canal reflect relative innervation of the torso, tail, forelimbs and hindlimbs of vertebrates. Cervical canal cross-sectional diameter in modern humans is large relative to body size when compared to other mammals, including non-human primates. (MacLarnon 1995) has attributed this enlargement to an increase in white matter (axons) rather than gray matter in the spinal cord. Such an enlargement correlates with increased cortico-spinal communication for cerebral motor processing related to fine motor processing (Noback and Moskowitz 1962; Weaver, Holliday, Ruff and Trinkaus 2000; White, Richards, Lucas and Purves, 1994 and references therein).

The absolute cross-sectional area of the C7 vertebra from the Nariokotome *H. erectus* skeleton falls at the lower end of the normal range of modern humans. The relatively greater transverse canal diameter of this specimen is also similar to that of modern humans and Neandertals.

However, if cross-sectional area of C7 is plotted against body mass, the Nariokotome skeleton falls well below modern humans (though significantly above *Pan troglodytes*) for this variable. The significance of this morphology is disputed. According to one interpretation, the relatively small vertebral canal may be related to a pathological condition such as axial dysplasia (Latimer and Ohman 2001). Other interpretations suggest that this individual had less well-developed cortico-spinal innervation to the upper limb than modern humans or less innervation of the intercostal muscles for breath control during vocalization (MacLarnon 1993).

Upper Limb Asymmetry

Modern human upper limbs also offer evidence of behavioral evolution as the human cognitive pattern emerged. Patterns of differential loading of the upper left and right limbs in fossil humans suggest that frequencies of right-handedness in Pleistocene hominids, dating back at least 1.6 million years ago, were similar to (or even more pronounced than) those observed in modern humans (e.g., Churchill 1994; Trinkaus, Churchill and Ruff 1994; Trinkaus, Churchill, Villemeur, Riley, Heller and Ruff 1991; Weaver et al. 2000).

Lithic debris apparently made by right-handed stone knappers supports the hypothesis that early hominids were right-handed (Toth, 1985).

Skeletal Indicators of Language Evolution

Several attempts have been made to discover skeletal indicators of adaptations for speech that can reveal the onset of linguistic functions in hominids.

Basicranial Flexion

A flurry of reports published in the 1970s and 1980s (e.g., Laitman and Heimbuch 1982; Laitman, Heimbuch and Crelin 1979; Laitman and Reidenburg 1988; Lieberman 1975; 1984a; 1994b; a; Lieberman and Crelin 1971; Lieberman, Laitman, Reidenburg and Gannon 1992; Lieberman, Pearson and Mowbray 2000) suggested that a low basicranial angle in certain fossil hominids, including Neandertals, would have reduced vocal resonance and limited the range of speech sounds available to these hominids. Since this early work, considerable evidence has accrued to suggest that it is inappropriate to exclude Neandertals, or any other fossil hominids, from the human speech community based on basicranial flexion:

- reconstruction of certain fossils, among them the key fossil La Chapelle-aux-Saints (Heim 1989);
- re-evaluation of the possible oral anatomy that might be reconstructed based on the basicranial and mandibular skeletal elements (Falk 1975); (Duchin 1990);
- fuller sampling of modern human populations, showing that Neandertals fall within the range of variation for Upper Paleolithic and Mesolithic Europeans for basicranial flexion (Frayer 1992);

analysis of a Neandertal hyoid bone from Kebara (Arensburg, Schepartz, Tillier, Vandermeersch and Rak 1990; Arensburg, Tillier, Vandermeersch, Duday, Schepartz and Rak 1989).

The Hypoglossal Canal

Kay, Cartmill and Balow (1998) conducted a study, which measured cross-sectional areas of the hypoglossal canal in extant humans, gorillas, chimpanzees and a sample of fossil hominids. These researchers found that in both absolute and relative size the hypoglossal canal, which carries the hypoglossal nerve, one of the innervators of the tongue, reached modern human proportions by approximately 300,000 years ago. However, a subsequent study based on larger sample size and a wider taxonomic range, showed an overlap in cross-sectional diameter of the hypoglossal canal for many non-human primates and fossil hominids (De Gusta 1999).

The Hand

Differences in carpal and metacarpal articulations in Late Archaic and Modern Humans suggest that Early Modern Humans employed precision grips more frequently than Late Archaic Humans, who relied more upon somatic effort (Churchill, Weaver and Niewoehner 1999; Niewoehner 2001).

Endocranial Indicators of Cognitive Evolution

Debate among paleoneurologists about cortical reorganization based on evidence from endocasts arises from at least three sources:

- gross morphology of the cortical surface is only a general indicator of functional organization. Superficial morphology does not reveal the interconnections between various cortical and sub-cortical structures that are involved in any given cognitive operation;

- Cognitive functional organization is characterized by considerable inter and intra-individual variability;

- even where cortical sulci correspond with functional regions, sulcal patterns are poorly marked on many endocrania, and most are non-existent in large-brained individuals.

Despite the difficulties of inferring behavioral capacities from endocranial morphology, a considerable body of evidence bears witness to phylogenetic changes in cortical organization during the Pleistocene. Pleistocene hominids exhibit differing patterns of cortical asymmetry, shifts in the relative proportions of cortical regions, and changes in cerebellar volume and form. (See Tables A-5 to A-9 for a summary of cortical changes observed in fossil hominid endocasts.)

Cortical asymmetries: Language and Handedness

In higher vertebrates, the sensory and motor cortices maintain contralateral as well as ipsilateral connections with the peripheral nervous system. Many aspects of sensory and motor function are neurologically symmetrical, assuring efficiency of perception and locomotion. However, in human populations many subfunctions are systematically lateralized (Efron 1990; Heillige 1993; Kosslyn and Koenig 1992). Efron (1990) and Heillige (1993) have emphatically pointed out that the interaction of the hemispheres cannot be formulated as a simple functional dichotomy. The complexity of the functions involved, the apparent randomness in hemispheric location of related subfunctions, and a high degree of individual variability all preclude simple generalizations. As Heillige has pointed out, “The distinction [in left and right hemisphere function] is sufficiently complex as to permit a variety of *post hoc* conclusions and sufficiently vague to prevent clear refutation.” (Heillige 1993).

In humans, the most salient functional and morphological cerebral morphological and functional asymmetries are correlated with language and manipulation. The majority of humans is right-handed (depending upon the criteria used to measure handedness, estimates vary from 70-95% (Heillige 1993). Most right-handed individuals show a left hemisphere dominance for many linguistic subfunctions. The consistency of the relationship of hand dominance with cerebral lateralization for language functions has led many researchers to hypothesize that there is a functional relationship between manipulative and linguistic functions in humans. Falk, for example, postulated a “field effect” wherein left hemisphere dominance for association areas influencing the vocal apparatus was extended to include nearby association areas influencing hand representation (Falk, 1987). Such a field effect, however, is not consistent with what has been learned about the neural network structure involved in cognition.

Corballis has proposed one of the more convincing explanations of the correlation of left hemispheric control of hand and language (Corballis 1991). Corballis has proposed that localization of praxic control in a single hemisphere would have the advantage of minimizing “crosstalk” from similar but slightly out-of-phase signals from the separate hemispheres.

Why there should be a species-level bias for left hemispheric representation of these functions is not known. A number of hemispheric specializations appear to be homologous in other species. Chicks, for example, exhibit right hemisphere dominance for emotional responses, including attack and copulation (Arnold and Bottjer 1985) as do rats for aggressiveness (Dennenberg 1981). Functional lateralization has been demonstrated in split-brain monkeys for tasks unrelated to communication or handedness, including visual discrimination, face recognition, and response to emotionally significant stimuli (e.g., Hamilton and Vermeire 1988). Normal monkeys show a left-hemisphere preference for species-specific vocal processing (Hefner and Hefner 1986; Petersen, Beecham, Zolotow and Stebbins 1978).

Some morphological and behavioral asymmetries seen in non-human primates may be homologous with those seen in humans. The question of hemispheric specialization in non-human primates remains open (MacNeilage, Studdert-Kennedy and Lindblom 1987). Considerable evidence suggests that for many functions, hemispheric specialization at a population level does not exist in non-human primates (Marchant and McGrew 1996 and references therein). However, there is some evidence for population-level lateralization of visual processing (Hamilton and Vermeire 1988), for left hand preferences for visually-guided reaching in monkeys (MacNeilage et al. 1987) and prosimians (Larson, Dodson and Ward 1989); (Colqhuhoun 1994) and visually guided manipulation in gorillas (Vauclair and Fagot 1988). Even in humans, handedness is variable in its expression, not only among individuals, but also for various tasks in the same individual. The degree and direction of hand preference across behaviors depends on environmental, hormonal, and developmental factors as well as genetic predisposition (Annett, 1972; 1985; Kim, Levine and Kertesz 1990; Heillige 1993).

Morphological asymmetries

A number of cerebral morphological asymmetries have been observed in humans as well as non-human primates. Given the frequency of prevalence of “atypical” patterning in humans, and “human-like” morphology in non-human primates, causal interpretations of such asymmetries must be viewed with caution.

Temporo-parietal asymmetries

In many humans, the Sylvian fissure is longer on the left than on the right. It is also longer in chimpanzees and macaques (Falk, 1978LeMay 1976; LeMay, Billig and Geschwind 1982; LeMay 1985). The posterior end of the Sylvian fissure is higher on the right in both African apes and modern humans (Falk, 1978).

The left planum temporale in humans is larger than the right in about 65% of cases in both human adults and fetuses (Geschwind and Levitsky 1978); (Habib, Robichon, Lévrier, Khalil and Salamon 1995). Larger left plana temporale have also been observed in chimpanzees (Gannon, Holloway, Broadfield and Braun 1998). Although macaques do not show significant asymmetries in the occipital cortex, they do exhibit they do exhibit a minor degree of parietal lobe asymmetry, with greater development in the left-hemisphere (Heilbroner and Holloway 1989).

Frontal Lobe Asymmetries

The frontal lobe is divided into three main divisions: the primary motor area (anterior to the central sulcus) the premotor area, and the prefrontal area, including dorsoventral and dorsolateral areas. “Broca’s area” occupies a portion of the left prefrontal area known as the third inferior frontal convolution, or inferior frontal gyrus (Brodmann’s areas 44 and 45). This region is may be subdivided into the pars opercularis and pars triangularis. Although it undoubtedly plays some role in speech production, the exact function of Broca’s area is not well defined. However, the authors of a recent PET study (Petersen and Fox 1988) associate this area with motor praxis (simple tongue movements, hand movements, and imagined hand movements) rather than linguistic production *per se*.

Broca’s area is often (but not inevitably) enlarged in modern humans. An enlarged Broca’s area has been occasionally observed in *Pan troglodytes* as well (Holloway 1983b). The fossil record reflects consistent enlargement of this cortical region in the genus *Homo*, beginning with *H. habilis*.

In modern humans, the anterior portion of the right hemisphere is often wider and protrudes further than its left counterpart (right frontal petalia) (Gilissen, Dabringhaus, Schlaug, Schormann, Steinmetz and Zilles 1996a; Gilissen, Steinmetz, Dabringhaus, Schlaug, Schormann and Zilles 1996b; Holloway and De La Coste-Lareymondie 1982). Frontal petalia have also been observed occasionally in monkeys, and are frequently present in African apes (Holloway and De La Coste-Lareymondie 1982). However, the human pattern is unique in that the frontal petalia is very well developed, extending both antero-posteriorly and mediolaterally. The frontal-polar prefrontal cortex is activated bilaterally when individuals hold in mind a primary goal while exploring and processing secondary goals (Koechlin, Basso, Pietrini, Panzer and Grafman 1999). In modern humans, frontal petalia typically occur on the right side and are frequently accompanied by left occipital petalia, especially in right-handed individuals (Gilissen et al. 1996b; Holloway and De La Coste-Lareymondie 1982). The right-frontal/left-occipital petalial pattern does not appear in Pongids. It is manifested irregularly in early *Homo*, but is found consistently in later hominids, including *Homo erectus*.

Some evidence exists for asymmetry in human frontal lobe sulcal patterns (White, Lucas, Richards and Purves 1994). Equivalent asymmetry has not been observed in other species (although the upper end of the central sulcus may vary more in position than the lower end) (LeMay 1976; 1982; 1985; LeMay et al. 1982; White, Richards, Lucas and Purves 1994).

Occipital Lobe Asymmetries

Modern humans frequently exhibit left occipital petalia, usually in combination with a right frontal petalia (see discussion above). Left occipital petalia have been observed in non-human primates, but differ in magnitude from those of hominids. Even when left occipital petalia occur in non-human primates, they are not consistently associated with right frontal petalia, as they are in modern humans (Holloway and De La Coste-Lareymondie 1982).

“Atypical” patterning of petalia is associated with non-right-handedness. It is also more common in females. Females and non-dextral individuals are also more frequently “atypical’ in terms of linguistic function and consistency of handedness (Heillige 1993). However, as many as 85% of humans deviate from the “classical” cerebral laterality pattern, either in direction or degree of hemispheric lateralization, intra-hemispheric organization, plasticity of one hemisphere in assuming the other hemisphere’s functions, or in hemispheric dominance for behavioral control (Robinson, Becker, Camp and Mansour 1985).

Occipital petalia are consistently found in the genus *Homo*, with the exception of *H. habilis,* where the pattern occurs in some, but not all, specimens (Tobias, 1987).

Cerebellar Asymmetries

In one MRI study, cerebellar morphological asymmetry was correlated with handedness and with asymmetry of the contralateral cerebral hemispheres (Snyder, Bilder, Houwei, Bogerts and Lieberman 1995). These results are somewhat paradoxical, as fMRI imaging has shown that the ipsilateral cerebellum is active during imagined as well as executed hand movements (Lotze, Montoya, Erb, Hulsmann, Flor, Klose, Birnbaumer and Grodd 1999). Complex hand movements are organized both ipsilaterally and bilaterally in the cerebellum (Kawashima, Matsumura, Naito, Waki, Nakamura, Matsunami, Fukuda and Yonekura 1998). The cerebellum also functions asymmetrically with respect to language processing, auditory memory, and spatial and visual sequential memory (Desmond et al. 1998; Iidaka et al. 2000; Riva and Giorgi 2000; Schlosser et al. 1998). Assessment of cerebellar asymmetries in fossil hominids is problematic, given the difficulty of distinguishing asymmetry of the lateral lobes themselves *versus* asymmetries imposed by the transverse sinuses. Further challenges arise from the ever-present problems of small sample-size and taphonomic distortion.

Qualitative Analyses of the Cerebellum and Posterior Cranial Fossa

Australopithecus

A number of authors have briefly discussed the morphology of the PCF, and by extension, the cerebellum, in fossil hominids. Holloway (1988) found that in the early “robust” australopithecine, KNM-WT 17000, the cerebellar lobes flare laterally and posteriorly as they do in chimpanzees. Both Holloway (1972) and Tobias (1967) observed that the cerebellum is enlarged in *Paranthropus* compared to *Australopithecus* and the great apes. Weidenreich (1947) suggested that the petrous part of the temporal bone could inhibit brain growth in the region of the inferior temporal lobes. However, Kochetkova’s analysis indicated the opposite effect, at least in the La Chapelle cranium (Kochetkova 1978). Dean has speculated that petrous compression in *Homo* and *Paranthropus* may be an accommodation of the slower-growing posterior cranium to the rapidly expanding cerebellum during prenatal development (Dean 1988, citing Ford 1956)). The PCF of later “robust” australopithecines appears more like that of Middle Pleistocene and modern humans in its vertical or even undercut posterior petrous surface (Aiello and Dean 1990)Seidler, Falk, Stringer, Wilfing, Müller, zur Nedden, Weber, Reicheis and Arsuaga 1997).

Homo habilis

Tobias reported that the cerebellar fossa in *Homo habilis* was variable in relative volume, but expanded posteriorly and superiorly (Tobias 1967). Based on a series of absolute and indexical measurements of endocranial casts, he also found that the cerebellum was more fully developed in *A. boisei* than in other early hominids (Tobias 1967; 1995).

Homo erectus

Tobias also observed that the PCF in *H. erectus* was expanded posteriorly and superiorly (Tobias 1967).

Archaic H. sapiens

The PCF in Neandertals is flattened posteriorly, but protruding and extended anteriorly; the cerebellar lobes are well separated (Boule and Anthony 1911; Heim 1976; Seidler et al. 1997).

Quantitative Analyses of the Cerebellum and PCF

As discussed above, relative cerebellar volume has been documented for a wide range of primates (Matano et al. 1985a; Stephan et al. 1970; Stephan 1972; 1981; 1988). However, sample sizes for hominoids (including modern humans) have been very small and few quantitative analyses have been conducted related to cerebellar evolution in fossil hominids.

One such study was conducted by Kochetkova (1978), who made linear measurements of the cerebellar portion of a series of hominid endocasts. Her analysis suggested that absolute and relative cerebellar dimensions increased steadily throughout hominid evolution, from *Australopithecus* through Early and Middle Pleistocene *Homo*, leveled off through the Late Pleistocene, then dropped abruptly in modern humans. In a preliminary study, D. White (1998) noted that cerebellar width relative to overall cerebral length in a sample of 11 African fossil hominids, 4 classic Neandertals, one European early *Homo sapiens*, and 30 living hominoids, including modern humans, exceeds expected width based on non-human primate baseline.

The morphology of the posterior cranial fossa is subject to a complex interaction among biomechanical and ontogenetic influences. In addition to the impressions of the lateral cerebellar lobes, the posterior cranial fossa reflects the morphology of other occipital and basicranial structures, including the transverse and sigmoid sinuses, the so-called “vermian” fossa, the subarcuate fossa, the foramen magnum, and, in some individuals, the occipital and marginal sinuses. The degree of basicranial flexion and the angle of the petrous processes also inform PCF morphology. Because these structures interact in poorly understood ways, it is inappropriate to assume that changes in cerebellar shape reflect changes in neurological organization or function of the cerebellum.

Holloway (1996) has tabulated 14 “major cortical regions in early hominid evolution.” As described above and summarized in Table A-3, histological and/or imaging studies have documented cerebellar connections with each of these areas.

Cerebellar evolution must have occurred in tandem with cortical reorganization for new adaptive cognitive/sensory-motor behaviors as they emerged. If this is the case, changes in cerebellar morphology, including changes in relative cerebellar volume, may be expected to correlate with evidence of cortical reorganization.

A strong, if still controversial case has been made for aspects of PCF morphology as phylogenetic indicators. For example, occipital-marginal sinuses are present in many of the known robust australopithecine fossils in which this area has been preserved. However, occipital-marginal sinuses are found occasionally even in modern humans and some apes. Therefore, the presence of an occipital-marginal sinus system in any fossil hominid is a statistical rather than a definitive indicator of taxonomic status.

Vermian Fossa

Similarly, the presence of a marked “vermian fossa,” a wide separation of the impressions of the cerebellar lobes, has been used as the basis for both phylogenetic and functional inferences e.g., (Boule and Anthony 1911; Seidler et al. 1997). However, Black (1915) examined the morphology of this trait and found it to be variable in modern humans and uncorrelated with cerebellar morphology.

Transverse sinuses

In the majority of hominoids, the superior sagittal sinus drains into the left transverse sinus and the straight sinus drains into the right transverse sinus at the confluence of the sinuses. Thus, the transverse sinuses are asymmetrical as they issue from the confluence. Impressions of the transverse and sigmoid sinuses vary among individual endocasts for at least two reasons. (1) there is an idiosyncratic tendency for some endocasts to be more strongly marked than others, regardless of the functional morphology of the adjacent soft tissues; (2) when occipital and marginal sinuses are present, they convey a variable amount of cerebral blood volume relative to that borne by the transverse sinuses.

Basicranial flexion

Phylogenetic variation among hominids in basicranial flexion has been observed in a number of studies (Laitman et al. 1979; Laitman and Heimbuch 1982; Laitman and Reidenburg 1988; Lieberman 1975; 1994 b; a; Lieberman and Crelin 1971; 1984a; Lieberman et al. 1992; Lieberman et al. 2000). The basicranial angle follows a complex ontogenetic trajectory and is correlated with overall brain volume (Lieberman et al. 2000). Basicranial morphology also appears to be influenced by the biomechanics of posture, hearing, respiration, mastication, cranio-facial allometry, negative allometry between short cranial base length versus body mass; and artificial modification of the cranial vault and (Anton 1989; Dean and Wood 1984; Lieberman et al. 2000; Strait 1999; Taylor and Dibennardo 1980). Basicranial flexion is customarily measured via landmarks on the external skull base. One study has been undertaken which examines the internal morphology of the basicranium with respect to basicranial flexion (Spoor 1997). However, to the present author's knowledge, in no study has the basicranial angle been considered with respect to the volume or shape of the cerebellum.

Petrous angle

Like basicranial flexion, the orientation of the petrous processes is subject to a number of biomechanical and ontogenetic influences whose interaction is not well-understood (Dean 1988; Dean and wood 1981; 1984). A more coronally-oriented petrous angle in early hominds compared to other hominoids corresponds with shortening of the skull base with downward deflection of the nuchal area, basicranial flexion, and the anterior migration of the foramen magnum and occipital condyles (Dean and Wood 1981). Petrous orientation is customarily measured on the exterior of the skull rather than the endocranium (but see Spoor 1997). Cerebellar volume and shape undoubtedly contribute to the morphology of the petrous processes (Dean 1988). However, cerebellar influence has not been the subject of any quantitative analysis of petrous morphology known to the present author.

Subarcuate fossa

In many mammals, including non-hominoid primates, the petrosal lobule of the cerebellar paraflocculus (PLP) occupies a lateral outpocketing petrosal wall of the posterior cranial fossa. The PLP, part of the paleocerebellum, receives neural input from the vestibular labyrinth related to coordination and balance. Subarcuate fossa volume varies from order to order. In primates, subarcuate fossa volume is highly correlated with PLP volume, and follows a linear negative allomeric trend with respect to brain and cerebellar volumes. It is absent in adult hominoids, with the exception of *Hylobates*. The PLP appears to be formed by bone resorption in response to parafloccular development. In hominoids, the PLP is not well differentiated and the paraflocculus accessorius, its anatomical homologue, does not impinge on the petrosal bone (Gannon, Eden and Laitman 1988). Consistent with the morphology of large-brained, large-bodied hominoids, no trace of a subarcuate fossa has been reported for fossil hominids.

5 COGNITIVE EVOLUTION:

ARCHAEOLOGICAL EVIDENCE AND MODELS

The following discussion is framed around Wynn's (1996) chronology of technological and cognitive change in the Paleolithic, as well as the taxonomic composition of the sample used in the present study. Traditional culture/stratigraphic divisions are used for ease of reference. The discussion focuses on issues pertinent to the role of the cerebellum in cognitive evolution. These issues are discussed under the following headings:

Taxonomy: (Which hominids made are responsible for what artifacts?). This has a direct bearing on what neurological morphology underlies the behaviors in question. The discussion under this rubric highlights the evidence that in no phase of the Paleolithic is there an unequivocal association of only one hominid taxon with one type of artifact industry.

Sources of Variability: (To what degree was variability intentional and/or influenced by cultural norms?). Assemblages may vary according to the variety of tool forms (typological variability) or by the proportions of different types of tools present in different assemblages (assemblage composition) (Dibble 1987, citing Bordes 1950; 1953; 1961). Factors to consider in discussing assemblage variability include the following:

- necessity/opportunity/expediency
- resource availability and changes therein

- social and demographic factors (stylistic norms; cultural repertory; modes of information storage; modes of information transfer; life span; population density)
- technological constraints
- curation strategies

\ Distributed Cognition: Cognition requires a context (i.e., it is *distributed* between the individual and an environment, which, in turn, is shaped by natural, social, cultural and technological structures and processes over time) (Vygotsky 1978; Hutchins 1995). For example, objects such as stone tools not only arise form but also contribute to the cultural environment (Holloway 1981a). Distributed cognition takes into account social organization within and between groups; mode of communication (lexical, gestural, etc.) and the media through which culture is stored and transmitted.

Neuro-cognitive Development: This is considered under three modalities: *Neocortical/Sensory-Motor* (what degree of fine motor control was required to produce the technology or behavior?); *Neocortical/Declarative* (what degree of conceptual or representational sophistication was required to produce the technology or behavior?); and *Cerebellar/Procedural* (to what degree did the cerebellum influence production of the technology or behavior?)

The division among neuro-cognitive functions is somewhat arbitrary, as any intentional motor behavior recruits all three modalities. However, there is a division of labor among neurological regions and structures that is reflected in the modalities selected. Different authors have constructed differently configured models for hominid cognitive evolution. These models often overlap with the "declarative/procedural" dichotomy, but are not entirely congruent with it:

Pelegrin's differentiation of "*conaissances*" and "*savoir-faire*" corresponds closely to the difference between procedural and declarative cognitive processes (Pelegrin 1991).

Wynn (1979; 1981; 1985; 1991; 1996a) has used a three-stage, recapitulationist, gradualist model based on the work of Piaget (1952). In Wynn's analysis, hominids passed through "sensory-motor", "concrete operational," and "formal operational" phases. Both "sensory-motor" and "concrete operational" stages invoke procedural cognitive strategies that would involve a cerebellar contribution. Wynn (e.g., 1985; 1991; 1996a; b; 2000) has also emphasized "spatial intelligence" as a focal area of human cognitive evolution The spatial abilities he refers to recruit specific regions of the parietal and frontal cortices which have demonstrated cerebellar connections and which are activated simultaneously with the cerebellum in visuo-spatial functions. Like most authors discussed, Wynn's discussions focus on the cerebral cortex, rather than subcortical structures such as the cerebellum.

Donald (1991) has proposed three major transitions in cognitive evolution: "mimesis" (voluntary copying and recall of motor routines); "lexical invention" (differentiation and labeling perceptions and concepts); and "externalization of memory" (visuo-symbolic invention, external memory records; and externally nested cultural products, or theories). Donald's "mimetic function" is largely a sensory-motor adaptation, and coincides in many, but not all respects, with

Wynn’s spatial intelligence and Piaget’s sensory-motor and concrete operational stages (Piaget, 1952).

Donald (1991) has made a distinction between left-hemispheric, generative and sequential neural control required for throwing and stone knapping and the more generalized, holistic right-hemispheric functions supporting “mimesis” (but see Calvin, 1983 and Corballis, 1991).

Mithen’s (1996b) recapitulationist, modular model relies heavily on the work of Fodor (1983) and Gardner (1993). Mithen has proposed that human cognitive evolution proceeded from a stage of “general intelligence” through a gradual elaboration of distinct “modules”: social, technical, and natural science. It is not until the Upper Paleolithic that the discrete modules become integrated. Mithen’s “technological intelligence” is similar to the sensory-motor, concrete operational, and spatial intelligences described above. Unlike Wynn and Donald, who have proposed stages of cognitive evolution in which visuo-spatial abilities are at least somewhat generalized to social and subsistence behaviors, Mithen has suggested that the technological and social intelligence modules remain utterly separate from the social intelligence module until the emergence of modern humans.

Like Mithen, many other authors vest modern human cognition in the development of a specialized symbolic capacity that appears late in hominid evolution and is unique to anatomically modern humans (e.g., Davidson and Noble 1993; Klein 1990; Mellars 1991). These authors find that the behavior of early modern humans is dramatically different from that of archaic humans, and they attribute this behavioral difference to neocortical evolution related to language. Even if this is the case, manipulation of symbols does involve the participation of the cerebellum and its interconnections with many areas of the neocortex.

For yet other authors, social complexity is the driving element of cognitive evolution. Holloway has proposed that human cognitive evolution was catalyzed by the generation and management of complexity in the context of increasingly important social interactions (Holloway 1967). As described by Holloway, complexity management requires the interaction of both declarative cognitive strategies (mediated by the temporal region of the neocortex) and procedural, rule-based cognitive strategies mediated by the frontal cortex, basal ganglia, and cerebellum (Ullman, in press). The archeological evidence suggests that the balance between these complementary cognitive modalities shifts during hominid evolution, as discussed below. Models that emphasize social factors have been proposed by Byrne (1996), Dunbar (1992), Gamble (1986) and Soffer (1992).

<u>Timing, Tempo and Mode of Transition</u>. Was the transition gradual or saltational? Are biological, cognitive and technological changes correlated? To what degree were “new” behaviors incipient in the previous phase? To what degree were the changes cumulative or part of an autocatalytic cycle?

Proponents of gradualist models emphasize early evidence of symbolic capacity, overlaps between culture-stratigraphic levels, and taxonomic ambiguities in the fossil record. On the other hand, proponents of punctuated models interpret the paleontological evidence as episodic, with clear distinctions among both archeological stages and the humans who made them.

Stages in Human Cognitive Evolution

6-2.5 mya (Pliocene)

Although the earliest hominids probably had a level of gestural, representational, and communicative sophistication, as well as tool-making ability, at least equal to that of modern apes, the known lithic record does not begin until c. 2.5 million years ago (Harris 1983) (Harris and Semaw 1989, cited in Klein 1999).

Holloway (1969, 1996) has proposed that "social intelligence" would have been enhanced in early *Australopithecus*. Bipedalism would have permitted new and more complex social dynamics and a range of natural experiments in social order based on aggression control, sexual division of labor, and cooperation.

2.5 – 1.6 mya (Early Lower Paleolithic/Oldowan (Mode 1); *Australopithecu*s and *Homo habilis)*

Taxonomic Issues

It is unclear which of the early hominid species regularly used stone tools. The first stone tools appear to have been contemporaneous with the emergence of the genus *Homo*, and stone tools have been consistently found in association with *H. habilis*. However, at least one australopithecine species may have made and used stone tools (Asfaw, White and Lovejoy 1999). Other instances are equivocal. When australopithecines have been found in association with lithics (e.g., at Swartkrans and Bed I, Olduvai), fossils from the genus *Homo* have also been present (Klein 1999). However, the robust australopithecines had hand morphology more similar to humans than to apes, with features related to precision grasping. Although early *Homo* is known from in artifact-bearing localities in the Shungura formation and the Turkana Basin, dating to 2.5 or 2.6 mya, the majority of hominid fossils represent robust australopithecines. It is possible and even likely that later australopithecines were tool users (Susman 1988; 1991; 1994).

The earliest stone tool industries used simple flaking techniques on pebble tools. They are generally referred to as Oldowan, or “Mode 1” industries (Clark 1977).

Sources of Variability

Mode 1 stone artifacts have been categorized according to their shape, size, and degree of retouch, with speculative labels related to their possible functions (e.g., Leakey 1971). However, variability in the Oldowan falls along a continuum and can be accounted for by the number of flakes removed as well as the size and composition of available raw materials, rather than formal intentionality or design criteria on the part of the makers (Isaac 1976; Klein 1999; Wynn 1996).

Distributed Cognition

Wynn (1981; 1996) has stated that techniques for Oldowan as well as Acheulean (“Mode 2 [Clark 1977]) tool manufacture and use could have been learned by imitation. It is not clear whether knapping techniques would have involved trial-and-error imitation, or more active “donation” of information by experienced knappers to less experienced ones (King 1991). However, in Donald’s (1991) model, Oldowan toolmakers had not yet developed mimesis (where motor routines can be voluntarily recalled and rehearsed). There is no evidence for linguistic categorization of tool forms or transmission of cultural norms around their manufacture (Isaac, 19796; Klein 1999; Wynn 1996).

It is possible that *H. habilis* may have lived in larger social groups than is usual in Pongids (Dunbar 1992; Mithen 1996b). The social context for learning may have been enriched in two senses: larger social groups permit more permutations of socially-constructed knowledge; and individuals who have well developed “social intelligence” may have a fitness advantage over less socially adept individuals (Byrne 1996; Mithen 1996b).

Mithen (1996) has credited *H. habilis* with a relatively well developed “social intelligence module.” He has suggested that *H. habilis* may have been able to cope with more “orders of intentionality” (Dennett 1988) than non-human primates. However, in Mithen’s model, the predominant cognitive mode was a rather primitive generalized intelligence.

Holloway (1969, 1996) has pointed out that the marked tendency for hemispheric lateralization in *H. habilis* would have enhanced socially important cognitive functions such as facial recognition and analysis of social behavioral complexity. He has speculated that the arbitrariness, duality of patterning, and productivity of Oldowan tool making are reflections of linguistic behavior.

Support for rudimentary language in the cultural repertory of *H. habilis,* comes from evidence for encephalization and cortical reorganization (Deacon, 1997; Falk 1983; 1992; Tobias 1980; 1983).

Neurocognitive/Sensory-Motor

Simple flake production involves both sensory-motor and superior parietal “association” areas of the neocortex, as well as the cerebellum (Stout, Toth and Schick 2000). Early Mode 1 tool-makers had developed visuo-spatial and sensory-motor functions which enabled them to judge the appropriate striking angle, as well as the precise control of ballistic actions involving accurate placement of blows and force of percussion (Gowlett 1986; 1996; Wynn 1996; Pelegrin 1991). In addition to fossil evidence for neocortical reorganization for greater hemispheric lateralization in *H. habilis*, the archeological evidence suggests that makers of the Oldowan preferred to use their right hands as the striking hand during unifacial flaking (Toth 1985; 1987).

Neurocognitive/Neocortical-/Declarative

Oldowan toolmakers appear to have surpassed the cognitive abilities of Pongids in that they were capable of greater planning depth (Binford 1985), rather than strictly episodic, *ad hoc* use of tools. The makers of the Oldowan recognized and sought out specific lithic resources, often transporting them several kilometers from their source. (Gowlett 1996, citing Leakey 1971; Schick and Toth 1993). They were able to conceptualize landscapes and resource distribution with sufficient consistency to practice routed foraging (Binford 1984) or to cache stone tools and return to the site with meat for processing (Potts 1988).

Oldowan toolmakers exhibited at least as much capacity to handle conceptual representations as chimpanzees who have reached Piaget's stage of "preoperational intelligence" (Parker and Gibson 1979; Wynn 1981). They exhibited an understanding of the concepts of boundary, proximity and order (Wynn 2000). They were also capable of a degree of representational complexity only reached by apes who have undergone long and intensive training (Langer 1993; 2000). Their ability to bring both stone tools and food to geographical locations independent of either resource suggests they were able to conceptualize correspondences between objects belonging to different representational sets (Langer 1993). Simple flake production involves both sensory-motor and superior parietal "association" areas of the neocortex, as well as the cerebellum (Stout, Toth and Schick 2000).

Mithen (1996) has credited *H. habilis* with an emerging "technological intelligence module", as well as an incipient "natural history intelligence module". However, he has denied both lexical and grammatical abilities to these early hominids, describing their dominant cognitive strategy as one of undifferentiated general intelligence. Mithen (1996) has pointed out that wood residues on some Oldowan stone tools indicate they were used to make other tools, again a sign of more complex representational sets than utilized by other primates.

Neurocognitive/Cerebellar-/Procedural

Mode 1 tool makers exhibit many behaviors enhanced by cerebellar involvement, including differentiation of motor functions (Leiner et al. 1986); activation of goal directed behaviors (Brodal and Bjaalie 1997; Daum, et al.

1993); judgment of the velocity of moving stimuli (Leiner et al. 1993); spatial event processing (Petrosini 1996); elementary visuospatial and memory functions (Brodal and Bjaalie 1997); and working memory (Middleton and Strick 1997).

Tempo and Mode of Transition – Oldowan to Acheulean

By the end of the Oldowan, the appearance of bifacially worked "discoids" indicates these hominids had developed the technical skill to produce the bifaces typical of the Acheulean ("Mode 2" [Clark 1977]) industrial complex (Wynn 2000). Gowlett (1996) has pointed out that Acheulean and Oldowan industries overlap chronologically. Oldowan-like assemblages may be found at 700 kya and beyond; and there are many instances of the symmetrical, bifacial tools which predate 700 kya. However, it does not appear that the makers of the earliest Mode I industries had made the conceptual step of "re-representation" (Karmiloff-Smith 1996) or imposing an intentional, pre-determined form on their tools (Gowlett 1996).

1.6 mya - 300 kya (Later Lower Pleistocene/Acheulean (Mode 2) /*Homo erectus*

Taxonomic Issues

Evidence for Acheulean industries in northern, eastern and southern Africa, Europe, and Southern and Western Asia. Bifacial industries are less common in East Asia, but have been reported in both China and Korea (although they often have a less finished appearance than typical African or European bifaces)(Klein 1999). The large bifacial tools characteristic of the Acheulean were made by both smaller-brained early *H. erectus* and later, larger-brained Middle Pleistocene hominids (Klein 1999 and references therein).

Sources of Variability

The Acheulean is noted for its relative consistency of form over a wide geographical area for many thousands of years, rather than for its variability. However, extensive variability has been observed with regard to tool morphology, as well as the distribution of tool forms from assemblage to assemblage.

Typological variability: The finished appearance of the artifacts varies depending upon the raw materials they are made of (Gowlett 1984). Some allometric variation is present. Larger bifaces, for example, tend to be proportionally narrower; and short bifaces tend to be proportionally wider. This type of variation may be related to two factors (1) preservation of the size and shape of the butt end of the biface so that it continues to fit the hand; and (2) considerations of weight and ease of handling, where proportions are secondary to functional considerations (Gowlett 1996). Acheulean bifaces, or large cutting tools, have been classically identified as “cleavers” and “handaxes.” Isaac (1977) and Gowlett (1996) have questioned whether these represent distinct, intentional forms in the minds of their makers. Gowlett (1984) has also speculated that there may be some stylistic influence on their appearance.

There is considerable diachronic variability in the Acheulean. Many innovations appear in the late Acheulean. Bifaces, which appear after about 500 kya exhibit congruent, bilateral symmetry in three dimensions (Wynn 2000).

Other innovations of the later Acheulean are more fully described in “Tempo and Mode of Transition to Middle Paleolithic,” below.

Assemblage variability: Although the Acheulean is generally signified by the presence of bifaces, many Early and Middle Pleistocene assemblages lack bifaces altogether, especially in East and Southeast Asia. Bifaces are missing from many European sites as well, including, for example, Atapuerca TD6, Isernia La Pineta, Bilzingsleben, Clacton, Arago, Vallonet, Schönigen, and Vértesszöllös (Klein 1999). Villa (1983) has observed that the distribution of bifaces appears to be independent of temporal, spatial, and environmental variables, at least in southern France.

Klein has attributed differences in distribution of biface forms to possible stylistic preferences (Klein 1999). Mithen (1986b), on the other hand, has described variability in curation, form and distribution of bifaces as a passive reflection of the environment, reflecting only undifferentiated general intelligence rather than an integrated set of intelligences (Mithen 1996b). Individual skill is also a factor that contributes to the form of the finished implement (White and Dibble 1986; Wynn 2000).

Distributed Cognition

The standardized forms of the Acheulean were made to conform a cultural pattern (Gowlett 1996; Wynn 1996). However, as Wynn (1996) has pointed out, the similarity of bifaces across continents and across hundreds of thousands of years suggests that the nature of cultural transmission in *Homo erectus* has no analogue in modern human culture.

Donald (1991) has credited *Homo erectus* with fully-developed mimetic capacity. For Donald, mimesis is independent of language, is at the heart of human social effectiveness, and is essential to group solidarity. He has emphasized the advantages of mimesis in social adaptedness.

Holloway (1967; 1981) has pointed out that the sociality and arbitrariness involved in biface manufacture are also characteristics of language. Calvin and Bickerton (2000), who, like Holloway, have proposed a gradualist scenario of linguistic evolution, have denied syntax to *Homo erectus*, but conceded a simple lexicon. However, other authors have denied language altogether to *H. erectus* (e.g., Klein 1990; 1992; 1999; Mellars 1989b; a; 1991).

Davidson and Noble, (1989) have recognized the importance mimicry, but have found evidence for it only in modern humans, co-incident with the appearance of representational depiction and language.

Mithen (1996b) has grouped *H. erectus* with Middle and Late Pleistocene humans. He has distinguished these groups with respect to language, however. He has attributed a well developed social intelligence to *Homo erectus,* and has proposed that they were capable of a limited “social language,” used for conveying emotional content. He has made the analogy that vocal communication in *H. erectus* was like an elaborate version of a cat purring.

Neurocognitive/Sensory-Motor

Production of symmetrical, bifacial stone tools may not have required greater sensory-motor coordination than production the bifacial tools seen in the Developed Oldowan (Gowlett 1996). However, many Acheulean tools are made on large flakes. They are heavy compared to the Oldowan. Simply manipulating and carrying such large objects required overall strength, which is reflected in the larger stature and body mass of post-habiline hominids. Both postcranial evidence and endocranial morphology suggest that makers of the Acheulean were right-handed at a population level (see Chapter 4 for a discussion of the fossil evidence).

The discoverers of long, well-crafted wooden spears at Schöningen in Eastern Germany have speculated that the spears were weighted for throwing rather than thrusting (Thieme 1997). If this is indeed the case, the individuals who wielded them would have needed considerable ballistic skill to bring down game successfully.

Neurocogntive/ Neocortical-Declarative

Mode 2 industries are distinguished from Mode 1 assemblages in several respects. In addition to sheer flake size (Isaac 1972), the most obvious distinction is the adherence to a generalized mental template and the arbitrary imposition of shape (Gowlett 1984; 1986; 1996; Holloway 1969; Pelegrin 1991; Robson Brown 1993). However, the limited formal variability of tools may imply only a limited symbolic capacity (Wynn 1996).

Mode 2 toolmakers had an appreciation of part-to-whole relations, involving manipulation of individual elements (length, width, thickness) while their proportional relationships remained constant (Gowlett 1996). Objects were not always produced *ad hoc*, but were systematically quarried, manipulated, and cached as sets (e.g. accumulations of bifaces at Olorgesailie, Isimila, Ubeidiya, and Kilombe). Middle Pleistocene hominids also had hierarchically organized, more complex operational chains characteristic of Piaget's "concrete operational" intelligence (Gowlett 1986; Isaac 1986; Langer 1993; Piaget 1952; Wynn 1981; 1985; 1996a). In this respect, their representational abilities exceeded those exhibited by intensively trained apes (Langer 2000; Toth, Schick, Savage-Rumbaugh, Sevcik and Rumbaugh 1993) and may approach modern human capacities for "concrete operational" intelligence (Wynn 1979; 1985; 1991; 1996a) or "savoir-faire" (Pelegrin 1991).

Mithen (1996b) has grouped *H. erectus* with Neandertals as "early Humans." He has credited both *H. erectus* and Neandertals with considerable technological intelligence (based on their mastery of bifacial knapping and prepared-core techniques). He has acknowledged that Middle Pleistocene hominids must have had well-developed natural history intelligence and social intelligences. However, he has advanced the hypothesis that the making of stone tools was not fully integrated with subsistence behavior, based on their lack of specialization for different tasks.

Neither cerebral hemispheric lateralization nor lithic forms offer definitive evidence about linguistic capacity in *H. erectus.* However, some authors have proposed that the neural substrate (both neocortical and cerebellar) that supported rapid, serial movements in ballistic aiming or even stone knapping could have been recruited for the rapid, serial oro-facial movements used in speech production (Calvin 1983; Corballis 1991). Donald (1991), however, has disagreed, suggesting that mimetic action patterns are analogue and metaphorical rather than symbolic and computational.

It is likely that Middle Pleistocene hominids had a limited lexicon related to their social and technological environment, but that the rule-based, hierarchical and representational aspects of language remained undeveloped (Calvin and Bickerton 2000).

Neurocognitive/Cerebellar-Procedural

Relative cerebellum volume is larger in *H. erectus* than in any other hominid, with the exception of recent humans. Cerebellar enlargement could have been contributing either to sensory-motor or to cognitive functions, or both. It is likely that cerebellar evolution underlay the highly developed sensory-motor, concrete-operational, and mimetic abilities of *H. erectus*. Given the ambiguity of the evidence for linguistic behavior or cognitive sophistication, it is less likely that the cerebellum had assumed the same role in manipulation of concepts that it plays in modern humans.

Stone-knapping skills required to produce typical Mode 2 artifacts may be equivalent to those needed to produce simple flake and chopper industries, but the ballistic skills needed for accurate throwing of spears (and probably stones) are considerable. The slight rise in relative cerebellar volume may be attributed to an increased cerebellar role in both ballistic throwing, as well as procedural cognitive functions related to production of standardized bifaces: visuospatial coordination (Brodal and Bjaalie 1997); spatial event processing (Petrosini, 1996); shape recognition (Gao et al., 1996); procedural memory processes

(Daum and Ackermann 1997); working memory (LaBar et al. 1999; Middleton and Strick 1997); scheduling of multiple goals (Roberts, Collins and Robbins 1996); regulation of changes in directed attention; shape recognition (Gao et al. 1996); pattern generation; counting, timing, sequencing; improved ballistic control; and judgment of the velocity of moving stimuli (Leiner et al. 1993).

Tempo and Mode of Transition within and beyond the Acheulean

Wynn (1985) has suggested that the transition from the Oldowan to the Early Acheulean is less marked than that from the Early to the Late Acheulean. The later Acheulean may be distinguished from the early Acheulean in several respects. Wynn (1985; 2000) has reported increased symmetry over time, although this may be attributable in part to raw material variation or stylistic differences (Gowlett 1984). More significantly, by the late Acheulean a number of technological innovations appear. Artifacts of wood, including throwing/-thrusting spears have been found, dating to the Middle Pleistocene (Clark 1969; Oakley et al., 1977; Thieme 1997). Given the perishability of wood, however, and microwear evidence for wood working as far back as the early Acheulean (Dominguez-Rodrigo, Serrallonga, Juan-Tresserras, Alcala and Luque 2001) and even the Oldowan (Keeley and Toth 1981), it is hard to know the degree to which this represents technological or conceptual innovation. Occasional objects of flaked bone and ivory appear as well, although they are crudely worked (Mania 1995).

Antecedents of prepared-core (Mode 3) techniques are found in the Acheulean, perhaps as early as one million years ago (Bordes 1950; Clark 1970;

Gowlett 1996; Isaac 1972, citing Biberson 196a; Sohnge, Visser and Van Riet Lowe 1937). However, they were not fully and consistently exploited in flake production until 200-300 thousand years ago (Gowlett 1996; Wynn 1996; Svoboda 1987).

The transition to Mode 3 technology may have occurred earlier in Africa than in Europe, in response to changing ecological conditions. Sangoan artifacts (including several radial and subradial cores, as well as large bifaces) underlie Middle Stone Age strata found at the Simbi site in Western Kenya (McBrearty, Bishop and Kingston, 1996).

300-150 kya: Late Middle Pleistocene, Late Acheulean/Early Middle Paleolithic *Homo sapiens*

Taxonomic Issues

Chronological ambiguities and a mosaic of skeletal and behavioral features do not permit easy classification of Late Middle Pleistocene hominids. The two hominids included in the present study are illustrative in this respect. Kabwe (Broken Hill), has been attributed to *H. heidelbergensis* (Rightmire 1976); *H. soloensis* (i.e., *H. erectus*) (Weidenreich 1943), and early *H. sapiens (Klein 1999).* Swanscombe is most frequently described as a pre-Neandertal or Neandertal (Breitinger 1952; 1955; Howell 1960; Klein 1999; Stewart 1955; Trinkaus 1986). The results of the present study support including Swanscombe with a Neandertal or pre-Neandertal group, despite its early date of 400 kya (Stringer and Hublin 1999a). On the other hand, in the present study, Kabwe groups with *H. erectus*, despite its large endocranial volume. For the sake of convenience, and for want of clearer taxonomic criteria, hominids of this period will be designated as “Middle Pleistocene *Homo sapiens.”*

Sources of Variability

Svoboda (1987) has suggested that late Middle Pleistocene assemblage variability may be related to both climatic and social factors.

Both Lower and Middle Paleolithic industries are characterized by a preponderance of heavy-duty artifacts made with coarse raw materials such as basalt, quartzite and limestone (Svoboda 1987). However, several assemblages of small, specialized tools, dating from as early as 700 kya, have been found in the Middle Pleistocene (e.g., at Isernia de la Pineta, [Coltorti et al. 1981]; at Soleihac (Bonifay et al., 1977); at Arago (de Lumley 1976); at Bilzingsleben (Vlcek 1980) and at Vértessöllös (Thoma 1966, cited in Svoboda 1987). These tools are usually produced by non-standardized processes without the extensive core preparation associated with later Mode 3 industries Middle Pleistocene hominids may also have replaced heavier stone implements with ones made of wood (Svoboda 1987).

Distributed Cognition

Despite their considerable technical abilities, Middle Pleistocene hominids were not culturally modern in any recognizable way (Wynn 1996). Cultural isolation, induced by low population density, may have played a part in maintaining a lower level of technological sophistication in the Middle Pleistocene small-tool industries in Europe (Clark & Lindly 1991; Stiner, Munro and Surovell 1999; Svoboda 1987; Whallon 1989). Transport distances for lithic raw materials suggest that intergroup interactions were confined to a relatively small geographical area (Roebroeks, Kolen and Rensink 1988).

In Africa, however, greater population densities may have led to greater opportunities for information exchange and led to the precocious appearance of more sophisticated technologies (Deacon, in press).

Neuro-cognitive/ Sensory-Motor

Sensory-motor skills developed in earlier time periods appear to have been adequate to produce and use the Mode 3 cultural artifacts of the Middle Pleistocene (Gowlett 19894; Wynn 1979; 1991; 1996; 2000). Technological advances were more likely due to neocortical expansion of neocortical association areas rather than primary sensory-motor regions.

Neuro-cognitive /Neocortical-/Declarative

Development of linear and recurrent prepared core techniques, soft hammer retouch, and indirect percussion permitted refined control of the working edge and overall shape (Boëda 1988; Chase 1990). The invention of these techniques appears to be more of a conceptual than sensory-motor development (Gowlett 1996). In fact, some authors consider the appearance of Mode 3 prepared-core techniques to be an important milestone in human cognitive evolution (Roebroeks et al. 1988; Rolland 1990, cited in Mellars, 1996).

Rare instances of “concept-mediated marking” (Bednarik 1995) or intentional, non-utilitarian alteration of raw materials have been reported for the Middle Pleistocene. The Steinrinne site at Bilzingsleben is associated with fossils attributed to late *H. erectus.* Several intentionally incised bone and ivory artifacts have been found at the site, which has been stratigraphically dated to 350 kya. Other Middle Pleistocene sites with incised or engraved objects have been found at Stránská Skála in the Czech Republic, Auditorium Cave at Bhimbetka, near Bhopal, and Berekhat Ram (Bednarik 1995). The markings resemble non-representational, non-utilitarian markings that have been found in Middle Paleolithic sites such as La Férrassie, Pech de l'Azé, Prolom 2 (Crimean peninsula),Tagliente Shelter from Grotta dell'Alto, Italy, Apollo Cave, and numerous Australian sites (Bednarik, 1995 and references therein). D'Errico and Villa (1997) have established that many marks attributed to human intentionality are the result of other taphonomic or biological processes. However, several incised artifacts appear to the result of intentional human activity.

The fine bifaces characteristic of the late Acheulean could have only been made by individuals who had mastered "spatio-temporal substitution" (Piaget and Inhelder, 1967). This has led Wynn to attribute "operational intelligence" characteristic of modern human adults to Middle Pleistocene hominids (Piaget 1952; Wynn 1996).

Whether operational intelligence in spatial operations extends to other cognitive domains is less clear. Mithen has attributed a high level of "technical intelligence" to Middle Pleistocene hominids. He has also suggested that the language capacity of Middle Pleistocene *Homo,* although lexically rich and grammatically complex, was confined to social interactions and did not extend to other intelligence modules. Mithen's model is the antithesis of the "distributed cognition" model outlined by Donald (2001), in that he sees each domain of intelligence as isolated from the others. Social context, for example, appears to make a minimal contribution to technological or natural history intelligences. How such information would be conveyed from individual to individual, much less from generation to generation within such a model is not clear.

Neurocognitive/Cerebellar-/Procedural

Makers of the Late Acheulean exhibited a high level of spatial cognition to makers of the late Acheulean, but has repeatedly commented on their failure to produce modern culture (Wynn 1979; 1985; 1991; 1996). In a recent publication (Wynn, 2000), in which he has incorporated both neurofunctional studies of spatial abilities (Kosslyn 1994) and modularity theory (Fodor 1983), Wynn has speculated the spatial abilities of *H. erectus* and Middle Pleistocene *Homo* required associations between concrete, primary sensory functions and information processed in the parietal and frontal lobes. Evidence from a recent functional PET study (Stout, Toth and Schick 2000) supports Wynn's hypothesis. There are clear indications of parietal and frontal lobe expansion in *H. erectus* and earlier hominids (e.g., Falk 1990; Holloway 1975a; 1976; 1996; Tobias 1987). Moreover, relative cerebellar volume is greater in *H. erectus* and Middle Pleistocene *Homo (*e.g., Kabwe) than in earlier hominids, reflecting its interconnectivity with the neocortical regions involved in spatial cognition and its role as a sensory-motor coordinator.

Tempo and Mode of Transition to Middle Paleolithic

Intentionally incised bone and ivory artifacts are rare in the Middle Pleistocene, but the ones that are discovered resemble those found in later, Middle Paleolithic sites such as La Férrassie, Pech de l'Azé, Prolom 2 (Crimean peninsula), the Tagliente Shelter from Grotta dell'Alto, Italy, Apollo Cave, and numerous Australian sites (Bednarik 1995). Prepared-core techniques also appear during the Middle Pleistocene, although they are not systematically used until the Middle Paleolithic (Gowlett 1996).

200-40 kya (Late Pleistocene/Mousterian/Middle Paleolithic (Mode 3)

The earliest known Mode 3 lithic production techniques (flakes struck from prepared cores; systematic blade production; soft-hammer and indirect percussion) appeared in at the terminal Middle Pleistocene, in Africa, as early as 250 kya at Kalambo Falls and by 200 kya at Kapthurin (McBrearty, Bishop and Kingston 1996).

Taxonomic Issues

Middle Paleolithic/Mousterian artifacts are most commonly associated with Late Archaic Humans. However, many Mode 3 forms appearing in earlier assemblages have been attributed to Middle Pleistocene hominids (Gowlett 1996). Moreover, early anatomically modern humans are found in association with Mode 3 artifacts as well, in Israel, for example (Léveque and Vandermeersch 1980; Vandermeersch 1981) as well as northern Africa (Hublin 1992). Despite their technological similarities, the ecological and behavioral contexts in which Early Modern humans made and used stone tools may have been somewhat different from those of Late Archaic *H. sapiens* (e.g., Niewoehner 2001; Shea 1994; 1998; Trinkaus 1983; 1992; Trinkaus, Ruff and Churchill 1998).

Sources of Variability

Typological Variability: Bordes identified 63 different categories of tools for Mousterian assemblages, based on the position and type of retouch and the technique of manufacture (Bordes 1961; Chase and Dibble 1987). Although Bordes attributed much of this variability to stylistic differences among human cultural groups, a number of authors have offered alternative explanations for both interassemblage and typological variability. Dibble, for example (1987) has described typological variability in Mousterian as continuous, and has attributed differences in tool form to reduction intensity.

Interassemblage Variability: Binford proposed a functional model for Middle Paleolithic interassemblage and typological variability, based on three basic assumptions: (1) there was a division of labor in Middle Paleolithic social groups, who carried out seasonally and spatially differentiated economic functions; (2) geographical patterning of resources affected the types of economic activities that were carried out; (3) different tools would have been utilized for different activities (Binford 1983; Binford and Binford 1966; 1969).

However, use-wear studies have provided evidence that different morphological forms were often used for overlapping functions (Keeley 1980; Beyries 1988; Plisson 1988), cited in (Mellars 1996). Variation within regional assemblages is often as great as variation among regions.

On the other hand, there are numerous examples of Middle Paleolithic assemblages that feature idiosyncratic, geographically restricted forms (e.g., Central and Eastern European bifacial foliate points; cordiform handaxes and extensively retouched back knives in southwestern France) (Chase and Dibble 1987; Mellars 1996). It is likely that these represent isochrestic variants (non-symbolic, but culturally transmitted styles) (Chase and Dibble 1987; Sackett 1982).

The rare bone or antler that artifacts appear in the Middle Paleolithic are made with the same knapping approaches used for stone, rather than by shaving, incising or grinding and polishing techniques which would be more appropriate for the medium Chase and Dibble (1987), citing (Jelinek 1977).

Distributed Cognition

Late Archaic Humans apparently had well-developed within-group social networks which could support disabled individuals, despite the rigors of life in the Late Pleistocene (Trinkaus 1989).

Interaction among groups, on the other hand, especially during the early Middle Paleolithic, may have been sporadic, due to low population densities, which limited intergroup contacts (Stiner, Munro and Surovell 2000). Although the intergroup networks of Middle Paleolithic humans were not as far-flung as those of later Upper Paleolithic humans, lithic raw materials were occasionally transported over considerable distances (Roebroeks et al. 1988).

Mithen (1996; 2000) has attributed a high degree of social intelligence, and possibly a social lexicon, to the makers of the Middle Paleolithic; but in

Mithen's model their social, technological, and natural history intelligences were not yet integrated.

Many authors have denied language to Late Archaic humans (e.g., (Davidson and Nobel 1993; Klein 1990; Mellars 1991; Lieberman 1984a). There is little support for this position, given their endocranial morphology, their sophisticated subsistence strategies, and their capacity to produce Upper Paleolithic cultural artifacts (see "Transition to Upper Paleolithic," below).

Neurocognitive/ Sensory-Motor

The prepared-core techniques utilized for much of Middle Paleolithic technology require long practice. However, humans had mastered the technical skills for production of these tools by at least 300,000 years ago (Pelegrin 1991; Wynn 1996).

Neurocognitive/Neocortical-/Declarative

To the extent that discrete tool types are the result of emic discrimination rather than etic imposition, they may represent different linguistic categories as well (Holloway, 1981). However, as Chase and Dibble (1987) have pointed out, many Middle Paleolithic artifact "types" fall along a continuum of variability and do not appear to represent discrete categories of deliberately produced end-products. Lithic forms reflect a learned set of behaviors, but not stylistic or symbolic intent or linguistic categories.

Deliberately incised and engraved bone and stone objects appear occasionally in the Middle Paleolithic. As in earlier Paleolithic periods, the meaning (or even the intentionality) of these "concept-mediated marks" is disputed (e.g., Bahn 1996; Bednarik 1995; Chase and Dibble 1987). The most impressive examples of deliberate marking include an engraved flint nodule from Quneitra, an inscribed nummulite and polished mammoth plaque from Tata, Hungary, and numerous shells, fossils and perforated teeth and bones (Bednarik, 1992; Marshack, 1985; 1990 and references therein).

Pigments, including manganese dioxide and iron ores, are frequently found in Middle Paleolithic contexts from Europe, Australia, and Africa (Bednarik, 1992; Demars, 1992; Watts, 1999; Wreschner 1985).

Neuro-cognitive/Cerebellar-procedural

Late Archaic humans had expanded their repertory of lithic types and refined their knapping techniques. The production of tools from prepared cores required long practice (Pelegrin 1991). However, tools of this type appear sporadically even in Middle Pleistocene contexts (Clark 1970; Gowlett 1996; Hublin 1993; Isaac 1972). Similarly, manufacture of Upper Paleolithic stone tools was within the competence of Late Archaic and even earlier humans (Brooks and Yellen 1996; Deacon McBrearty and Kingston 1996; Meignen and Bar-Yosef 1988; Rigaud 1997). It is unlikely that additional cerebellar evolution was required to cope with the technological aspects of either Middle or Upper Paleolithic lithic industries.

Tempo and Mode of Transition from Middle Paleolithic to Early Upper Paleolithic

As described above, the signature technology of the Middle Paleolithic is the routine production of prepared-core stone tools. The Early Upper Paleolithic, on the other hand, is characterized by a suite of behavioral and technological innovations described below ("40-20 kya/Early Upper Paleolithic").

As Ambrose and Lorenz (1990), Jelinik (1990), Marks (1990), and Straus (1995; 1997) have pointed out, the transition from the Middle to Upper Paleolithic was gradual, mosaic, and context-dependent. In Sub-Saharan Africa, for example, where there is both biological and archeological continuity, the transition appears to have occurred largely *in situ* in response to fluctuating environmental conditions (Allsworth-Jones 1993; Ambrose and Lorenz 1990; Deacon, 1992; Phillipson 1985). The transition was gradual in parts of the Near East and the Russian Plain (Bar-Yosef 1989; Soffer 1989). In parts of France, by contrast, the transition may have been rather abrupt (Harrold 1989). In many other European contexts, the transition was more gradual in all aspects of human adaptation, including lithic technology, raw material characteristics, patterns of faunal exploitation, evidence for symbolic behavior, and settlement patterns (Clark 1992).

Many of the behaviors attributed to the Upper Paleolithic appear sporadically in earlier Middle Pleistocene contexts, including

- the presence of coloring pigments (Bednarik, 1992; de Lumley and de Lumley 1973; Demars, 1992; Marshack 1976; 1989; Watts, 1999; Wreschner 1985);
- small-scale stone tool and/or blade-rich industries (e.g., Ambrose and Lorenz 1990; Bower, 1998; Deacon 1989; Brooks and Yellen 1996;

McBrearty and Kingston 1996; Otte 1990; Phillipson 1985; Svoboda 1984; 1987);

- the presence of apparently symbolic objects in burials (Movius, 1953; Leroi-Gourhan, 1975; Soleki 1975);
- pierced animal teeth; occasional instances of bone working (Freeman 1978; Marshack 1976; 1989; Thoma 1966);
- long distance lithic transport strategies (Roebroeks et al. 1988);
- engraved or incised patterns on stone, bone, and ivory (e.g., (Bednarik 1992; Marshack 1976; Perony 1934);
- and evidence of systematic hunting and shell fishing after 55 kya (Marean and Kim 1998; Stiner et al. 1999; Straus 1997).

The initial Upper Paleolithic may have emerged independently from many localized Middle Paleolithic contexts by convergence, rather than diffusion or replacement (D'Errico, et al. 1998; Straus, 1997). The precocious appearance of Upper Paleolithic blade-rich assemblages in Southern and Eastern Africa (Deacon 1992; McBrearty and Yellen 1996) and Israel (Meignen and Bar-Yosef 1988), even when later hominids produced typical Mousterian tools in the same region, suggests that many aspects of Upper Paleolithic technology are a response to environmental exigency, rather than cognitive developments. Overall behavioral patterns, reflected in skeletal morphology as well as functional archeological studies, may be a better indicator of cognitive evolution in later Pleistocene hominids than tool typology *per se* (Ambrose and Lorenz 1990; Clark and Straus 1983; Klein 1975; 1979; 1992; Trinkaus and Smith 1985).

40-20 kya Early and Middle Upper Paleolithic (Mode 4)

For many authors (e.g., Klein 1992; Mellars 1996; R. White 1982) the Upper Paleolithic is produced by a profoundly different set of cognitive behaviors from the Middle Paleolithic. However, as outlined above, many Upper Paleolithic behaviors are prefigured in earlier times. In addition, diachronic cultural variation occurs within the Upper Paleolithic itself, in several domains, including intra-and inter-site complexity, land-use patterns, hunting strategies, non-depictive notational markings, personal ornamentation, elaboration of tool types, medium and style of representational “art,” and technological complexity (Bailey 1983; Clark 1997; Straus 1995).

The earliest known Upper Paleolithic (Mode 4 industries, featuring blade-rich assemblages, and worked bone artifacts [Clark 1977]) appeared in the Levant about 45 kya (Marks 1990); in Anatolia 41-43 kya (Kuhn, Stiner, Reese and Gülek 2001); in Central Europe and Spain approximately 40-42 kya (Allsworth-Jones 1990; Bischoff, Soler, Marato, and Julia 1989; Svoboda, Lozek and Vlcek 1996); and by 37-38 kya in other regions of Western Europe (D’Errico et al. 1998; Gamble 1986; Straus 1995). These early industries were followed by Middle Upper Paleolithic industries such as the Pavlovian and Gravettian, which appeared approximately 30 kya, possibly as a response to worsening of climatic conditions (Straus 1995; Gamble 1986).

Early Upper Paleolithic industries are characterized by a suite of technological innovations, including the following (from Binford 1982; Klein 1992; Mellars 1989b; a; 1991 Rigaud 1989).

- a shift from “flake” dominated to “blade” dominated assemblages;
- greater standardization of tools and more economic use of lithic resources;
- increased variety and complexity of tool forms; and a more rapid rate of technological change;
- use of organic materials (bone, ivory, and antler) for artifacts;
- the proliferation of non-utilitarian objects, including beads, pendants, pierced animal teeth, marine shells, and representational objects and paintings;

Taxonomic Issues

Early Upper Paleolithic artifacts are associated with both Late Archaic and Early Modern humans. In Western Europe, the Châtelperronian industry is found in association with Neandertals at Arcy-sur-Cure and St. Césaire (Leroi-Gourhan 1958; Léveque and Vandermeersch 1980; Stringer, Hublin and Vandermeersch 1984). In Central and Eastern Europe, the Bohunician, Szeletian, Jankovichian, and Kostienki-Streletskaya and possibly the Aurignacian Upper Paleolithic industries are attributed to Neandertals (Allsworth-Jones 1990; Karavanic 1995; Smith 1984; Svoboda, Lozek and Vlcek 1996). However, with the exception of the Vindija Neandertals there are no diagnostic remains securely associated with these industries (Smith, et al. 1999). On the other hand, both blade-based and microlithic (i.e. Mode 4) assemblages are known from several Middle Pleistocene contexts, and have been attributed to Archaic humans: e.g., the Kapthurin Formation in Kenya (McBrearty and Kingston 1996); the Middle Awash in

Ethiopia (Brooks and Yellen 1996); Hayonim Cave in Israel (Meignen and Bar-Yosef 1988); and the Howieson's Poort assemblages in South Africa (Allsworth-Jones 1993; Deacon 1992).

Distributed Cognition

The Early Upper Paleolithic was characterized by an intensification of developments related to distributed cognition. "Concept mediated marks," which appear sporadically in the Middle Pleistocene (Bahn 1996; 1997; Marshack 1996) became more common, although their symbolic significance is a matter of continued debate (e.g. Bednarik 1992; Byers 1994; Chase and Dibble 1992; Wynn 1991). Beads, pendants and pierced teeth, as well as abundant coloring pigments, reflect a focus on personal ornamentation, and increased concern for formalized social differentiation and personal identity (R. R. White 1982; 1989a; 1996).

A still open, but crucial, question in terms of distributed cognition is whether and how Archaic and Early Modern humans may have interacted with each other to influence technological, symbolic, and social behaviors. As D'Errico et al. (1998) have observed, an implicit biological determinism informs most models of this interaction, in which limited (or no) symbolic capacity is attributed to Late Archaic humans (e.g., Chase and Dibble 1987; Farizy 1990; Harrold 1983; Klein 1992; Mellars 1989; 1996; 1991; Noble and Davidson 1993; Otte 1990; Stringer and Gamble 1993; R. 1996; but see Mellars 1998 and R. White 1998 for a more equivocal position). Upper Paleolithic artifacts associated with Late Archaic humans are interpreted as the result of trade or imitation, whose invention is outside the capabilities of archaic humans The almost simultaneous appearance of Upper Paleolithic technologies and Early Modern humans in Europe is taken as evidence that Early Modern humans were the inventors of those technologies. Another assumption behind the “imitation model” is that information transfer was unilateral rather than mutual, from the Early Modern to the Late Archaic group (notwithstanding the accumulated knowledge and successful strategies developed by archaic humans over thousands of years for coping with glacial environments).

However, as outlined above, many Upper Paleolithic behaviors, including symbolic elements, are prefigured in earlier times, and many of the earliest Upper Paleolithic industries represent continuous, indigenous developments arising *in situ* from the Middle Paleolithic (Allsworth-Jones 1993; Ambrose and Lorenz 1990; Bar-Yosef 1989; Clark 1992; Deacon, 1992; Phillipson 1985; Svoboda, Lozek and Vlcek, 1996; Vandermeersch 1997). Svoboda (1998, p. S27) has suggested that models based on “independence, variability, parallelism, convergence, or analogy” reflect the data better than acculturation models. Resolution of this question has been hampered by the lack of diagnostic human fossils with Early Upper Paleolithic archeological assemblages and by chronological ambiguities (Smith et al. 1999; Trinkaus 1986).

Regardless of phylogenetic/technological affinities, shifts in population density related to climatic changes would have affected the frequency and complexity of inter- and intra-group contacts, information exchange, and competition (Bailey 1983; Clark and Straus 1983; Gamble 1986; Richards, Pettitt, Stiner and Trinkaus 2001; Soffer 1990; Stiner, Munro and Surovell 2000; Straus 1996). Intergroup contact and competition in densely populated areas (e.g. glacial refugia) may have led to more systematic social organization (Bailey 1983; Mellars 1991). In regions where harsh environments led to small, widely distributed populations, humans may have depended upon a far-flung social “safety-net,” with regional, public information systems sharing common stylistic conventions (Gamble 1986).

Sources of Variability

All of the factors affecting variability in earlier technological stages (intentionality, style, curation strategies, material constraints, convention, function, and individual skill) were still operative. But other factors came into play as well in the Early Upper Paleolithic. As described above, a number of new artifact types proliferated, including carefully-worked bone, antler and ivory artifacts; personal ornaments in the form of perforated teeth and marine shells; and depictive “art.” The examination of non-utilitarian objects removes the issue of technological function from the question of style. Non-utilitarian objects exhibit both geographical and diachronic variability. D’Errico et al. (1998) have attributed the clear differences between Aurignacian and Châtelperronian to independently developed, cultural traditions maintained by distinct human groups. The Gravettian style, on the other hand, was a widely distributed, temporally constrained, regional phenomenon associated exclusively with Early Modern humans (Gamble 1986).

Diachronic change may be observed on a broader scale as well. Recognizable, representational figures of humans and other animals did not appear in the earliest Upper Paleolithic. The first known representational figures, even those from Aurignacian contexts, occurred in Europe only after 32 kya, including cave painting at the French Grotte de Chauvet (c. 32 kya); a female figurine from Galgenberg, Austria (c. 31 kya); an ivory statuette from Hohlenstein-Stadel, Germany (c. 30 kya); a carved mammoth from Geissenklösterle, Germany (30-32 kya); and a collection of ivory statuettes from Vogelherd (c. 30 kya) (Bahn Chauvet, Deschamps and Hillaire 1996; Gamble 1986; Marshack 1976; 1989). Non-representational intentional markings were produced very early in Australia, e.g. at Wharton Hill (c. 42 kya); but recognizable figures appeared only much later (Bahn 1997). In Africa, bones which appear to be deliberately notched and grooved are found from very ancient sites like Klasies River Mouth (c. 100 kya) but the earliest known figurative paintings from Africa are found at Apollo Cave (c. 25 kya) (Bahn 1997).

Neuro-cognitive/Sensory-Motor

Early Upper Paleolithic artifacts require a wide range of both fine and gross motor skills and require committed practice for their manufacture and use. However, the basic level of technological competence required to make them appears to have been place by the time of the Late Acheulean (Pelegrin 1991; Wynn 1979; 1985; 1991; 1996a; b; 2000).

Neuro-cognitive/Neocortical-Declarative

Many analyses of Upper Paleolithic "art" and technology have assumed that from the beginning they were produced by humans who were cognitively fully modern (Conkey 1987). For example, Klein (1992) has proposed that the Upper Paleolithic arose from a neurologically based mutation enhancing the individual's ability to manipulate culture via symbolic language. Donald (1991), whose archaeological chronology is somewhat vague, has speculated that intensive, specialized computational demands made by external memory devices developed during the Upper Paleolithic required cerebral reorganization. From the perspective of these authors, putative cognitive differences between Middle and Upper Paleolithic humans are biologically based, but diachronic changes in art during the Upper Paleolithic should be attributed to cultural variability. Given the cultural capacities demonstrated by Archaic Humans who produced Upper Paleolithic artifacts, as well as the significant cultural development that occurred during the Upper Paleolithic itself (Straus 1995; Straus and Heller 1988), the conventionally accepted timing of neurobiological evolution is open to question.

Neuro-cognitive/Cerebellar-procedural

Cerebellar functions that may have been invoked to produce or utilize such art may be related to fine motor coordination, and possibly cognitive aspects of linguistic behavior such as verbal memory or sequencing and recall of narrative material. However, the very large NetBrain and relatively small cerebellum in Middle Pleistocene and Late Archaic humans suggests that neurological evolution in these hominids was related to development of declarative rather than procedural cognitive functions. The manufacture of even simple stone tools by an experienced knapper involves activation of several neocortical regions, especially the superior and inferior parietal regions, as well as the cerebellum (Stout, Toth and Schick 2000). Production of less standardized objects with aesthetic and symbolic significance, as well as a functional context, would be expected to invoke an even greater involvement of the neocortex.

Tempo and Mode of Transition to Late Upper Paleolithic

A number of authors have observed an important cultural transition at the Last Glacial Maximum (18-20 kya) (e.g. Clark and Lindly 1989; Clark and Straus 1983; Rigaud and Simek 1987; Straus 1995). Whether cultural intensification arose from widely-dispersed social network systems or social competition in densely populated environments, or both, the pace of cultural innovation accelerated in the Late Upper Paleolithic.

20-10 kya /Late Upper Paleolithic

Many stone-age cultural innovations were developed well after 40 kya, the date traditionally marking the onset of the Upper Paleolithic (Bailey 1983; Clark and Straus 1983; Rigaud and Simek 1987; Straus 1997; Straus and Heller 1988). Especially after the Last Glacial Maximum, changes in economic and social organization occurred that are reflected in specialized and/or systematic resource exploitation and their supporting technology. Resource procurement became both highly specialized and diverse. In Vasco-Cantabrian Spain and Gascony, for example, elusive or dangerous prey such as ibex and wild boar were rarely sought in the Early Upper Paleolithic, but became common in the Later Upper Paleolithic. Technological advances include eyed needles, harpoons, fishhooks, weirs, traps, projectile weapons such as atlatls, and possibly bows (Straus 1987; Straus and Heller 1988).

Taxonomic Issues

Late Upper Paleolithic cultural remains are exclusively associated with anatomically modern humans.

Distributed Cognition

Increased densities and climatic deterioration during the last Glacial Maximum may have led to intensification of subsistence strategies and the need to regulate more complex social relations through art and technology (Bailey 1983; Clark and Straus 1983; Straus 1991; 1997; R. White 1998). the proliferation of culture in the Upper Paleolithic would have transformed the context in which children's minds developed, leading to restructured neural networks (Mithen 2000).

Several authors have offered hypotheses about the role of "group memory," borne by external memory systems such as language and cultural artifacts, in sustaining the "extended mind" in the Upper Paleolithic (e.g. Clark and Chalmers 1998; Donald 1993; Hutchins 1995; Mithen 2000; Vygotsky 1978; Wallon 1989). As Donald (1993; 2001) has observed, such external memory systems permit almost unlimited "distributed cognition." However, the possibility of continued neurobiological evolution in Late Upper Paleolithic or Holocene humans is not explicitly addressed.

Sources of Variability

As in earlier periods, variability was a product of functional as well as cultural dynamics. Demographic fluctuations intensified the pressures to establish both individual identities and group boundaries (Clark 1994; Gamble 1982; 1991; Mithen 1991). Paradoxically, frequent inter-group encounters would have also offered more frequent opportunities for trade and diffusion of ideas as well, accelerating the rate of technological innovation and the proliferation of variants and new combinations of elements.

Neurocognitive/Declarative

An increasing number of objects, object-categories, concepts related to social stratification and the regulation of intergroup contacts led to escalating cultural complexity (Holloway 1969) and resulted in what Gowlett (1996) has referred to as “declarative multiplicity.”

Byers (1994) coined the term “effortless reflexivity” to describe the cognitive facility underlying all of modern human behavior. Effortless reflexivity enables humans to monitor routinely and to modify consciously their behavior in light of their own mental contents. Byers has contended that effortless reflexivity underlies all rule-based behavior as well as self-consciousness, and that it is essential for all symbolic activities, including language and depiction of absent objects. Several authors have acknowledged the possible usefulness of Byers’ conceptual framework, but questioned whether the acquisition of reflexive facility was as abrupt as Byers contends; or that it coincided with the Middle-to-Upper Paleolithic transition (e.g., De Beaune 1994; Clark 1994; Shanks 1994; Straus 1994; Wynn 1994).

Neuro-cognitive/Cerebellar-Procedural

Both "declarative multiplicity" and "effortless reflexivity" involve cognitive manipulation of multiple, complex mental representations. Cognitive reflexivity, whenever it arose, would have been supported by the neocortex, at least, and possibly by subcortical structures such as the cerebellum. At some point in hominid evolution, merely increasing the computational network size, embodied in the neocortex, may have become an inefficient mechanism for managing increased representational complexity (Kien 1992).

Late Archaic and Early Modern Humans have the largest brains of all hominids. The data collected in the present study support the hypothesis that their neocortical size reached a critical mass in terms of network computational capabilities. Cerebellar evolution is a plausible mechanism for increased ability to cope with rule-based, procedural, computational organization across many domains. In later humans, cerebellar circuitry may have been exapted from control of serial timing of motor functions to serial timing of larger computational units (e.g., longer and more complex motor functions; multiple motor and conceptual representations; "thoughts;" more complex linguistic productions). Specific cognitive behaviors that may have emerged or became more important during the Late Upper Paleolithic include analysis of complex scenes or texts (Leiner et al. 1993) verbal intellectual capacities; creative, flexible nonverbal thinking and design fluency (Conn 1995); working memory (Middleton and Strick 1997); and retention of complex narrative material (Paradiso et al. 1997).

Late Archaic and Early Upper Paleolithic Modern Humans exhibit many behavioral similarities. As demonstrated below (Chapter 11, “Data Analysis and Results”), they may have similar relative cerebellar volumes. However, at some point between the earliest modern humans and Recent humans, the cerebellum became relatively larger. The timing and tempo of this increase, whether it occurred at the Late Glacial Maximum, when the pace of technological innovation accelerated, or even later, can only be determined by an examination of Late Pleistocene and Holocene endocrania.

Summary

Cognitive evolution during the Paleolithic was a complex and mosaic process. At times, biological adaptations enabled new behaviors to emerge. At other times, culture drove neurological changes, both through ontogenetic plasticity and genetically-based cortical reorganization. Traditional culture-stratigraphic attributions are undermined by functional analyses. Models which rely on strict biological determinism are inadequate to account for the association of many hominid groups with any given Paleolithic industry or “mode” of production.

The earliest toolmakers (Mode 1) exhibited advanced sensory-motor abilities, “preoperational intelligence” and a capacity for representational complexity that was somewhat more sophisticated than that of living pongids (Langer 1993; 2000; Parker and Gibson 1979; Wynn 1981).

Makers of the Acheulean (Mode 2) had a well developed “operational intelligence,” and social mechanisms through which isochrestic “styles” could be conserved from generation to generation.

By the Middle Pleistocene, hominids had well developed procedural, technical and sensory-motor “intelligence.” However, there is little agreement about their symbolic and linguistic capacities. Neurological changes and behavioral changes as registered in the surviving archeological record support divergent views for the timing of linguistic and other symbolic behavior. Many biological anthropologists and neuroanatomists are advocates of early linguistic development (e.g., Calvin and Bickerton 2000; Deacon, 1997; Holloway 1967; Falk 1983; Tobias 1980; 1983). They cite the neurological changes observed in endocranial morphology in early hominids. Archeologists and neuropsychologists, on the other hand, are more likely to advocate a late-language model (Davidson and Noble 1993; Donald 1991; Klein 1992; Mellars 1989a; 1991; Mithen 1996b). They draw their conclusions based on the late appearance of unequivocally symbolic artifacts. In light of the challenges of associating behavior with neuroanatomy, even in living species, and the role of culture in informing behavior regardless of genetic predisposition, the impasse is presently unresolvable.

On the other hand, there is a consensus that from at least Gravettian times onward, humans were capable symbol-makers and symbol users. It is taken for granted that both their symbolic behavior and neuroanatomy were fully modern. However, modern humans have undergone considerable, mosaic skeletal morphological change over the last 30,000 years, (e.g. Holliday 1997; Stringer 1992; Trinkaus and Smith 1985). They have also changed dramatically in terms of behavior, especially in their ability to produce and maintain cultural and social complexity at an accelerating rate from the Last Glacial Maximum to the present. It is appropriate to explore they possibility that they have also evolved neurologically during the Late Pleistocene and perhaps even during the Holocene as well.

Scenarios of Cognitive Evolution

Many synthetic attempts have been made to account for human cognitive evolution. In addition to the models described in detail above, the models outlined in the Appendix, Table A-10, are noteworthy. Each has influenced the analysis that follows. Where appropriate, these individuals have been cited in the body of the text.

6 ENDOCRANIAL VOLUME

Historical Perspective

A time-ordered series of fossil hominid endocranial volumes strikes the observer with one immediate, unequivocal fact: hominid cranial capacity has increased dramatically over time. The interpretation of this fact has been clouded for several reasons: (1) Though absolute cranial capacity has increased, the relationship of brain volume to body mass has followed a more ambiguous trajectory; (2) global size is not a meaningful gauge of the specific cognitive functions and underlying neurological organization informing the behavior of living organisms; (3) a "cerebral chauvinism" arising from the Cartesian dualism and an outdated *scala natura* biological model (Searle 1984).

Measures of Encephalization

Notwithstanding speculation about a cerebral "rubicon" separating human from non-human cognitive potential, even the earliest students of endocranial morphology in fossils recognized that brain size must be allometrically related to body size. Cuvier introduced the concept of relative brain weight in animals as early as 1845, relating intelligence (I) to brain weight (E = encehalon) to body weight (C = corpus) by a straightforward isometric equation: $I = E_{gr}/C_{gr}$ (Cuvier, 1845, cited by Stephan 1988). In 1891 Snell developed an allometric model, expressed as a bivariate power function, to describe the dependency of brain size on body size: $y = bx^{\alpha}$, where y is the dependent variable, b is an empirically determined constant, and α is an empirically determined “allometric coefficient” (Snell 1891, cited in Deacon 1990a and in Jerison 1973). Snell observed that log/log transformation of the power function ($\log y = \alpha \log x$) makes it amenable to regression analysis, permitting the slope and intercept to be easily determined. Following Snell, Dubois based his “cephalization index” on the assumption that the systematic allometric equation represented a surface-to-volume functional connection between the peripheral sensory organs and the brain. The regression line represented the somatencephalon, or body-brain; shifts in the intercept revealed progressive phylogenetic levels of development of the psychencephalon, or mind-brain relative to the somatencephalon (Dubois 1897, cited in Deacon 1990a).

The fallacies of mind-body dualism and progression (“bigger is smarter”) (Deacon 1990a) have informed and distorted most subsequent studies of encephalization. Nonetheless, encephalization indices continue to be useful in identifying large-scale diachronic or phylogenetic trends. As Gould (Gould 1966) has pointed out, the bivariate power function is a “quick and dirty,” accessible, statistically “adequate,” and biologically interpretable way to model changes in size, scale and proportion. The allometric approach was given theoretical support by Huxley (1932) and its application to encephalization in particular was extended by von Bonin (von Bonin 1937), who meticulously measured a sample of over 100 mammals, arriving at a value for α of 2/3. As the value of $\alpha = 2/3$ was congruent with regression of the surface area of the brain scaled to the surface area of the body, and consistent with received wisdom (Bauchot 1978, citing

Brandt 1867), the correlation was believed to represent a causal surface-to-volume relationship and was widely accepted (Bauchot 1978; Gould 1966; Jerison 1973).

Jerison (1973) assumed a functional relationship between brain and body size in a large range of taxa, superimposing a series of lines with a slope of 2/3 on points related by “grade. Jerison further refined the application of allometry to the problem of encephalization by conceptualizing it as the analysis of residuals, defining an "encephalization quotient" (EQ) as the relationship between measured and predicted brain size, based on the allometric regression. He employed a “criterion of subtraction,” assuming that an EQ which deviated significantly from the value predicted by the allometric regression line for a given grade represented a departure also in terms of information processing/mental capacity based on the availability of “extra-neurons”.

While Jerison’s allometric predictions were based on the mean value of a range of mammal species across with a wide range of body sizes, Bauchot and Stephan took a somewhat different approach, basing their line on an extensive sample of "basal" insectivores, whose brain and body sizes were presumably representative of the earliest primate groups (but see Deacon’s (1990b) argument that they may occupy too specialized a set of niches to be truly representative of early primates).

Martin derived a new α value of 0.76 based on data collected from 309 species of placental mammals across 18 orders (Martin 1981). Martin proposed that this value for α is based on its correlation with maternal basal metabolic rate.

Martin also pointed out that for individual species values of brain size may vary by a factor of five on either side of the predicted value, suggesting that other factors (e.g. gestation period; natural foraging behavior) may be involved. Harvey and Krebs have pointed out weaknesses in the maternal metabolism hypothesis, but do find a correlation of the 0.76 α value with fetal development patterns (Harvey, Krebs and Brains 1990).

Martin interpreted the vertical separation (shift of intercept) in regression lines of similar slopes across taxa as a "grade" distinction related to adaptational shifts (Martin 1982; 1983).

Problems in Interpreting Allometrically Derived Data

Allometric data are often robust enough for broad-brush analyses in "mouse-to-elephant/mouse lemur-to-gorilla" comparisons. A number of problems arise, however, when more limited taxonomic ranges are considered. The data are subject to distortions arising from a daunting list of sources, discussed briefly below:

Extrapolation to Size Ranges beyond the Empirical Data

Allometric regressions are empirically determined and apply only to size ranges represented by the actual data (Gould 1966). Outside this range, distortions may be introduced, limiting predictive confidence (Deacon 1990a). This is problematic in many studies of human encephalization, because human values fall outside the trend. If they are included, they may introduce bias; if they are excluded, interpretation of human values may fall beyond the range of predictive confidence.

Interdependence of Allometric Constant and Coefficient

The allometric constant and the allometric co-efficient are interdependent. Their point of intersection determines the correlation between any two allometric regressions. A change in measurement units, for example, produces a shift in the point of intersection. Care must be taken in choosing measurement units to ensure that the correlations drawn have underlying biological meaning (Gould 1966)

Line Fitting

Linear regression results will be affected by two factors, based on the theoretical criteria for fitting the lines: the distribution of variance between the x and y variables and the correlation coefficient (Aiello 1992 and references therein; Deacon 1990b; a; Martin 1982; Sokol and Rohlf 1981). Each of the common statistical line-fitting techniques (least squares regression, major axis and reduced major axis regression) makes different assumptions about these factors. All linear regression equations tend to underestimate the slope in closely related taxa, where the ratio of error to variance is greater (Harvey et al. 1990). As in most statistical comparisons, sample size also affects the breadth of the confidence intervals for the slopes, and therefore the sensitivity of comparison tests.

Data Transformation vs. Higher Degree Equations

The bivariate function itself is usually analyzed by a log/log transformation of the data, which in itself adds a level of distortion to the results. Although a bivariate function is relatively easy to calculate, the fit may force a fit even where the data depart in a systematic way from a straight line. Higher order equations are more sensitive to the data. Bauchot (1978), citing Count (Count 1947) pointed out that a higher-order (second-degree) polynomial equations fit the actual allometric trajectory of brain regression on body weight. Because of the difficulty of fitting higher-order regression lines, Bauchot proposed the use of a hyperbolic function. Modern computerized statistical analyses can incorporate higher order regressions, but their application to encephalization studies has not been extensively explored. Deacon pointed out that the downward curvilinearity of a second degree equation fitted through a broad sample of mammals (log brain weight/log body weight) may reflect either a curvilinear allometric function or a systematic skewing of mammalian orders with different mean body sizes to one side or the other of the line (Deacon 1990a).

Unknowablity of Residuals

No matter what allometric approach is used, fossil studies are vulnerable to another analytical pitfall: unknowability of the residuals (Smith 1996). Meaningful allometric signals can be swamped by “noise” arising from many sources, including

(a) loosely-fitting or improperly constructed analogies with extant organisms;

(b) accumulated imprecision from broad confidence intervals related to small sample size and non-normal distributions;

(c) individual variability resulting from sex, age, nutritional status and other factors;

(d) measurement imprecision resulting from normal measurement error and compounded by the condition of fossil material, which is often unassociated, incomplete, and distorted.

(e) Use of the allometric power function assumes that the line passes through the origin (a biologically impossible “0” point with little theoretical justification (Albrecht and Gelvin 1987; Deacon 1990a).

Choice of Reference Group

The choice of reference group has profound results on the analysis (Bauchot 1978; Begun and Walker 1993; Deacon 1990b; a; Harvey et al. 1990; Holloway and Post 1982; Martin 1981). For example, when Martin’s (1981) line including 18 orders of mammals is used, almost all primates score high; but only half of primates fall above a line derived from primate data only. Lines that incorporate a broad taxonomic range do not take into account the considerable variation from order to order. On the other hand, if a more limited taxonomic range is used, taxa that share a common ancestor will weight the line in favor of the ratio they represent. Moreover, higher-order taxa with many descendant groups will be over-represented (Harvey et al. 1990).

Holloway and Post have suggested that the choice of allometric exponent could be based on a known functional equivalence (e.g. the 2/3 exponent’s hypothetical relationship to surface areas) (Holloway and Post 1982). The functionally-based regression line would provide a reference point for analyses based on a “criterion of subtraction.” They have pointed out, however, that unless the theoretical functional cause is confirmed (which is not the case for the 2/3 exponent), our assumptions may be based on mere coincidence, and other, more valid causal relationships may be overlooked. They issued a caveat about reifying EQ, suggesting that they are best seen as an initial way to evaluate evolutionary trends or generate testable, biologically relevant hypotheses.

Brain and body masses are not independent variables. A statistical distortion may be introduced when the volume or a part is regressed upon the volume of a whole without first subtracting the volume of the part (e.g., when brain mass is regressed upon body mass, without first subtracting brain mass from body mass). However, as the brain constitutes only a small proportion of body mass, and as brain weight-body weight correlations within populations are not statistically significant (Henneberg 1990, citing Holloway 1980; Pakkenberg and Voigt 1964). Covariance of brain weight and body weight is not likely to distort the regression analysis, as brain weight represents only a small fraction of body weight (Deacon 1990a). However, when the part under consideration represents a large fraction of the whole, as is the case with the telencephalon, neocortex, and cerebellum, which constitute a large fraction of total brain volume, deviations from the allometric trend may be masked unless an adjustment is made by subtracting the part from the whole prior to the regression analysis (Deacon 1990a).

Biological Justification

The biological justification for assuming that departures from allometry represent extra (or diminished) information-processing capacity is not well established. In the first place, the psyche-vs.-soma dualism is fallacious (see discussion below). In the second place, it is likely that other biological constraints intervene (e.g., maternal basal metabolism) (Deacon 1990a) and references therein. In the third place, it is inappropriate to assume that brain size is the variable under selective pressure. Species which deviate negatively from the allometric trend may have been under selection for relatively larger body size (e.g. gorillas, Neandertals) rather than reduced relative brain size. In these cases, the “bigger is smarter” fallacy for brain size may be especially insidious.

Brain Size Does Not Equal Intelligence

Finally, as many researchers have insisted (Deacon 1990a; Holloway, 1966; 1972; 1981; 1982; 1996), no organism functions by a nebulous capacity to process more or less information. Effective information processing is specific and highly organized, depending upon memory, minutely organized neuroendocrine communications networks, and hierarchically interdependent, topologically patterned interconnections of peripheral and central nervous system.

Interpretation of Encephalization Data

Despite the dangers of misrepresentation, misinterpretation, and overinterpretation of the data, paleoneurological studies based on endocranial volume continue to generate and explore useful hypotheses about functional and behavioral changes over the course of human evolution. Both the regression formula and the reference group must be chosen with a degree of skepticism and caution. Allometric studies of relative brain size in hominids and other primates have focused on a wide range of issues:

1. tempo and mode of encephalization (Conroy, Weber, Seidler, Tobias, Kane and Brunsden 1998; Henning and Clausen 1989; Holloway 1975b; 1979; 1983b; 1995; 1996; 1999; Passingham 1975; Sacher and Staffeldt 1974; Ruff, Trinkaus and Holliday 1997).
2. social interactions (Byrne 1996; Dunbar 1992; Sawaguchi 1988; 1989).
3. metabolic, ecological, and dietary implications (Aiello, 1995; Armstrong 1983; Beals, Smith and Dodd 1984; Deacon 1990a; Falk 1990; Foley 1991; Kleiber 1947 and Martin 1981; Milton 1981; 1988).
4. obstetrical and reproductive costs, benefits and implications (Abitol 1987; Berge, Orbjan-Segebarth and Schmid 1984; Leutenegger, 1974; 1982; 1987; Lynch, 1983; Pagel and Harvey 1988; Parker 1990; Tabue and Lovejoy 1986);
5. life history patterns (Harvey and Clutton-Brock 1985);
8. generalized information-processing capacity (Jerison 1982; Lumsden 1982; Kein 1991);
9. phylogenetic relationships (Gabow 1977).

Establishing the variables: Measuring Brain and Body Size

Every model of the relationship between brain size (weight/mass or volume) and body size (weight/mass or stature) depends on measurement of the variables of interest. Such measurement presents several important challenges.

Measuring Brain Size

Post mortem measurements

Postmortem measurement of brains and brain regions in preserved specimens has historically provided most of the published data for these variables. Any preserved brain will be subject to an arbitrary amount of shrinkage due to the fixation process.

In vivo measurements

Radiographic imaging (MRI, PET, fMRI, and CT) has permitted measurement of the brains of living organisms, eliminating concerns about preservation but introducing other concerns. Most medical scans involve pathology, and given that the risks of radiography are not negligible, appropriate, high quality, full-head scans of non-elderly individuals are rare. Even scarcer are scans of living primates.

Even with powerful software, identifying and delineating areas of interest is subject to variability in scan quality, the judgment of the observer, ambiguity in the scans themselves, and the choice of threshold values used to distinguish different tissue types. Validation is an important and unresolved issue, as there is usually no way to confirm volumes obtained from radiographic imaging except by dissecting the subject, an option whose limitations are self-evident. Scans obtained by computed tomography (CT scans) register bone very clearly, but provide poor images of soft tissue. Magnetic Resonance Images (MRI) scans register soft-tissue details, but more dense tissues (bone and meninges) are more ambiguous. Nonetheless, an increasing body of literature bears testimony to the value of such techniques in obtaining brain measurements from living subjects (e.g., (Andreasen, Cohen, Harris, Cizadlo, Parkkinen, Rezai and Swayze II 1992; Andreasen, Cizadlo, Harris, Swayze II, O'Leary, Cohen, Ehrhardt and Yuh 1993a; Andreasen, Flaum, Swayze, O'Leary, Alliger, Cohen, Ehrhardt and Yuh 1993b; Andreasen, Harris, Cizadlo, Arndt, O'Leary, Swayze II and Flaum 1994; Andreasen, Rajarethinam, Cizaldo, Arndt, Swayze II, Flashman, O'Leary, Ehrhardt and Yuh 1996); (Rilling and Insel 1998); (Snyder et al. 1995); (Semendeferi and Van Hoesen 1997; Semendeferi and Damasio 2000).

Measurement of fossils

Fossil endocranial volumes can be measured directly, by filling the skull with water, mustard seed, shot, or sintered glass beads. Variations in packing and settling of the filler material can introduce measurement error (Gould 1978; 1996). Ambiguities in incomplete and damaged fossils add to the difficulty of accurate volume determination. Post-mortem distortion is another source of error.

Indirect measurement of endocranial volumes from endocasts is generally done by measuring the volume of water displaced when the endocast is immersed in a large, spouted beaker. As fossil skulls tend to be distorted, damaged, and more or less filled with foreign material (matrix), every estimate requires careful judgment and consideration of many factors, and endocast reconstruction, especially of ambiguous materials, is subject to repeated reevaluation. Reevaluations of the endocasts incorporate new comparative fossils as they are discovered, as well as new methods of reconstruction (e.g. (Braun 1996; Conroy et al. 1998).

Endocranial Volume vs. Brain Volume

As Symington (1916) observed, endocranial volume is only a proxy for brain volume, although published studies treat them as if they were equivalent (Beals et al. 1984; Falk 1980; Henneberg 1990). To determine the relationship between these two variables, the brain must be removed from the skull without damage to either structure. Perhaps this accounts for the scarcity of data relating these variables. In a study of 29 human cadavers, Pickering established a strong correlation between brain volume and internal skull volume ($r^2 = 0.805$). For fresh brains, he found that brain volume averaged 85.98 per cent of skull volume in this sample (Pickering 1930). Ruff et al. used a regression formula based on published values of brain mass and cranial capacity for 27 primate species: brain mass = 1.147 * cranial capacity $0.^{976}$ ($r^2 = 0.995$) (Ruff et al. 1997, citing Stephan et al. 1970 and Martin 1990).

Radiographic scans using modern imaging techniques provide an opportunity for in vivo measurements for endocranial and brain comparisons (See chapter 3, Materials and Methods, for a more detailed discussion of making soft and hard tissue comparisons from MRI scans).

Body Size (Weight/Mass or Stature)

Body size (usually calculated as body mass or body weight), the second variable utilized in encephalization studies, is, like brain size estimates, subject to error from a number of sources.

The first and most obvious (and intractable) source of error in estimating body mass from fossil materials is that such materials are fragmentary, and sample sizes are small. A second source of error is that the range of variation for taxa that are no longer living cannot be known. Estimations derived from living populations may be derived from inappropriate analogies (Mathers and Henneberg 1995; Smith 1996). A third source of error arises from the statistical methods used to estimate body mass from an intervening variable such as tooth area, long bone diaphyseal cross sectional area, or joint size. Error from these sources is reflected in disparate estimates of body mass from extinct hominids using ape and modern human reference samples with a variety of statistical methods and a number of intervening variables (Kappleman 1996; McHenry 1992b; a; 1994; Rightmire 19886; Ruff et al. 1997). However, Ruff et al., using two independent indicators (femoral head breadth and reconstructed stature combined with body breadth) and an extensive sample of fossil and contemporary humans have produced concordant body mass estimates for Pleistocene hominids (Ruff et al. 1997). These estimates have been incorporated into the present study (see Chapter 4, Data Analysis).

7 COMPUTER IMAGING

Computed Radiography

Introduction

Since the 1970s, computerized radiographic techniques (magnetic resonance imaging [MRI], functional MRI [fMRI], positron emission tomography [PET] computed x-ray tomography [CT]), regional cerebral blood flow (rCBF) and others, have permitted highly detailed, non-invasive, *in vivo* exploration of structure/function relationships in the human brain. Coupled with sophisticated graphics analysis tools, these techniques have been successfully applied in quantitative as well as qualitative analyses of both normal and pathological human anatomy and development. Like film-based radiography, computed radiography has found good use in paleontological and comparative primate studies as well.

MRI

MRI images are produced when protons are first excited by radiofrequency pulses and then return to their unexcited state, releasing detectible energy as they do so. The phase, amplitude, and frequency of the signal are mapped onto a two-dimensional plane or a three-dimensional block of elements. Variations in signal intensity are rendered as shades of gray in a grayscale image, which can be viewed on a computer monitor. Conventionally, black represents the lowest intensity and white represents the highest.

Different tissues and organic substances (e.g., gray matter, white matter, cerebro-spinal fluid) comprise different proportions of fat and water, and thus have different proton densities, producing different signal intensities, which show up on the screen as varying shades of gray. Mineralized bone, which contains very little water or fat, is rendered as a pixel-free void. Details of bone morphology are visible, however, by examining areas where the void is contiguous with soft tissue (Spoor, Jeffrey and Zonneveld in press).

Constraints and Advantages

Aside from practical issues in acquisition of the images (Spoor et al. in press) image analysis presents a number of challenges related to correct identificaion of regions of interest (ROIs), replicability, and labor intensity.

Previous Studies

Medical applications

Manual, semi-automated and automated volumetric MRI analyses of the relationship between CSF and brain volume have been applied to studies of Alzheimer’s disease, normal aging, schizophrenia, alcoholism, multiple sclerosis, hydrocephalus, edema related to head injury, and other brain pathologies. Intracranial volume *per se* has not been the focus of medical diagnostic study. As described below in “Methods,” the measurement protocol takes advantage of the fact that the volume of a fossil endocranial cast reflects brain volume + subdural CSF volume.

Cerebellum and Posterior Cranial Fossa

MRI volumetric studies of posterior cranial fossa structures, particularly the cerebellum, have also been conducted in medical diagnostic studies of autism (Karmiloff-Smith, Klima, Bellugi, Grant and Baron-Cohen 1995 and references therein); various ataxias (Wüllner, Klockgether, Peterson, Naegele and Dichgans 1993). Other studies have focused on psychometric correlations of cerebellar volume (e.g. Paradiso et al. 1997).

A recently acquired series of MRIs of anthropoids, from a project designed by Katerina Semendeferi, has provided data for several anthropological studies including the present one (MacLeod et al. 2000; Semendeferi and Damasio 2000; Semendeferi and Van Hoesen 1997; Rilling and Insel 1998).

With the exception of the present work, these studies have involved soft tissues only. Despite different measurement protocols, the authors have all reported that humans have relatively smaller cerebellar volumes than would be expected for a primate of our body weight.

3-Dimensional Imaging and Analysis

Introduction

Three-dimensional representation of cranial and endocranial structures enhances an observer’s ability to visualize and quantify spatial relationships between anatomic regions. The anthropological literature offers numerous examples of three-dimensional reconstructions of fossil cranial and endocranial materials made from MRIs as well as CT scans. (e.g., Conroy, Falk, Guyer, Weber, Seidler and Recheis 2000; Conroy et al. 1998; Conroy and Vannier 1985; Conroy, Vannier and Tobias 1990; Seidler et al. 1997; Spoor 1997; Spoor, Wood and Zonneveld 1994; Weber, 1998; Weber and Seidler (in press) Zollikofer, Ponce de Léon and Martin 1998). Data related to basicranial architecture, inter-osseous morphology, and endocranial capacity have emerged from these studies.

Another approach to three-dimensional data acquisition is based on recording of coordinate data using stereolithic photography or contact digitization of surface landmarks (e.g., Falk, Hildebolt and Vannier 1989; Niewoehner, 1999). Software devoted to brain image analysis has proliferated in the 1990s (Andreasen et al. 1992; Andreasen et al. 1993a; Andreasen et al. 1993b; Andreasen et al. 1994; Subramaniam, Hennessey, Rubin, Beach and Riess 1997). A growing number of statistical morphometric studies of brain structures from radiographic data sets attests to the potential for shape analysis in clinical as well as comparative functional applications (e.g., (Bookstein 1997; Bookstein, Schafer, Prossinger, Seidler, Fieder, Stringer, Weber, Arsuaga, Slice, Rohlf, Recheis, Mariam and Marcus 1999).

Even with the advent of laser scanners for rapid prototyping, coordinate data collection tends to be extremely labor intensive. Hardware for 3-dimensional digitization is expensive, requires computer memory and processing speeds that have only recently been achievable, and generally sacrifices portability for power. Three internet sites provide access to three-dimensional endocranial data. The first derives from the research of the present author, in collaboration with Professor Jeffrey Clark and Aaron Bergstrom at North Dakota State University: <http://atl.ndsu.edu/wev/>.

At least two other research groups have made available digital images of "virtual endocasts" of fossil hominids and other vertebrates. The Institute of Virtual Anthropology (Weber, Kim and Prossinger 2000), is developing a three-dimensional archive based on CT scans of Middle-Pleistocene hominid crania. It may be viewed at: <http://www.anthro.univie.ac.at/virtanth/virtanth.html >

A small number of non-primate endocasts scans can be viewed on a Web Page at the Museum of Health and Medicine, University of Wisconsin and Michigan State University (Jerison): <http://www.neurophys.wisc.edu/brain/evolution/paleo/>.

Most 3-dimensional acquisition and display software has been developed for entertainment or design applications. Software for comparison and quantification of three-dimensional data in biological applications has lagged behind. For morphometric comparisons, the images must be rotatable (able to be spun on an axis) and translatable (able to move within a given coordinate system). Once three-dimensional data is acquired, comparable landmarks must be identified and marked and appropriate statistical analyses applied. The application of geometric morphometrics and neuroimaging holds considerable promise for endocranial shape comparisons (Bookstein 1997).

For example, in one recent study arising from the "morphometric synthesis (Bookstein et al. 1999), CT scans of modern and archaic human frontal bones showed stability in anterior brain morphology in anatomically modern and archaic late Pleistocene humans. As Holloway demonstrated in his early analysis of fossil endocrania using coordinate data (Holloway 1981c), three-dimensional studies offer many advantages in quantifying morphological differences as well as permitting surface area and geometric profile comparisons of fossil materials.

The Present Study

While the endocast scans and MRI materials utilized in the present study have great potential for complex morphometric comparisons of endocranial morphology, the focus of the study relies upon volumetric comparison of distinct endocranial regions.

8 SUMMARY AND RATIONALE FOR PRESENT RESEARCH

Since the late 1980s, when technical advances in neuroimaging permitted the cerebellum to be included in functional studies, increasing attention has been directed to cerebellar function.

The cerebellum contributes to cognition in at least three ways:

1. Cortical organization during ontogeny. Cerebellar input contributes to representations (patterns of activation across neural networks) which later form the basis for cognitive processing. The cerebellum participates in a wide range of functions via its connections with diverse subcortical and cortical areas, including the basal ganglia, thalamus, posterior parietal cortex, premotor cortex, ocular cortex, and prefrontal cortex (including Broca's area).
2. Sensory-motor and cognitive integration. The conceptual separation of "purely sensory," "purely motor," and even "purely cognitive" functions is becoming more tenuous. In functions such as "language production," for example, neural representations include phonemic analysis, motor planning for vocal articulation, inaudible rehearsals of words, and word searches for verbal completion, and all of these dispersed functions must be coordinated to occur in the appropriate sequence.
3. Computational functions related to timing, sequencing, integration and praxis contributing to both cognitive and non-cognitive complex functions. Timing

precision in ballistic movements (including throwing and aspects of linguistic production) is greatly improved by utilizing redundant information in a parallel processing structure (Calvin 1983; Holloway 1967). Such redundancy may be provided by computations that involve the cerebellum. Based on the stereotyped circuitry of the cerebellum a number of reviewers have advanced hypotheses attributing a master computational role to the cerebellum (i.e., it may perform similar operations on diverse types of input). The cerebellum appears to contribute to efficient performance of complex tasks by promoting smooth control of both thoughts and motor sequences (Paradiso et al. 1997; Penhune, Zattore and Evans 1998).

In a hierarchical, epigenetic connectionist, weak modularity model, the cerebellum contributes to horizontally organized functions, which emerge with development and must have appeared mosaically during hominid evolution.

Important cortical functions contributing to hominid cognitive evolution are (at least partially) localized in cortical areas whose morphology changed during hominid evolution. Each of these cortical areas participates in afferent and efferent communication with the cerebellum.

The cerebellar lateral lobes appear to have increased in relative volume during anthropoid evolution, but decreased in relative volume some time after the divergence of African great apes and hominids. Congruence between allometric changes in relative cerebellar volume and the motor or cognitive skills reflected in archeological and/or other fossil evidence is directly informative of the cognitive specializations that were evolving. Disjunction between these factors suggests a greater role for plasticity and cultural/environmental influences.

Previous studies of relative cerebellar volume in fossil hominids have used linear measurements of the posterior cranial fossa (PCF) without regard to the fact that the cerebellum extends rostrally beyond the PCF or the fact that the PCF contains structures other then the cerebellum. The present study relates PCF volume to cerebellar volume, and employs volumetric rather than linear data derived from computer imaging, including MRIs of living hominoids as well as three-dimensional scans of fossil hominid endocasts.

9 MATERIALS

Description of Sample

A total of 29 individuals (or samples including more than one individual) was used in the data analysis. They are listed in Tables A-21 and A-22. For samples of more than one individual, the number of individuals is indicated in parentheses. The specimens were assigned to the groups indicated. The medium (CT, MRI, cadaver, scanned 3-D model) in which the variables were measured is indicated as well.

Three-Dimensional Endocast Scans (Holloway Collection)

Sixteen three-dimensional virtual models of endocasts from the collection of Dr. Ralph Holloway were scanned and virtual models assembled using a Minolta Vivid 700 non-contact laser digitizer and Polyworks InnovMetric Software (ImMerge, ImCompress, and ImEdit) belonging to the Archeology Technologies Laboratory, North Dakota State University. Dr. Jeffrey Clark, Department of Sociology and Anthropology, North Dakota State University provided access to the scanner. Aaron L. Bergstrom, a graduate student at NDSU, provided technical assistance in scanning and constructing the models. The models were measured for endocranial volume and posterior cranial fossa volume. See Chapter 10, “Methods” for a full description of construction and measurement of the virtual models.

MRI Scans of Anthropoids

Two sets of MRI scans were used to measure posterior cranial fossa volume and cerebellar volume. A set of MRI scans of living primates was provided by Katerina Semendeferi, University of San Diego, designer of the Primate MRI project; and James R. Rilling and Thomas Insel, of the Yerkes Regional Primate Research Center, Emory University. The Yerkes MRIs were T1-weighted images of the entire brain acquired with a 1.5 Tesla Philips NT scanner. Slice thickness, field intensity, matrix size, field of view, and scan orientation varied from specimen to specimen.

The second set of MRI scans was included full-brain scans of 15 normal human male subjects, provided by Dr. John Csernansky of Washington University. The scans were high-resolution T1-weighted images acquired with a General Electric scanner and converted to NIH Image format by Dr. Lei Wang of Washington University.

CT scans of La Ferrassie I, La Chapelle I, and Cro-Magnon I

Three Computed Tomography (CT) scans of fossil hominids were also used in the study. Dr. Jean-Jacques Hublin, Laboratoire d’Anthropologie, Musée de l’Homme, Paris; and Dr. Marc Braun, Service De Neuroradiologie, Hôpital St.Julien, Nancy, France provided the scans.

10 METHODS

Introduction

In order to evaluate cerebellar proportions in fossil hominids it is necessary to develop methods to relate cerebellar and PCF volumes; to determine whether this relationship is consistent from taxon to taxon; and to relate cerebellar volume to both brain volume and body mass.

The present study uses magnetic resonance images ("MRIs") to determine that cerebellar volume and PCF volume are consistent from taxon to taxon. PCF volume in fossil hominids is measured from three-dimensional virtual models ("scanned models") of hominid endocasts and computed tomography (CTs). PCF volumes from the MRIs, the CTs, and the scanned models are then calibrated. Cerebellar volume for the fossil hominids is calculated from the calibrated PCF measurements.

PCF and Cerebellar Volume from Magnetic Resonance Images

MR Images permit visualization of hard and soft tissues (endocranial PCF and cerebellum), but a number of technical problems must be addressed for reliable quantitative analysis of their relationship. The sample of MRIs used in this study included modern humans (n = 16) and non-human hominoids (n = 15), described above under "Materials" and listed in the Appendix in Tables A-1 and A-2. The images were analyzed with the software NIH Image and Object Image for Macintosh, public domain programs developed at the U.S. National Institutes of Health and available on the Internet at http://www.info.nih.gov/nih-image.

Identifying Landmarks of the Posterior Cranial Fossa

The superior PCF border is an imaginary plane projected from landmarks of the lateral, posterior, and anterior skull that are not always distinguishable in radiographic images. In MRIs, adjacent soft tissues can help to identify the boundaries of the plane.

Anterior Border: the superior border of the dorsum sellae and the antero-superior petrous ridges

The optic chiasma rest directly superior to the sella turcica. Where the petrous ridges are indistinct in the images, the antero-superior PCF border was defined on the slice immediately inferior to the slice in which the optic chiasma is first visible. Where the dorsum sellae is ambiguous, the anterior point of the PCF plane was determined to be on the midline at a point immediately anterior to the vertebral artery.

Posterior Border: the confluence of the sinuses at the internal occipital protuberance

Where the internal occipital protuberance was ambiguous (which was frequently the case), the confluence of the sinuses was taken as the postero-superior landmark for the PCF. Among hominoids, including *Homo sapiens*, the left transverse sinus is usually the recipient of the straight sinus, while the right transverse sinus drains the superior sagittal sinus. Thus, the confluence of the sinuses and the bony structure of the internal occipital protuberance are somewhat asymmetrical both antero-posteriorly and medio-laterally.

Taking these asymmetries into account, the confluence of the sinuses can be identified as follows:

- Identify the superiormost and inferiormost slices in which each sinus appears
- Select the slice midway between the superiormost and inferiormost slices, and mark the confluence of the sinuses on the midline at the interface of sinus and bone.

Adjustment for MRI Scan Angle

The angle of the MRI and the plane of the PCF were rarely, if ever, coincident. Adjustments for scan angle were necessary for both medio-lateral and antero-posterior deviations from the PCF plane.

Medio-Lateral Deviation

The degree of medio-lateral deviation of the MRI plane from the PCF plane can be estimated by determining the inferiormost slice in which one of the ocular lenses appears, then counting the number of slices between it and the inferiormost slice in which the other lens appears. In cases where left-right deviation is significant, left and right halves of the MRI can be individually considered for inclusion in the PCF.

Antero-Posterior Deviation

As the MRI scans move supero-rostrally, many slices contain portions of the cerebellum that are external to the PCF. In these slices, the portion of the cerebellum included within the PCF can be determined as follows:

1. Determine the vertical distance (number of slices) and the horizontal distance along the y-axis of the image between the confluence of the sinuses and the superior border of the dorsum sellae at midline.

2. Divide the horizontal distance by the number of slices to obtain the adjustment for scan angle per slice

2. Use this value to determine the position of a line perpendicular to the midline on each slice, bisecting the slice into an anterior portion (included within the PCF) and a posterior portion (excluded from the PCF) (Figure 10-1).

Reconstruction of the Inferior and Lateral Borders of the PCF

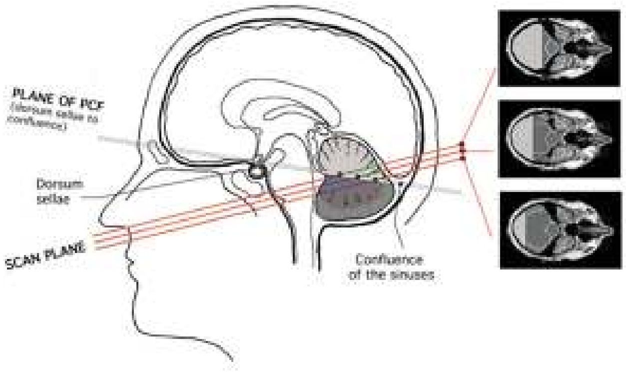


Figure 10-1: Adjustment for Scan Angle

Thresholding and Segmentation

Each tissue type has a characteristic radiographic density, which registers as a grayscale value between zero (white) and 255 (black) on the image. Although NIH Image can register and display 255 shades of gray, the human eye can distinguish only about 30 shades of gray (Russ 1999). Image thresholding, which labels all pixels above a certain density as “background” and those below it as “object,” can be used to identify and delineate structures of interest (segmentation).

Cerebrospinal fluid, meninges, and bone in particular are difficult to distinguish by the human eye. However, density sampling of unambiguous areas reveals that the mean, median and modal density values of these tissues are significantly different (p = 0.0001). By setting the threshold levels to exclude pixels above a certain density, the regions of interest can be consistently segmented and measured. Ambiguous regions are minimized by this procedure and can be manually resolved. For the present analysis, the threshold settings include the closely adhering pia and arachnoid mater as part of the cerebellum. The PCF threshold setting excludes bone and dura mater.

Indexed color rendering, observation of textural differences, anatomical information, and inspection of adjacent slices permitted consistent and credible manual completion of ambiguous outlines. Intra-rater coefficient of variation for repeated measurement (n = 25 slices): 1.0-1.5%.

Interpolation and Volume Calculations

Areas in NIH Image are calculated by counting the pixels in the area of interest and calibrating them with the pixel width and length provided in the original scaling information for the MRIs. Volume in NIH Image is calculated by multiplying the summed area of the measured slices by slice thickness and slice number (interpolation). When the slice thickness of the original MRIs is on the same scale as the pixel dimensions, volume interpolation is straightforward. However, if slice thickness is on a different scale, and the original MRIs are rendered as voxels rather than pixels, problems may arise with interpolation (Spoor, In press) When the voxels are converted to pixels, the conversion algorithm assumes that the volume information is equally distributed in the x, y and z dimensions. If this is not the case, then it becomes very difficult to backtrack and correctly calibrate the area dimensions and slice thickness.

For the MRIs used for the present study, the algorithm appears systematically to distort the volume dimensions. Volumes with fewer numbers of slices are underestimated; volumes with a greater number of slices are overestimated. As the cerebellum occupies more slices than the PCF, this systematic distortion underestimates PCF volume relative to cerebellar volume. It is necessary to perform a calibration to evaluate PCF and cerebellar volumes with respect to the endocast virtual models.

Fortunately, non-human primate and primate MRIs can be validated for cerebellar volume, because there are three other sets of cerebellar measurements of the same data, taken by other researchers using voxel-based image analysis programs (Rilling and Insel 1998); (Semendeferi and Damasio 2000); McLeod (unpublished data, personal communication). Although there are measurement differences among these researchers, their results are consistent with the cerebellar volume measurements produced by the present study.

Cerebellar Volume and PCF Volume in Hominoids

A Least Squares Linear Regression of Cerebellar Volume (VCBLM) on PCF volume (VPCF) in the present sample indicates that these variables are strongly correlated ($r^2 = 0.89$; $n = 34$). These results confirm the for humans (1988). The prediction equation for CBLM from VPCF is:

$$\mathbf{CBLM = 3.25 + 1.22\ PCF.}$$

VCBLM/PCF is normal normally distributed, with a sample mean of 1.26 /- 0.021. Cerebellar volume relative to PCF volume remains consistent from taxon to taxon. A non-parametric Wilcoxon Kruskal/Wallace test fails to refute the null hypothesis of equality of means among hominoid groups (Chi-Square = 5.58; DF = 5; p = 0.349). The mean values for *Pongo* and *Hylobates*, however, do appear to be somewhat lower than the mean for the other hominoid groups.

Mean Cerebellum Volume/mean PCF volume is not significantly different when the sample is divided into two groups comprising humans and non-human primates (Wilcoxon Kruskal/Wallace test for equality of means: chi-squared = 1.10; df = 1; p = 0.29; n = 34).

The present analysis of relative cerebellar volume proceeds on the assumption that PCF volume is a valid and consistent indicator of cerebellar volume in hominoids, including fossil hominids.

Summary of Results for Cerebellar volume/PCF volume in MRIs

Cerebellar volume measurements for the MRI sample are consistent with observations of other researchers. Cerebellar volume is strongly correlated with PCF volume. Cerebellar volume relative to PCF volume is consistent from taxon to taxon in the present sample of hominoids. In terms of the null hypotheses set forth in Chapter 1, “Introduction”:

Null hypothesis $\mathbf{H_{02}}$ is not rejected: In modern humans, total posterior cranial fossa volume (PCF) is correlated with total cerebellar volume (CBLM):

$$\mathbf{H_{02}} : \quad \mathbf{PCF_{human} := k * CBLM_{human}}$$

Null hypothesis $\mathbf{H_{03}}$ is not rejected. In modern apes, total PCF volume (PCFV) is correlated with total cerebellar volume (CBLM):

$$\mathbf{H_{03}: \quad PCF_{nonhuman} = k * CBLM_{nonhuman}}$$

Null hypothesis $\mathbf{H_{04}}$ not rejected. The slopes of the Least Squares Regression lines for modern humans and non-human primates are equal:

$$\mathbf{H_{04}: \; PCF/CBLM_{nonhuman} = PCF/CBLM_{human}}$$

Measuring PCF Volume in CTs

Determination of PCF Boundaries in CTs

The problematic issues raised by the MRIs are simplified in the fossil hominid computed tomography scans (CTs). Only one tissue type is registered (bone), and it is unambiguous on the images (although in some CTs matrix may register as well). The CT scan angle is coincident with or very close to the PCF angle. The conversion algorithm does not distort the interpolation because the slice thickness is proportionate to the pixel width and length.

The most problematic issue arising from the CTs is the incomplete nature of the fossils. Manual editing is required to complete the boundaries of the regions of interest before they can be measured. There are no soft tissue clues to help determine the location of landmarks.

Reconstruction of the Superior and Anterior Borders of the PCF

Where the clivus and sella turcica were missing, their position was digitally reconstructed as follows: The width of the foramen magnum on the x-axis was used to estimate the width of the clivus. Lines were drawn from the lateral margins of the foramen magnum until they intersected with lines extended along the visible portion of the petrous ridges. The anterior border of the PCF was marked at the point of intersection of the lines on the right and left sides.

Reconstruction of the Inferior and Lateral Borders of the PCF

Where portions of the inferior or lateral borders of the PCF were missing, their position was digitally reconstructed by extending lines between structures that were visible, following the implied contour as closely as possible.

As in the MRIs, the total area of the PCF from all the slices is multiplied by slice thickness and slice number to determine PCF volume.

Summary of CT Results

PCF volumes for the three individuals who were sufficiently complete for PCF measurements are summarized in Table 10-1 below:

Specimen	**PCF Volume**
La Ferrassie	142.35
La Chapelle	140.46
Cro-Magnon	135.25

Table10-1: PCF Volume, CTs in Late Archaic Humans

Construction, Manipulation, and Measurement of Virtual 3-D Models

Three-dimensional digital models of the endocasts described in Chapter 9, “Materials” were constructed by the following methods:

Laser Scanning

Each endocast selected for digitization was positioned on a supporting medium (e.g., modeling clay) approximately 70 cm in front of a Minolta Vivid 700 3-D laser scanner. A laser beam emitted from the scanner was reflected from the object back to an optical lens, and the scanner calculated the location of each point from which the laser began its return trip. For this study, data from the scanner was communicated directly to a Sony VAIO PCG XG9 laptop computer or to an IBM Workstation and stored there for assembly. The scanner also captured a digital color photograph of the scanned object. After each scan, the endocast being modelled was repositioned and a new, overlapping area was similarly scanned. This process was repeated until the entire surface of the object was covered.

Scale

Scaling is automatic. The Minolta Vivid software calculates the distance between the scanner and the object and interpolates this information into the images to produce accurate scaling.

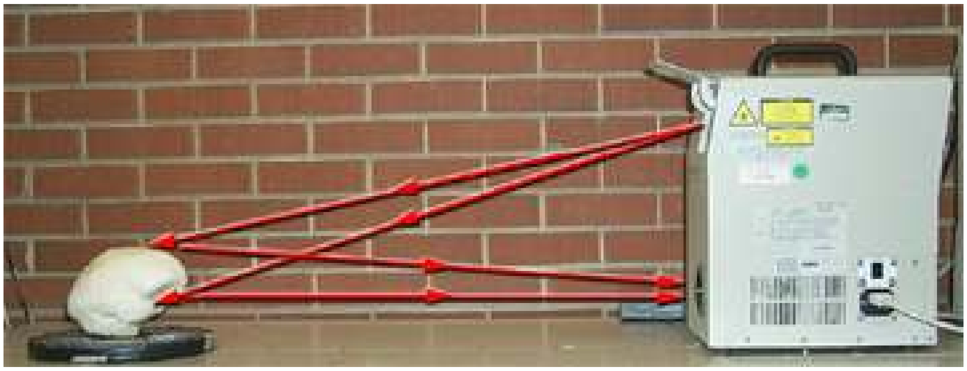


Figure 10- 2: Scanner set-up

Assembly of Digital Models

The multiple overlapping surface-area scans of the endocast were then imported into the PolyWorks Modeler software. Assembly of the 3-D models was performed on either a Sony Vaio PCG XG9 laptop computer or an IBM Workstation in the Archeology Technologies Laboratory at North Dakota State University. The IMAlign module ensures that the 3D polygonal mesh images produced by the scanner software are properly aligned in relation to one another by matching operator-selected common points in the overlapping scans. For some scans, only one common point needs to be defined; for other scans, multiple points are required to perform the alignment. The number of scans required to complete a digital endocast model varies from as few as 15 for chimpanzees to 50 or more for Neandertals.

The PolyWorks module IMMerge was used to convert the aligned 3-D meshes into a complete 3-D model file. The files may be stored in a number of formats, including PolyWorks, VRML 2.0/97, STL, IGES, and Wavefront. For the present study, the PolyWorks format was retained. Once properly merged, the models were examined in the IMEdit module, which allows for filling of minor holes, topology error correction, and smoothing (removal of digitizer error, which is 300 microns for the Vivid 700).

IMCompress evaluates the shape of an edited model to identify redundant data that can be removed without changing the overall shape, size and surface configuration. Compression is actually a resolution reduction process that allows the operator to specify a tolerance (as low as 1/1000 of a micron) so that he/she can decide how much detail should be retained. While compression can affect the resolution of surface detail, it has little effect on either volumetric or linear distances, as discussed below (also see http://atl.ndsu.edu/props/using3d/compare.htm; ATL 2000c; and Weaver, Bergstrom and Holloway, in press).

Some problems were encountered during scanning. The most persistent and problematic was the tendency of the laser beam to create its own interference when it is irregularly reflected in deep and narrow crevices. The problem is exacerbated by the tendency for both matrix and casting artifacts to accumulate in small spaces. The “noise” produced by such interference results in small holes and unattached polygons. Particularly problematic are deeply invaginated regions of the ventral surface, especially the petrous ridge, and the medial curvature of the temporal lobes. Hand editing, polygon by polygon, was required to compensation for laser distortion. As demonstrated below (see

“Validation”), such distortion appears to have a negligible effect on volumetric or linear measurements.

Measurement

Once the digital models are constructed, the PolyWorks software IMEdit permits linear (chord) and volumetric measurements. PolyWorks determines volumes by an interpolation method. The virtual model is divided into serial slices, their surface area measured, and the total area multiplied by slice thickness. The precision of volumetric measurements is determined by the user, who selects the number of slices to be interpolated. All endocast volumes recorded in the present study used a slice number of 100.

To obtain linear (chord) measurements, the user selects points (polygons or vertices) on the digital model and the PolyWorks IMEdit software automatically calculates the distance between them. Linear values used in the present study represent the mean of multiple measurements (usually three) by the author,

Comparisons of Scanned Models and Published Values

(For summaries of Scanned and Published Volumes, See Appendix, Table A-13; for summaries of Scanned and Published Linear Measures, see Appendix, Table A-14)

The 3-D endocast models are both precise (+/- 300 microns) and accurate.

Comparisons were made for Volume, AP length (frontal pole - occipital pole), and maximum parietal breadth for the scanned models against published values. For all dimensions, scanned values were strongly correlated with published measurements (r-squared = 0.96 -0.998). Highly sensitive matched-pairs t-tests showed slight but statistically significant differences between sample means for scanned and published values, with means for scanned measurements tending to be lower than published values.

Linear AP measurements for the scans were within 2% of the published values. Greater differences (up to 4.8%) were observed for parietal breadth, especially for values taken from the literature on endocasts other than the ones scanned. Fluctuation of residuals for linear measurements is attributed to landmark ambiguity, casting artifacts, and differences between original endocasts and inter-observer error.

Like the linear values, published volumes were taken from a number of sources. Most volume discrepancies are attributable to the fact that different versions of the original endocasts were used. However, scan values differed by an puzzling 8% for both KNM-ER 3733 and 3883.The discrepancies in these measurements may be due to an anomalous interaction of the laser beam with the reflective surface of resin endocasts, or to some unknown source of error, which requires further investigation.

In studies utilizing the digital models only, no compensation for differences in means is required, as measurements will be internally consistent, However, in studies utilizing measurements from both digital models and actual endocasts, the slight difference in means should be taken into account.

AP Length (Scanned vs. Published)

A Least Squares Linear Regression of scanned on published AP length confirms that the variables are highly correlated ($r^2 = 0.999$; $n = 17$). Absolute differences between scanned and published values for AP length range from 0.00 – 5.50 mm. Absolute values for residuals range from 0.08 – 5.32 mm, with a mean of 1.90 mm. The mean Coefficient of Variation for the residual is 0.01. Residuals are normally and randomly distributed. Linear AP values do not appear to show a systematic discrepancy related to the material or volume of the original scanned endocast.

Scanned measurements for AP Length fall slightly but consistently below published values. A non-parametric test of paired means suggests that the null hypothesis of equality of means between Published and Scanned AP length should be rejected ($p = 0.99$; $\alpha = 0.05$). A test for differences of paired means confirms that scanned values fall outside the confidence interval generated when Scanned values are plotted on the Y axis and Published values are plotted on the X axis.

The negligible difference between Scanned and Published values and the random fluctuation of residuals can be attributed to ambiguity of the landmarks, especially for intra and inter-observer error, differences between scanned and measured endocasts, and the fact that the measurements were performed in different media.

Breadth (Scanned vs. Published)

A Least Squares Linear Regression of Scanned on Published Breadth measurements shows the high correlation between the variables ($r^2 = 0.999$; n = 15). Absolute differences between Scanned and Published values for W range from 0.04 – 10.92 mm, with a mean of 3.67 mm. Absolute values for residuals range from 0.09 – 5.42 mm, with a mean of 2.22 mm. The mean Coefficient of Variation for residuals is 0.02. The residuals are normally and randomly distributed, with no indication of a systematic effect of volume or material on the discrepancies.

Scanned measurements for Breadth fall slightly but consistently below published values. A non-parametric test of paired means suggests that the null hypothesis of equality of means between published and scanned AP length should be rejected ($p = 0.99$; $\alpha = 0.05$). A test for differences of paired means (Sall and Lehman, 1996) confirms that scanned values fall outside the confidence interval generated when Scanned values are plotted on the Y axis and Published values are plotted on the X axis.

The small fluctuations in residuals between Scanned and Published values can be attributed to ambiguity of the landmarks, intra and inter-observer error, and the fact that some of the published values came from different endocasts than the ones that were scanned.

“Virtual Dissection” of the Posterior Cranial Fossa

PCF volumes are obtained by “virtual dissection,” which permits isolation of selected regions of the model. The “virtual dissections” were created as follows:

A marker was placed on the virtual model at the intersection of the mid-clivus and the dorsum sellae. Additional markers were placed along the left and right petrous ridges and along the midline of the left and right transverse sinuses, and across the internal occipital protubrance. IMEdit then created a line between the markers, and the model was separated along the line. The modeling software requires that the model segment be closed, or “capped” before measuring the volume. Given that the border of the PCF undulates, a certain amount of vertical filling-in is required in order to fit the plane of the cap. To define the plane for the cap, the operator must select three points. For the present study, the mid-clivus/dorsum sellae, internal occipital protubrance, and one additional point were selected. The third point was somewhat arbitrarily selected, and depended upon a visual assessment of how well the cap fit, with an eye to minimizing the amount of vertical fill for each model. Once the models are capped, PolyWorks’ IMEdit automatically calculates the volume. PCF volumes were calculated using a resolution of 100 slices.

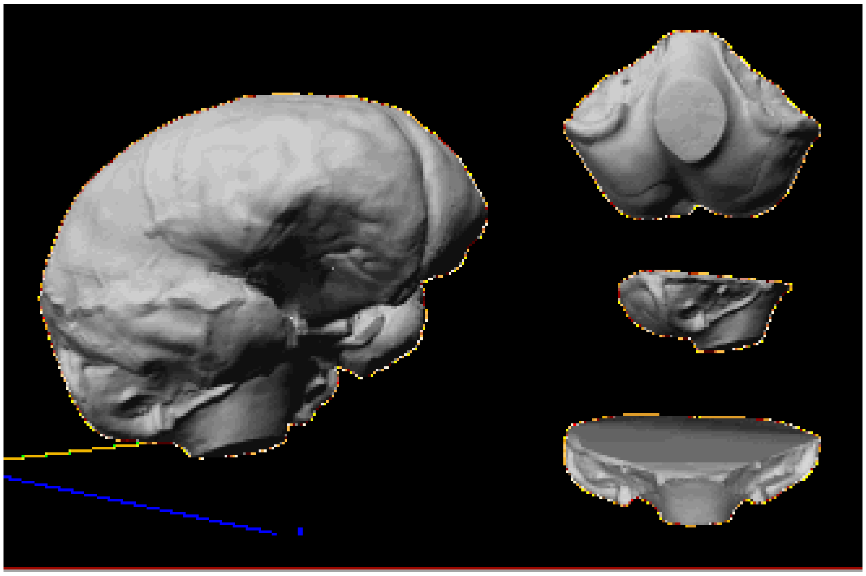


Figure 10-3: Screen shot showing Zhoukoudian, Locus LI and “virtual dissection” of PCF

In addition to allowing volumetric measurements, the filling and capping procedure renders the “virtual PCF” consistent with the CT scan data, where analogous vertical fill-in occurs due to the way the scan is represented by serial slices.

Calibration of Measurements from MRIs and Virtual Scans

Differences in measurement protocols between the MRIs and the virtual endocast models (described below), as well as the tendency of the conversion algorithm for the MRIs to underestimate volumes with fewer slices, require a calibration between the MRIs and the virtual models for PCF volume. When this is accomplished, a much larger sample can be incorporated to calculate relative cerebellar volume in both hominids and non-human primates. The following data analysis is based on a calibrated estimated cerebellar volume for the endocast scans. The calibration coefficient was calculated as follows:

The regression equation for cerebellar volume (CBLM) on PCF volume (VPCF) for the MRIs is VCBLM= 3.66 +1.22 VPCF. When this equation is used to predict cerebellar volume from the Chimp 1 endocast, the result is a *predicted* cerebellar volume of 67.67 cc for the endocast. This is an overestimation: mean cerebellar volume for *Pan troglodytes* is 45.9 cc. (Rilling and Insel 1998; Semendeferi and Damasio 2000). Assuming that the scanned individual falls near the mean for cerebellar and PCF volume, the actual cerebellar volume for the endocast should be 45.9/67.67 = 68% of the predicted value. The "calibration co-efficient" would be 0.68. The calibration is based on the assumption that the overestimate effect is linear and consistent across specimens. (See below for support for this assumption.)

Cerebellar volume for the endocasts is derived from the regression formula of Cerebellar Volume on PCF volume for the endocasts, multiplied by the calibration coefficient:

$$\text{calibrated CBLM} = 0.68 * (3.66 + 1.22\ \text{VPCF}).$$

Justification for the Calibration

The practical effect of the calibration is to lower the intercept for the estimated cerebellar value for the endocast scans to 68% of the predicted value across for the hominids. The internal relationships among the scanned taxa are left intact. That is, if only the uncalibrated predicted values are used, the "trajectory" for the groups still follows the same pattern. The *Homo erectus* group still has the highest mean; Late Archaic humans still have the lowest; and Middle Pleistocene humans are intermediate.

Assumptions for the Calibration

The assumptions underlying the calibration can be supported as follows:

CBLM/PCF is linear in the MRIs; and PCF/Endocranial volume is linear in the endocast scans. Therefore, the assumption that the relationship between predicted and actual values for the scans is linear appears to be correct.

The assumption that the scanned *Pan troglodytes* individual is representative of its taxon appears to be correct. Estimates for cerebellar volume in *Pan* range from 41.2 cc to 48.9 cc (Rilling and Insel 1998; Semendeferi and Damasio 2000); McLeod (unpublished data).

Given the range of published cerebellar volumes in *Pan* is, the calibration coefficient could be as low as 41.2/67.7, requiring a calibration of 0.61; or as high as 48.9, requiring a calibration coefficient of 0.72. The appropriateness of these calibration fractions can be evaluated by examining how the scanned endocasts are integrated.

Cerebellar Volume for Pan troglodytes	ratio of actual/predicted cerebellar volume	calibration fraction
41.2	41.2/67.67	0.61
45.9	45.9/67.67	0.68
48.9	48.9/67.67	0.72

Table 10-2: Effect of High and Low Calibration Coefficients

High and low values of cerebellar volume can be used to recalculate the regression equation, with the following results (see Table I0-1 above):

High chimp value assumed (calibration coefficient 0.61): r-squared = 0.87; CBLM $= 5.95 + 0.32\ \mathrm{NetBrain}_{high}$

Low chimp value assumed (calibration coefficient 0.72): r-squared = 0.82; CBLM $= 16.36 + 0.80\ \mathrm{NetBrain}_{low}$

Mean chimp value assumed (calibration coefficient 0.68): r = 0.84;

$$\mathrm{CBLM} = 15.33 + 0.09\ \mathrm{NetBrain}_{mean}$$

The equations for mean and low assumed values are very close. The equation for a high chimp value produces a disjunction between scanned and MRI datasets, with the scanned chimp value appearing at a dramatically higher level than the MRI chimp value. The equation for a high chimp value also produces second disjunction appears between all of the other hominids and modern humans. A model with two such severe disjunctions is less credible than the other two models, which show close agreement between the scanned and MRI values for the chimpanzee, and between the hominids as a whole and modern humans.

In addition, the modern human MRI values are in close agreement with other published measurements for both cerebellar volume and brain mass (e.g. (Beals et al. 1984; Harper and Kretschmann 1989; Klekamp et al. 1987; Klekamp, Riedel, Harper and Kretschmann 1989; Snyder et al. 1995). The disjunctions that appear when a high estimate for the scanned chimpanzee is used are not credible.

Once the calibration is established, values for additional anthropoid taxa, including Old World and New World Monkeys, can be included in the analysis (Rilling and Insel 1998).

11 DATA ANALYSIS AND RESULTS

Description of Variables

Three raw variables are employed in the data analysis (cerebellum volume, “CBLM”; brain mass, “BrMass”’ and body mass, “BoMass”). Three derived variables are also employed in the data analysis (net brain mass, “NetBrain”; cerebellar quotient (“CQ”); encephalization quotient (“EQ”); and cerebellar coefficient (“CEQ”). The variables are described in Tables 11-1 and 11-2. All derived variables except EQ are empirically based, using the present sample only. Exact values of EQ are consistent with, but vary slightly from, previously published values based on larger sample sizes (e.g., Ruff et al. 1997). (Data for all variables is summarized in the Appendix, Table A-13).

Table 11-1: Raw Variables

Description	Abbreviation	Definition
Cerebellar Volume	CBLM	MRI volume or calibrated volume from virtual endocast models
Body mass	BoMass	Directly measured for living taxa; estimated by formula for fossil taxa, using sources indicated in Notes to Table A-13)
Brain mass	BrMass	Estimated from measured brain volume for living taxa; estimated from endocranial volume for fossil taxa, using formula provided in (Ruff et al. 1997)

Table 11-2: Derived Variables

Description	Abbreviation	Definition
Net Brain Mass	NetBrain	BrMass – CBLM
Cerebellar Quotient	CQ	CBLM/NetBrain
Encephalization Quotient	EQ	NetBrain/BoMass
Cerebellar Coefficient	CEQ	CQ/EQ

Univariate Analysis

None of the variables is random; and they are all functionally and phylogenetically interdependent and co-linear. Although a Shapiro-Wilk W test for normality shows some of the distributions to be normal, the test fails to detect serious problems with the distributions (see comments in Appendix, Table A-14). Based on the violation of the assumptions necessary for the use of parametric statistical tests, non-parametric tests are used in the data analysis.

Figures 11-1 to 11-3 show mean values and standard deviations for cerebellum volume, body mass, and brain mass for the taxa represented in the sample.

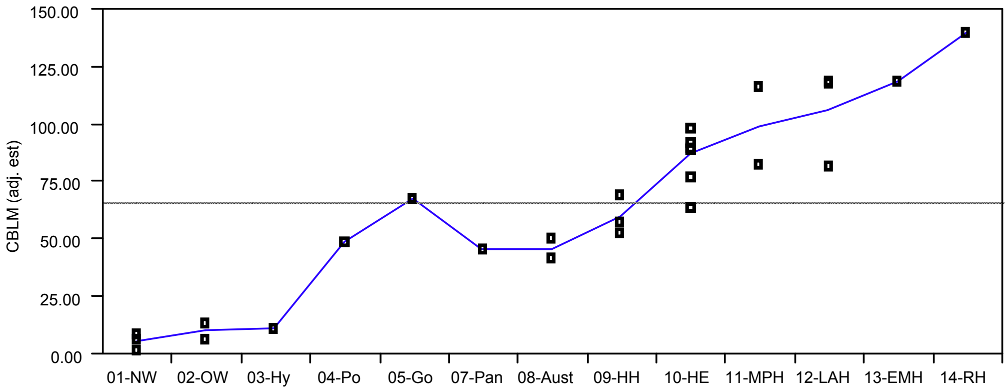


Figure 11-1: Cerebellum Volume in Anthropoids

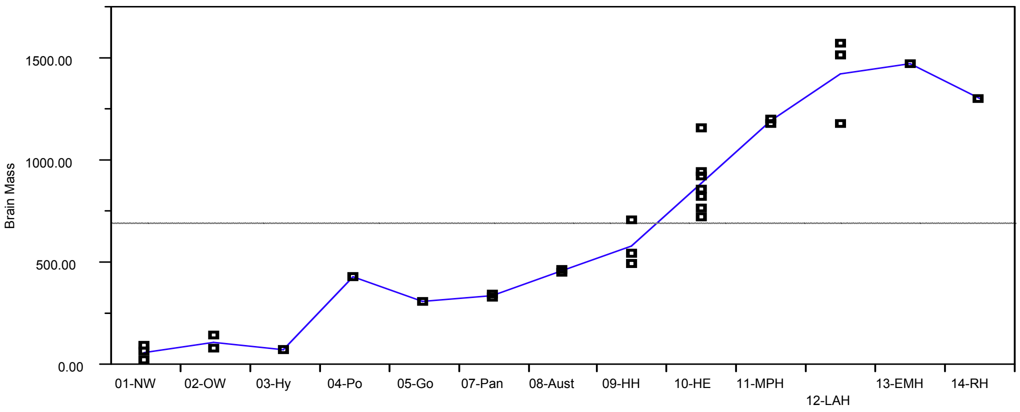


Figure 11-2: Brain Mass in Anthropoids

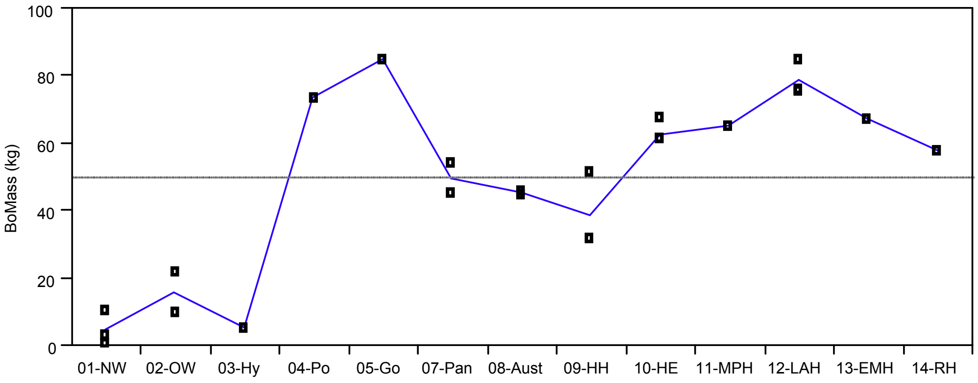


Figure 11-3: Body Mass in Anthropoids

Each of the variables has a general tendency to increase across a "phylogenetic trajectory", with notable deviations occurring for the large-bodied hominoids, *Pongo* and *Gorilla*. However, the variables do fluctuate with respect to each other. The following multivariate analyses are undertaken in order to explore the significance of these fluctuations.

Multivariate Analysis

Multiple correlation analysis shows the variables BoMass, BrMass and CBLM to be well correlated for anthropoids. (See Correlation Matrix for Anthropoids, Table 11-3.) In the anthropoid sample, cerebellar mass is more highly correlated with brain mass (r^2 = 0.94) than it is with body mass (r^2 = 0.82).

Table 11-3: Multiple Correlations – Anthropoids

Variable	CBLM (g)	BoMass (Kg)	BrMass (g)
BoMass (Kg)	0.8218	1.0000	0.7663
BrMass(g)	0.9392	0.7663	1.0000

Cerebellar volume correlates more strongly with brain mass among hominoids (r^2 = 0.89) than it does with body mass (r^2 = 0.50) (Table 11-4).

Table 11-4: Multiple Correlations – Hominoids only			
Variable	CBLM (g)	BoMass (Kg)	BrMass (g)
CBLM (g)	1.0000	0.5039	0.8942
BoMass (Kg)	0.5039	1.0000	0.5126
BrMass(g)	0.8942	0.5126	1.0000

Correlations for hominids are similar to hominoids (see Multiple Correlation matrix, Table 11-5).

Table 11-5: Multiple Correlations – Hominids only			
Variable	CBLM (g)	BoMass (Kg)	BrMass (g)
CBLM (g)	1.0000	0.6729	0.8778
BoMass (Kg)	0.6729	1.0000	0.8200
BrMass(g)	0.8778	0.8200	1.0000

Each of the three variables (cerebellar volume, body mass, and brain volume) tends to increase along a “phylogenetic trajectory,” from monkeys through hominids.

Departures from Allometry

The purpose of the present investigation is to evaluate possible departures from allometry among the variables CBLM, NetBrain, and BoMass for each taxon. The following analysis uses the variable “CQ,” calculated as actual/predicted cerebellar volume with respect to NetBrain, in a manner analogous to the accepted calculation of an encephalization quotient, or “EQ” (actual/predicted brain volume with respect to body mass). While both CQ and EQ are useful tools for comparisons among groups, they should not be reified as entities in themselves: they are simply scales for comparison. As discussed in greater detail below, absolute values for CQ and EQ vary with sample composition and line-fitting technique.

Reduced Major Axis Regression and “CQ”

Because neither CBLM nor NetBrain can be regarded as analogous to a “fixed” treatment, sample error should be allocated equally to each of the variables in regression analyses. Accordingly, reduced major axis regression formula (RMA) is used to calculate predicted CBLM from NetBrain. The RMA regression line was calculated using the equation developed by Jolicoeur (1990) and discussed in detail in Conrad and Gutman (1996). Reduced Major Axis (RMA) regression of cerebellar volume (CBLM) on net brain mass (NetBrain) gives the following regression formula:

For anthropoids (present sample):

$$\mathbf{CBLM = 7.3 + .094\ Net\ Brain}$$

Figure 11-4 shows the RMA regression line superimposed upon the scatterplot for CBLM/NetBrain. Examination of the plot suggests that at least two “grades” for relative cerebellar volume may be present in Pliocene and Pleistocene hominids.

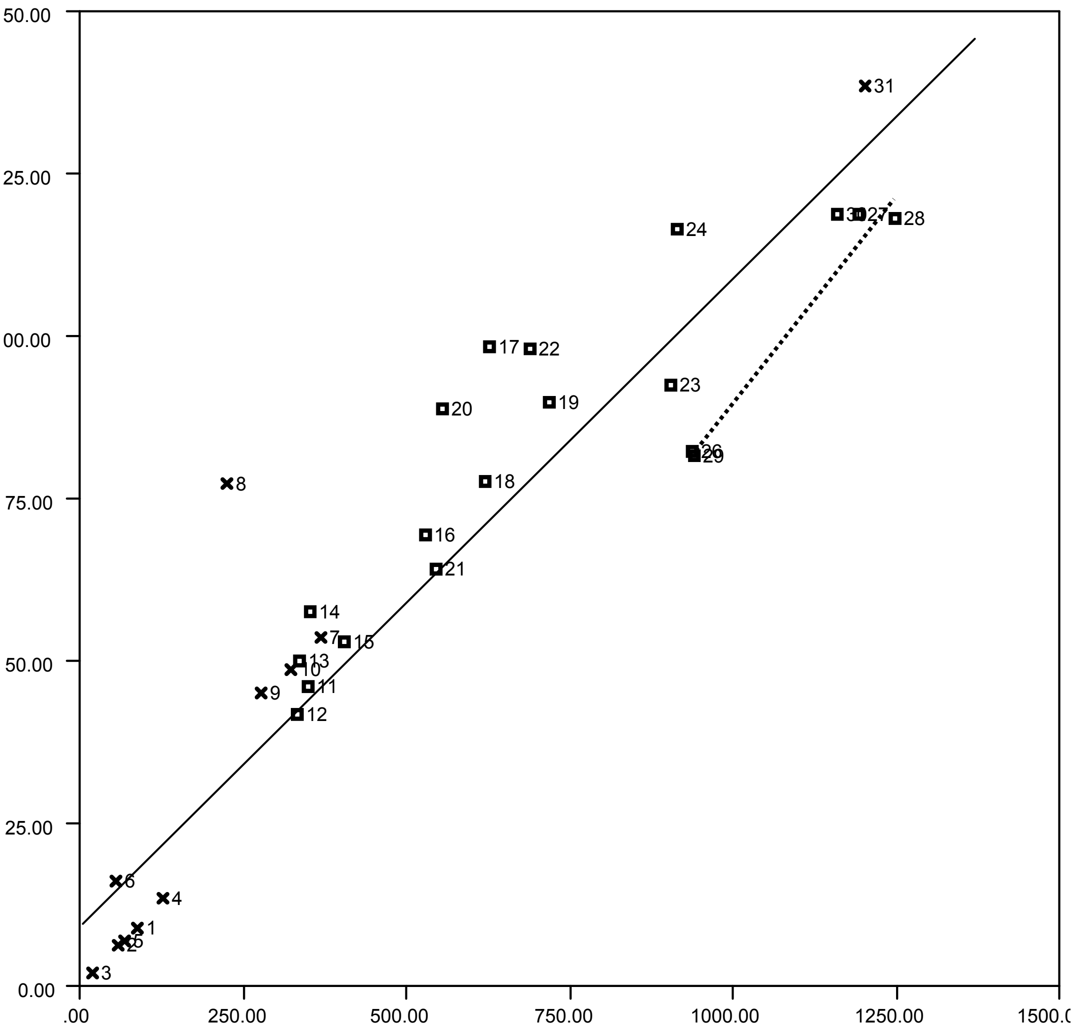


Figure 11-4: Scattergram: calibrated Cerebellum Volume/Net Brain Volume for all specimens with RMA line superimposed (CBLM = NetBrain)

List of specimens:

1. *C. atys* (n = 4)
2. *C. apella* (n = 4)
3. *S. sciureus* (n = 4)
4. *P. cynoceph* (n = 4)
5. *M. mulatta* (n = 4)
6. *Hylobates* (n = 4)
7. *Pongo* (n = 4)
8. *Gorilla* (n = 2)
9. Bonobo n = 4)
10. Chimp(MRI) (n = 6)
11. Chimp I Scan
12. STS 19-5
13. KNM-ER 23000
14. KNM-ER 1813
15. KNM-ER 1805
16. KNM-ER 1470
17. Zh Loc E /skull III
18. KNM-WT 15000
19. Pitih VII /Sangiran 12)
20. KNM-ER 3733
21. KNM-ER 3883
22. Trinil/Pith I/Sangiran 2
23. Zhoukoudian Locus LI
24. Broken Hill/Kabwe
26. Swanscombe
27. La Chapelle I
28. La Ferrassie I
29. Gibraltar/Forbes Quarry
30. Cro-Magnon I
31. *Homo sapiens* (n = 6)

A Tukey-Kramer test for Honest Significant Differences of CQ among the means including all groups finds the a limited number of significant differences between groups, summarized in Table 11-6:

Table 11-6: Tukey-Kramer Test for Honest Significant Differences of CQ in Anthropoids

	Go	Pan	RH	Po	HH	HE	Aust	MPH	EMH	Hy	LAH	OW	NW
Go		Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
Pan	Y										Y	Y	Y
RH	Y												Y
Po	Y												Y
HH	Y												Y
HE	Y											Y	Y
Aust	Y												Y
MPH	Y												
EMH	Y												
Hy	Y												
LAH	Y												
OW	Y	Y				Y							
NW	Y	Y	Y	Y	Y	Y	Y						

Less generalized results are produced when the groups are consolidated into an “early” group, including the australopithecines, *H. habilis* and *H. erectus*; a “late” group, comprising Late Archaic and Early Modern Humans; and the Recent Human group. In a Wilcoxon/Kruskal Wallace test for equality of means, the Early and Late groups are found to be significantly different (chi-squared = 8.42; df = 2; p = 0.014; alpha = 0.05/3 = 0.017) (See Figure 11-5).

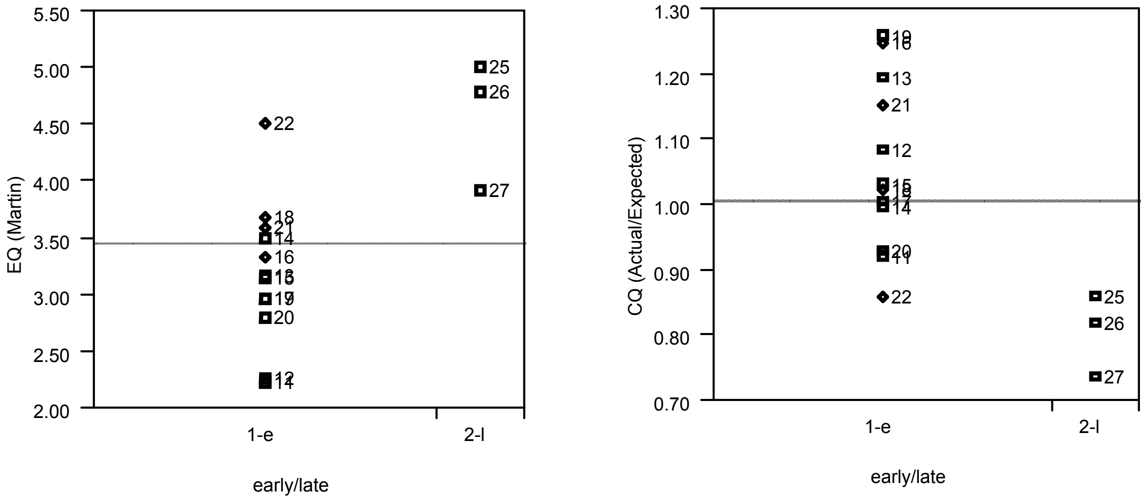
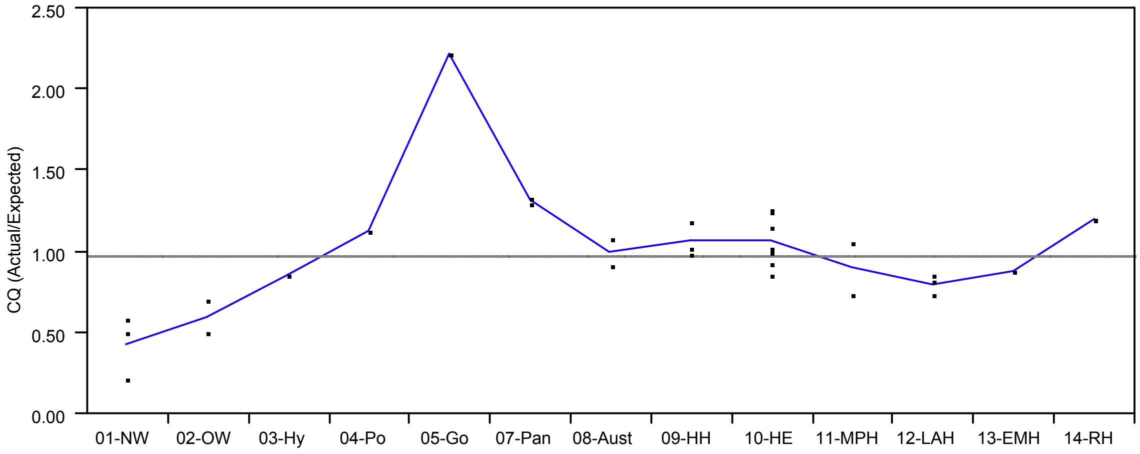


Figure 11-5: EQ (left) and CQ (right) in early hominids vs. Late Archaic *Homo sapiens*

Early and Late Archaic Human groups tend to fall along a line with a similar slope, but lower intercept, than do all other homionids. It is possible that Recent Humans fall on a higher slope than either the early hominid groups or the Archaic *Homo sapiens* groups, but it is difficult to evaluate this hypothesis because the present sample comprises only a single taxon mean. Figure 11-6 shows group means and standard deviations for CQ.



Level	**Number**	**Mean**	**Std Dev**	**Std Err Mean**
01-NW	3	0.43326	0.192802	0.11131
02-OW	2	0.60395	0.140366	0.09925
03-Hy	1	0.85831	•	•
04-Po	1	1.12628	•	•
05-Go	1	2.22513	•	•
06-Bo	1	1.33754	•	•
07-PanS	1	1.30281	•	•
08-Aust	2	1.00231	0.114821	0.08119
09-HH	3	1.07271	0.106297	0.06137
10-HE	7	1.06750	0.155292	0.05869
11-EAH	2	0.90342	0.224510	0.15875
12-LAH	3	0.80460	0.062664	0.03618
13-EMH	1	0.88097	•	•
14-RH	1	1.20621	•	•

Figure 11-6: CQ in Anthropoids (Actual /Expected). Means and Standard Deviations (based on Sample 01, RMA Line)

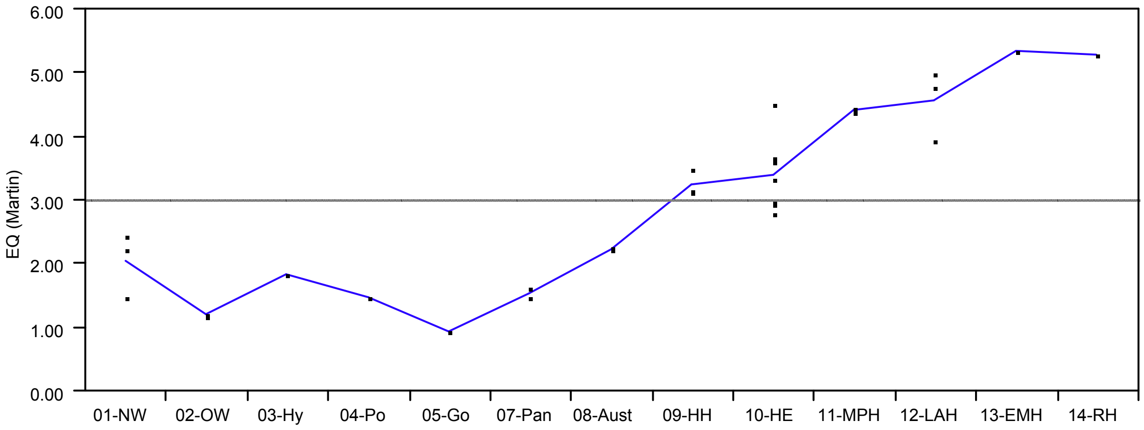
Calculation of EQ

The well-tested regression equation of Martin (1990) for mammals was used to calculate the encephalization quotient ("EQ") for the present analysis. The resulting values for EQ differ little from those produced by an empirical formula derived from the present sample. Use of this equation, rather than an equation based upon the present sample only has at least two advantages. (1) Martin's equation derives from a much larger sample of 27 primate species. (2) EQ values are directly comparable to those obtained in other studies (See Figure 11-7 and Appendix, Table A-13 for EQ values for the present sample.)

Inter and Intra-Groups Comparisons of Relative Cerebellar Volume in Anthropoids

Like the raw variables CBLM, BoMass and NetBrain, the derived variables CQ and EQ tend to rise over time in a "phylogenetic trajectory" from monkeys to recent humans. However, the interplay among the variables is highlighted when the CQ is compared to EQ for each taxon. The high CQ residual for *Gorilla*, for example, is not matched by a high relative brain mass with respect to body mass. In fact, *Gorilla*s have much smaller brains, as well as a much smaller cerebella, than would be predicted for their body mass. By contrast, the Late Archaic humans, whose mean body mass is equal to that of the *Gorilla* sample, have very large brains and small cerebella for their body size.

All comparisons were made using non-parametric, Wilcoxon/Kruskal Wallace Rank Sums tests for equality of means, unless otherwise indicated.



Level	Number	Mean	Std Dev	Std Err Mean
01-NW	3	2.05568	0.503587	0.29075
02-OW	2	1.20620	0.024110	0.01705
03-Hy	1	1.83318	•	•
04-Po	1	1.47314	•	•
05-Go	1	0.95363	•	•
06-Bo	1	1.63053	•	•
07-PanS	1	1.48314	•	•
08-Aust	2	2.24593	0.029474	0.02084
09-HH	3	3.26959	0.194858	0.11250
10-HE	7	3.41058	0.589411	0.22278
11-EAH	2	4.43132	0.054434	0.03849
12-LAH	3	4.57980	0.571411	0.32990
13-EMH	1	5.35763	•	•
14-RH	1	5.28782	•	•

Figure 11-7: EQ in Anthropoids (based on Martin's (1990) formula EQ = BrMass/11.22*BoMass $^{0.76}$) Means and Standard Deviations (based on Sample 01, RMA Line)

CQ and EQ in Non-Human Primates

The CQ trajectory rises from New World Monkeys to Old World Monkeys, and from Monkeys to Hominoids. The monkeys are small-bodied and small brained with compared to the rest of the sample. Three New World Monkey species, which have very high EQ due to their small body size, skew the significance test. Nevertheless, CQ in the small-bodied *Hylobates* falls well above the mean CQ for the monkeys. Extremely high relative cerebellar volume in the *Gorilla* sample produces an elevated group mean for CQ in the Pongids; however, even when *Gorilla* is excluded from the analysis, the Pongids are distinguishable from the monkey sample (chi-squared = 6.0; df = 1; p = 0.014). The Pongid sample is not significantly different from the monkey sample for EQ (chi-squared = 0.000; df = 1; p = 1.0). However, this result is in part an artifact of the line-fitting algorithm, which reduces the residual for both small monkeys and large apes.

The net effect of interplay among the variables in the Monkey vs. Hominoid comparison is one in which brain volume increases with respect to body mass, but the cerebellum appears to expand more rapidly than the NetBrain.

CQ and EQ in Pongids and australopithecines

EQ for the australopithecine sample just misses being significantly higher in the australopithecines than in *Pan* (*troglodytes* + *paniscus*) in a Wilcoxon-Kruskal Wallace test (chi-squared = 2.4; df = 1; p = 0.12). CQ is lower in the australopithecine group, but the again the difference just misses significance for alpha = 1 (chi-squared = 2.4; df = 1; p = 0.12).

The net effect of the interplay among the raw variables in the Pongid / australopithecine comparison is one of little or slight encephalization, with the NetBrain expanding more rapidly than the cerebellum.

Homo habilis

CQ for the *Homo habilis* sample is not significantly different from the australopithecines (chi-squared = 0.33; df = 1; p = 0.56). However, EQ is significantly different for alpha = 1 (chi-squared = 3.0; df = 1; p = 0.083). The highest CQ occurs in KNM-ER 1813. KNM-ER 1813 and KNM-ER 1470 have very similar EQs, but KNM-ER 1470 and KNM-ER 1805 are more similar in term of CQ. As with the australopithecines, body mass assignments are problematic.

The net effect of the interplay among the raw variables in the *H. habilis* to australopithecine comparison is one of overall encephalization. Both the cerebellum and the NetBrain expand non-allometrically; but the cerebellum appears to expand at a faster rate than the NetBrain.

Homo erectus

The *Homo erectus* sample is not significantly different from the *H. habilis* group with respect to CQ (chi-squared = 0.013; df = 1; p = 0.91) or EQ (chi-squared = 0.013; df = 1; p = 0.91). Although there is an increase in mean cerebellar volume and brain mass, this expansion was accompanied by an increase in body mass. Both cerebellar expansion and net brain expansion appear to have been isometric for this group.

The net effect of the interplay among the variables in the *H. erectus* vs. *H. habilis* comparison is one in which the cerebellum expanded more rapidly than the NetBrain.

***Middle Pleistocene* Homo sapiens**

The Middle Pleistocene *H. sapiens* sample as a group does not differ significantly from the *H. erectus* sample in terms of CQ (chi-squared = 0.77; df = 1; p = 0.38). The group mean EQ is higher than that of the *H. erectus* group, and the difference comes close to, but does not reach, significance for alpha = 0.1 (chi-squared = 2.14; df = 1; p = 0.14). EQ in both individuals in the sample (Swanscombe and Kabwe) is very similar. However, CQ is much lower in Swanscombe. Kabwe's CQ of 1.06 falls very close to the *H. erectus* mean of 1.07. Swanscombe, however, falls well below it, with a CQ of 0.74. In terms of CQ, Swanscombe is much more similar to the Late Archaic *H. sapiens* CQ mean of 0.80.

The net effect of the interplay among the raw variables in the *H. erectus* vs. Middle Pleistocene *H. sapiens* comparison results in overall encephalization, in which the NetBrain expands much more rapidly than the cerebellum. The two individuals in the sample, however, while similar in overall EQ, have very different values for CQ.

Late Archaic *Homo sapiens*

Mean CQ in the Late Archaic group is significantly lower than it is *H. erectus* (chi-squared = 5.73; df = 1; p = 0.17); or for all earlier hominids as a group (chi-squared = 7.04; df = 1; p = 0.008). Mean EQ, by contrast, is significantly higher for the Late Archaic sample than it is for *H. erectus* (chi-squared = 4.69; df = 1; p = 0.03); or for all earlier hominids as a group (chi-squared = 5.14; df = 1; p = 0.02). The net effect of the interplay of the raw variables in the Late Archaic vs. Middle Pleistocene *H. sapiens* samples is one of overall encephalization, in which the NetBrain expands with respect to body mass, but raw cerebellar volume does not increase, resulting in a drop in CQ.

Early Modern Homo sapiens

The single individual in this group has a higher EQ than the Late Archaic humans, but the difference is not significant (chi-squared = 1.80; df = 1; p = 0.18). This individual falls at the high end of the Late Archaic Distribution for CQ, which no significant difference between him and the Late Archaic Group (chi-squared = 1.80; df = 1; p = 0.18). The absolute brain mass for Cro-Magnon I (1477 cc) is somewhat smaller than the brain mass for La Chapelle I and La Férrassie I (1517 cc and 1576 cc, respectively); but the cerebellar volume of 118. cc is identical to both of these Late Archaic humans.

Although the range of variation for CBLM and CQ is unknown for the population to Cro-Magnon I belonged, it can be estimated by using the co-efficient of variation (CV) to calculate a standard deviation, as follows (CVs for CBLM and CQ in the study sample are summarized in Appendix, Table A-16):

Scenario 1: Assume Cro-Magnon I's population is as variable as hominids as a whole, and his CBLM falls at the mean for his population:

CBLM Mean = 118.92
CV (SD/Mean) = 0.31
x/118.92 = 0.31
x = 118.92 *0.31 = 36.87
max 118.92 + 36.87 = 155.78

min 118.92 – 36.87 = 82.05

CQ Mean = 0.88
CV (SD/mean) = 0.16
x/0.88 = 0.16
SD = x = 0.16*0.88 = 0.14
max = 0.88 + 0.14 = 1.02
min = 0.88 – 0.14 = 0.74

Scenario 2: Assume Cro-Magnon I's population is as variable as genus *Homo* and his CQ falls at his population mean

CBLM Mean = 118.92
CV (SD/Mean) = 0.27

x/118.92 = 0.27
SD = x = 118.92 * 0.27 = 32.11
max 118.92 + 32.11 = 151.01
min 118.92 – 32.11 = 86.81

CQ Mean = 0.88
CV (SD/Mean) = 0.17
x/00.88 = 0.17
SD = x = 0.17*0.88 = 0.15
max = 0.88 +0.15 = 1.03
min = 0.88 – 0.15 = 0.73

The results of the estimates for standard deviation suggest that the ranges of variation for CQ and CBLM in Early Modern humans overlap with both Recent humans and Late Archaic humans,

The net effect of the comparison between Late Archaic and Early Modern *H. sapiens* is a faster drop in body mass than in brain mass, resulting in a slightly higher EQ. Absolute cerebellar volume, however, remains static, resulting in a slightly higher CQ in this specimen.

Recent **Homo sapiens**

This group has the highest CQ of all the anthropoids, but an EQ that is almost identical to that of Cro-Magnon I. The Recent Human mean CQ and EQ are not significantly different from CQ and EQ for Late Archaic and Early Modern humans (for the Late Archaic group, for both EQ and CQ Late Archaic group, chi-squared = 1.80; df = 1; p = 0.18. For CQ and EQ for Early Modern Cro-Magnon I, chi-squared = 1.0; df = 1; p = 0.32).

However, when an expanded sample of individual CQ values is used in the comparison (from Rilling 1999 and Klekamp, Riedel, Harper and Kretschmann 1989), rather than the Recent Human mean, the power of the test is improved. For the expanded sample, CQ is significantly different between Recent and Late Archaic Humans (chi-squared = 7.43; df = 1; p = 0.006). EQ is not significantly different (chi-squared = 0.33; df = 1; p = 0.86).

For the expanded sample, CQ in Early Modern and Recent Humans is significantly different for $\propto = 0.1$ (chi-squared = 2.71; df = 1; p = 0.1), but EQ is not significantly different (chi-squared = 0.98; df = 1; p = 0.32). Mean absolute brain mass and body mass are lower in Recent humans than in than they are for the Late Archaic and Early Modern Humans, but mean absolute cerebellar volume is greater than in any other group of anthropoids, including fossil hominids.

The net effect of the interplay among the raw variables in the comparison of Recent and Early Modern *Homo sapiens* is a very similar EQ, accompanied by a sharp rise in cerebellar volume and concomitant rise in CQ.

Effect of Sample Composition and Line-Fitting Technique

As described more fully in Chapter 6, “Endocranial Volume,” both sample composition and line-fitting technique affect the regression formula (Bauchot 1978; Begun and Walker 1993; Deacon 1990b; a; Harvey et al. 1990; Holloway and Post 1982; Martin 1981). In order to assess the effect of sample composition and reference group on CQ, nineteen different linear regression formulae were calculated (See Appendix, Table A-17, for a description of the samples and regression formula used.)

While all of the equations reflected the high correlation between NetBrain and CBLM, three of the reference samples produced particularly high correlation coefficients (> 0.98):

Sample 08: Living Primates using raw variables; including Insectivores, Prosimians; and Anthropoids; excluding Fossil Hominids and Recent Humans.

Sample 05: Living Anthropoids using raw variables; excluding Insectivores, Prosimians and *Gorilla*; and including an expanded sample of Recent *H. sapiens* (18 Australian males; Klekamp, Reidel, Harper and Kretschmann 1987).

Sample 10: Living Primates, using log-transformed variables; including Insectivores, Prosimians; and Anthropoids; excluding Fossil Hominids and Recent Humans.

Because these samples produce a particularly close fit with the data, they were selected for comparison with the reference sample (Sample 01) used for the data analysis described above.

Wilcoxon-Kruskal Wallace comparisons of means were performed to evaluate whether selected groups are statistically different, and whether the sample composition or regression formulae affected the significance of the group comparisons. Table A-18 (Appendix) compares the results of selected regression formulae. Figures 11-8 to 11-12 below depict the effects of line-fitting on the selected samples. Although the selected formulae affect the relationship of the group means to the whole sample mean, the relationships among the groups are retained.

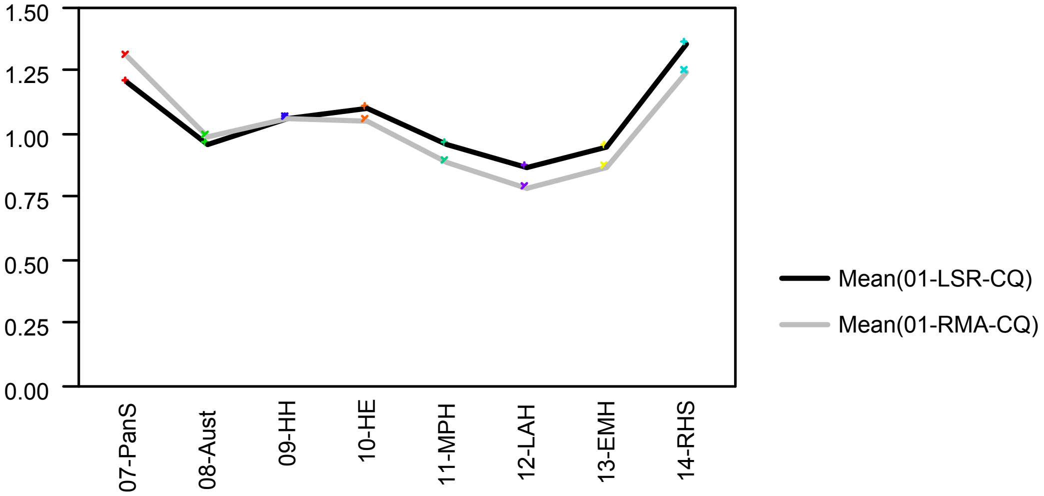


Figure 11-8: LSR and RMA CQ comparisons (Formula 01)

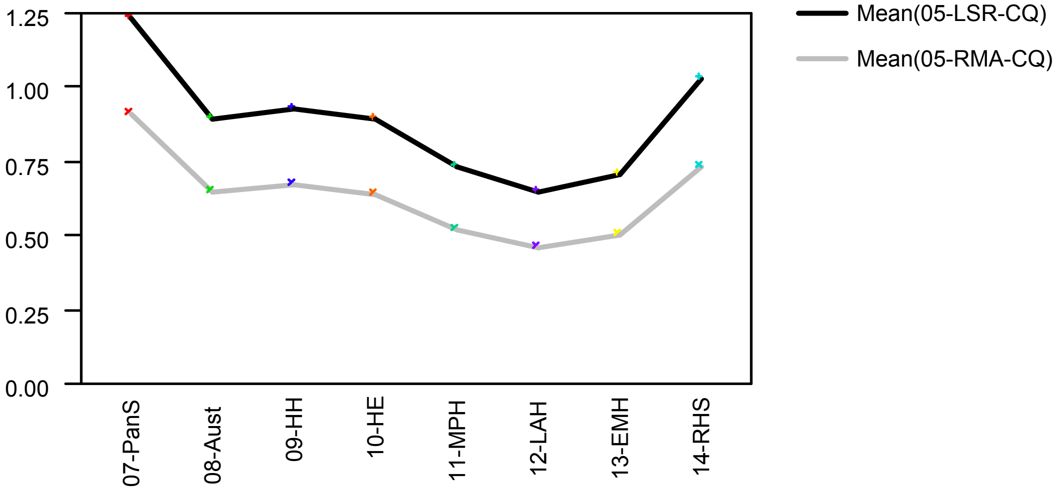


Figure 11-9: LSR and RMA CQ Comparisons (Sample 05)

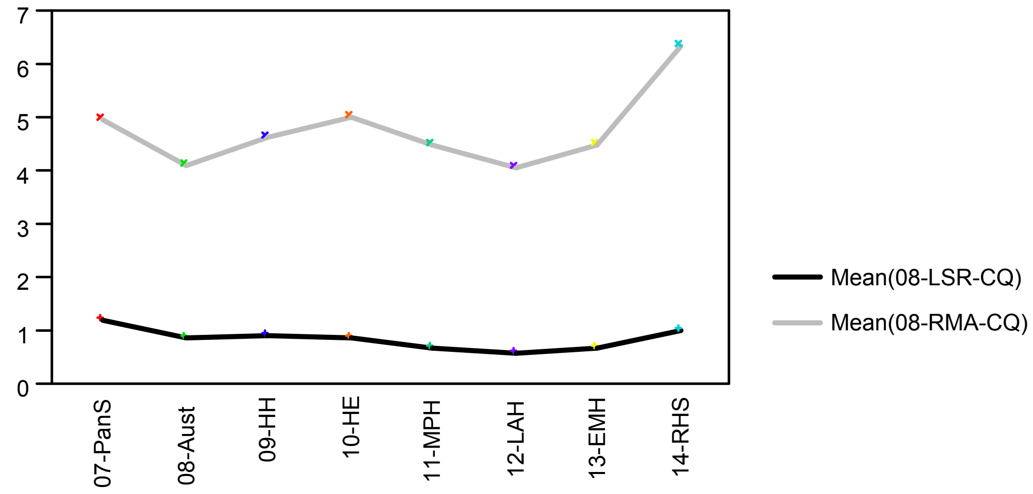


Figure 11-10: LSR and RMA CQ Comparisons (Sample O8)

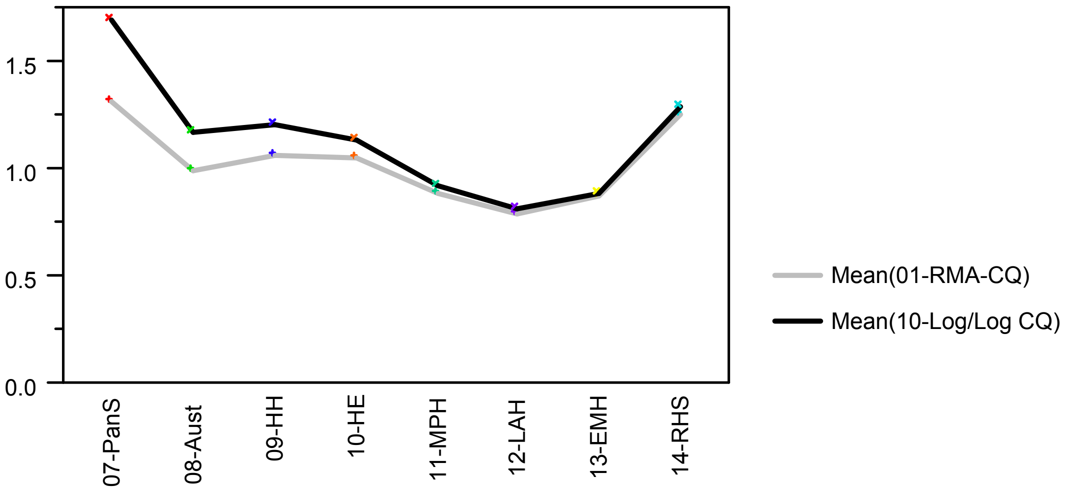


FIGURE 11-11: LSR and RMA Comparisons (Sample 01, RMA Formula and Sample 10)

Results of Comparison of CQ Using Different Sample Composition and Different Line-Fitting Techniques

For each of the comparison formulae, the Late Archaic humans are significantly different from the *H. erectus* group (p = 0.006). Neither Late Archaic nor Early Modern humans are significantly different from Recent humans when compared to the Recent human mean (p = 0.18). The power of the test is improved by using an expanded comparison sample including 18 Australian males (Klekamp, Riedel, Harper and Kretschmann 1987). When the expanded sample is used in the comparison, both Late Archaic and Early Modern Humans are significantly different from Recent *H. sapiens* for $\propto$ - 0.1. Such consistent results in between-group comparisons suggest that the between-group differences are robust reflections of an underlying phenomenon, not a statistical artifact based on sample composition or line-fitting technique. (See Appendix, Table A-18 for details of the formula comparisons.)

Constant Proportions for CQ for all Formulae

Although the absolute values of CQ and residuals vary depending upon the sample composition and line-fitting technique employed, the relationships among the groups remain stable. For example, the following values are found for $CQ_{\text{La Chapelle I}}/CQ_{\textit{H. sapiens}\text{ mean}}$: Formula LSR-01: 0.72; Formula RMA-01: 0.71; Formula LSR-05: 0.7; Formula RMA-05: 0.7; Formula LSR-08: 0.71; Formula RMA –08: 0.73; Formula LSR-09: 0.7; Formula RMA-09: 0.73; LSR-10: 0.7.

CQ and EQ Comparisons in Perspective

From a comprehensive ("tree shrew-to-gorilla") point of view, all later hominids have unremarkable CQs and high EQs . Figure 11-12 illustrates how the large difference in scale for EQ between Insectivores and hominids flattens depiction of the CQ trajectory.

When all CQ values are multiplied by 5, the overwhelming effect of encephalization on the CQ trajectory is compensated for, and the slight (but statistically significant) differences in CQ among the groups are brought into focus (Figure 11-13).

Although the Late Archaic and Early Modern groups have extremely high EQs, for primates as a group as well as for hominids, for all of samples and regression formula except RMA-08 they have the lowest CQ of any hominid. CQ declines steadily with respect to EQ from *Pan* through the fossil hominids, reaching its lowest value with Late Archaic and Early Modern humans, then it rises again in Recent humans.

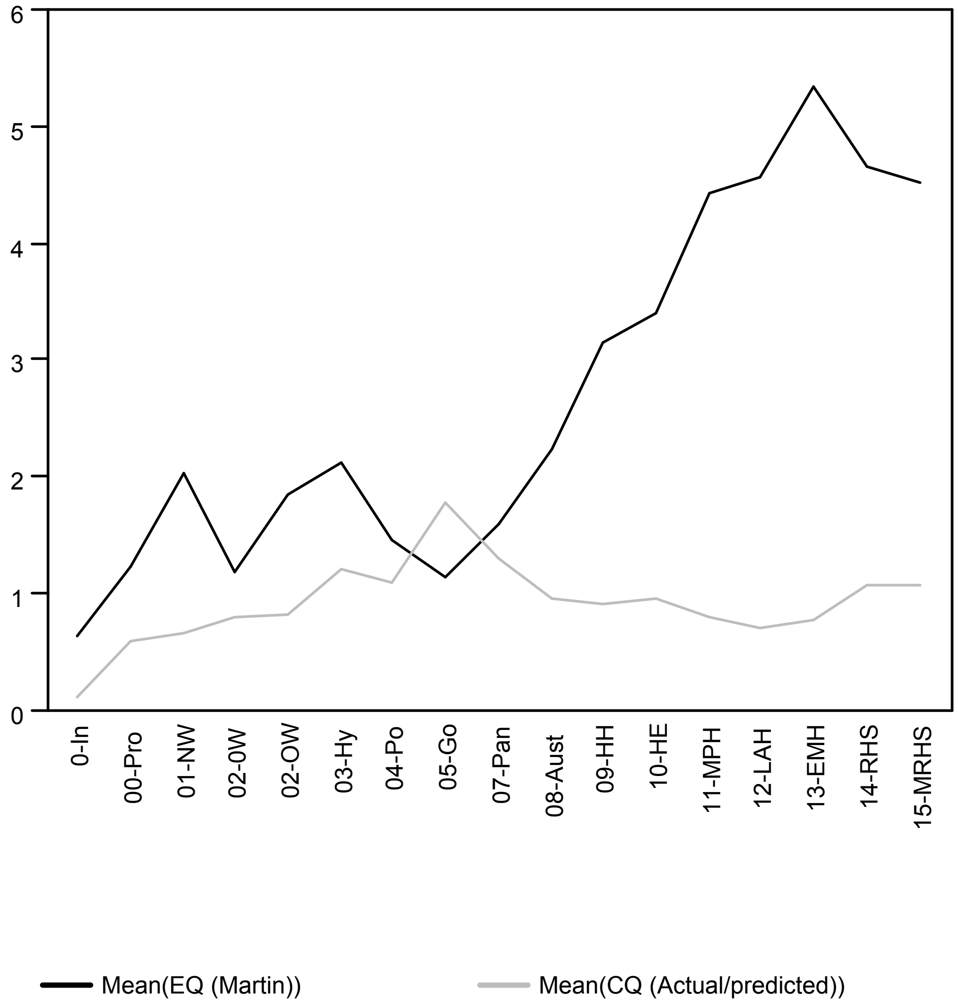


Figure 11-12 “Tree Shrew-to-Gorilla” comparison of CQ and EQ

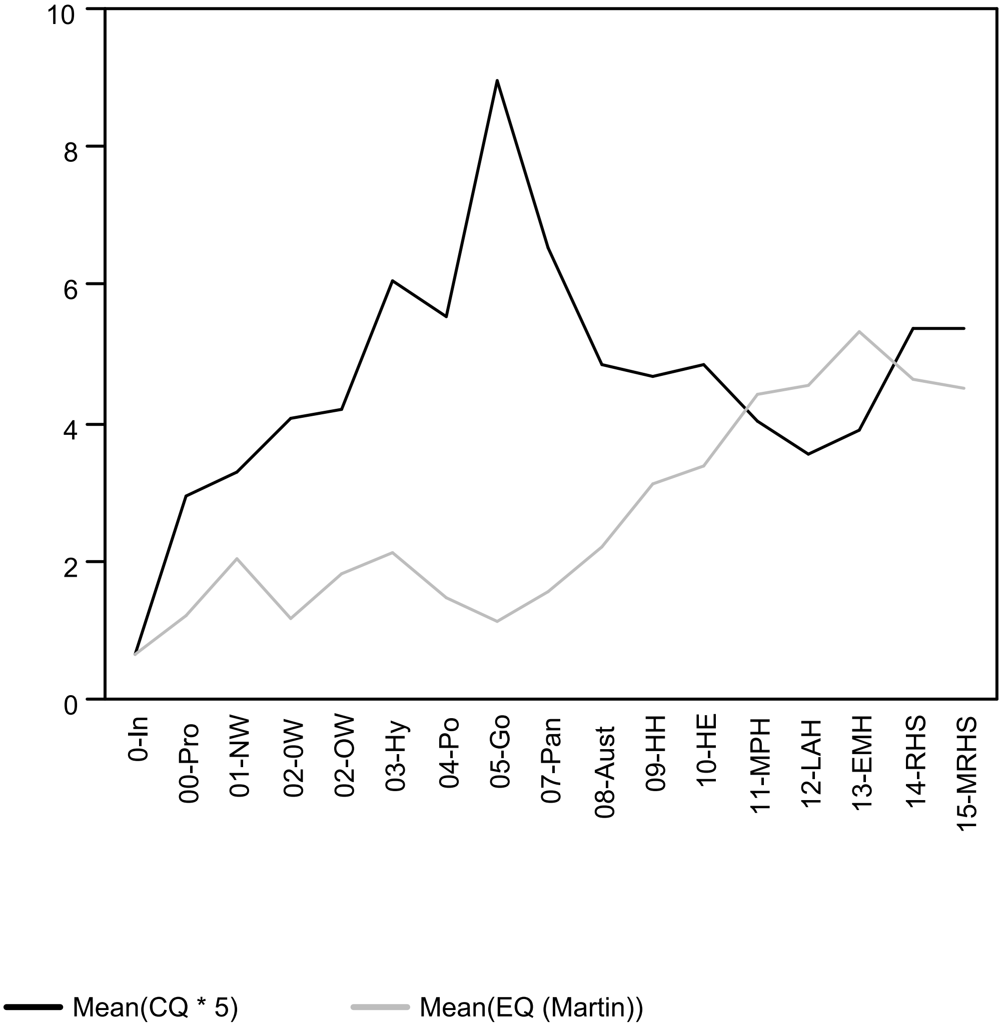


Figure 11-13: CQ and EQ follow Independent Trajectories (Group Means based on Sample 10, LSR formula for log CBLM and log NetBrain. CQ * 5 for adjustment of scale.

“Cerebellar Coefficient” (CQ/EQ)

Another approach to analyzing relative cerebellar volume is the “Cerebellar Coefficient” (CQ/EQ). This ratio incorporates (Values are calculated from Reference Sample 10, using logged values for CBLM, NetBrain, and BoMass). The results of the CQ/EQ comparison are congruent with the CQ comparisons described above. Differences among groups for the Cerebellar Coefficient are concordant with those for CQ. (See Appendix, Table A-19.)

Effect of Sample Composition and Line-Fitting Technique on Residuals

Yet another way to compare relative cerebellar volume is to compare residuals (actual – expected values). Residuals reflect the percentage by which cerebellar volume departs from expected volume. Although the absolute values of the residuals vary, depending upon sample composition and line-fitting technique, the *pattern* of residuals is similar to that of CQ, as shown in Figure 11-14. A summary of residuals is listed in the Appendix, Table A-20.

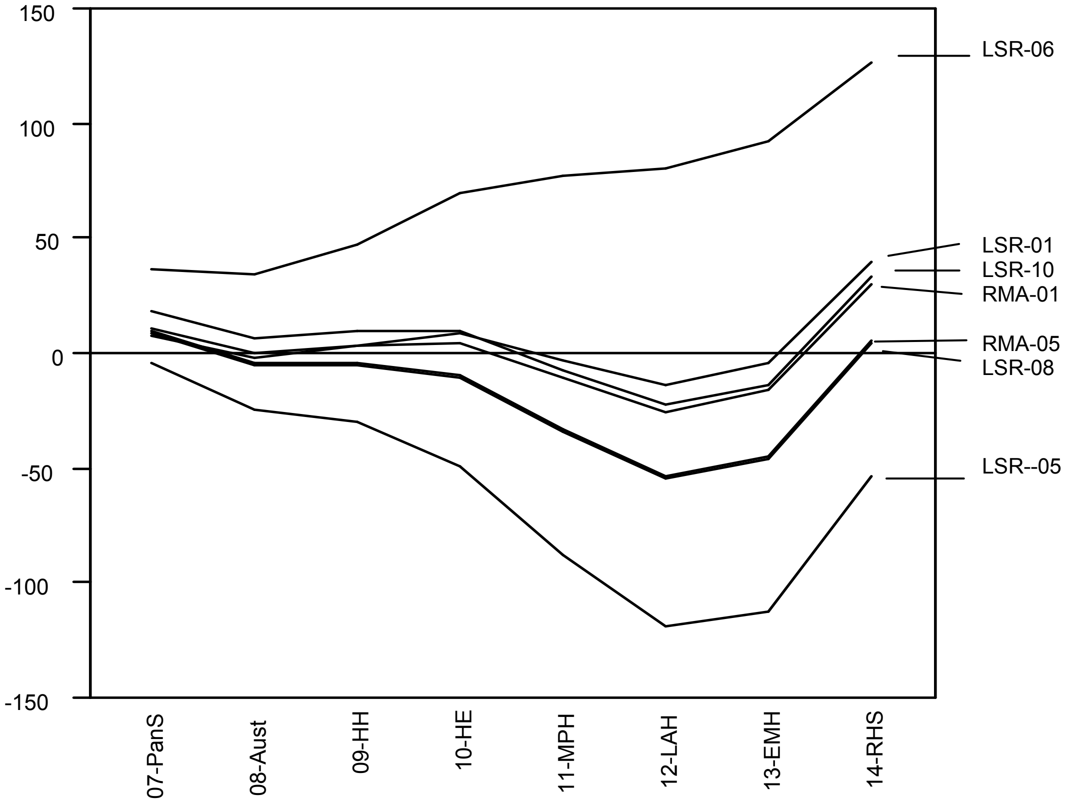


Figure 11-14: LSR and RMA Residual Comparisons

Mean CQ and Mean EQ Follow Independent Trajectories

Clark, Mitra, and Wang (2001) have argued that CBLM/BrainVol falls consistently between 0.11 and 0.15 in many living taxa, with a mean of 0.13. However, as illustrated in Figures 11-8 and 11-9, there are systematic phylogenetic differences in CQ among vertebrates. Insectivores and Prosimians fall consistently well below the mean CQ. New World Monkeys fall randomly on either side of the mean. The sample Old World Monkeys all fall slightly above the mean. Pongids have consistently high values, falling well above all other taxa in the sample. Contemporaneous humans fall consistently well above the mean, but below the Pongids. Most fossil hominids also fall above the mean, in the range of contemporary humans; however, Late Archaic and Early Modern humans fall only slightly above the mean and significantly below the other fossil hominids.

As Clark et al. (2001) have reported, mean CBLM/BrainVol = 0.11 +/- 0.02. However, a finer-grained examination shows that there are systematic, phylogenetically-based deviations from the mean, consistent with the observations of Matano and Hirisaki (1996; 1997), Rilling (1998), MacLeod et al. (2000), and Semendeferi et al. (2000). CQ in contemporary humans and for most other anthropoids *does* fall within the range of variation described by Clark et al. (2001). However, the Middle Pleistocene, Late Archaic, and Early Modern large-brained hominids are exceptional, not only for their large brains, but for their unique cerebellar proportions. Relative cerebellar volume (CBLM/BrMass) in the sampled Late Archaic Humans ranges from 0.7 to 0.8, with a mean of 0.74. That is, relative cerebellar volume in Late Archaic humans falls almost two standard deviations below the population mean observed by Clark et al.

Absolute cerebellar volume is in Middle Pleistocene, late Archaic and Early Modern humans is larger than in earlier hominids. Relative cerebellar volume is reduced in later hominids because NetBrain expansion outpaced cerebellar expansion.

Cerebellar expansion in Middle Pleistocene, late Archaic and Early Modern humans kept pace with body mass expansion. Presumably, the cerebellum in these hominids continued to function with respect to basic proprioception and sensory-motor integration much as it did in earlier hominids. However, rapid cerebellar expansion in Recent Modern humans suggests that additional demands were made on the cerebellum. As outlined in Chapter 3 “Neural Architecture,” the cerebellum appears to be extensively involved in cognition. The sensory-motor repertories of Recent Modern humans appear to be indistinguishable from those of earlier humans. Therefore, it is reasonable to hypothesize that cerebellar expansion in Recent Modern Humans is related to cerebellar participation in cognitive functions.

Summary of Data Analysis and Results

The derived variables CQ and EQ can be used as a reference scale for comparison of relative cerebellar and brain volume in fossil hominids. Although the absolute values of CQ and EQ may vary, based upon sample composition and the line-fitting technique employed, significant differences can be observed for relative cerebellar volume can be observed in fossil hominids for CQ alone, for CQ with respect to EQ, and for deviations from expected values (residuals). The phylogenetic trajectory for relative cerebellar volume follows a consistent, robust pattern that is emerges no matter what line-fitting technique, sample composition, or ratio is employed.

Six phases of cerebellar evolution can be discerned in fossil hominids, based upon the interaction of CQ and EQ over time. The cognitive and behavioral implications of the phases are more fully elaborated in Chapter 13, “Discussion.”

In the first, transitional phase from Pongids to australopithecines, encephalization involved a slight expansion of the NetBrain, at the expense of relative cerebellar volume.

In the second phase, marked encephalization in *H. habilis* involved a non-allometric expansion of both NetBrain and Cerebellum.

In the third phase, relative cerebellar expansion continued in *H. erectus*, possibly at the cost of NetBrain expansion, reflected in little or no change in EQ.

In the fourth phase, the NetBrain of Early and Late archaic *H. sapiens* expanded very markedly with respect to Body Mass, but the cerebellum expanded at a much slower rate.

In the fifth phase, absolute cerebellum volume in Early Modern *H. sapiens* did not change significantly; but CQ increased slightly. Body Mass decreased at a slightly greater rate than Brain mass, resulting in a net increase in EQ

In the sixth phase, Body Mass decreased at a greater rate than Brain Mass, which was also reduced; but absolute and relative cerebellar volume increased markedly.

Cerebellar volume change was gradual and continuous in hominid evolution. Cerebellar evolution did not involve significant differences between mean CQ in successive hominid taxa; in fact, the only significant differences occur between early hominids (australopithecines, *H. habilis* and *H. erectus*) and Late Archaic Humans; and between Late Archaic humans and Recent *Homo sapiens.* Clear distinctions among the groups are obscured by the presence of several apparently transitional individuals (e.g., Kabwe, Swanscombe, and Cro-Magnon I). The mixed morphology of these individuals highlights the mosaic nature of the evolutionary process.

Results with Respect to Null Hypotheses

The results of the data analysis with respect to the null hypotheses informing the study are as follows:

Null Hypothesis: H_{01}: For all groups CQ scales non-allometrically with EQ:

$$\mathbf{H_{01}: \quad CQ = k * EQ}$$

Result: $\mathbf{H_{01}}$ is refuted. (See "Data Analysis," above, for details of between-group comparisons. Also see Chapter 13, "Discussion" for an expanded discussion of the implications of these results.

Null Hypothesis: H_{02}: In modern humans, total posterior cranial fossa volume (PCF) is correlated with total cerebellar volume:

$$\mathbf{H_{02} \; : \quad PCF_{human} := k * CBLM_{human}}$$

Result: $\mathbf{H_{02}}$ is not falisified (See Chapter 10, “Methods” for elaboration).

Null Hypothesis: H_{03}: In modern apes, PCF is highly correlated with total cerebellar volume:

$$\mathbf{H_{03}:\quad PCF_{nonhuman} = k * CBLM_{nonhuman}}$$

Result: Null hypothesis is not falsified. (See Chapter 10, “Methods,” for full description.)

Null Hypothesis: H_{04}: The ratio CBLM to (PCF) in apes is equal to the ratio of CBLM to PCF in modern humans.

$$\mathbf{H_{04}:\ PCF/CBLM_{nonhuman} = PCF/CBLM_{human}}$$

Result: Null hypothesis is not falsified. (See Chapter 10, “Methods,” for full description.)

12 DISSUSSION: PHYLOGENETIC CHANGES IN RELATIVE CEREBELLAR VOLUME

Introduction

The interaction between the variables cerebellar volume (CBLM), body mass (BoMass) and brain mass ((BrMass) in Pliocene and Pleistocene hominids is a complex one. A reference scale based on derived the variables CQ and EQ can be used for exploring phylogenetic differences in relative cerebellar and brain volume in fossil hominids. The concept of a “phylogenetic trajectory” is a helpful in visualizing how the proportions among the variables differ from group to group. However, modern human morphology is not an inevitable cognitive “endpoint”. Each of the taxa included in the graph has its own evolutionary history and ecological context and related adaptive patterns.

Comparison of Modern Human Cerebellum with non-Human Primates

The cerebellum has undergone evolutionary changes in the relative volume of the cerebellar deep nuclei, lateral lobes, and vermis. Cerebellar reorganization must have occurred mosaically, in tandem with evolution of the neocortex and other subcortical structures, especially the pons, thalamus and basal ganglia, which transmit and receive neural impulses to and from the cerebellum. The modern human cerebellum differs from that of other anthropoids in five important respects, listed below.

(1) It is absolutely larger than that of other primates (present analysis; Rilling and Insel 1998; Semendeferi and Damasio 2000; MacLeod et al. 2000; Matano et al 1985a; Matano et al. 1985b; Matano and Hirasaki 1966; 1997)

(2) It is larger than would be predicted by overall brain volume compared to other anthropoids (present analysis; but see (Rilling and Insel 1998) (Semendeferi and Damasio 2000) and (MacLeod et al. 2000).

(3) In comparison to other anthropoids, the lateral cerebellar lobes are larger than would be predicted by overall brain volume or by cerebellar vermis volume (MacLeod et al. 2000).

(4) Compared to other anthropoids, the modern human dentate nucleus is smaller than would be predicted by cerebellar volume or cerebellar hemisphere volume (MacLeod et al. 2000); but see (Matano and Hirasaki 1997).

(5) It is possible that the ventral half of the dentate is larger than would be predicted for overall dentate size, as well (Matano 2001), but this has not been confirmed (C.E. MacLeod, personal communication; unpublished data, March 27, 2001).

Cognitive Behavioral Distinctions between Humans and Non-Human Primates

Non-human primates differ from each other and from humans in many cognitive dimensions. The most extensive studies of primate cognition have related to linguistic behavior (e.g., Cheney and Seyfarth, 1990; Gardner, Gardner and van Cantford 1989; Greenfield and Savage-Rumbaugh 1990; Savage-Rumbaugh, Romski, Hopkins and Sevcik 1989)

Other studies of cognition in primates have addressed social interactions and cultural complexity (e.g., McGrew 1992; Whiten 1990). The construction of sets and cognitive hierarchies is of particular interest in the context of the present study.

Set Construction

Differences in set construction ability (composing objects together on the basis of their similarities) are among the most fundamental and pervasive cognitive distinctions between humans and non-human primates (Langer 2000). Monkeys can learn to group objects together in single sets of fewer than three objects, but do not construct multiple sets. By the time they are five years old, chimpanzees can learn to group objects into two contrasting sets, permitting linear comparisons, but they apparently cannot construct more than three sets. By their third year, human infants spontaneously compose three or more sets containing an increasing number of objects, enabling them to construct cognitive hierarchies.

Cognitive Mapping

The following summary of cognitive development is taken from Langer (2000). By the time they are two years old, human children spontaneously compose sets of objects that correspond to each other numerically and spatially. They then exchange objects between the sets while preserving the spatial and numerical correspondence. Chimpanzees learn to exchange objects within one of their two constructed sets, but do not exchange objects between sets. The behavior of the human children is evidence of their ability to employ recursiveness, where groups of objects, rather than single objects, are manipulated in relation to each other. *The elements of cognition are no longer objects, but concepts*. This means that humans, unlike other primates, can reflect upon and cognitively manipulate the relationships among groups of objects. Once a basic hierarchical conceptual organization is achieved, the hypotheticodeductive formal operations unique to humans can be developed (Inhelder and Piaget 1958; Langer 2000).

The Cerebellum and Set Construction

One hypothesis about the contribution of the cerebellum to human cognition is that its role in sequencing, timing and integration of sensory-motor functions can be extended to the serial timing and integration of thoughts as well (Ito 1993). Serial timing and integration may be as fundamental to manipulation of cognitive categories, as they are to sets of sensory-motor patterns. As the number of cognitive categories increased during human evolution (as a result of greater working memory, complexity of set construction, recursiveness, and cultural enrichment), there would have been an increased demand for serial timing and integration of cognitive hierarchies (rather than single objects or sets of objects). Individuals who were capable of formal operational thought (Piaget 1952) or “externally nested cultural products”, i.e. theories (Donald 1991) would have been more successful in procuring resources in many cultural contexts.

The cerebellum, with its extensive connections with many areas of the neocortex, would have been the logical candidate to handle this increased demand for handling hierarchical, nested representations.

Demands on the cerebellum would have increased as cultural elaboration continued and the number of objects and concepts to be manipulated increased.

Limitations of the Data

The preceding data analysis rests on data that are subject to three significant limitations:

(1) The sample sizes for all taxa are small and the specimens included are somewhat arbitrary. MRIs of anthropoids, especially the large-bodied apes, are rare. Few endocasts are available for any hominid taxon, and the present sample of scans can only be suggestive of the pattern of allometric change in cerebellar volume in the taxa represented.

(2) In addition to small sample sizes, the articulation of bodies of data obtained from different media is a loose one at best. With only one overlapping species between the MRIs and the 3-D scans, and only two overlapping species between the CTs and the 3-D scans (and no overlap between the MRIs and the CTs), the derivation of a single regression equation for cerebellar volume from the present data may be flawed. However, even if the line falters at the points of articulation, the relationships among the taxa *within* the data sets will remain constant. That is, relative cerebellar volume among the hominids or among the non-human primates does not change, no matter how the intercept is shifted. The pattern that emerges is consistent with what is known about cerebellar volumes in living taxa (Rilling and Insel 1998) and (Semendeferi and Damasio 2000), although, in contrast to the present work, these authors both found relative cerebellar volume in recent humans to be less than expected for an

anthropoid of equal body mass. The addition of the hominids depresses the slope of the anthropoid regression line and alters the position of recent humans with respect to relative cerebellar volume. With the addition of the hominid taxa, the strong effect of *Gorilla* on the slope of the line is mitigated.

(3) Many of the endocasts are reconstructed from partial evidence. Reconstruction of missing portions for many endocasts has relied upon morphology known from other, more complete specimens, or from contours that are only intimated by broken edges (e.g. the Zhoukoudian endocasts). Swanscombe and Arago are an extreme example of mutual composites. Even the most complete endocasts (e.g. KNM-ER 1470) have been distorted during fossilization. Many endocasts have been taken from crania pieced together from fragments.

All inferences drawn from such data must be provisional. However, the internal consistency of the evidence suggests that the underlying signal is robust, and offers support for the framework of allometric cerebellar change that is suggested by the results.

EQ and CQ in Anthropoids

Monkeys and Pongids

The focus of the present work is on Pliocene and Pleistocene hominids. However, a brief discussion of CQ and EQ in the non-human primate sample will place the later discussion in context.

Cerebellar volume, net brain mass, body mass, and CQ follow an increasing “phylogenetic trajectory” from New World monkeys to Old World monkeys to Pongids. Mean CQ for Cerebellar volume in non-human primates is highly correlated with body mass ($r^2 = 0.92$). By contrast, the cerebellum in the genus *Homo* is uncorrelated with body mass ($r^2 = 0.3$). Cerebellar volume is only weakly correlated with net brain size in either group ($r^2 = 0.5$).

The trajectory for EQ is also correlated with body mass, but the picture is more complicated than it is for CQ. EQ is negatively allometric with respect to body mass for both monkeys and non-human hominoids. However, there is a "grade" distinction for EQ between the two groups. Hominoids have higher EQs than monkeys of similar body mass (e.g., *Hylobates* versus S*. sciureus*). Higher EQ in the hominoids is manifested in their more sophisticated behavior in problem-solving tool use, self-recognition, and incipient symbolic capacity.

Higher CQ in hominoids than in monkeys may be related to their considerable manual dexterity and/or to their versatile locomotor repertory (Matano and Hirasaki 1997; Rilling and Insel 1998). It may also be a function of larger body mass in hominoids.

Australopithecines

The two australopithecines in the sample (KNM-ER 23000 and STS 19) have larger brains than the *Pan* sample, but small brains compared to the rest of the hominids. Cerebellar volume for KNM-ER 23000 is larger than in *Pan*; but STS 19 is smaller. Endocranial volume for KNM-ER 23000 (assigned to *A. boisei)* is 471.74 (from the scanned model; no published volume available). This is represents an increase of approximately 5% above the mean for *A. africanus* (440-450 cc). STS 19, which has been assigned to *Australopithecus africanus*, is fragmentary. Its total endocranial volume of 436 cc was estimated by formula (Holloway 1975a; 1978). The endocranial capacity of this individual falls just below the mean endocranial capacity for *A. africanus* of 440-450 cc (Tobias 1975; Holloway 1995). Assignment of body weights to the earliest hominids is problematic. Endocranial capacity in both *A. africanus* and *A. boisei* as a whole may reflect a non-allometric increase relative to body weight (Holloway 1995).

To the extent that encephalization occurred in australopithecines, it appears to be a result of net brain expansion (neocortex and/or subcortical structures not discernible from the endocast) rather than cerebellar expansion.

Encephalization in australopithecines occurred in tandem with cortical reorganization (expansion of the posterior parietal region; reduction of the striate cortex; and possibly increased functional lateralization) (Holloway 1966; 1967; 1972b; a; 1973; 1975a; 1976; 1978; 1979; 1983a; b; 1984; 1985; Holloway and De La Coste-Lareymondie 1982; Holloway and Kimbel 1986).

Although CQ is lower in the australopithecine sample, it is likely that neocortical reorganization was accompanied by cerebellar reorganization involving an expansion of the lateral cerebellar lobes at the expense of the vermis. Bipedalism makes fewer demands on the cerebellum than the complex arboreal repertories of other primates (Matano and Hirasaki 1997). Increased lateral lobe capacity would have permitted a greater cerebellar contribution to functions of the posterior parietal cortex such as serial timing of gestures, and enhanced sensory integration related to visuo-spatial abilities. Only two individuals, representing only two of the many australopithecine species, are represented in the sample. It is impossible to determine whether these particular individuals were typical in terms of their behavior or neuromorphology.

Possible behavioral indicators of neocortical and cerebellar reorganization for enhanced manual dexterity are lacking for the earliest australopithecines, but present in the stone tools made and used by approximately 2.5 mya (e.g., Asfaw et al. 1999; Harris 1983; Harris and Semaw 1989; Kimbel, Walter, Johanson, Reed, Aronson, Assefa, Marean, Eck, Bobe, Hovers, Rak, Vondra, Yemane, York, Chen, Evensen and Smith 1996; Semaw, Renne, Harris, Feibel, Bernor, Fesseha and Mowbray 1997). Sensory integration and freedom of the forelimbs may have led to enhanced gestural communication to accompany vocalization as well; but the paleontological evidence is silent with regard to this speculation.

***Early* Homo/Homo habilis**

Three individuals are included in the *Homo habilis* (*sensu lato*) sample: KNM-ER 1813; KNM-ER 1805; and KNM-ER 1470. As with the australopithecines, evaluating encephalization in the early members of the genus *Homo* is problematic, due to the lack of associated postcranial materials. Of the present sample, only KNM-ER 1470 may be associated with postcranial bones permitting an estimation of body weight, and the attribution of these bones to the same individual is tenuous (Trinkaus 1984).

CQ has risen only slightly, if at all in this group; but EQ has increased significantly in comparison to the australopithecines. Encephalization appears to be the result of NetBrain expansion, accompanied by an isometric expansion of the cerebellum.

NetBrain expansion was accompanied by extensive, if variable, neocortical reorganization (compared to the australopithecines) in all three of the *H. habilis* individuals. Neocortical evolution in this group includes changes in frontal lobe shape (in KNM-ER1470 and KNM-ER 1805); expansion of the parietals (in KNM-ER 1805, and KNM-ER 1470); right-frontal/left occipital petalia (variable; observed by Holloway in all three (but see Begun and Walker did not entirely agree with Holloway with respect to their degree of development); presence of and expanded Broca's area (in KNM-ER 1470) (Begun and Walker 1993; Falk 1983; Holloway 1983a); and possible modifications of the caudal orbital frontal sulcal morphology (Falk 1983). Many landmarks are ambiguous, due to poor preservation.

Encephalization in *H. habilis* can be attributed to a very slight increase in relative cerebellar volume accompanying a more significant increase in net brain volume.

Behavioral evolution in *H. habilis* appears to be related to non-allometric expansion of the neocortex and/or subcortical structures not discernable in endocasts. In addition to tool use, cognitive developments in this taxon included long-range planning; as well communication and conceptual skills related to procuring and distribution of raw materials for meat processing (Potts 1988). These are activities that would have been supported by the parietal lobe expansion observed for this taxon (Geshwind 1966; Holloway 1972b; 1981c; Schepers 1946; Tobias 1975; 1987).

Though cerebellar expansion was slight, it is plausible that cerebellar reorganization may have been initiated or continued, as new neocortical functions increased demands for motor learning, motor coordination and sensory integration related to tool-making, manual dexterity, visuo-spatial skills, navigation skills, and communication efficiency. In addition, a small increase in cerebellar volume may signal a large increase in neocortical efficiency.

Homo erectus

The sample includes seven individuals classified as *Homo erectus.* Mean CQ in the *H. erectus* group is identical to that of the *H. habilis* group. Mean EQ is slightly lower in the early African *H. erectus* (KNM-ER 3733, KNM-ER 3883, and KNM-WT-15000) sample than in either *H. habilis* or later Asian *H. erectus*, but not significantly so. The only individual for whom reliable body mass estimates are available in this sample is KNM-ER 15000, an adolescent who was not skeletally or neurologically mature (Walker and Leakey 1993).

Mean cerebellar volume and mean brain mass are both higher in the later Asian *Homo erectus* specimens than in the earlier African *Homo erectus* specimens, and the early *Homo erectus* group mean for these variables is, in turn, higher than in the *H. habilis* group. At the same time, body mass has increased from the *H. habilis* group to the *H. erectus* group. Individual estimates of body mass are not available for most of these specimens, so they have all been assigned the same estimated mean body size (except for KNM-WT 15000, for whom associated postcranial bones are available). Therefore, making individual encephalization estimates is problematic.

Absolute cerebellar volume increases from a group mean of 46.2 in the australopithecine sample to 87.2 in the *Homo erectus* sample. The rise in CQ does reach significance. Nonetheless, mean CQ in the early hominids is greater than it is in later hominid groups (with the exception of recent humans).

The apparently increased behavioral sophistication seen in *H. erectus* compared to *H. habilis* is accompanied by a slight rise in CQ, but an isometric increase in body weight and brain volume. Thus, the behavioral and technological sophistication of *H. erectus* is correlated with an increase in cerebellar volume relative to overall brain size, but not in brain size with respect to body mass. Perhaps this accounts for the skilled, but typologically limited, lithic repertory produced by Middle Pleistocene hominids. *Homo erectus* had highly developed procedural learning abilities, bolstered by excellent visuo-spatial skills (Gowlett 1984; 1986; 1996; Wynn 1979; 1985; 1991; Robson-Brown 1993). A high level of visuo-spatial integration is indicated by neocortical reorganization of the posterior parietal cortex in this taxon (Begun and Walker, 1993). Visuo-spatial skills would have also been strongly influenced by a cultural heritage in which individuals learned the elements and standards of toolmaking (and probably other, unrecorded behaviors) according to a pattern assimilated by procedural, rather than declarative learning. Toolmaking skill was related to well-developed sensorimotor and concrete-operational abilities mediated by the cerebellum, rather than on formal operations mediated by the neocortex (Piaget 1952; Piaget and Inhelder 1967).

Cognitive behavioral differences observed between *H. habilis* and *H. erectus* may have been related to consolidation of neocortical reorganization incipient in *H. habilis*, accompanied by enhanced integration mediated by the expanded cerebellum.

Middle Pleistocene Humans

Two individuals are included in this group: Kabwe and Swanscombe. Their group assignment is related to their chronological position, endocranial volume, and ambiguous, apparently transitional morphology (Stringer 1974). In the present analysis, they appear to be quite distinct. CQ for the Kabwe individual falls at the mean for the *H. erectus* group. Swanscombe, on the other hand, has the second-lowest CQ in the entire anthropoid sample, falling only slightly above Gibraltar/Forbes Quarry. The specimens have similar endocranial volumes from which brain mass was calculated (for Swanscombe, the endocranial volume of 1225 cc is estimated by formula, based on the Swanscombe occipital and parietal bones (Le Gros Clark 1938). The endocranial volume of 1248 for Kabwe is taken from the scanned virtual model. These individuals have been assigned identical body weights, based on mean values for their taxon.

Thus, cerebellar volume relative both to body weight and to brain volume is very high in Kabwe, but very low in Swanscombe. At least two (not mutually exclusive) explanations may account for difference in CQ between these specimens. (1) Geographical separation. These archaic humans belonged to populations widely separated geographically. (3) Phylogenetic separation. There may be significant genetic differences between the parent populations from which these individuals came. Some researchers have aligned Swanscombe with the Atapuerca, Reilingen, Petralona, and Arago hominids as pre-Neandertal based on occipital morphology (e.g. (Breitinger 1952; 1955; Howell 1960; Stewart 1960, cited in Day 1986). The present evidence offers support for this hypothesis. Kabwe, also, has been described as a pre-Neandertal (Smith 1928; Weinert 1931), although other authors have preferred to include it within *Homo erectus* (Arambourg 1963, cited in Day 1986). The present analysis aligns it with *Homo erectus* in terms of CQ; but it is distinct in that its large cranial capacity results in a high degree of encephalization compared to *H. erectus*. In any case, in contrast to Swanscombe, the cerebellum in the Kabwe individual is quite large compared to the rest of the brain.

Mean CQ declines in the Middle Pleistocene group and reaches its lowest level in late archaic humans. The Kabwe and Swanscombe individuals are very distinct from each other with regard to CQ, although their overall brain and body masses are similar. Their inclusion in a single group with in an analysis of CQ may not be appropriate.

The Swanscombe remains were found in association with Middle Acheulean tools. The Kabwe cranium has no clearly associated lithic materials, although some *ad hoc* scrapers were found within the cave site, and some bifacial tools were found at some distance away (Delson, Tattersal, Van Couvering and Brooks 2000). In terms of the archeological evidence, these particular individuals are not unequivocally distinguishable from each other or from *Homo erectus*.

Lithic and other remains from other sites suggest that by the middle Middle Pleistocene humans were capable of manufacturing very fine bifacial tools (Wynn 1979; 1996b; 2000) . They had developed an incipient prepared-core technology (Clark 1970; Gowlett 1996; Isaac 1972),and were skillfully crafting wooden spears, (Oakley, Andrews, Keeley and Clark 1977; Thieme 1997) .

However, based on the present evidence, it is impossible to determine whether cerebellar evolution affected the cognitive behavior of either Kabwe or Swanscombe or their contemporaries. These individuals were not associated with advanced technology or other indicators of cognitive evolution; and cerebellar volume data are not yet available for individuals who *are* associated with such technology. Just as the taxonomic status of these individuals is indeterminate, so are details of encephalization and behavior.

Late Archaic Humans

Three Late Archaic Humans have been included in the present sample, and they are all Western European Neandertals. Although their cerebella are absolutely large (only recent humans have larger cerebellar), their relative cerebellar volume falls well below the mean for all earlier hominids. When the intermediate and ambiguous Middle Pleistocene humans are excluded, mean CQ in late archaic humans is found to be significantly lower than the pooled mean CQ for all three early hominid groups.

Mean cerebellar volume is higher in the Late Archaic group (106.3 +/- 21.34 cc) than in the Middle Pleistocene group (99.5 +/- 23.97 cc) or the *Homo erectus* group (87.2 +/- 12.27 cc). Mean brain mass is considerably higher in the Late Archaic group, which includes the La Ferrassie I and La Chapelle I, who have the highest overall endocranial capacity for the entire sample 1641 cc and 1548 cc, respectively). The mean endocranial capacity of 1426 cc for the present sample of Late Archaic humans, which includes the rather small Gibraltar/Forbes Quarry specimen, falls slightly below the Late Archaic mean of 1492 cc reported for a more inclusive sample of 14 individuals (Ruff et al. 1997). However, regardless of their individual endocranial capacities, all of the Late Archaic humans in the sample have very low relative cerebellar volumes.

The mean EQ of 16.7 for the present sample of Late Archaic humans is identical to the mean EQ for the Middle Pleistocene group. Mean CBLM/BoMass in the Late Archaic group falls below the mean for either *Homo erectus* or the Middle Pleistocene group, but not significantly so (Wilcoxon/Kruskal-Wallace test; chi-squared = 0.66; df = 2; p = 0.72). The brain mass increase in Late Archaic humans appears to be isometric with respect to body mass; but although *absolute* cerebellar volume has *increased*, *relative* cerebellar volume appears to have *decreased* with respect to both body and brain size. The sample Late Archaic mean cerebellar volume of 106 cc falls approximately two standard deviations below the Recent Human mean (140.5 +/- 19.0 cc). Both La Ferrassie I and La Chapelle I, with cerebellar volumes of 118 and 119 cc, respectively, fall barely below one standard deviation from the modern mean, and well within the

Recent Human range of variation (91.98 – 194 cc), as does Kabwe/Broken Hill. The Gibraltar individual, whose estimated cerebellar volume is 81.71, falls within three standard deviations of the recent human mean, as do all of the *Homo erectus* specimens except KNM-ER 3883 and KNM-WT 15000.

The very low values for cerebellar volume, and low CQ in the Late Archaic Human sample are somewhat surprising, given that they have the largest brain mass of any anthropoid. Several proposed hypotheses are presented may explain follow:

Hypotheses related to Measurement Error

Hypothesis 1: Late Archaic Humans have cerebella that are systematically larger than values derived from the Least Squares Regression prediction equation.

Perhaps population heterochronic factors (timing differences in maturation of the cerebellum or cerebral hemispheres) compared to other hominids result in a different relationship of PCF to cerebellar volume in Late Archaic Humans. Given the consistency of PCF to Cerebellar volume in the MRI sample across a wide range of anthropoid taxa, however, this seems unlikely. One way to explore this hypothesis, however, would be to recalculate the Late Archaic Cerebellar volumes, using a reasonable, but higher value to predict CBLM from PCF for these individuals. The mean ratio of CBLM to PCF volume in anthropoids is 1:1.26, +/1 0.028. As a reasonable outside estimate, the mean + one standard deviation value (1.26 + 0.028 = 1.288) can be used to replace the 1.22 value of b derived from the LSR prediction equation, giving the results summarized in the Table 12-1 below.

Table 12-1: PCF Volume/CBLM Variability in Late Archaic Humans

Specimen	**VPCF (from scanned Model)**	**Predicted CBLM from LSR 0.68*(3.24 + 1.22VPCF)**	**Recalculated CBLM 0.68 *(3.24 + 1.288VPCF)**
Gibraltar/Forbes Quarry	96.54	81.71	86.76
La Chapelle I	140.46	119.01	125.22
La Ferrassie I	139.63	118.92	124.5

Even if the proportion of the cerebellum contained within the measured PCF is a full standard deviation away from the anthropoid mean for CBLM/VPCF, the Late Archaic Humans still fall below of the Recent Human mean. The recalculation places both La Chapelle I and La Ferrassie I (but not Gibraltar/Forbes Quarry) securely within one standard deviation of the Recent Human mean for absolute cerebellar volume.

Hypothesis 2: The scanned volumes for the endocast PCF could be inaccurate.

However, as the same methodology employed for all of the scanned endocasts, the relationship of PCF volume to endocranial volume would be equally underestimated for all the hominids. In this case, the early hominid values would be low as well – and they are not.

Hypotheses related to Environmental Deficits

Hypothesis 3: Nutritional deficits could have lead to underdevelopment of the cerebellum in Late Archaic Humans.

The cerebellum is functionally highly plastic in infancy and childhood. The cerebellar deep nuclei, including the dentate nucleus, develop in the early embryonic period. However, many cerebellar cells, including the microneurons, which are the short-axoned basket, stellate, and granular cells, are generated postnatally, at least in the rat. One hypothesis about the function of microneurons is that they provide the macroneurons of the input and output elements (such as the dentate nucleus) with “endless ‘associative’ connections” (Altman and Bayer 1997, p. 751). In other words, the microneurons are the associative and storage elements of the cerebellum. Generation of microneurons is correlated with early development of complex motor patterns in the rat, and presumably in humans as well.

Nutritional stress in early ontogeny in Late Archaic and Early Modern Humans could have contributed to reduced cerebellar volume. In modern humans, nutritional stress may lead to developmental delays in cerebellar development leading to smaller cerebellar volumes (Klekamp et al. 1989; Riedel et al. 1989). It is possible that nutritional deficits are related to relatively smaller cerebella in Late Archaic Humans, but additional data are required to explore this hypothesis. What specific behaviors are correlated with cerebellar development in humans? What is the range of variation for timing of cerebellar development in humans? What degree of nutritional stress affects cerebellar development, and to what degree?

Hypothesis 4: Cultural impoverishment could have led to less stimulation and reduced cerebellar development.

Perhaps Late Archaic Human children were not exposed to opportunities to develop complex motor and cognitive skills, especially in infancy and early childhood, when, presumably, the cerebellar microneurons are at their height of plasticity. However, their environments must have been at least as complex as those of *H. erectus* and Middle Pleistocene Humans. In addition, infants of all species engage in complex ways with their environments.

Hypotheses related to differences in cognitive functioning

Hypothesis 5: Cognitive evolution related to the distribution of cognitive functions and/or differences in neural organization.

Late Archaic humans lived in a culturally rich environment, full of objects and sets of objects, which they manipulated with great skill. Their large brains are testament to their neocortical capacity for storage of neural impressions, based on an extensive and complex neural network. There is no reason to think they did not have an extensive spoken vocabulary to describe the objects around them. However, the efficiency of a neural network decreases as the size of the size of the network increases. It is possible that individuals who were more efficient at integration and serial timing of cognitive categories had an improved ability to manipulate concepts hierarchically and recursively. That is, the cerebellum may have been invoked for algorithmic manipulation of larger and more groups of objects. The increased role of the cerebellum may have permitted a reduction in neocortical volume and cognitive operations were consolidated. As neural efficiency improved, an equal or even greater number of cognitive operations could have been performed without an increase in overall brain mass.

Late Archaic Humans have the largest brains of all hominids. Perhaps their neocortical size represents a critical mass in terms of network computational capabilities. Increasing cultural and behavioral complexity would have provided a selective advantage to individuals whose brains were more computationally efficient (Kien, 1992). In later humans, the cerebellum's circuitry may have been exapted from control of serial timing of motor functions to serial timing of larger computational units (e.g., longer and more complex motor functions; "thoughts," more complex linguistic productions).

Early Modern Homo sapiens

The single individual, Cro-Magnon I, represents the Early Modern *Homo sapiens* group. With an EQ of 20.11 in the context of the present sample, Cro-Magnon I has undergone an allometric Net Brain expansion with respect to Body Mass. This is consistent with EQ values reported for larger samples of Early Modern humans (e.g., Ruff et al. 1997). However, this individual, whose CQ is 0.09, is barely (and not significantly) above the sample mean CQ of 0.08 for Late Archaic humans. Cerebellar volume for this individual (118.92 cc) is similar to that of La Ferrassie I and La Chapelle I, and is approximately one standard deviation below the Recent Human mean.

Although there was no increase in absolute cerebellar volume in this individual, the cerebellum is proportionately larger compared to the NetBrain. Two (not mutually exclusive) hypotheses can be invoked to explain the rising CQ in Upper Paleolithic hominids: (1) Differences in fine manual dexterity. Functional hand anatomy of Early Modern humans suggests they had developed neurological as well as skeletal adaptations for precise manual control (Niewoehner 2001). It is possible that more precise neurological control of fine motor behaviors enabled early hominids to expand their cultural repertories over time. On the other hand, the direction of causality may have gone the other way. A shift in cognitive strategies enabling Early Modern humans to conceptualize objects at a finer scale may have preceded the manipulative behaviors required to produce such objects.

(2) A shift in cognitive strategies. Cro-Magnon I was found in association with an Evolved Aurignacian Early Upper Paleolithic archeological assemblage, including flint tools, pierced animal teeth, and many shells (some of them pierced) (Day 1986; Klein 1973).

Late Archaic humans apparently had sufficiently developed procedural memory, concrete-operational skills and kinesthetic intelligence required to produce Upper Paleolithic artifacts as well (Leroi-Gourhan 1958; Léveque and Vandermeersch 1980). However, Late Archaic humans did not produce surviving parietal or representational art, as did Early Modern Humans (Bahn 1998; Bednarik 1992). The NetBrain expansion seen in Cro-Magnon I could account for this behavioral difference. No matter what his aesthetic achievements were (and our best archeological evidence is for his “artistic” as opposed to his “mathematical” or “linguistic” intelligences), it is possible that his cognitive strategies were more similar to those or Late Archaic Humans than they were to later humans.

Late Upper Paleolithic material culture can be distinguished from Early Upper Paleolithic material culture by its variety, its generativity, its innovation, and its complexity (Donald 1991; Straus 1985; 1988; Straus, Bischoff and Carbonell 1993; Straus 1995; Wynn 1996). The present evidence suggests that, as skilled as they may have been in many ways, Early Upper Paleolithic humans were not yet fully modern in their cognitive behavior, or its neurological underpinnings. Pending investigation of larger samples, this remains an untested, if intriguing hypothesis.

Recent Homo sapiens

Cerebellar volume increases much more rapidly than brain mass between Late Archaic, Early Modern and Recent Modern humans. A drop in body mass and a less marked drop in brain mass accompany this rise in cerebellar volume. Although Late Archaic, Early Modern, and Recent Modern humans are not significantly different in terms of mean absolute cerebellum volume or CQ, the data suggest that there was a gradual shift towards larger cerebella in modern humans.

This non-allometric change in relative cerebellar size may be explained by a need for more precise motor control in the manipulation of objects. However, earlier hominids had achieved a degree of fine motor control, “savoir-faire” (Pelegrin 1991) and technological expertise that would enabled them to make characteristic Upper Paleolithic artifacts (Léveque and Vandermeersch 1980; Hublin, Spoor, Braun, Zonneveld and Condemi 1996; Wynn 1996).

A second, and more likely, explanation is that there was a shift in cognitive strategies. Earlier hominids, who had large, lateralized brains, advanced concrete operational intelligence, and complex material culture, would have already developed syntactical language, supported by both cerebellar/procedural and neocortical/declarative neural functions. However, they may not have fully developed the formal operational intelligence that characterizes many contemporary human societies.

Range of Variation in Under-represented Taxa

When sample sizes are small, as are the australopithecine, *H. habilis*, Middle Pleistocene, and Early Modern groups, the coefficient of variation (CV = SD/mean) for relative and absolute cerebellar volume can be estimated by analogy with other groups. Table A-12 summarizes the CV for non-human primate and hominids, including and for recent humans.

Summary

Differences in cerebellar proportions in Pliocene and Pleistocene hominids are correlated with behavioral changes. As cultural complexity increased, different cognitive strategies were developed to deal with it. Australopithecines had only slightly higher relative brain volume and relative cerebellar volume, but both the cerebellum and the neocortex may have undergone some reorganization related to parietal lobe functions. A gradual rise in relative cerebellar volume in early *H. habilis* and *H. erectus* is followed by a puzzling drop in CQ in Early and Late Archaic *H. sapiens*, although they have the largest relative brain size of any hominids. Recent humans have smaller brains, but very large cerebella relative to both body mass and brain mass. It is likely that the cerebellum in Recent Humans has developed efficient procedural algorithms to execute cognitive functions that were previously performed by the neocortex.

13 SUMMARY AND CONCLUSIONS

“Most skilled acts, from running a maze to playing a musical phrase or speaking a sentence, involve a timed series of actions which cannot be accounted for as a simple chain of conditioned reflexes. . .The serial timing of actions is among the most important and least studied of behavioral problems.” (Lashley 1950), p. 474

The cerebellum is involved in proprioception, balance, attentional mechanisms, sensory-motor integration, and serial timing of motor and probably cognitive behavior. It evolved in concert with neocortical changes in Pliocene and Pleistocene hominids as their motor (and cognitive) repertories became more elaborate. The cerebellum, like the neocortex, emerged mosaically through complex and changing response to a wide variety of selective pressures operating at different times as cultural complexity increased (Holloway 1964; 1966; 1967; 1969).

Hominid cerebellar and cognitive evolution can be described by a three-stage model, comprising six-phases related to changes in cognitive strategies. The cerebellum and neocortex, which perform complementary cognitive operations, evolved reciprocally, but at different rates. As the neocortex expanded and reorganized, the cerebellum was recruited to support new cognitive functions. As the cerebellum expanded its functions to control conceptual as well as motor representations, cognitive efficiency increased.

Stage 1: Neocortical and Cerebellar Expansion and Reorganization

The australopithecines in the present sample do not represent the earliest known hominid species. However, the switch to habitual bipedalism undoubtedly affected cerebellar organization. EQ rose somewhat in the australopithecines, then rose more steeply in *H. habilis*, tapering off in *H. erectus.* A gradual shift in technological complexity occurred as well. Consistent, culturally transmitted tool forms emerged, requiring procedural learning mediated by the cerebellum.

Phase I: Divergence of Pan and earliest hominids from common ancestor.

The data suggest that little significant encephalization occurred; but NetBrain volume expanded slightly with respect to cerebellar volume. However, bipedalism may make fewer demands cerebellum than the more complex, versatile ancestral locomotor repertory typical of other hominoids (Matano and Hirasaki 1996; 1997; Rilling and Insel 1998). Although the cerebellum did not become larger, the lateral lobes may have expanded at the expense of the vermis (Matano et al. 1985a; MacLeod et al. 2000). Cerebellar reorganization supported neocortical reorganization (Increased hemispheric differentiation; relative expansion of posterior parietal region; expansion of the third inferior frontal convolution). Cerebellar function may have shifted to coordinate visuo-spatial functions related gestural communication or incipient tool manufacture in some species. *Directly associated* archeological evidence is lacking for australopithecine tool use (except in the singular instance of *A. gahri* (Asfaw et al. 1999)).

Phase II: Marked encephalization in **H. habilis** *involving a non-allometric expansion of both the NetBrain and the cerebellum*

The observed increase in relative cerebellar volume in these early members of the genus *Homo* would have supported a number of sensory-motor and cognitive functions, including bimanual coordination and serial timing of complex bimanual movements involved in stone-tool manufacture and/or gestural communication.

Cerebellar evolution was accompanied by neocortical reorganization. The parietal lobes had expanded (Begun and Walker 1993; Geshwind 1965; Holloway 1972b; 1981c; Tobias 1975; 1987) and sulcal patterns had become more "*"Homo*-like" on the orbital surface of the frontal lobe in some individuals (Falk 1983). Cerebral lateralization and right-hand dominance became common (Begun and Walker 1993; Holloway and De La Coste-Lareymondie 198; Toth 1985). "Broca's area" also underwent development in this group (Tobias 1987) (Begun and Walker 1993; Falk 1983; Holloway 1983b; Tobias 1987).

Cerebellar evolution supported well-developed procedural learning routines and ballistic skills emerged to effectively strike flakes from cores (Calvin and Bickerton 2000; Wynn 1981). "Technological intelligence" or "preoperational intelligence" became more refined (Mithen 1996b; Wynn 1981, after Piaget 1952). The capacity for representational complexity began to exceed that of laboratory-trained chimpanzees (Mignault 1985; Langer 1993; Toth et al. 1993).

Brain structures adapted for serial control of ballistic movements and motor praxis would have been available to support complex gestural or oro-facial motor routines in service of communication (Bickerton 1995; Calvin and

Bickerton 2000; Corballis 1991; Donald 1991; Holloway 1969;Kien 1992; Steklis and Harnad 1976).

Phase III: relative cerebellar expansion continues in **H. erectus***, possibly at the expense of NetBrain expansion.*

The repertory of procedural knowledge increased as culturally-defined forms were imposed on bifaces (Wynn 1985; 1991; 1996a; b).

Recursive conceptual structures emerged to relate multiple dimensions of symmetry and to re-evaluate and match emerging shape of blank with internal template (Robson Brown 1993). Hominids developed their capacity for sustained, voluntary directed attention (which would have been mediated by the cerebellum via its connections with the parietal and frontal lobes) (LaBar et al. 1999). Conceptual as well as motor representations became subject to voluntary recall (Donald 1991).

Microwear on bifaces suggests that stone tools were used to make other tools, as complex fine motor routines became embedded in a recursive conceptual structure (Mithen 1996b). Object sets became even more complex as additional raw materials (wood, hides) were added to the material culture (Thieme 1997; Oakley et al. 1977).

It is likely that a more complex gestural (and probably vocal) communication system emerged, employing a larger number of semi-arbitrary and arbitrary signs for cultural objects and related activities (Calvin 1983; Calvin and Bickerton 2000; Deacon 1997; Holloway 1975b).

Stage 2 Neocortical and Cerebellar Expansion

In this stage both the neocortex and cerebellum expanded, but there was little increase in relative cerebellar volume. The visuo-spatial skills and procedural learning and memory capacities developed in earlier hominids sufficed to produce Middle Paleolithic artifacts (Wynn 1985; 1991; 1996a) .

The neocortex expanded dramatically, however, providing an expanded capacity for declarative cognitive processes. Humans were capable of more numerous and more complex representations of objects and concepts.

Phase IV: Rapid Expansion of NetBrain relative to cerebellum

Non-allometric expansion of NetBrain with respect to body mass is seen in Middle Pleistocene and Late archaic *H. sapiens*, but the cerebellum expanded little if at all. Cultural innovations, including prepared-core technology and use of soft-hammer percussion (Boëda 1988; Chase 1990) reflected conceptual complexity. Gowlett (1996, p. 210) has described this period as one of "declarative multiplicity."

In this phase, the neocortical association areas, as well as subcortical areas involved in long and short term memory, expanded to accommodate an ever-increasing number of cultural objects and the actions related to their manufacture, use, and distribution. Many complex sets of objects and concepts had to be kept in mind and manipulated. Neocortical and subcortical structure expanded to accommodate the amount and complexity of information to be learned and assimilated. As neural networks expanded, their efficiency was reduced. A successful neuro-cognitive strategy based on sheer size reached its limits (Kien 1992).

Stage 3: Marked Cerebellar Expansion

In the third stage of cerebellar evolution, the sheer number of connections in the neocortex reduced computational efficiency (Kien 1992). In addition, cultural knowledge exceeded the capacity of the declarative memory system of the neocortex. The cerebellum was recruited for hierarchical organization of the multiplicity of representations stored in the neocortex. The cerebellum enhanced the individual's capacity for formal operational intelligence and management of information available in distributed cognitive systems.

Phase V: The Division of Labor between Neocortex and Cerebellum Shifts to Increase Computational Efficiency

In the fifth phase of cerebellar evolution, body mass decreased, accompanied by a less steep decrease in brain mass. However, the cerebellum did not become smaller, either in absolute or in relative terms. The brain of Cro-Magnon I (presumably like the brains of his contemporary early modern humans) was somewhat smaller than mean brain size of Late Archaic humans, but his cerebellum was the same size as theirs. His NetBrain, was relatively smaller with respect to his body size than his cerebellum.

Although early modern humans were producing highly skilled representational depictions of the world around them, the lithic repertory of Early Modern humans is not characterized by the variety, innovation, or stylistic volatility of later people (Donald 1991; Straus 1988; Straus, Bischoff and Carbonell 1993; Straus 1995; Wynn 1996).

Phase VI: The cerebellum assumes a greater role in cognition, as information previously processed by the neocortex is subsumed into more complex conceptual hierarchies

The trend towards somewhat smaller brains and larger cerebella became very marked in Recent *Homo sapiens.* Fine manual dexterity is highly valued and may have provided measurable fitness advantage for Early Modern and Recent Humans.

Late Upper Paleolithic humans produced more complex cultural artifacts, requiring a greater number of embedded steps for their manufacture. An increased descriptive lexicon and array of procedural routines would have given the advantage to individuals who were efficient information managers. Involvement of the cerebellum in cognitive operations may have increased in response to the increased complexity of object sets and their conceptual representations. As the cerebellum subsumed certain declarative mental functions into a procedural framework, a relatively smaller NetBrain was able to operate with increased efficiency.

Cerebellar involvement facilitated functions involving precisely timed, algorithmic sequencing for composing, decomposing, and recomposing representational elements into representations according to syntactical constraints (Corballis 1991) Cerebellar involvement enabled humans to manage the complexity (Holloway 1969) and “declarative multiplicity” (Gowlett 1996) of their own distributed cognitive creations.

Significance of the Research

Data from the study described above extends our understanding of cerebellar function and cognitive evolution in hominids. It adds six new large-bodied, large-brained groups to the anthropoid database for relative cerebellar volume. The regression line of cerebellar volume on NetBrain volume is lowered, as the influence of the large-bodied, hominoids *Gorilla* and *Pongo* is mitigated.

The model described above has broad explanatory power. It offers a parsimonious explanation for the following aspects of human cognitive evolution:

- distributed, hierarchical, emergent, representative, computational, nature of cognition and the neuroanatomical substrate from which it emerged;
- the temporal pattern of complexity of the archaeological record;
- neural reorganization in Pliocene and Pleistocene hominids over time;
- encephalization in Pliocene and Pleistocene hominids over time;
- the emergence of complex social, linguistic, technological, spatial, biological, mathematical, and musical “intelligences” in Pleistocene hominids.

APPENDIX

Table A-1: Documentation of cerebellar connections with Holloway's "major cortical regions in early hominid evolution"

Brodman's Area	Documentation of cerebellar role, cortical connections
Parietal: areas 5, 7, 39, 40	(Osherson et al. 1998) Imaging study with normal individuals; cerebellum and mesial frontal cortex implicated in both probabalistic and deductive reasoning; but probabalistic reasoning also activates left dorso-lateral cortex; whereas deductive reasoning involves associative parietal and occipital regions, primarily of the right hemisphere (Middleton and Strick 2000) Review of studies indicating that neurons within the basal ganglia and cerebellar circuits resemble the neurons within the cortical areas subserved by these circuits. Thus, neuronal activity within cerebellar loops connected to motor cortex is correlated with movement; whereas neuronal activity within loops connected to areas of prefrontal cortex are correlated with cognitive function (Kakei et al. 1995) Evoked field potential analysis and histological analysis of parietal cortex in cats shows both afferent and efferent connections of areas 5 and 7 with motor cortex and cerebellum cerebellar as well as parietal regions are part of a network of brain areas that mediate the short-term storage and retrieval of phonologically coded verbal material (Schumacher et al.) PET study of normal individuals; concluded verbal working memory is modality independent and is mediated by a circuit involving frontal, parietal, and cerebellar mechanisms (Bioulac, Burbaud and Varoquequx 1995) comparison of arm movements in monkeys after dentate nucleus lesioning and ablation of areas 4 and 5 suggest that the neocerebellum enhances excitability of area 5 movement-related neurons
Temporal: areas 22, 37	(Grasby, Frith, Friston, Bench, Frackowiak and Dolan 1993) PET imaging on normal volunteers during auditory-verbal memory tasks shows increases in regional cerebral blood flow in thalamus, left anterior cingulate, right parahippocampal gyrus, superior temporal gyrus and cerebellum, suggesting a distributed system for aspects of verbal processing and storage
Frontal: areas 44, 45, 46 "Broca's area"; also areas 8, 9, 10	(Desmond et al. 1998)brain imaging study of normal individuals concluding that complementary roles of the left middle frontal gyrus and left caudate nucleus; right cerebellar hemisphere in word selection and search (Abe et al. 1997) MRI study of patients with chronic Broca's aphasia; concluded cerebellum contributes to language through connections with inferior frontal gyrus (Middleton and Strick 2000) review of studies indicating that neurons within the basal ganglia and cerebellar circuits resemble the neurons within the cortical areas subserved by these circuits. Thus, neuronal activity within cerebellar loops connected to motor cortex is correlated with movement; whereas neuronal activity within loops connected to areas of prefrontal cortex are correlated with cognitive function (Schmahmann and Pandya 1995) corticopontine projections project to the cerebellum in rhesus monkeys from a number of cortical association areas, including areas 8A, 46 dorsal, 9 and 10 as well as medial and ventro lateral cortices, reinforcing the hypothesis that the cerebellum participates in the organization of cognitive functions (Strick and Middleton 1994) viral tracers used to document cerebellar connection with area 46 of the primate neocortex, which is involved in spatial working memory (Middleton and Strick 1997) summarizes research in which (1) viral tracers in monkey brains show that cerebellar dentate nucleus projects to premotor, oculomotor, and prefrontal cortices as well as primary motor cortex, including area 8 (frontal eye field), areas 46 and 9 (which participate in aspects of 'working memory' and guidance of behavior based on transiently stored information rather than external cues); (2) fMRI studies of normal humans confirm dentate activity in cognitive tasks
	(Osherson et al. 1998) imaging study with normal individuals; cerebellum and mesial frontal cortex but probabalistic reasoning also activates left dorso-lateral cortex; whereas deductive reasoning involves associative parietal and occipital regions, primarily of the right hemisphere

Table A-2: Recent Studies of Cerebellar Function

Reference	Synopsis
(Abe et al. 1997)	MRI study of patients with chronic Broca's aphasia; concluded cerebellum contributes to language through connections with inferior frontal gyrus
(Ackerman 1997)	neurological testing of individuals with cerebellar damage; concluded cerebellum acts as an internal clock, responsible for temporal computations in motor and perceptual functions involved in speech perception
(Ackermann et al. 1998)	fMRI imaging study of normal individuals indicating cerebellar activation is related to the articulatory level of speech production rather than to cognition
(Ackermann, Graber, Hertrich and Daum 1999)	dysfunction study concluding that cerebellum processes temporal cues related to phonemic identification
(Akshoomoff et al. 1997)	neurobehavioral, neurophysiological, and neuroimaging data to supports hypothesis that cerebellum plays a role in attentional functions. Cerebellum modeled as a master computational system that anticipates and adjusts responsiveness in a variety of brain systems (e.g., sensory, attention, memory, language, affect) to efficiently achieve goals determined by cerebral and other subcortical systems
(Andreasen et al. 1993b)	imaging study of normal volunteers found that IQ is significantly correlated with intracranial, cerebral, temporal lobe, hippocampal, and cerebellar volume
(Arriada-Mendicoa et al. 1999)	review article concluding that the cerebellum plays a central role in coordinating and regulating thought as well as movement
(Barinaga 1996)	commentary on Fox (p. 545 of same issue of Science); outlines controversy related to cerebellar contributions to cognition; points out that a definitive theory about cerebellar function is still being constructed, as adequate data are lacking
(Bioulac et al. 1995)	comparison of arm movements in monkeys after dentate nucleus lesioning and ablation of areas 4 and 5 suggest that the neocerebellum enhances excitability of area 5 movement-related neurons
(Bracke-Tolkmitt, Linden, Canavan, Rockstroh, Scholz, Wessel and Diener 1989)	neurological testing of 5 patients with cerebellar lesions compared to 10 normal controls suggests cerebellum contributes to a particular type of mental skill, but reserve judgement about cerebellar contribution to frontal lobe functions
(Braitenberg et al. 1997)	new cerebellar functional model based on cerebellar histology wherein well-timed inhibitory volleys "sculpt" motor sequences
(Creutzfeldt 1979)	proposed hypothetical basis of consciousness: symbolic self representation results from the synthesis of distributed cortical representations of the world as it is fed back to neocortical areas via the midbrain-cerebellum and basal ganglia. In brains with linguistic competence, the self-reflective loop is symbolically encoded, permitting self consciousness
(Daum et al. 1993)	neurological testing of patients with cerebellar pathology, patients with both cerebellar and brainstem pathology, and normal controls suggest that cerebellar damage did not effect skill acquisition; authors question role of cerebellum in procedural learning
(Daum and Ackermann 1997)	review article discussing role of cerebellum in non-declarative memory
(Decety et al. 1990)	measurements of regional cerebral blood flow during imagined tennis movements and silent counting tasks suggests cerebellar involvement in mental function; authors propose cerebellum plays a role in temporal organization of neuronal events related to cognition
(Desmond et al. 1998)	brain imaging study of normal individuals concluding that complementary roles of the left middle frontal gyrus and left caudate nucleus; right cerebellar hemisphere in word selection and search
(Doyon et al. 1997)	performance test of patients with lesions resulting from idiopathic Parkinson's disease and normal controls indicate that acquisition of new visuomotor skills depends upon integrity of striatum and cerebellum, but not of the frontal lobes
(Ebner and Qinggong 1997)	measurement of spikes generated by activation of Purkinje cell neurons suggests that Purkinje cells remap sensory space onto motor space to enable visuo- motor coordination during hand movement
(Fox et al. 1985)	positron emission tomography is a viable tool for investigation of cerebellar function and anatomical correlates
(Fulbright et al. 1999)	imaging study of normal individuals concluding that cerebellum differentially activates in response to phonologic and semantic tasks, contributes to the cognitive processes integral to reading

Table A-2 Continued

Reference	Synopsis
(Gao et al. 1996)	MRI imaging of dentate nucleus output confirms cerebellar activation during passive and active sensory tasks; the authors propose that demands on the lateral cerebellum to process sensory data cause it to be involved in motor, perceptual and cognitive performance
(Grafman, Litvan, Massaquoi, Stewart, Sirigu and Hallett 1992)	cognitive testing of 12 patients with cerebellar atrophy and 12 normal controls suggests a functional link between the cerebellum, basal ganglia, and frontal lobe during cognitive planning tasks
(Grasby et al. 1993)	PET imaging on normal volunteers during auditory-verbal memory tasks shows increases in regional cerebral blood flow in thalamus, left anterior cingulate, right parahippocampal gyrus, superior temporal gyrus and cerebellum, suggesting a distributed system for aspects of verbal processing and storage
(Haggard, Jenenr and Wing 1994)	study of a patient with unilateral cerebellar damage suggests hat proprioceptive representations provided by the normal cerebellum contribute in an important way to coordination of multi-joint movements
(Iidaka 2000)	PET study of encoding and retrieval of episodic memory showed preferential activation of left association temporal and posterior cingulate areas in encoding tasks and preferentially right-sided activation of the association parietal cortex, cerebellum, and posterior cingulate in retrieval tasks.
(Ito 1990)	model of cerebellar function in which cerebellum acts as an adaptive controller and contributes to adaptive learning capacity in voluntary motor control and probably some cortical activities
(Ito 1993)	commentary on Leiner, Leiner and Dow, 1993; advances computational model for cerebellar contribution to "dynamics learning," where cerebellum's consistent circuitry would control both movement and thought with the same neural mechanisms. Proposes that cerebellum is a multi-purpose learning tool which assists in motor, autonomic, verbal, and non-verbal behaviors
(Levitt et al. 1999)	MRI volumetric study found hypertrophy of vermis, left cerebellar hemisphere in schizophrenic patients correlated with severity of positive symptoms and thought disorder and with impairment in verbal logical memory
[Jenkins, 1993 #238]	PET investigation of cerebellar function has been hampered by technical limitations of PET cameras; recent advances will enable more studies of this important brain region, which is implicated in cognition & motor activities
(Jenkins and Frackowiak 1997)	imaging study of normal individuals indicated participation of cerebellum in parkinsonian tremor, motor learning, and cognition
(Kakei et al. 1995)	evoked field potential analysis and histological analysis of parietal cortex in cats shows both afferent and efferent connections of areas 5 and 7 with motor cortex and cerebellum
(Kawashima et al. 1998)	PET study of eight normal, dextral males in unimanual two-ball rotation task showed bilateral activation of primary motor area, premotor area and cerebellum; but activation of supplementary motor area only in contralateral hand movements, suggesting that complex hand movements are organized bilaterally in complex hand movements.
(Kim, Ugurbil and Strick 1994)	MRI study of normal humans, who showed greater bilateral activation of dentate nucleus during cognitive task than during a task involving simple movement
(Klatzky et al. 1987)	performance test suggested that on-line motor responses result from the interplay of both perceptual and more cognitive sources of information, blurring the distinction between "cognitive" and "motor" behaviors
(Leiner, Leiner and Dow 1986)	authors advance an hypothesis about how signals from the neodentate may function to manipulate ideas in a manner analogous to the way the older dentate areas coordinate movement
(Leiner, Leiner and Dow 1989)	behavioral evidence suggests that the cerebellar connections to the frontal motor areas as well as adjacent association areas and Broca's area can enable the cerebellum to improve skills related to specific motor and cognitive functions
(Leiner, Leiner and Dow 1993)	brief review of neuroanatomical, neuroimaging and behavioral reports of cerebellar involvement in language functions; functional expansion of neocerebellum related to evolutionary changes during hominid evolution related to development of language
(Lotze et al. 1999)	fMRI study of ten normal, dextral subjects showed activation of ipsilateral cerebellum in imagined as well as executed hand movements, but foci of peack activation were different. Results support hypothesis that motor imagery and motor performance rely upon similar neural networks.

Table A-2 Continued

Reference	Synopsis
(Middleton and Strick 1997)	summarizes research in which (1) viral tracers in monkey brains show that cerebellar dentate nucleus projects to premotor, oculomotor, and prefrontal cortices as well as primary motor cortex, including area 8 (frontal eye field), areas 46 and 9 (which participate in aspects of 'working memory' and guidance of behavior based on transiently stored information rather than external cues); (2) fMRI studies of normal humans confirm dentate activity in cognitive tasks
(Middleton and Strick 2000)	review of studies indicating that neurons within the basal ganglia and cerebellar circuits resemble the neurons within the cortical areas subserved by these circuits. Thus, neuronal activity within cerebellar loops connected to motor cortex is correlated with movement; whereas neuronal activity within loops connected to areas of prefrontal cortex are correlated with cognitive function
(Mushiake and Strick 1993)	monitoring of dentate nucleus in monkeys indicates cerebellum is involved in control of higher order aspects of skeletomotor behavior
(Osherson et al. 1998)	imaging study with normal individuals; cerebellum and mesial frontal cortex but probabilistic reasoning also activates left dorso-lateral cortex; whereas deductive reasoning involves associative parietal and occipital regions, primarily of the right hemisphere
(Paradiso et al 1997)	MRI study, cognitive testing of normal individuals found that cerebellar volume is significantly correlated on of cerebellar volume with verbal memory and fine motor dexterity, and non-significantly correlated with general IQ
(Parkins 1997)	review article suggesting that the cerebral cortex and cerebellum function as two fundamentally different types of representation and information processing systems which reciprocally evaluate and correct each other, forming the basis for a self-correcting adaptive control system
(Petrosini 1996)	procedural spatial event processing impaired in rats subjected to surgical hemicerebellectomy
(Price et al. 1999)	study of normal, bilingual individuals confirming cerebellar involvement in cognitive control of language processes
(Riva and Giorgi 2000)	cerebellar pathology in children; confirms role of right cerebellar hemisphere in auditory sequential memory and language processing, left cerebellar hemisphere in spatial and visual sequential memory; cerebellum is a modulator of mental and social functions
(Salmon and Butters 1995)	cerebellum and basal ganglia contribute to motor skill learning, possibly through indexing or temporal ordering of events (cerebellum) and sequencing of component acts of a motor program (basal ganglia)
(Schlosser et al. 1998)	fMRI study of verbal fluency task in 6 males, 6 females revealed activation of left prefrontal, right cerebellar regions. Slight differences in parietal and orbitofrontal activation were correlated with sex
(Schmahmann and Sherman 1998)	neurological & imaging examination of individuals with lesions of the posterior lobe of the cerebellum and vermis showed: impairment of executive functions such as planning, set-shifting, verbal fluency, abstract reasoning and working memory; difficulties with spatial cognition including visual-spatial organization and memory; personality change with blunting of affect or disinhibited and inappropriate behavior; and language deficits, including agrammatism and dysprosodia. Lesions of the anterior lobe of the cerebellum impaired executive and visual-spatial functions. Conclusions: the cerebellum modulates neural circuits involving prefrontal, posterior parietal, superior temporal and limbic cortices
(Schmahmann and Pandya 1995)	corticopontine projections project to the cerebellum in rhesus monkeys from a number of cortical association areas, including areas 8A, 46 dorsal, 9 and 10 as well as medial and ventro lateral cortices, reinforcing the hypothesis that the cerebellum participates in the organization of cognitive functions
(Schumacher et al.)	PET study of normal individuals; concluded verbal working memory is modality independent and is mediated by a circuit involving frontal, parietal, and cerebellar mechanisms

Table A-2 Continued

Reference	Synopsis
(Seitz, Canavan, Yaguez, Herzog, Tellmann, Knorr, Huang and Homberg 1994)	Imaging study of normal individuals, suggesting that learning of new movement trajectories involves the cerebellum, while overlearned trajectorial movements engage the premotor cortex
(Silveri et al. 1994)	study of a patient who developed right hemicerebellar syndrome and agrammatic speech, without other cognitive impairment, supporting hypotheses that the cerebellum regulates temporal interplay among neural structures during sentence production
(Silveri et al. 1998)	lesion study concluding that the cerebellum takes part in the planning of speech production at a level that does not require an overt articulation
(Snyder et al. 1995)	cerebellar left-right asymmetries are correlated with cerebral hemisphere asymmetries as well as handedness
(Strick and Middleton 1994)	viral tracers used to document cerebellar connection with area 46 of the primate neocortex, which is involved in spatial working memory
(Iidaka et al. 2000)	fMRI study of encoding and word retrieval task with seven normal subjects documented activation of right cerebellum and left prefrontal dorsal and ventral cortices with word encoding; and right cerebellum with left dorsal prefrontal cortex in pattern encoding and retrieval. The authors suggest that this pattern of activation reveals a common neural network for encoding regardless of the type of material..
(Thach, Goodkin and Keating 1992)	the stereotyped and stylized circuitry of the cerebellum suggests a model of cerebellar function in which the body is mapped separately within each of the three deep cerebellar nuclei, with each nucleus controlling a different mode of bodily movement, based on the input and output connections of the nucleus. The authors suggest that the cerebellum coordinates the elements of movement; adjusts old movement strategies; and learns new movement strategies
(Tracy, Faro, Mohamed , Pinsk and Pinus 2000)	fMRI study of normal individuals; confirms role of cerebellum as a repository of codes for time processing, but also implicates temporal lobe structures in time-keeping functions
(van Dongen, Catsman-Berrevoets and van Mourik 1994)	a study of 15 children who had undergone removal of a cerebellar tumor suggests that brainstem dysfunction rather than cerebellar function alone, was a factor in cerebellar mutism and dysarthria
Fox and Parsons, 1999	PET study : cerebellum is involved in interpreting rhythm, melody, in PET study of eight conductors of a Bach chorale. Also see study by Gottfried Schlaug of Beth Israel Deaconess Medical Center in Boston which found that the cerebella of male musicians were 5% larger than those of non-musicians. Also mentions 12 November article in Nature, showing that verbal memory is enhanced in musicians, and referring to studies showing that the planum temporale is enlarged in musicians.

Table A-3: Frontal Lobe Evolution in Hominids

Author	Morphology	Fossil
(Tobias 1987)	transversely expanded, anteriorly squarish frontal lobe; with well-marked sulci. Overall resemblance to KNM-ER 1470, H. erectus (citing (Holloway 1978), motor speech area Homo-like (citing (Falk 1983), (Tobias 1975); right frontal petalia	OH 16
(Tobias 1987)	transversely expanded, anteriorly squarish frontal lobe; with well-marked sulci. Overall resemblance to KNM-ER 1470, H. erectus (citing (Holloway 1978), right frontal petalia suggested (although some reconstruction in this area)	OH 24
Tobias, 1975	strong development of inferior frontal convolution (but see Begun & Walker, who have noted that this areas is not preserved in OH 24, and that 1470 is also distorted	OH 24 KNM-ER 1470
(Begun and Walker 1993)	intermediate frontal lobe morphology, compared to KNM-WT 15000 and KNM-ER 1813 on the one hand (low, narrow frontal lobes) and KNM-ER 1470, KNM-ER-3733 and KNM-ER-3883 on the other hand (taller, broader); damage to frontal poles; no petalia visible	KNM-ER 1805
(Falk 1983)	pongid-like fronto-orbital sulcal pattern \ similar to that of apes and early South African australopithecines; no clear evidence of asymmetry of third inferior frontal convolution	KNM-1805
(Begun and Walker 1993)	frontal lobes very similar in shape to KNM-WT 15000 -- elongated, low, mediolaterally constricted with prominent poles well-marked fronto-petalia (though less marked than on KNM-WT 15000) damaged in region of third inferior frontal convolution	KNM-ER 1813
(Tobias1975, cited in Begun & Walker 1993)	well developed Broca's cap	KNM-ER 1470
(Falk 1983)	human-like frontal lobe & fronto-orbital sulcus, increased convolution of Broca's area	KNM-ER 1470
(Begun and Walker 1993)	smaller, but relatively short, broad and high compared with those of KNM-WT 15000 larger, inflated left Broca's area, left third inferior frontal convolution; but less protuberant than on KNM-WT 15000	KNM-ER 1470
(Tobias 1987)	motor speech area Homo-like (citing (Falk 1983), (Tobias 1975)	OH 7
(Holloway 1981b)	right frontal petalia - lateral (also left occipital; see below)	Sangiran 2 (Pith II/1937)
(Holloway 1981b)	petalia "uncertain"	Sangiran 17 (Pith VIII/1969)
Holloway, 1983	well developed Broca's cap	KNM-ER 1470 (Holloway has noted that chimpanzees may also have well developed Broca's caps)

Table A-3 continued		
Author	**Morphology**	**Fossil**
(Begun and Walker 1993)	frontal lobes relatively broad, and more rounded compared to KNM-WT 15000 viewed laterally, frontal lobes are relatively flat (like KNM-WT 15000) orbital surfaces flat to slightly concave clearly defined right fronto petalia, anteriorly projected but only slightly broader than the left (perhaps due to asymmetric development of the frontal sinuses) Broca's caps less well preserved than KNM-WT 15000, but more rounded, projecting laterally and inferiorly right inferior frontal convolution surrounded by deeper sulci (in contrast to left, where sulci appear to be "filled in"	KNM-ER 3883
(Begun and Walker 1993)	frontal lobes relatively broad, and more rounded compared to KNM-WT 15000 in lateral view, frontal lobes are more vertically oriented than in KNM-ER 3883 or KNM-WT 15000 less pronounced asymmetry between frontal lobes than in KNM-ER 3733 Broca's caps less well preserved than KNM-WT 15000, but more rounded, projecting laterally and inferiorly right inferior frontal convolution surrounded by deeper sulci (in contrast to left, where sulci appear to be "filled in"	KNM-ER 3733
(Begun and Walker 1993)	inferior frontal convolution significantly larger and more projecting, both ventrally and laterally on left than on right right inferior frontal convolution appears "deflated" and is surrounded by strongly marked sulci; whereas sulci on left appear more "filled in"	KNM-ER 15000
(Dubois 1897)	narrow frontal lobes, resembling modern human condition of trigocephaly, which occurs when the metopic suture closes prematurely fairly well developed inferior frontal convolution	Pithecanthropus
(Begun and Walker 1993)	no frontal petalia evident; sagittal keel continues anteriorly from parietal region, extends between frontal lobes, with broad, well-marked depressions to either side, immediately anterior to coronal suture; frontal keel ends anteriorly as a broad, antero-superiorly facing bulge	Zhoukoudian 2
(Begun and Walker 1993)	no frontal petalia evident; frontal keel ends anteriorly as a broad, antero-superiorly facing bulge	Zhoukoudian 3
(Begun and Walker 1993)	no frontal petalia evident; frontal keel ends anteriorly as a broad, antero-superiorly facing bulge	Zhoukoudian 10
(Begun and Walker 1993)	no frontal petalia evident; sagittal keel continues anteriorly from parietal region, extends between frontal lobes, with broad, well-marked depressions to either side, immediately anterior to coronal suture; frontal keel ends anteriorly as a broad, antero-superiorly facing bulge	Zhoukoudian 12

Table A-3 Continued		
Author	**Morphology**	**Fossil**
(Holloway 1980)	right frontal petalia; well developed Broca's area	Solo (Ngandong) I
(Holloway 1980)	right frontal petalia; Broca's cap on left "particularly pronounced;" right is smaller	Solo (Ngandong) V
(Holloway 1980)	right frontal petalia; well developed Broca's area	Solo (Ngandong) VI
(Holloway 1980)	left frontal petalia	Solo (Ngandong) X
(Holloway 1980)	right frontal petalia; Broca's area more pronounced of left	Solo (Ngandong) XI
(Holloway 1981)	right frontal petalia (both A/P and M/L)	Salè
(Holloway 1981)	right frontal petalia (both A/P and M/L)	Spy I
(Holloway 1981)	right frontal petalia (both A/P and M/L)	Spy II
(Holloway 1981)	right frontal petalia (both A/P and M/L)	Djebel Irhoud I

Table A-4: Parietal Lobe Evolution in Fossil Hominids

Author	Morphology	Fossil
(Dart 1925)	lunate sulcus pushed backward by bulging of parieto-temporo-occipital association areas	Taung
(Schepers 1946)	Dart's assessment of posterior position of lunate sulcus confirmed	Taung
(Le Gros Clark 1947; 1964, cited by Tobias 1987)	position of lunate inconclusive	Taung
(Keith 1831, cited by Tobias 1987)	lunate in more anterior, monkey-like position	Taung
(Holloway 1975a)	posteriorly placed lunate sulcus (uses indirect evidence)	Sk1585
(Holloway 1975a)	posterior position of lunate	Taung
(Holloway 1972c; 1981c; Tobias 1975)	parietal lobule expanded transversely; a trended noted also in Australopithecines by but here the superior parietal region is well developed as well); left supero-parietal region more developed than right supero-parietal region (Tobias suggests this may be classified as a "petalia"); inferior parietal region (aka supramarginal & angular gyri; Brodman's areas 39 & 40 & others; forms part of Wernicke's area) more strongly developed than in apes or Australopithecines	OH 16
(Tobias 1975) (Schepers 1946; Geshwind 1965; Holloway 1972c) (Dart 1925); (Holloway 1981c))	parietal lobule expanded transversely and postero-superiorly, a trended noted also in Australopithecines by but here the superior parietal region is well developed as well left supero-parietal region more developed than right supero-parietal region (Tobias suggests this may be classified as a "petalia"); inferior parietal region (aka supramarginal & angular gyri; Brodman's areas 39 & 40 & others; forms part of Wernicke's area) more strongly developed than in apes or Australopithecines (citing	OH 24
(Begun and Walker 1993)	high (typical of H. erectus); maximum height posteriorly placed, as in KNM-ER 3733, 3883	KNM-ER 1470
(Dart 1925; Holloway 1972; 1981 c; Schepers 1946; Tobias 1975)	parietal lobule expanded transversely and postero-superiorly, a trended noted also in Australopithecines by but here the superior parietal region is well developed as well left supero-parietal region more developed than right supero-parietal region (Tobias suggests this may be classified as a "petalia"); inferior parietal region (aka supramarginal & angular gyri; Brodman's areas 39 & 40 & others; forms part of Wernicke's area) more strongly developed than in apes or Australopithecines (citing (Schepers 1946; Geshwind 1965; Holloway 1972c);	OH 13
(Holloway 1981c; Tobias 1975)	parietal lobule expanded transversely and postero-superiorly, a trended noted also in Australopithecines by (Dart 1925; Schepers 1946); but here the superior parietal region is well developed as well; inferior parietal region (aka supramarginal & angular gyri; Brodman's areas 39 & 40 & others; forms part of Wernicke's area) more strongly developed than in apes or Australopithecines (citing (Schepers 1946; Geshwind 1965; Holloway 1972c); Sylvian sulcus well-marked on left; suggestions of steeper angle on right; suggests well developed parietal operculum on left, correlated with right handedness	OH 7
(Begun and Walker 1993)	strongly developed sagittal keel, parietal surface slightly depressed on either side of keel, oriented at a somewhat acute angle to mid-sagittal plane parietal region broadest bilaterally adjacent to temporal lobes; in lateral view the mid-parietal region angles in toward parietal keel	Zhoukoudian 2

Table A-4 Continued

Author	Morphology	Fossil
(Begun and Walker 1993)	strongly developed sagittal keel parietal region broadest bilaterally adjacent to temporal lobes; in lateral view the mid-parietal region angles in toward parietal keel	Zhoukoudian 3
(Begun and Walker 1993)	strongly developed sagittal keel parietal region broadest bilaterally adjacent to temporal lobes; in lateral view the mid-parietal region angles in toward parietal keel	Zhoukoudian 10
(Begun and Walker 1993)	strongly developed sagittal keel, parietal surface slightly depressed on either side of keel, oriented at a somewhat acute angle to mid-sagittal plane; parietal region broadest bilaterally adjacent to temporal lobes; in lateral view the mid-parietal region angles in toward parietal keel	Zhoukoudian 12

Table A-5: Temporal Lobe Evolution in Fossil Hominids

Author	Morphology	Fossil
(Begun and Walker 1993)	intermediate in terms of projection between KNM-ER 1813 and KNM-ER 1470	KNM-ER 1805
(Begun and Walker 1993)	relatively smaller, narrower and less projecting than KNM-ER 1470	KNM-ER 1813
(Begun and Walker 1993)	large, bilaterally flared; in lateral view, temporal lobes face laterally, so that the endocast is broadest near the mid temporal region; basal temporal region partially preserved, appear flat and inferiorly oriented	Zhoukoudian 2
(Begun and Walker 1993)	large, bilaterally flared; in lateral view, temporal lobes face laterally, so that the endocast is broadest near the mid temporal region	Zhoukoudian 10
(Begun and Walker 1993)	large, bilaterally flared; in lateral view, temporal lobes face laterally, so that the endocast is broadest near the mid temporal region	Zhoukoudian 12

Table A-6: Occipital Lobe Evolution in Fossil Hominids

Author	Morphology	Fossil
(Begun and Walker 1993)	relatively small, less projection than in KNM-ER 1470; no clear asymmetry	KNM-ER 1813
(Begun and Walker 1993)	relatively small, less projection than in KNM-ER 1470; no clear asymmetry	KNM-ER 1805
(Begun and Walker 1993)	occipital lobes appear somewhat large relative to cerebellum than on KNM-WT 15000	KNM-ER 3883
(Holloway 1981b)	slight left A/P definite left lateral occipital petalia;	Trinil 2 (Pith I /1891)
(Holloway 1981b)	definite left A/P, slight left lateral occipital petalia	Sangiran 2 (Pith II/1937)
(Holloway 1981b)	slight left AP, slight left lateral occipital petalia	Sangiran 4 (Pith IV/1938)
(Holloway 1981b)	slight left A/P, slight left lateral occipital petalia	Sangiran 10 (Pith VI/1963)
(Holloway 1981b)	uncertain petalial pattern, but many indicators of overall left occipital/right frontal petalia	Sangiran 17 (Pith VIII/1969)
(Begun and Walker 1993)	occipital lobes dorso-ventrally flattened, broad, with strong posterior projection; project well beyond the cerebellar surfaces; no occipital petalia	Zhoukoudian 2
(Begun and Walker 1993)	occipital lobes dorso-ventrally flattened, broad, with strong posterior projection; project well beyond the cerebellar surfaces; no occipital petalia; cerebellar lobes poorly preserved; situated well anterior to occipital lobes	Zhoukoudian 3
(Begun and Walker 1993)	occipital lobes dorso-ventrally flattened, broad, with strong posterior projection; project well beyond the cerebellar surfaces; some development of occipito petalia evident (the authors do not state which side); cerebellar lobes poorly preserved; situated well anterior to occipital lobes	Zhoukoudian 10
(Begun and Walker 1993)	occipital lobes dorso-ventrally flattened, broad, with strong posterior projection; project well beyond the cerebellar surfaces cerebellar lobes poorly preserved; situated well anterior to occipital lobes	Zhoukoudian 12
(Holloway 1981)	left occipital petalia (both A/P and M/L)	Salè
(Holloway 1980)	left occipital petalia	Solo (Ngandong) I
(Holloway 1980)	left occipital petalia	Solo (Ngandong) V
(Holloway 1980)	left occipital petalia	Solo (Ngandong) VI
(Holloway 1980)	unclear (cf. left frontal petalia)	Solo (Ngandong) X
(Holloway 1980)	left occipital petalia	Solo (Ngandong) XI

Table A-7: Evolution of the Posterior Cranial Fossa in Fossil Hominids

Author	Morphology	Fossil
(Holloway 1981b)	no indication of occipital/marginal sinus (but see Falk...)	Omo L338y-6
(Holloway 1988)	cerebellar lobes flare laterally, protrude posteriorly (they resemble Pan in this respect); less tucked under than in OH5 and SK 1585 (more “human-like”) in this trait	KNM-WT 17000
(Begun and Walker 1993)	no occipital/marginal sinuses evident	KNM-ER 3733
(Begun and Walker 1993)	right transverse sinus larger than left; no occipital/marginal sinuses evident	KNM-WT 15000
(Begun and Walker 1993)	right transverse sinus larger than left; no occipital/marginal sinuses evident	KNM-ER 3883
(Begun and Walker 1993)		Zhoukoudian 2
(Begun and Walker 1993)	large transverse sinuses; “right side dominant”; directly continuous with strongly marked superior sagittal sinus; superior sagittal sinus best developed just anterior to confluence; sigmoid sinuses well preserved, of roughly equal caliber	Zhoukoudian 3
(Begun and Walker 1993)	large transverse sinuses; “right side dominant”; directly continuous with strongly marked superior sagittal sinus; superior sagittal sinus best developed just anterior to confluence	Zhoukoudian 10
(Begun and Walker 1993)	large transverse sinuses; “right side dominant”; directly continuous with strongly marked superior sagittal sinus; superior sagittal sinus best developed just anterior to confluence	Zhoukoudian 12
(Holloway 1980)	superior sagittal sinus appears to drain into right transverse sinus	Solo (Ngandong) I
(Holloway 1980)	superior sagittal sinus drains into right transverse sinus	Solo (Ngandong) V
(Holloway 1980)		Solo (Ngandong) VI
(Holloway 1980)	superior sagittal sinus drains into right transverse sinus	Solo (Ngandong) X
(Holloway 1980)	transverse sinuses obscure; in author’s opinion, right side is more likely	Solo (Ngandong) XI

Table A-8: Scenarios for Human Cognitive Evolution

Author	Central Premise	Model
[(Holloway 1967; 1981)	emphasizes the autocatalytic nature of human cognitive evolution. He models cognitive/brain evolution as a dialectical process. Socio-cultural environment becomes a central dynamic of natural selection	"initial kick" (selection for social behavior within cultural context, e.g., hunting, tool-making, division of labor, cooperative sharing of food and child care) ⇔ increased perceptual discrimination, proprioceptive control, attention ⇔ symbolic elaboration enhances communication as culturally-shared activities become more complex ⇔ sensory-motor & visuo-spatial integration ⇔ expansion of posterior parietal cortex ⇔change in endocrine target tissue ⇔ reduced aggression, increased cooperation, rates of pre- and post-natal brain and body growth, sexual dimorphism ⇔ cognitive complexity/neural complexity
(Mithen 1996b; a).	recapitulationist approach; cognitive structure oscillated between more horizontal and more vertical (modular) organization, until culminating in "fluid intelligence" characteristic of modern humans	generalized intelligence, bipedalism, relaxation of constraints on brain size ⇒ free hands for carrying, toolmaking, descent of larynx, breath control ⇒ exploitation of scavenging niche ⇒ cognitive "arms race" as social pressures increased ⇒ new or expanded cognitive modules (e.g., "technical intelligence," "social intelligence," & simple language; "natural history intelligence") ⇒ still more complex social groups ⇒ function of language shifts from mediation of social relationships to vehicle for generalized information storage ⇒ increased cognitive demands ⇒ longer infant dependency creates selection pressure related to provisioning of females & dependents ⇒ intra-modular information flow ⇒ fluid, general intelligence
(Donald 1991)	Punctuationist model: three stages or "punctuations," beginning with a "supramodal" capacity for motor modeling ("mimesis"). Mimesis is a content-independent, horizontally operating function that enabled voluntary retrieval of stored mental representations. Mimesis operates as a self-triggered rehearsal loop, capable of gaining voluntary access to its own outputs. Mimesis permitted independence from immediate environmental cues, and enabled individuals to deliberately reflect upon events and to voluntarily and systematically rehearse behaviors. Mimesis is grounded in an early motor adaptation that permitted early hominids to use the whole body as a multimodal representational device.	serial motor skill (many unique representational possibilities) ⇒ mimesis (body as a multimodal representational device) ⇒ voluntary modeling and modifying of behavior (rehearsal enables deliberate control of outputs) ⇒ previously stereotyped emotional behaviors become rehearsable, refinable, and deliberate ⇒ intentional communication employing facial, vocal, and whole-body expression in social exchanges ⇒ vocal mimetic skill ⇒ lexical invention based on representational complexity, shared social context, and vocal skill ⇒ proto-linguistic behavior (distinct from motor skills related to tool manufacture and use) ⇒ lexical representations organized systematic, socially shared, rule-based system enabling information storage, organized knowledge for shared narrative tradition, explicit recall & reflection

Table A-8 Continued

Author	Central Premise	Model
(Bickerkton 1995)	Language is determining attribute of human cognition; all other unique aspects arise from it. Language is not simply a system of communication – it is a representational tool that permits multiple levels of intentionality and infinite complexity. Representation permits “off-line thinking” – computations carried out on internal representations of objects. Bickerton takes a superficial approach to the Pleistocene archaeological record, using only (Noble and Davidson 1996) (Dibble 1987) and (Mellars 1989a) as his only cited sources. He does not address the issue of how language, as a prime mover, could account for the complexity of the Upper Paleolithic. Although he cites both (Falk 1993) and (Tobias 1971) with respect to brain size increases, he does so only to refute their gradualist perspective, without addressing any of the complexities of encephalization or cortical reorganization. On the other hand, Bickerton is almost unique in discussing the role of the cerebellum as the ultimate node in a neural network permitting the emergence of syntax.	
(Lieberman 1984b).	Lieberman has proposed a horizontal model for human cognitive behavior, postulating a “central, distributed neural computer” (p. 16) with specialized input-output devices that enable language. He has emphasized the importance of a broad and versatile phonological repertory for complex vocal communication. In this model, language depends upon (1) general (content-independent) cognitive neural structures; (2) anatomical adaptations for speech production; (3) neural adaptation governing syntax	neural mechanisms for motor control ⇒complex, structured motor acts ⇒ facilitated automization of motor control ⇒ rule-governed, syntactic behavior ⇒ syntactical organization of communication to reduce ambiguity ⇒ anatomical adaptations for efficient vocal expression and interpretation of syntactically based vocal communication ⇒ enhancement of general cognitive efficiency ⇒ accelerated exchange of conceptual information ⇒ elaboration of language as a cultural medium for information storage and processing

Table A-8 Continued

Author	Central Premise	Model
(Deacon 1997)	Language is its own “prime-mover” Symbolic representation provides a unique medium for consciousness	indexical and iconic representation (a characteristic of all nervous systems) ⇒ “subjective distance” from original stimulus ⇒ co-evolved complex of adaptations arrayed around symbolic representation (e.g., representational freedom, self consciousness, self control, empathy) ⇒ symbolic representation of self ⇒ social complexity, “distributed cognition” ⇒ selection favors ability to cross the “symbolic threshold” ⇒ evolution of ever greater language complexity ⇒ neural adaptations for sensorimotor efficiency (controlled vocalization), lexical memory, grammatical processing
(Falk 1992)		bipedalism releases constraints on brain size related to homeothermy ⇒ shifts in developmental timing necessitated by pelvic constraints ⇒ increased cerebral lateralization (incipient in earlier species) ⇒ asymmetric distribution of neurotransmitters & pattern of cortical connectivity ⇒ related to complex motor demands of vocal signaling ⇒ communication skills enhanced, selective advantage to hominids with good social skills ⇒ full-blown language, reflectivity, self-recognition, ⇒ increased general intelligence
(Pinker 1990; 1995; 1997; 1999)	Pinker argues, contra the conventional wisdom embraced by many linguists who follow the standard social sciences model, that natural selection is the only mechanism through which language capacity could have evolved. He rejects motor control mechanisms as homologues of syntactical control mechanisms, on the basis that motor control programs require multi-level, open, continuous time and space parameters. According to Pinker, a better precursor for syntactical control mechanisms would be cognitive operations based on the conceptualization of topology and antagonistic forces. Hierarchality and seriality are common features of many, perhaps all, complex systems, including neural systems. There is no reason to believe that syntax rests on seriality and hierarcality based on motor mechanisms.	visual emphasis ⇒ world perceived as distinct three-dimensional objects which exist in space + group living + bipedalism (hands free for manipulation) + hunting ⇒ efficiency of information sharing ⇒ social interactions enhanced by linguistic behavior ⇒
(Cosmides 1997; Cosmides and Tooby 1995; Tooby and Cosmides 1995)	modular, domain-specific model of human cognitive evolution, giving credit to the seminal conception of William James that humans are distinguished from other animals by the number of their cognitive specializations (a greater number of “instincts”). They have rejected what they have referred to as the “standard social sciences model,” and propose a Darwinian explanation of neuro-cognitive evolution. The brain is an amalgamation of adaptive problem-solving devices. Modern human	Hunter-gatherer lifestyle/environment ⇒ specialized modules to meet specific ecological contexts. Evolved problem-solving” is content-dependent. Innate domain-specific modules act as “crib sheets” to enhance computational speed and efficiency. They emphasize an epigenetic perspective: human cognition emerges as the innate structure of the mind is exposed to environmental stimuli. Cosmides’ and Tooby’s published work has focused on he cognitive dynamics of social exchange and “social contract algorithms”.

	cognition a set of functionally specialized neural adaptations that evolved in response to the complex demands of Pleistocene hunter-gatherer life. Functional integration of the separate modules is accomplished by another module specialized for that task. “	

Table A-8 Continued

Author	Central Premise	Model
Stone Cache Model (Potts 1988)	Taphonomic evidence suggests that early hominids minimized time spent at sites where bone/stone accumulations are found. Based on evidence of competition between hominids and carnivores over meat; danger to hominids from other carnivores when they were in possession of meat; incomplete processing of bones; repeated visits during which bones were accumulated. Potts refutes home base hypothesis in favor of scenario where hominids optimized energy expenditure by transporting meat & other food resources to caches of stone tools	widely separated food and tools ⇒ transportation to same area + controlled use of fire ⇒ safety against predators ⇒ focus of social activity and food processing in same place ⇒ home-bases/campsites
Variability Selection Model (Potts 1996)	Erratic climatic regimes gave adaptive advantage to hominids that could cope with unpredictable, diverse ecological circumstances.	widely distributed, patchy, seasonal, resource distribution ⇒ increased body size increased mobility ⇒larger foraging area ⇒ wider geographic dispersal ⇒ biological adaptations for protection against heat stress, water loss + climatic change ⇒ advantage of more generalized behavior ("intelligence") ⇒ costs and benefits of encephalization ⇒ longer juvenile dependency period ⇒ longer learning period ⇒ intensified social bonds ⇒ transmission of culture ⇒ language ⇒ technological innovation
(Isaac 1978)	Introduced the "home-base" model, which integrated social/reproductive behavior, bipedalism, dietary adaptations, encephalization, technology, and culture. A central dynamic of food-sharing drives the interplay among these elements	Hunting ⇒ tolerated scrounging + bipedalism ⇒ tool use ⇒ hunting/gathering ⇒ food sharing ⇔ division of labor re: technology/home bases ⇔ elaboration of culture: formalized kinship structures, formalized social structure, formalized intergroup interactions; technological innovation
(Lovejoy 1981)	Early behavioral/ecological model. Mosaic, patchy environments & sparse distribution of food sources favor a generalist strategy of resource exploitation, separation of sexes during foraging.	patchy resource distribution ⇒ separation of males and females during foraging + lower mobility of females with young ⇒ linear displacement of males, who become wider-ranging ⇒ advantage of polygeny declines as feeding divergence increases ⇒ sex ratio close to parity ⇒ monogamous pair bonding (males avoid competition with their mates & biological offspring without losing assurance of consortship) ⇒ male provisioning (facilitated by hand carrying) ⇒ establishment of "home bases" ⇒ selection for efficient bipedality and enhancement of material culture ⇒ elaboration of material culture ⇒ continuous female sexual receptivity, ⇒ sequestration of ovulation ⇒ enhancement of epigamic characteristics ⇒ marked sexual dimorphism ⇒ "nuclear family" structure ⇒ shortened interbirth interval, increased ⇒ longer learning period ⇒ enhanced infant survivorship

Table A-8 Continued

Author	Central Premise	Model
(Wynn 1979; 1981; 1991; 1996a)	Piaget's theoretical framework & recapitulationist approach; evaluates developmental stages in intelligence (organizational ability) demonstrated by stone tool manufacture. Brain morphology + experience are both necessary to develop intelligence. Only minimum competence necessary to produce artifacts can be evaluated; nothing can be said about unutilized potentials of long-dead individuals.	Oldowan stone tool typology suggests that its makers had attained a pre-operational stage of intelligence. These tools require very simple spatial abilities (concept of proximity) to manufacture. They do not suggest that these hominids were capable of operational functioning (order, direction, reversal, and topological geometry). By the late Acheulean, toolmakers had achieved concrete operational thinking (part-to-whole relationships; classification; reversibility; precorrection of errors). Operational thinking is first applied in a narrow range of domains, then applied to more and more situations. Kinship, politics, religion all require concrete operational thinking. Piaget's stage of formal operational intelligence may be a product of culturally "distributed cognition," rather than a biologically based innovation (although some evidence that it depends of neural development can is suggested by the late myelnation of the frontal lobes in adolescents
(Calvin and Bickerton 2000)	authors focus on the step from proto-language to syntactically organized language, Syntax is an emergent process arising from proto-language coupled with either (1) cognitive categories arising from reciprocal altruism or (2) planning circuits necessary for ballistic planning. Syntax enables long range planning, procedural games, music, and creative disposition of elements. These behaviors may well have a content-independent, common neural machinery based on sequencing and exapted for language and other functions.	⇒ arbitrary word sequences ⇒ assignment of thematic roles to certain words ⇒ recognition of obligatory arguments based on nature of verbs ⇒ modifiers, relational word intermediaries between words and complete utterances (= phrase and clause boundary markers) ⇒ hierarchical, embedded utterances (thalamus and cerebellum invoked for coordination; temporal and parietal lobes (in sites surrounding Sylvian fissure) ⇒sequencing of oro-facial expressive movements and phoneme sequencing; ⇒ associations between representation & production by redundant spatiotemporally resonant neural firing patterns. Proto-language distinct from syntax. Social intelligence prime mover for syntax; mechanisms for cortical coherence derived from syntactical algorithms become domain general

Table A-9: Sample of Scanned Endocasts

Specimen/ Taxon	n	Group	Medium	Age	Comments
Chimp I/ Pan troglodytes	1	07-PanS	Scanned Endocast Model	recent	latex endocast made by Dr. R.L. Holloway from the skull collection of the American Museum of Natural History
STS 19 A. africanus	1	08-aust	Scanned Endocast Model	3.0-2.5 mya	Unreconstructed basicranial fragment, PCF intact Endocranial volume of 436 cc estimated by Holloway from formula [Holloway, 1975 #251]
KNM-ER 23000 A. boisei	1	08-aust	Scanned Endocast Model		No published description
KNM-ER 1813 H. habilis (sensu lato)	1	09-HH	Scanned Endocast Model	2.0-1.8 mya	Almost complete cranium, missing only part of cranial base; reconstruction of endocast by Dr. R.L. Holloway 1970s
KNM-ER 1805 H. habilis (sensu lato)	1	09-HH	Scanned Endocast Model	2.0-1.8 mya	Reconstruction of the PCF follows fragmentary contours, as the basicranium was not well preserved
KNM-ER 1470 H. habilis (sensu lato)	1	09-HH	Scanned Endocast Model	2.0-1.8 mya	Reconstruction of cranium by Dr. A. Walker. Endocast originally prepared 1970s by Dr. R.L. Holloway
Zhoukoudian, Locus E, III H. erectus	1	HE-10	Scanned Endocast Model	400 + kya	Reconstruction by Weidenreich, 1937. Cranial base required some reconstruction; adolescent or juvenile
KNM-WT 15000 H. erectus/ergaster	1	10-HE	Scanned Endocast Model	1.6 mya	Reconstruction by Dr. A. Walker; basicranium well preserved
Pithecanthropus VIII (Sangiran 17) H. erectus	1	10-HE	Scanned Endocast Model	800 kya - 1.7mya	Well preserved basicranium, except in for orbital surface of frontal lobes & temporal pole Endocast r reconstruction by Dr. R.L. Holloway 1970s
KNM-ER 3733 H. erectus/ergaster	1	10-HE	Scanned Endocast Model	~ 1.8 mya	Fairly well preserved, relatively undistorted Endocast reconstruction by Dr. R.L. Holloway
KNM-ER 3883 H. erectus/ergaster	1	10-HE	Scanned Endocast Model	~ 1.8 mya	Endocranium mostly intact, although somewhat flattened; skull was reconstructed from many fragments. Endocast reconsruction by Dr. R.L. Holloway
Zhoukoudian, Locus L, 1 "Skull X" H. erectus	1	10-HE	Scanned Endocast Model	400 + kya	PCF intact; ; anterior/inferior portion required extensive reconsruction
Kabwe/Broken Hill early archaic H. sapiens	1	11-EAH	Scanned Endocast Model	200-500 kya	Very well preserved; intact cranial base
Swanscombe early archaic H. sapiens	1	11-EAH	Scanned Endocast Model	200-300 kya	Occipital & parietals articulate closely ; PCF well-preserved
La Chapelle I late archaic H. sapeins	1	12-LAH	Scanned Endocast Model/CT scan		PCF reconsruction follows contours of broken skull base
La Ferrassie I late archaic H. sapiens	1	12-LAH	Scanned Endocast Model/CT scan	~ 70 kya	some damage to anterior PCF; foramen magnum missing
Gibraltar/Forbes Quarry late archaic H. sapiens	1	12-LAH	Scanned Endocast Model		basicranium well preserved
Cro-Magnon I early modern H. sapiens	1	13-EMH	CT scan	~ 30 kya	Good preservation; basicranium intact

Table A-10: MRI Sample

Specimen/ Taxon	Number of Individuals	Group/ Abbreviation	Medium	Age	Comments
C atys	4	New World Monkey/ 01-NW	MRI	recent	provided by Semendeferi, Rilling & Insel
C. apella	4	New World Monkey/ 01-NW	MRI	recent	provided by Semendeferi, Rilling & Insel
S. sciureus	4	New World Monkey/ 01-NW	MRI	recent	provided by Semendeferi, Rilling & Insel
P. cynoceph	4	Old World Monkey/02-OW	MRI	recent	provided by Semendeferi, Rilling & Insel
M. mulatta	4	Old World Monkey/02-OW	MRI	recent	provided by Semendeferi, Rilling & Insel
Hylobates	4	Hylobates/03-Hy	MRI	recent	provided by Semendeferi, Rilling & Insel
Pongo	4	Pongo/04-Po	MRI	recent	provided by Semendeferi, Rilling & Insel
Gorilla	2	Gorilla/05-Go	MRI	recent	provided by Semendeferi, Rilling & Insel
Pan paniscus	4	Bonobo/06-Bo	MRI	recent	provided by Semendeferi, Rilling & Insel
Pan troglodytes	6	Pan/07-PanM	MRI	recent	provided by Semendeferi, Rilling & Insel
Homo sapiens	for population mean brain volume, n = 52 from [Beals, 1984 #30]; for population mean cerebellum volume, n = 51 from [Snyder, 1995 #208][Semendeferi, 2000 #180][Klekamp, 1987 #406] and present study	Recent Homo sapiens/14-RHS	MRI	recent	cadaver specimens for whole brains and most human cerebellar volumes; MRI scans for non-human cerebellar volumes

Table A-11: PCF and CBLM Volume from MRI Scans

Specimen	Taxon	PCF Volume	CBLM Volume	CBLM/PCF
Gi1	Gi	7.11	9.32	1.31
Gi2	Gi	18.36	18.81	1.02
Gi3	Gi	19.82	25.98	1.31
Gi4	Gi	9.37	11.2	1.19
Or1	O	55.06	52.7	0.96
Or2	O	53.43	49.19	0.92
Or3	O	54.5	62.38	1.14
Or4	O	45.74	51.22	1.12
GO1	Go	49.38	65.71	1.33
GO2	Go	76.2	89.24	1.17
Pan1	C	37.34	56.12	1.5
Pan2	C	43.76	55.84	1.28
Pan3	C	31.38	43.46	1.38
Pan4	C	35.23	40.47	1.15
Bo1	B	37.75	54.07	1.43
Bo2	B	30.99	39.41	1.27
Bo3	B	37.51	41.82	1.11
YH2	H	141.59	153.35	1.08
YH3	H	105.1	145.47	1.38
CS1519	H	89.28	123.16	1.38
Cs1520	H	129.29	125.94	0.97
CS1523	H	86.83	100.97	1.16
CS1533	H	126.85	134.75	1.06
Cs1541	H	118.66	177.63	1.5
Cs1544	H	91.28	129.44	1.42
Cs1503	H	116.93	156.45	1.34
Cs1501	H	123.99	155.75	1.26
Cs1504	H	105.5	147.44	1.4
Cs1506	H	122.39	159.73	1.31
Cs1507	H	91.29	116.39	1.27
Cs1513	H	127.5	144.57	1.13
CS1516	H	115.93	125.84	1.09
CS1517	H	93.91	156.3	1.66
CS1518	H	75.95	147.43	1.94

Table A-12: Cerebellum Volume Comparison

Hominoid MRIs

Author	Recent Hum	Pan	Bonobo	Gorilla	Pongo	Hylobates
Semendeferi	155.1	41.2	45.8	69.3	52	10.7
Rilling	134.1	46.4	41.3	64.7	46	10.9
McLeod/Low	136.08	46.4	41.3	60.2	48.8	11
McLeod/High	133.6	46.7	44.9	68.6	47.1	12
Weaver	134.15	48.9	45.3	73.6	.	11.3
Mean	138.6	45.9	43.7	67.28	48.5	1.18
SD	9.26	2.83	2.23	5.06	2.62	0.51
SE Mean	4.15	1.27	1	2.26	1.31	0.23

Table A-13 Comparison of Scanned/Published Volumes			
Specimen	**Scan Vol**	**Published Vol**	**Source Pub Values**
La Chapelle I	1578.7	1625	Holloway ‘96
La Ferrassie I	1640.82	1640	Holloway ’96
Gibraltar/Forbes Quarry	1225.49	1235	Vlcek ’69
Broken Hill/Kabwe	1247.94	1280	Kochetkova ’78
Arago	1114	1166	Kochetkova ’78
Swanscombe		1325	Kochetkova ’78
KNM-WT 15000	844	880	Begun et al. ‘93
Pitih VIII /Sangiran 17)	976.01	1004	Holloway ’96
KNM-ER 3733	782.71	848	Holloway ’96
KNM-ER 3883	738.06	804	Holloway ’96
KNM-ER 1813	501.29	510	Holloway ’96
KNM-ER 1805	554.03	582	Holloway ’96
KNM-ER 1470	727.8	752	Holloway ’96
STS 19-5	455	436	Holloway ’96
KNM-ER 23000	471.74	436	Holloway ’96
Trinil/Pith I/Sangiran 2	954.09	953	Hol ’96
Zhoukoudian Locus LI	1201.71	1225	Begun ’93 (after Black ’43)
Zhoukoudian Locus E /skull III	881.84	915	Tobias ’71 (after Weidenreich ’43)

Table A-14: Comparison of Scanned and Published Linear Measurements

Specimen	Scan A/P	Published A/P	Scan W	Published W	Source Pub. Meas.
AL 23000	117.5	.	91.86	.	
KNM-ER 1813	129.02	127	129.02	97	Begun & Walker '93
KNM-ER 1805	124.56	135	95.94	100	Begun & Walker '93
KNM-ER 1470	129.7	136	97.4	116	Begun & Walker '93
KNM-ER 3883	134.6	150	110.15	122	Begun & Walker '93
KNM-ER 3773	149.1	143	119.86	120	Begun & Walker '93
KNM-WT15000	140.18	158	118.18	116	Begun & Walker '93
Zhoukoudian Locus L1	152.7	171	113.9	128	Begun & Walker '93
Zhoukoudian Locus E, Skull III	170.88	157	123.64	120	Begun & Walker '93
Trinil/Pith I/Sangiran 2	157.15	156	117.21	125	Holloway '81
Pith VIII/Sangiran 17	134.72	161	125.62	130	Holloway '81
La Chapelle I	180.24	182	142.37	113	Kochetkova '78
La Ferrassie I	179.62	184	146.94	151	Heim '70
Gibraltar/Forbes Quarry	162.25	169	128.08	139	Vlcek '69
Swanscombe	.		128.11	139	Kochetkova '78
Kabwe/BrokenHill	170.09	171	102.6	103	Kochetkova '78

Table A-15: Data for Raw and Derived Variables

Specimen	Group	CBLM (cc)	BoMass (kg)	BrMass (g)	NetBrain (g)	CQ (actual/	EQ (Martin)
C. atys (n = 4)	01-NW	9.2	10.5	99.7	90.5	0.58	1.49
C. apella(n = 4)	01-NW	6.5	3.2	66.5	60	0.5	2.45
S. sciureus (n = 4)	01-NW	2	0.9	23.1	21.1	0.22	2.23
P. cynoceph (n = 4)	02-OW	13.7	21.9	143.3	129.6	0.7	1.22
M. mulatta (n = 4)	02-OW	7.1	10.4	79.1	72	0.5	1.19
Hylobates (n = 4)	03-Hy	11.33	5.4	74.1	62.77	0.86	1.83
Pongo (n = 4)	04-Po	48.9	73.5	433.13	384.23	1.13	1.47
Gorilla (n = 2)	05-Go	67.6	85	313.14	245.54	2.23	0.95
Bonobo (n = 4)	06-Bo	45.8	45.4	332.42	286.62	1.34	1.63
Chimp I	07-PanS	46.22	54.2	345.95	299.73	1.3	1.48
STS 19	08-Aust	42.09	45	450.59	408.5	0.92	2.23
KNM-ER 23000	08-Aust	50.32	46	466.76	416.44	1.08	2.27
KNM-ER 1813	09-HH	57.8	32	495.28	437.48	1.19	3.17
KNM-ER 1805	09-HH	53.29	32	546.07	492.78	0.99	3.49
KNM-ER 1470	09-HH	69.65	52	710.95	641.29	1.03	3.15
Zh Loc E /III	10-HE	98.37	61.8	859.54	761.17	1.25	3.34
KNM-WT 15000	10-HE	77.73	68	823.52	745.79	1	2.97
Pith VIII /Sangiran 17	10-HE	90.05	61.8	949.01	858.96	1.02	3.68
KNM-ER 3733	10-HE	89.11	61.8	765.1	675.99	1.26	2.97
KNM-ER 3883	10-HE	64.29	61.8	722.47	658.19	0.93	2.8
Trinil 2/Pith I	10-HE	98.32	61.8	928.2	829.89	1.15	3.6
Zhoukoudian Locus LI	10-HE	92.59	61.8	1162.65	1070.06	0.86	4.51
Broken Hill/Kabwe	11-EAH	116.48	65.6	1205.39	1088.92	1.06	4.47
Swanscombe	11-EAH	82.58	65.6	1184.63	1102.06	0.74	4.39
La Chapelle I	12-LAH	119.01	76.41	1516.76	1397.74	0.86	5.01
La Ferrassie I	12-LAH	118.33	84.99	1575.83	1457.5	0.82	4.8
Gibraltar/Forbes Quarry	12-LAH	81.71	76	1185.58	1103.87	0.74	3.93
Cro-Magnon	13-EMH	118.92	67.55	1477.34	1358.42	0.88	5.36
Homo sapiens (MRI)	14-RH	140.5	58.2	1302	1161.5	1.21	5.29

Notes for Table A-15

Brain and cerebellar volumes for Old and New World Monkeys and Pongids from MRIs

Brain Volume and Body Mass for recent *Homo sapiens* from (Beals et al. 1984)

Cerebellar Volume for recent *Homo sapiens* = mean published volumes from (Snyder et al. 1995)**,**(Riedel et al. 1989) (Semendeferi and Damasio 2000) **and** (Rilling and Insel 1998)

Formula for conversion of Cranial capacity to Brain Volume and for Brain Volume to Brain Mass: (Ruff et al. 1997)

Body Mass for *Homo erectus*, early and late archaic *Homo sapiens,* and early modern *Homo sapiens* from (Ruff et al. 1997)

Cerebellar and endocranial volumes for fossil hominids from 3-D virtual scanned models

Body mass for australopithecines and *Homo habilis* from (McHenry 1992b)

Table A-16: Shapiro-Wilk W Test for Normal Distribution of Variables		
Variable	p-value (Shapiro-Wilk W test for normality)	Comments
CBLM	0.3 (normal)	
BoMass	0.006	Skewed to high end of distribution
BrMass	0.1 (normal; but see comment)	discontinuous; multimodal
NetBrain	0.1 (normal; but see comment)	discontinuous; multimodal
CQ	0.0	Gorilla, Hylobates are extreme outliers
EQ	0.8 (normal)	
CQR	0.3 (normal; but see comment)	bimodal; Gorilla an extreme outlier
EQR	0.0	bimodal; Gorilla an extreme outlier

Table A-17: Summary of Group Comparisons

Comparison	CQ	Significant for ∝ = 0.05?	EQ	signifi-cant?	Net Effect
Monkeys vs. Hominoids	higher	yes	same*	no	
Australopithecines vs. *Pan*	lower	no	higher	equivocal	Expansion of NetBrain
H. habilis vs. Australopithecines	higher	no	higher	yes	Expansion of both CBLM and NetBrain; CBLM more rapidly than NetBrain
H. erectus vs. *H. habilis*	higher	no	same	no	Expansion of CBLM at cost of NetBrain
Middle Pleistocene H. sapiens vs. H. erectus	lower	no	higher	equivocal	Expansion of NetBrain
Late vs. Early Archaic *H. sapiens*	lower	no	Higher	no	Expansion of NetBrain
Late Archaic *H. sapiens* vs. pooled Early Hominids	lower	yes	higher	yes	Expansion of NetBrain
Early Modern *H. sapiens* vs. Late Archaic *H. sapiens*	higher	no	higher/ same	no	CBLM expansion at cost of NetBrain
Recent H. sapiens vs. Early Modern *H. sapiens*	higher	no	higher/ same	no	CBLM expansion at cost of NetBrain
*inclusion of three New World Monkey taxa skews significance test					

Table A-18: Coefficients of Variation for CBLM and CQ in Anthropoids

Group	CBLM	CV	CQ	CV
New World + Old World Monkeys 5 groups, total n = 25	Mean 7.7 Range 2.0 – 13.7 SD 4.25	4.25/7.7 = 0.55	Mean 0.50 Range 0.22 – 0.70 SD 0.18	0.18/0.50 = .36
Hominoids (non-human) 5 groups, total n = 18	Mean 44.0 Range 11.3 – 67.6 SD 20.34	20.34/44.0 = 0.46	Mean 1.37 Range 0.86 – 2.22 SD 0.51	0.51/1.37 = 0.37
Pongids 4 groups, total n = 14	Mean 52.13 Range 45.8 – 67.6 SD 10.40	10.4/52.13 = 0.2	Mean 1.5 Range 1.12 – 2.22 SD 0.5	0.5/1.5 = .33
Recent Humans n = 51	Mean 140.5 Range 91.98 - 194 SD 19.01	19.01/140.5 = 0.14	Mean Range SD	
Australopithecine n = 2	Mean 46.2 Range 42.1 – 50.3 SD 5.82	5.82/46.2 = 0.12	Mean 1.0 Range 0.92 – 1.08 SD 0.11	0.11/1.0 = 0.11
H. habilis n = 3	Mean 60.25 Range 53.29 – 69.65 SD 8.45	8.45/60.25 = 0.14	Mean 1.07 Range 0.99 – 1.19 SD 0.12	0.12/1.07 = 0.11
H. erectus + Kabwe n = 8	Mean 90.87 Range 64.29 – 116.48 SD 15.37	15.37/90.87 = 0.17	Mean 1.07 Range 0.86 – 1.26 SD 0.14	0.14/1.07 = 0.13
Late Archaic H. sapiens + Swanscombe n = 4	Mean 100.41 Range 81.71 – 119.01 SD 21.09	21.09/100.41 = 0.21	Mean 0.79 Range 0.74 – 0.86 SD 0.06	0.06/0.79 = 0.76

Table A-16 continued

Group	CBLM	CV	CQ	CV
Hominids (excluding Cro-Magnon I) n = 17 + Recent Humans Mean	Mean 87.43 Range 42.09 – 140.5 SD 27.24	27.24/87.43 = 0.31	Mean 1.0 Range 0.74 – 1.26 SD 0.16	0.16/1.0 = 0.16
Genus Homo n = 15 + Recent Humans Mean	Mean 90.61 Range 53.29 – 140.5 SD 24.18	24.18/90.61 = 0.27	Mean 1.0 Range 0.74 – 1.26 SD 0.17	0.17/1.0 = 0.17
Cro-Magnon I	(Estimated) Hominid Mean 118.92 Range 82.05 – 155.78 SD36.87 Homo Mean 118.92 Range 886.81 – 151.01 SD 32.11		(Estimated) Hominid Mean 0.88 Range 0.74 – 1.02 SD 0.16 Homo Mean 0.88 Range 0.73 – 1.03 SD = 0.15	

Table A-19: Description of Samples and Regression Formulae

Sample #	Sample Composition for Calculation of Regression Formula	r^2	Prediction Equation	
			LSR	RMA
01	01-Full Sample used in Data Analysis (+ Anthropoids; + Fossil Hominids; + mean RHS)	0.86	Cblm = 14.30 + 0.08 * NetBrain	Cblm =7.15 + .094 Net Brain
02	02-Living Anthropoids (- RHS)	0.79	Cblm = -1.43 + 0.165 * NetBrain	Cblm =-3.88 + 0.24 * Net Brain
03	03-Living Anthropoids (- Gorilla; - RHS)	0.96	Cblm = -1.71 + 0.15 * NetBrain	Cblm =- 1.54 + 0.17 * Net Brain
04	04-Living Anthropoids (- Fossil Hominids; + RHS)	0.92	Cblm = -5.05 + 0.12 * NetBrain	Cblm =-0.48 + 0.14 * Net Brain
05	05-Living Anthropoids (- Go; - Fossil Hominids; + mean RHS)	0.987	Cblm = 1.70 + 0.12 * NetBrain	Cblm = 0.24 + 0.17 * Net Brain
06	06- Living Anthropoids (– Go, + Fossil Hominids; + mean RHS)	0.89	Cblm = 11.52 + 0.08 NetBrain	Cblm = 4.52 + 0.096 * Net Brain
07	07-Living Primates (+ Insectivores; + Prosimians; + means for expanded Anthropoid sample; + Means for Hominid Groups + mean RHS)	0.92	Cblm = 2.05 + 0.097 * NetBrain	Cblm = 9.58 + 0.009 * Net Brain
08	08- Living Primates + Insectivores; + Prosimians; +expanded Anthropoids; – Hominids; - RHS)	0.98	CBLM = 0.81 + 0.12* NetBrain	Cblm =4.43 + 0.016 * Net Brain
09	09 Living Primates (Insectivores; + Prosimians; + expanded Anthropoids; - RHS)	0.93	Cblm = - 0.53 + 0.15 * NetBrain	Cblm = 4.17 + 0.016 * Net Brain
10-Log/Log	10-Living Primates (+Insectivores; + Prosimians; + expanded Anthropoids; - Fossil Hominids; - RHS)	0.99	Log CBLM = - 2.01 + 0.099 * Log NetBrain	

Table A-20: Comparisons of Group Means with Selected Regression Formulae					
Formula	Groups	Results Wilcoxon/ Kruskal-Wallace test			Significant for ∝ = 0.05?
RMA-01		Chi-squared	Df	P =	
	Pan vs. Aust	2.4	1	0.12	n
	LAH vs. HE	5.73	1	0.017	y
	LAH vs. mean RHS	1.8	1	0.18	n
	LAH vs. exp. RHS	7.43	1	0.006	y
	EMH vs. exp. RHS	2.71	1	0.1	y for ∝ = 0.1
LSR-01	Pan vs. Aust	2.4	1	0.12	n
	LAH vs. HE	4.68	1	0.03	y
	LAH vs. mean RHS	1.8	1	0.18	n
	LAH vs. exp. RHS	7.43	1	0.006	y
	EMH vs. exp. RHS	2.71	1	0.1	y for ∝ = 0.1
RMA-03	Pan vs. Aust	2.4	1	0.12	
	LAH vs. HE	5.73	1	0.017	y
	LAH vs. RHS	1.8	1	0.18	n
	LAH vs. exp. RHS	7.43	1	0.006	y
	EMH vs. exp. RHS	2.71	1	0.1	y for ∝ = 0.1
LSR-03	Pan vs. Aust	2.4	1	0.12	n
	LAH vs. HE	5.73	1	0.017	y
	LAH vs. RHS	1.8	1	0.18	n
	LAH vs. exp. RHS	7.43	1	0.006	y
	EMH vs. exp. RHS	2.71	1	0.1	y for ∝ = 0.1
LSR-05	Pan vs. Aust	2.4	1	0.12	n
	LAH vs. HE	5.73	1	0.017	y
	LAH vs. mean RHS	1.8	1	0.18	n
	LAH vs. exp. RHS	7.43	1	0.006	y
	EMH vs. exp. RHS	2.71	1	0.1	y for ∝ = 0.1
RMA-05	Pan vs. Aust	2.4	1	0.12	
	LAH vs. HE	5.73	1	0.017	y
	LAH vs. mean RHS	1.8	1	0.18	n
	LAH vs. exp. RHS	7.43	1	0.006	y
	EMH vs. exp. RHS	2.71	1	0.1	y for ∝ = 0.1
RMA-08	Pan vs. Aust	2.4	1	0.12	n
	LAH vs. HE	5.73	1	0.017	y
	LAH vs. mean RHS	7.43	1	0.006	y
	EMH vs. exp. RHS	2.71	1	0.1	y for ∝ = 0.1
LSR-08	Pan vs. Aust	2.4	1	0.12	n
	LAH vs. HE	3.75	1	0.052	y
	LAH vs. mean RHS	1.8	1	0.18	n
	LAH vs. exp. RHS	7.43	1	0.006	y
	EMH vs. exp. RHS	2.71	1	0.1	y for ∝ = 0.1
10-LSR-log/log	Pan vs. Aust	2.4	1	0.12	n
	LAH vs. HE	5.73	1	0.01	y
	LAH vs. mean RHS	1.8	1	0.18	n
	LAH vs. exp. RHS	7.43	1	0.006	y
	EMH vs. exp. RHS	2.71	1	0.1	y for ∝ = 0.1

Table A-21: CQ/EQ – Wilcoxon/Kruskal-Wallace Comparison of Means for Cerebellar Coefficient

Comparison	Chi-squared	Df	p	Significant for ∝ = 0.05?
Pan vs. australopithecines	1.5	1	0.22	n
H. erectus vs. LAH	5.72	1	0.017	y
LAH vs. Mean RHS	1.8	1	0.18	n
LAH vs. expanded RHS	5.95	1	0.015	y

Table A-22: Formula Comparisons for CQ

Specimen	Group	LSR-01 CQ	RMA-01 CQ	LSR-02 CQ	RMA-02 CQ	LSR-03 CQ	RMA-03 CQ	LSR-04 CQ	RMA-04 CQ
C. atys (n = 4)	01-NW	0.43	0.59	0.68	0.52	0.78	0.66	1.58	0.75
C. apella(n = 4)	01-NW	0.34	0.51	0.77	0.62	0.89	0.75	3.02	0.82
S. sciureus (n = 4)	01-NW	0.13	0.22	0.97	1.69	1.37	0.98	-0.79	0.81
P. cynoceph (n = 4)	02-OW	0.56	0.71	0.69	0.5	0.77	0.67	1.3	0.78
M. mulatta (n = 4)	02-OW	0.35	0.51	0.68	0.53	0.78	0.66	1.98	0.74
Hylobates (n = 4)	03-Hy	0.59	0.87	1.27	1.01	1.47	1.24	4.56	1.36
Pongo (n = 4)	04-Po	1.09	1.13	0.79	0.55	0.87	0.77	1.19	0.92
Gorilla (n = 2)	05-Go	1.99	2.24	1.73	1.23	1.92	1.68	2.77	1.99
Bonobo (n = 4)	06-Bo	1.23	1.34	1	0.71	1.11	0.97	1.56	1.16
Chimp I	07-PanS	1.21	1.31	0.96	0.68	1.07	0.94	1.49	1.11
STS 19	08-Aust	0.9	0.92	0.64	0.45	0.71	0.62	0.96	0.74
KNM-ER 23000	08-Aust	1.06	1.09	0.75	0.52	0.83	0.73	1.12	0.87
KNM-ER 1813	09-HH	1.17	1.2	0.82	0.57	0.9	0.79	1.22	0.95
KNM-ER 1805	09-HH	0.99	1	0.67	0.47	0.74	0.65	0.99	0.78
KNM-ER 1470	09-HH	1.06	1.03	0.67	0.46	0.74	0.65	0.97	0.78
Zh Loc E /III	10-HE	1.31	1.25	0.79	0.55	0.87	0.77	1.14	0.93
KNM-WT 15000	10-HE	1.05	1.01	0.64	0.44	0.71	0.62	0.92	0.75
Pitih VIII /Sangiran 17	10-HE	1.08	1.02	0.64	0.45	0.71	0.62	0.92	0.75
KNM-ER 3733	10-HE	1.3	1.26	0.81	0.56	0.89	0.79	1.17	0.95
KNM-ER 3883	10-HE	0.96	0.93	0.6	0.42	0.66	0.58	0.87	0.7
Trinil 2/Pith I	10-HE	1.22	1.15	0.73	0.5	0.8	0.7	1.04	0.85
Zhoukoudian Locus LI	10-HE	0.93	0.86	0.53	0.37	0.58	0.51	0.75	0.62
Broken Hill/Kabwe	11-MPH	1.15	1.06	0.65	0.45	0.72	0.63	0.93	0.77
Swanscombe	11-MPH	0.81	0.75	0.46	0.32	0.5	0.44	0.65	0.54
La Chapelle I	12-LAH	0.94	0.86	0.52	0.36	0.57	0.5	0.73	0.61
La Ferrassie I	12-LAH	0.9	0.82	0.49	0.34	0.55	0.48	0.7	0.58
Gibraltar/Forbes Quarry	12-LAH	0.8	0.74	0.45	0.31	0.5	0.44	0.64	0.53
Cro-Magnon	13-EMH	0.97	0.88	0.53	0.37	0.59	0.52	0.75	0.63
Homo sapiens (MRI)	14-RHS	1.31	1.21	0.74	0.51	0.81	0.72	1.05	0.87

Table A-22 continued

Specimen	Group	LSR-05 CQ	RMA-05 CQ	LSR-06 CQ	RMA-06 CQ	LSR-07 CQ	LSR-10 CQ	LSR-10 CQ/EQ
C. atys (n = 4)	01-NW	0.73	0.59	0.49	0.7	0.77	1.32	0.89
C. apella(n = 4)	01-NW	0.73	0.62	0.4	0.63	0.75	1.65	0.68
S. sciureus (n = 4)	01-NW	0.47	0.52	0.15	0.31	0.46	25.35	11.36
P. cynoceph (n = 4)	02-OW	0.79	0.62	0.63	0.81	0.84	1.27	1.04
M. mulatta (n = 4)	02-OW	0.69	0.57	0.41	0.62	0.71	1.39	1.17
Hylobates (n = 4)	03-Hy	1.23	1.04	0.68	1.07	1.27	2.69	1.47
Pongo (n = 4)	04-Po	1.02	0.75	1.16	1.18	1.1	1.36	0.92
Gorilla (n = 2)	05-Go	2.17	1.61	2.17	2.41	2.33	3.03	3.18
Bonobo (n = 4)	06-Bo	1.27	0.94	1.33	1.43	1.36	1.74	1.07
Chimp I	07-PanS	1.23	0.9	1.3	1.39	1.32	1.67	1.13
STS 19	08-Aust	0.83	0.6	0.95	0.96	0.9	1.1	0.49
KNM-ER 23000	08-Aust	0.97	0.71	1.12	1.13	1.05	1.28	0.57
KNM-ER 1813	09-HH	1.07	0.77	1.24	1.24	1.15	1.4	0.44
KNM-ER 1805	09-HH	0.88	0.63	1.05	1.03	0.95	1.14	0.33
KNM-ER 1470	09-HH	0.89	0.64	1.11	1.05	0.96	1.13	0.36
Zh Loc E /III	10-HE	1.06	0.76	1.36	1.27	1.15	1.34	0.4
KNM-WT 15000	10-HE	0.85	0.61	1.09	1.02	0.92	1.08	0.36
Pitih VIII /Sangiran 17	10-HE	0.86	0.62	1.12	1.04	0.93	1.08	0.29
KNM-ER 3733	10-HE	1.08	0.77	1.36	1.28	1.17	1.37	0.46
KNM-ER 3883	10-HE	0.8	0.57	1	0.95	0.86	1.02	0.36
Trinil 2/Pith I	10-HE	0.97	0.7	1.26	1.17	1.05	1.23	0.34
Zhoukoudian Locus LI	10-HE	0.71	0.51	0.95	0.86	0.77	0.89	0.2
Broken Hill/Kabwe	11-MPH	0.88	0.63	1.18	1.07	0.96	1.1	0.25
Swanscombe	11-MPH	0.62	0.44	0.83	0.75	0.67	0.77	0.18
La Chapelle I	12-LAH	0.7	0.5	0.96	0.86	0.76	0.87	0.17
La Ferrassie I	12-LAH	0.67	0.48	0.92	0.82	0.73	0.83	0.17
Gibraltar/Forbes Quarry	12-LAH	0.61	0.43	0.82	0.74	0.66	0.76	0.19
Cro-Magnon	13-EMH	0.72	0.51	0.99	0.88	0.79	0.9	0.17
Homo sapiens (MRI)	14-RHS	1	0.71	1.35	1.21	1.08	1.24	0.24

Table A- 23: Effect of Sample Composition and Line Fitting on Residuals (Actual – Expected Cerebellar Volume)

Specimen	Group	LSR-01	RMA-01	LSR-05	RMA-05	LSR-O8	RMA-08	LSR-09	RMA-09	LSR-10
C. atys (n = 4)	01-NW	0.43	0.59	0.73	0.59	0.79	1.57	0.79	1.64	1.32
C. apella(n = 4)	01-NW	0.34	0.51	0.73	0.62	0.81	1.21	0.81	1.27	1.65
S. sciureus (n = 4)	01-NW	0.13	0.22	0.47	0.52	0.6	0.42	0.6	0.44	25.35
P. cynoceph (n = 4)	02-OW	0.56	0.71	0.79	0.62	0.84	2.11	0.84	2.19	1.27
M. mulatta (n = 4)	02-OW	0.35	0.51	0.69	0.57	0.75	1.27	0.75	1.33	1.39
Hylobates (n = 4)	03-Hy	0.59	0.87	1.23	1.04	1.36	2.08	1.36	2.19	2.69
Pongo (n = 4)	04-Po	1.09	1.13	1.02	0.75	1.04	4.62	1.04	4.74	1.36
Gorilla (n = 2)	05-Go	1.99	2.24	2.17	1.61	2.23	8.09	2.23	8.35	3.03
Bonobo (n = 4)	06-Bo	1.23	1.34	1.27	0.94	1.3	5.08	1.3	5.23	1.74
Chimp I	07-PanS	1.21	1.31	1.23	0.9	1.26	5.01	1.26	5.15	1.67
STS 19	08-Aust	0.9	0.92	0.83	0.6	0.84	3.84	0.84	3.93	1.1
KNM-ER 23000	08-Aust	1.06	1.09	0.97	0.71	0.99	4.54	0.99	4.65	1.28
KNM-ER 1813	09-HH	1.17	1.2	1.07	0.77	1.08	5.06	1.08	5.17	1.4
KNM-ER 1805	09-HH	0.99	1	0.88	0.63	0.89	4.33	0.89	4.42	1.14
KNM-ER 1470	09-HH	1.06	1.03	0.89	0.64	0.9	4.74	0.9	4.83	1.13
Zh Loc E /III	10-HE	1.31	1.25	1.06	0.76	1.07	5.92	1.07	6.02	1.34
KNM-WT 15000	10-HE	1.05	1.01	0.85	0.61	0.86	4.75	0.86	4.83	1.08
Pitih VIII /Sangiran 17	10-HE	1.08	1.02	0.86	0.62	0.87	4.96	0.87	5.03	1.08
KNM-ER 3733	10-HE	1.3	1.26	1.08	0.77	1.09	5.84	1.09	5.95	1.37
KNM-ER 3883	10-HE	0.96	0.93	0.8	0.57	0.81	4.3	0.81	4.37	1.02
Trinil 2/Pith I	10-HE	1.22	1.15	0.97	0.7	0.98	5.55	0.98	5.63	1.23
Zhoukoudian Locus LI	10-HE	0.93	0.86	0.71	0.51	0.72	4.3	0.72	4.35	0.89
Broken Hill/Kabwe	11-MPH	1.15	1.06	0.88	0.63	0.89	5.33	0.89	5.39	1.1
Swanscombe	11-MPH	0.81	0.75	0.62	0.44	0.62	3.74	0.62	3.79	0.77
La Chapelle I	12-LAH	0.94	0.86	0.7	0.5	0.71	4.44	0.71	4.49	0.87
La Ferrassie I	12-LAH	0.9	0.82	0.67	0.48	0.67	4.26	0.67	4.3	0.83
Gibraltar/Forbes Qu.	12-LAH	0.8	0.74	0.61	0.43	0.61	3.7	0.61	3.74	0.76
Cro-Magnon	13-EMH	0.97	0.88	0.72	0.51	0.73	4.55	0.73	4.59	0.9
Homo sapiens (MRI)	14-RHS	1.31	1.21	1	0.71	1	6.1	1	6.17	1.24

DEFINITIONS

cognitive: “any mental operations and structures that are involved in language, meaning, perception, conceptual systems and reason” including “aspects of . . . [the] sensory-motor system that contribute to our abilities to conceptualize and to reason”. Cognition includes both conscious and unconscious processes. (Lakoff and Johnson 1999)

cortical area: a group of processing units that performs specific mental functions

declarative memory: “memory accessible to conscious mind, encodable into symbols and language” (Purves, Augustine and Fitzpatrick 1997)

domain: “set of representations sustaining a specific area of knowledge: language, number, physics, and so forth” (Karmiloff-Smith 1996) p. 6; “an organized set of activities within a culture, one typically characterized by a specific symbol system and its attendant operations.” ((Gardner 1999), p. 82

engram: “Physiological embodiment of a memory in neural machinery due to either 1) changes in efficacy of synapses; 2) changes in synaptic connections” (Purves et al. 1997)

epigenetic: from Greek “epi” = “upon;” “related to the doctrine that the entity that will develop into a viable system (e.g., the germ cell developing into an organism) is acted upon and depends both on the conditions in its environment as well as its internal coding (i.e., it is both the phenotype and genotype that determines the emergence of the living organism)”

(Heylighen 2001); pertaining to molecular signals external to a cell which control cell differentiation by initiating the active state of expression of the genes within the cell. The epigenetic model " . . . stresses the fact that every embryological [developmental] step must be built upon the status quo ante" (Bateson 1979), p. 47. For Bateson, as for Waddington, epigenesis ideally "resembles the development a complex tautology . . . in which nothing is added after the axioms and definitions have been laid down" (ibid.). The epigenetic model of brain development, however, explicitly embraces additional information from the environment in informing the cerebral cortex.

<u>function/subfunction</u> (uncapitalized): a fundamental mental operation or process which relies on a specific neuron or group of neurons (e.g. phoneme recognition; edge detection).

<u>Function</u> (capitalized): a complex cognitive activity involving several different functions and relying on multiple distributed groups of neurons or neural networks (e.g. word retrieval; face recognition.

<u>intelligence</u>: "Using knowledge of how things work to attain goals in the face of obstacles" (Pinker 1997, p. 188).

<u>microdomain</u>: subset within particular domains e.g. gravity within the domain of physics; pronoun acquisition within the domain of language (Karmiloff-Smith 1996, p. 6).

<u>module:</u> "an information-processing unit that encapsulates the knowledge of a domain and the computations on it. . . domain specific does not

necessarily imply modularity. . . the storing and processing of information may be domain-specific without being encapsulated, hard-wired, or mandatory." (Karmiloff-Smith 1996, p. 6).

network (neural): a group of subnetworks activated in service of a function or subfunction (e.g., groups of neurons in the posterior parietal and temporal cortices, which identify the shape, and spatial location of objects).

neuropsychology: study of the relationship between brain and behavior (Churchland 1986, p. 154)

phase model: recurrent phase changes at different times across different microdomains and repeatedly within each domain (c.f. stage model)

praxis/praxic skills: "internally generated, purposive skills that are unconstrained by spatial features of the environment" (e.g. speech) (Corballis 1991)

procedural memory: "memory of unconscious skills or associations" (Purves et al. 1997)

processing unit (cortical) a vertically organized column of cortical cells

representation: a mapping of input to neural structures created when the environment impinges on the senses.

stage model: overarching changes occur simultaneously across different domains (c.f., phase model)

Standard Social Sciences Model: the contents of human minds are primarily (or entirely) free social constructions, and the social sciences are autonomous and disconnected from any evolutionary or psychological foundation (Cosmides and Tooby 1995).

subnetwork: (a group or groups of neurons, localized or distributed, which are activated in service of a specific function. E.g., neurons in the visual cortex sensitive to edges, color, texture)

REFERENCES CITED

Abe, K., H. Ukita, S. Yorifuji and T. Yanagihara (1997). Crossed cerebellar diaschisis in chronic Broca's aphasia. Neuroradiology, 39(9), 624-626.

Abitol, M. M. (1987). Obstetrics and posture in pelvic anatomy. Journal of Human Evolution, 16, 243-255.

Ackermann, H., S. Graber, I. Hertrich and I. Daum (1997). Categorical speech perception in cerebellar disorders. Brain and Language, 60(2), 323-331.

________. (1999). A Cerebellar contribution to the perception of temporal cues within the speech and nonspeech domain. Brain, 67(3), 228-241.

Ackermann, H., D. Wildgruber, I. Daum and W. Grodd (1998). Does the cerebellum contribute to cognitive aspects of speech production? A functional magnetic resonance imaging (fMRI) study in humans. Neuroscience Letters, 247(2-3), 187-190.

Aiello, L. C. (1992). Allometry and the analysis of size and shape in human evolution. Journal of Human Evolution, 22, 127-147.

Aiello, L. C. and C. Dean (1990). An introduction to human evolutionary anatomy. San Diego, Academic Press.

Akshoomoff, N. A., E. Courchesne and J. Townsend (1997). Attention coordination and anticipatory control. International Review Neurobiology, 41, 575-598.

Albrecht, G. H. and B. R. Gelvin (1987). The simple allometry equation reconsidered: Assumptions, problems, and alternative solutions. American Journal of Physical Anthropology, 72, 174.

Allsworth-Jones, P. (1990). The Szeletian and the stratigraphic succession in Central Europe and adjacent areas: Main trends, recent results, and problems for resolution. In Mellars, P. (Ed.), Emergence of Modern Humans: An archeological perspective (pp. 160-242). Ithica, New York: Cornell University Press.

________. (1993). The archaeology of Archaic and Early Modern *Homo sapiens*: An African perspective. Cambridge Archaeological Journal 3(1),21-39.

Altman, J. and S. A. Bayer (1997). Development of the cerebellar system in relation to its evolution, structure, and functions. Boca Raton, CRC Press.

Ambrose, S. H. and Lorenz, K. G. (1990). Social and ecological models for the Middle Stone Age in Southern Africa. In Mellars, P. (Ed.), Emergence of Modern Humans: An archeological perspective (pp. 3-33). Ithica, New York. Cornell University Press.

Andreasen, N. C., T. Cizadlo, G. Harris, V. Swayze II, D. S. O'Leary, G. Cohen, J. Ehrhardt and W. T. C. Yuh (1993a). Voxel processing techniques for the antemortem study of neuroanatomy and neuropathology using magnetic resonance imaging. Journal of Neuropsychiatry, 5(2), 121-130.

Andreasen, N. C., G. Cohen, G. Harris, T. Cizadlo, J. Parkkinen, K. Rezai and V. Swayze II (1992). Image processing for the study of brain structure and function: Problems and programs. Journal of Neuropsychiatry and Clinical Neurosciences, 4, 125-133.

Andreasen, N. C., M. Flaum, V. d. Swayze, D. S. O'Leary, R. Alliger, G. Cohen, J. Ehrhardt and W. T. C. Yuh (1993b). Intelligence and brain structure in normal individuals. American Journal of Psychiatry, 150(1), 130-134.

Andreasen, N. C., G. Harris, T. Cizadlo, S. Arndt, D. S. O'Leary, V. Swayze II and M. Flaum (1994). Techniques for measuring sulcal/gyral patterns in the brain as visualized through magnetic resonance scanning: Brainplot and brainmap. Proceedings of the National Academy of Sciences, USA, 90, 93-97.

Andreasen, N. C., R. Rajarethinam, T. Cizaldo, S. Arndt, V. W. Swayze II, L. A. Flashman, D. S. O'Leary, J. C. Ehrhardt and W. T. C. Yuh (1996). Automatic atlas-based volume estimation of human brain regions from MR images. Journal of Computer Assisted Tomography, 20(1), 98-106.

Ankney, C. D. (1992). Sex differences in relative brain size: The mismeasure of woman, too? Intelligence, 16, 329-336.

Annett, M. (1972). The distribution of manual asymmetry. British Journal of Psychology, 63(3), 343-358.

________. (1985). Left, right, hand and brain: The right shift theory. London: Earlbaum.

Anton, S. C. (1989). Intentional cranial vault deformation and induced changes of the cranial base and face. American Journal of Physical Anthropology, 79, 253-267.

Arambourg, C. (1963). La corrélation Eurafricane du Quarternaire. Bulletin de la Société Préhistorique Française, 59(Parts I-II).

Arensburg, B., L. A. Schepartz, A. M. Tillier, B. Vandermeersch and Y. Rak (1990). A reappraisal of the anatomical basis for speech in Middle Paleolithic hominids. American Journal of Physical Anthropology, 83, 137-146.

Arensburg, B., A. M. Tillier, B. Vandermeersch, H. Duday, L. A. Schepartz and Y. Rak (1989). A Middle Paleolithic human hyoid bone. Nature, 338, 758-760.

Armstrong, E. (1980). A quantitative comparison of the hominoid thalamus. III. A motor substrate - the venterolateral complex. American Journal of Physical Anthropology, 52, 405-419.

________. (1981). A quantitative comparison of the hominoid thalamus. IV: Posterior association nuclei - the pulvinar and lateral posterior nucleus. American Journal of Physical Anthropology, 55, 369-383.

________. (1982). Mosaic evolution in the primate brain: Differences and similarities in the hominoid thalamus. In Armstrong, E. and D. Falk (Eds.), Primate brain evolution: Methods and concepts (pp. 131-161). New York and London: Plenum Press.

________. (1983). Relative brain size and metabolism in mammals. Science, 220, 1302-1304.

Arnold, A. P. and S. W. Bottjer (1985). Cerebral lateralization in birds. In Glick, S.D. (Ed.), Cerebral lateralization in non-human species. London: Academic Press.

Arriada-Mendicoa, N., E. Otero-Siliceo and T. Corona-Vazquez (1999). Current concepts regarding the cerebellum and cognition. Revue Neurologique, 29(11), 1075-82.

Asfaw, B., T. D. White and C. O. Lovejoy (1999). *Australopithecus gahri*: A new species of early hominid from Ethiopia. Science, 284, 629-635.

Austin, E. (1995). Right is right. In Jacoby, R. and Glauberman, N. (Eds.), The bell curve debate: History, documents, references (pp. 302-304). New York: Times Random House.

Azari, N. P. and R. J. Seitz (2000). Brain plasticity and recovery from stroke. American Scientist, (September-October).

Bahn, P. G. (983). Late Pleistocene economies of the French Pyrenees. In Bailey, G.N. (Ed.), Hunter-gatherer economy in prehistory: A European perspective (pp. 168-186). New York: Cambridge University Press.

Bailey, G. (1983). Economic change in Late Pleistocene Cantabria. In Hunter-gatherer economy in prehistory: A European perspective (pp. 149-165). In Bailey, G. N., (Ed.), New York: Cambridge University Press.

Bar-Yosef, Ofer. (1989).Geochronology of the Levantine Middle Paleolithic. In Mellars, P. and Stringer, C. (Eds.), The Human Revolution: Behavioral and Biological Perspectives on the Origins of Modern Humans (pp. 598-610). Princeton: Princeton University Press.

Barinaga (1996). The cerebellum: Movement coordinator or much more? Science, 272: 482-483.

Bateson, G. (1979). Mind and nature: A necessary unity. New York: E.P. Dutton.

Bauchot, R. (1978). Encephalization in vertebrates. Brain Behavior and Evolution, 15, 1-18.

________. (1982). Brain organization and taxonomic relationships in insectivora and primates. In Armstrong, E. and Falk, D. (Eds.), Primate brain evolution: Methods and concepts (pp. 163-175). New York: Plenum Press.

Bauchot, R. and H. Stephan (1966). Données nouvelles sur l'encéphalisation des insectivores et des prosimiens. Mammalia, 30, 160-196.

________. (1969). Encéphalisation et niveau évolutive chez les simiens. Mammalia, 33, 235-275.

Beals, K. L., C. L. Smith and S. M. Dodd (1984). Brain size, cranial morphology, climate and time machines. Current Anthropology, 25, 301-330.

Bednarik, R. G. (1992). Paleoart and archaeological myths. Cambridge Archaeological Journal, 2(1): 27-57.

________. (1995). Concept-mediated marking in the lower Palaeolithic. Current Anthropology, 36: 605-634.

________. (1992). Paleoart and archaeological myths. Cambridge Archaeological Journal, 2:272-43.

Begun, D. and A. Walker (1993). The endocast. In Walker, A. and R.E. Leakey (Eds.), The Nariokotome *Homo erectus* skeleton (pp. 326-358). Cambridge: Harvard University Press.

Bell, C. C., V. Z. Han, Y. Sugawara and K. Grant (1997). Synaptic plasticity in a cerebellum-like structure depends on temporal order. Nature, 387, 278-281.

Berge, C., R. Orbjan-Segebarth and P. Schmid (1984). Obstetrical interpretation of the australopithecine pelvic cavity. Journal of Human Evolution, 13, 573-587.

Beyries, S. (1988). Functional variability of lithic sets in the middle Paleolithic. In Dibble, H. I. and A. Montet-White (Eds.), Upper Pleistocene prehistory of western Eurasia (pp. 214-223). Philadelphia, The University Museum, University of Pennsylvania.

Biberson, P. (1961). Le Paléolitique Inférieur du Maroc Atlantique. Rabat, Publications du Service des Antiquités du Maroc.

Bickerkton, D. (1995). Language and human behavior. Seattle, University of Washington Press.

Binford, L. (1982). Comment on R. White 'Rethinking the Middle/Upper Palaeolithic transition'. Current Anthropology, 23, 177-181.

Binford, L. (1984). Butchering, sharing and the archaeological record. Journal of Anthropological Archaeology, 3, 235-257.

Binford, L. and S. Binford (1966). A preliminary analysis of functional variability in the Mousterian and upper Paleolithic. American Anthropologist, 68, 236-295.

Binford, S. and L. Binford (1969). Stone tools and human behavior. Scientific American 220, 70-84.

Bioulac, B., P. Burbaud and D. Varoquequx (1995). Activity of area 5 neurons in monkeys during arm movements: Effects of dentate nucleus lesion and motor cortex ablation. Neuroscience Letters, 192: 189-192.

Bischoff, J. N. Soler, J. Maroto and R. Julia. 1989. Abrupt Mousterian/Aurignacian boundary at c. 40 ka bp: Accelerator 14C dates from L'Arbreda Cave (Catalunya, Spain). Journal of Archaeological Science, *16*, 553-576*.*

Boëda, E. (1988). Le concept Levallois et evaluation de son champ d'application. L'homme de Néandertal. Meudon-Bellevue, France, U.R.A. 28 du C.R.A. du C.N.R.S. 4, La Technique, 13-26.

Bonin, G. von (1937). Brain weight and body weight in mammals. Journal of General Psychology, 16, 379-389.

Bookstein, F. (1997). Biometrics and brainmaps: The promise of the morphometric synthesis. In Koslow, S.H. and M. F. Huerta (Eds.), Neuroinformatics: An overview of the human brain project (pp. 203-254). New Jersey, Lawrence Erlbaum.

Bookstein, F., K. Schafer, H. Prossinger, H. Seidler, M. Fieder, C. Stringer, G. W. Weber, J. L. Arsuaga, D. E. Slice, F. J. Rohlf, W. Recheis, A. J. Mariam and L. F. Marcus (1999). Comparing frontal cranial profiles in archaic and modern *Homo* by morphometric analysis. Anatomical Record, 257(6), 217-224.

Bordes, F. (1950). L'évolution buissonante des industries en Europe occidentale: Considérations théoretiques sur le Paléolitique ancien et moyen. L'Anthropologie, 54, 393-420.

________. (1953). Essai de classification des industries Moustériennes. Bulletin de la Société Française, 50, 457-466.

________. (1961). Mousterian cultures in France. Science, 134(3482), 803-810.

Bouchard, T. J. (1993). The genetic architecture of human intelligence. In Vernon, P.A. (Ed.), Biological approaches to the study of human intelligence (pp. 33-85). Norwood, NJ, Ablex.

Boule, M. M. and R. Anthony (1911). L’encéphale de l’homme fossile de La Chapelle-aux-Saints. L'Anthropologie, 23, 9-196.

Bower, B. (1998). Cutting-edge pursuits in stone age. Science News, 153, 238.

Bracke-Tolkmitt, R., A. Linden, A. G. M. Canavan, B. Rockstroh, E. Scholz, K. Wessel and H.-C. Diener (1989). The cerebellum contributes to mental skills. Behavioral Neuroscience, 103, 442-446.

Braitenberg, V., D. Heck and F. Sultan (1997). The detection and generation of sequences as a key to cerebellar function: Experiments and theory. Behavioral and Brain Sciences, 20, 229-277.

Brandt, A. (1867). Sur le rapport du poids du cerveau à celui du corps chez différents animaux. Bulletin de la Société Impériale des Naturalistes de Moscou, 40, 525-543.

Braun, M. (1996). Applications de la scanographie a rx et de l'imagerie virtuelle en paléontologie humaine, 1 & 2. Paris, Museum Nationalle d'Histoire Naturelle.

Breitinger, E. (1952). Zur morphologie und systematischer stellung des schädelfragmentes von Swanscombe. Homo 3, 131-133.

________. (1955). Das schädelfragmentes von Swanscombe und das 'praesapiens-problem.' Mitteilungen der Anthropologischen Gesellschaft in Wien, 84/85, 1-45.

Brennan, M. U. (1997). Nonspecific indicators of stress in the Upper Paleolithic. 1997. Mary Ursula Brennan. Paper for AAA 86th Annual Meeting. November 20, 1997. New York: New York University.

Broca, M. P. (1861). La forme du cerveau: Suivant les individus et suivant les races. Paris, Typographie Hennuyer.

Brodal, P. and J. G. Bjaalie (1997). Salient anatomic features of the cortico-ponto-cerebellar pathway. Progress in Brain Research, 114, 227-249.

Brodmann, K. (1909). Vergleischende lokalisationslehre der groshirnrinde. Leipzig, J. A. Barth.

Brooks, A. and J. Yellen. (1996, April). "The Middle Stone Age of the Middle Awash: A preliminary report of recent research in Ethiopia. Paleoanthroplogy Society Abstracts (p. 3). Paper presented at the annual meeting of the Paleoanthropology Society, New Orleans.

Browne, B. and R. M. T. Simmons (1983). Quantitative studies of the evolution of the thalamus in primates. Journal für Hirnforschung, 25, 261-74.

Burt, C. (1909). Experimental tests of general intelligence. British Journal of Psychology (London), 3, 94-177.

Byers, A. M. (1994). Symboling and the Middle-Upper Paleolithic transition. Current Anthropology, 35, 369-399.

Byrne, R. (1996). Relating brain size to intelligence in primates. In Mellars, P. and Gibson, K. (Eds.), Modelling the early human mind (pp. 49-56). Cambridge: McDonald Institute for Archaeological Research.

Calvin, W. H. (1983). A stone's throw and its launch window: Timing precision and its implications for language and hominid brains. Journal of Theoretical Biology, 104, 121-135.

Calvin, W. H. and D. Bickerton (2000). Lingua ex machina: Reconciling Darwin and Chomsky with the human brain. Cambridge: The MIT Press.

Chase, P. G. (1990). Tool-making tools and middle Paleolithic behavior. Current Anthropology, 31, 443-447.

Chase, P. G. and H. I. Dibble (1987). Middle Paleolithic symbolism: A review of current evidence and interpretations. Journal of Anthropological Archaeology, 6, 263-296.

________. (1992). Reply to Bednarik. Cambridge Archaeological Journal, 2, 43-51.

Chomsky, N. (1980). On cognitive structures and their development: A reply to Piaget. Language and learning: The debate between Jean Piaget and Noam Chomsky. M. Piattelli-Palmarini. Cambridge: Harvard University Press.

Churchill, S. E. (1994). Human upper body evolution in the Eurasian later Pleistocene. Unpublished Doctoral dissertation. Albuquerque, New Mexico, University of New Mexico.

Churchill, S. E., A. H. Weaver and W. A. Niewoehner (1999). Late Pleistocene human technological and subsistence behavior: Functional interpretations of upper limb morphology. In Bietti, W. and S. Grimaldi (Eds.), Reduction processes (chaînes opératoires) in the European Mousterian. Quaternaria. Nova, 6.

Churchland, P. S. (1986). Neurophilosophy. Cambridge: The MIT Press.

Clark, A. and D. Chalmers (1998). The extended mind. Analysis 58(1), 7-19.

Clark, G. A. (1977). World prehistory. Cambridge: Cambridge University Press.

________. (1992). Continuity or Replacement? Putting Modern Human Origins in an Evolutionary Context. In Dibble, H. and P. Mellars (Eds.), The Middle Paleolithic Adaptation, Behavior and Variability (pp. 626-676). University Symposium Series #78. University of Pennsylvania.

Clark, J. D. (1969). Kalambo falls prehistoric site. Cambridge: Cambridge University Press.

________. (1970). The prehistory of Africa. New York: Praeger.

________. (1977). World prehistory: A new perspective. Cambridge: Cambridge University Press.

Colqhuhoun, I. C. (1994). Drinking behavior and left-handed preference among Eulemur Macaco macaco at Ambato Massi, Madagascar (Abstract). American Journal of Physical Anthropology (Supplement 18), 69.

Coltorti, M., M. Cremaschi, M. C. Delitatala, D. Esu, M. Fornaseri, A. N. McPherron, M., R. Van Otterloo, C. Peretto, B. Sala, V. Schmidt and J. Sevink (1981). Isernia de la Pineta: Lower Paleolithic with fauna before 0.7 my in the upper Bolturno basin, central Italy: First report. J. D. Clark and G. Isaac. México, UISPP. X Congresso, Comisión VI.

Conn, P. M. (1995). Neuroscience in medicine. Philadelphia, J.B. Lippincott Company.

Conrad, R. H. and J. L. Gutman (1996). Conversion equations between fork length and total length for chinook salmon (Oncorhynchus tshawytscha). Northwest Fishery Resource Bulletin. Project Report Series No. 5.

Conroy, G. C., D. Falk, J. Guyer, G. W. Weber, H. Seidler and W. Recheis (2000). Endocranial capacity in STS 71 (*Australopithecus africanus*) by three-dimensional computed tomography. The Anatomical Record, 258, 391-396.

Conroy, G. C. and M. W. Vannier (1985). Endocranial volume determination of matrix filled fossil skulls using high resolution computed tomography. In Tobias, P.V. (Ed.), Hominid evolution: Past, present and future (pp. 419-426). New York: Alan R. Liss.

Conroy, G. C., M. W. Vannier and P. V. Tobias (1990). Endocranial features of *Australopithecus africanus* revealed by 2- and 3-d computed tomography. Science, 247, 838-841.

Conroy, G. C., G. W. Weber, H. Seidler, P. V. Tobias, A. Kane and B. Brunsden (1998). Endocranial capacity in an early hominid cranium from Sterkfontein, South Africa. Science, 280, 1730-1731.

Corballis, M. C. (1991). The lopsided ape: Evolution of the generative mind. New York: Oxford University Press.

Cosmides, L. and J. Tooby (1995). From function to structure: The role of evolutionary biology and computational theories in cognitive neuroscience. In Gazzaniga, M.S. (Ed.), The cognitive neurosciences (pp.1199-1210). Cambridge: The MIT Press.

Count, E. W. (1947). Brain and body weight in man. Their antecedents in growth and evolution. Annals of the New York Academy of Sciences 446, 993-1122.

Creutzfeldt, O. D. (1979). Neurophysiological mechanisms and consciousness. Ciba Foundation Symposium 69, 217-233.

Crosby, E. C., T. Humphrey and E. W. Lauer (1962). Correlative anatomy of the nervous system. New York: The MacMillan Company.

De Beaune, S. (1994). Commentary on Symboling and the Middle-to-Upper Paleolithic transition. Current Anthropology, 35, 369-400.

D'Errico, F., J. Zilhão, D. Baffier, M. Julien and J. Pelegrin (1998). Neanderthal acculturation in western Europe. Current Anthropology, 39 (Supplement): S1-S44.

Damasio, A. R. (1994). Descartes' error: Emotion, reason, and the human brain. New York: Avon Books.

Dart, R. A. (1925). *Australopithecus africanus*: The man-ape of south Africa. Nature, 115, 195-199.

Daum, I. and H. Ackermann (1997). Nondeclarative memory -- neuropsychological findings and neuroanatomic principles. Fortschritte der Neurologie-Psychiatrie (Stuttgart), 65(3), 122-132.

Daum, I., H. Ackermann, m. M. Schugens, C. Reimold, J. Dichgans and N. Birnbaumer (1993). The cerebellum and cognitive functions in humans. Behavioral Neuroscience, 107(3), 411-419.

Davidson, I. and D. Nobel (1993). On the evolution of language. Current Anthropology, 34, 165-170.

Day, M. H. (1986). Guide to fossil man. Chicago, University of Chicago Press.

De Gusta, D. (1999). Hypoglossal canal size and hominid speech. Proceedings of the National Academy of Sciences USA, 96, 1800.

Deacon, H. J. (1989). Late Pleistocene palaeoecology and archaeology in the southern Cape, South Africa. In Mellars, P. and C. Stringer (Eds.), The human revolution: Behavioral and biological perspectives in the origins of modern humans (pp. 547-464). Edinburgh: Edinburgh University Press.

Deacon, T. W. (1990a). Fallacies of progression in theories of brain-size evolution. International Journal of Primatology, 11(3), 193-235.

________. (1990b). Problems of ontogeny and phylogeny in brain-size evolution. International Journal of Primatology, 11(3), 237-282.

________. (1997). The symbolic species. New York: W.W. Norton & Company.

Dean, C. and B. A. Wood (1981). Metrical analysis of the basicranium of extant hominoids and Australopithecus. American Journal of Physical Anthropology, 54, 63-71.

Dean, M. C. (1988). Growth processes in the cranial base of hominoids and their bearing on morphological similarities that exist in the cranial base of *Homo* and *Paranthropus*. In Grine, F.E. (Ed.), Evolutionary history of the "robust" australopithecines (pp. 107-111). New York: Aldine de Gruyter.

Dean, M. C. and B. A. Wood (1984). Phylogeny, neoteny and growth of the cranial base in hominoids. Folia Primatologica (Basel), 43, 157-180.

Decety, J., H. Sjöholm, E. Ryding, G. Stenberg and D. H. Ingvar (1990). The cerebellum participates in mental activity: Tomographic measurements of regional cerebral blood flow. Brain Research, 535, 313-317.

Delson, E., I. Tattersal, J. A. Van Couvering and A. S. Brooks (2000). Kabwe. Encyclopedia of human evolution and prehistory. New York: Garland Publishing, Inc.

Dennenberg, V. H. (1981). Hemispheric laterality in animals and the effects of early experience. Behavioral and Brain Sciences 4, 1-50.

________. (1996). Kinds of minds: Toward an understanding of consciousness. New York: Basic Books.

Dennett, D. C. (1988). The intentional stance in theory and practice. In Byrne, R. and A. Whiten (Eds.), Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes and humans. Oxford, Clarendon Press.

Desmond, J. E., J. D. E. Gabrieli and G. H. Glover (1998). Dissociation of frontal and cerebellar activity in a cognitive task: Evidence for a distinction between selection and search. Neuroimage, 7, 368-376.

Dibble, H. I. (1987). Reduction sequences in the manufacture of Mousterian implements of France. In Soffer, O. (Ed.), The Pleistocene Old World: Regional perspectives (pp. 33-44). New York: Plenum Press.

Dominguez-Rodrigo, M., J. Serrallonga, J. Juan-Tresserras, L. Alcala and L. Luque (2001). Woodworking activities by early humans: A plant residue analysis on Acheulean stone tools from Peninj (Tanzania) (Abstract). Journal of Human Evolution 40, 289-299.

Donald, M. (1991). Origins of the modern human mind. Cambridge: Harvard University Press.

________ . (2001). A mind so rare: the evolution of human consciousness. New York. W.W. Norton & Company.

Doyon, J., D. Gaudreau, R. J. Laforce, M. Castonguay, P. J. Bedard, F. Bedard and J. P. Bouchard (1997). Role of the striatum, cerebellum, and frontal lobes in the learning of a visuomotor sequence. Brain and Cognition, 3, 218-45.

Dubois, E. (1897). Sur le rapport du poids de l'encéphale avec la grandeur du corps chez mammifières. Bulletin et Mémoires de la Société d'Anthropologie de Paris, 4, 337-376.

Duchin, L. E. (1990). The evolution of articulate speech: Comparative anatomy of the oral cavity in *Pan* and *Homo*. Journal of Human Evolution, 19, 687-697.

Dunbar, R. I. M. (1992). Neocortex size as a constraint on group size in primates. Journal of Human Evolution, 20, 469-493.

Duncan, J., R. J. Seitz, J. Kolodny, D. Bor, H. Herzog, A. Ahmed, F. N. Newell and H. Emslie (2000). A neural basis for general intelligence. Science, 289, 457-460.

Ebner, T. and F. Qinggong (1997). What features of visually guided arm movements are encoded in the simple spike discharge of cerebellar Purkinje cells? In De Zeeuw, C.I. and Voogd, J. (Eds.), Progress in Brain Research (pp. 431-446). Amsterdam, Elsevier Publishers.

Eccles, J. C. (1989). Evolution of the brain: Creation of the self. London and New York: Routledge.

Efron, R. (1990). The decline and fall of hemispheric specialization. Hillsdale, NJ, Lawrence Erlbaum Associates.

Elman, J. L., E. Bates, M. H. Johnson, A. Karmiloff-Smith, D. Parisi and K. Plunkett (1996). Rethinking innateness: A connectionist perspective on development. Cambridge: The MIT Press.

Eysenck, H. J. (1993). The biological basis of intelligence. In Vernon, P.A. (Ed.), Biological approaches to the study of human intelligence(pp. 1-32). Norwood, N.J., Ablex.

Falk, D. (1975). Comparative anatomy of the larynx in man and the chimpanzee: Implications for language in Neanderthals. American Journal of Physical Anthropology, 43, 123-132.

________. (1980). Hominid brain evolution: The approach from paleoneurology. Yearbook of Physical Anthropology, 23, 72-78.

________. (1983). Cerebral cortices of east African early hominids. Science, 221, 1072-1073.

________. (1990). Brain evolution in *Homo*: The "radiator" theory. Behavioral and Brain Sciences, 13, 333-381.

________. (1992). Braindance. New York: Henry Holt and Company.

________. (1993). Sex differences in visuospatial skills: Implications for hominid evolution. In K. Gibson and T. Ingold (Eds.), Tools, language and cognition in human evolution (pp. 216-229). Cambridge: Cambridge University Press.

Falk, D., J. Guyer, J. Redmond, G. C. Conroy, W. Recheis, G. W. Weber and H. Seidler (in press). Early hominid brain evolution: A new look at old endocasts. Journal of Human Evolution.

Falk, D., C. Hildebolt and M. W. Vannier (1989). Reassessment of the Taung early hominid from a neurological perspective. Journal of Human Evolution, 18, 485-92.

Flourens, P. (1824). Recherches expérimentales sur les propriétés et les fonctions du système nerveux dans les animaux vertébrés. Paris, Crevot.

Fodor, J. A. (1983). The modularity of mind: An essay based on faculty psychology. Cambridge: The MIT Press.

Ford, E. H. R. (1956). The growth of the fetal skull. Journal of Anatomy (London), 90, 63-72.

Fox, P. T., M. E. Raichle and W. T. Thach (1985). Functional mapping of the human cerebellum with positron emission tomography. Proceedings of the National Academy of Sciences USA, 82, 7462-7466.

Fox, P. T., and L. M. Parsons. (1999). Neural basis of the comprehension of musical harmony, melody and rhythm. In Duke, R.A. (Editor), Texas Music

Education Research (pp. 21-24). Austin, Texas Music Educators Association.

Frayer, D. W. (1992). Cranial base flattening in Europe: Neanderthals and more recent *Homo sapiens* (abstract). American Journal of Physical Anthropology, (Supplement 14), 77.

Freeman, L. G. (1978). Mousterian worked bone from Cueva Morín (Santander, Spain): A preliminary description. In L. G. Freeman (Ed.), View of the past (pp. 29-51). The Hague, Mouton.

Fulbright, R. K., A. R. Jenner, W. E. Mencl, K. R. Pugh, B. A. Shaywitz, S. E. Shaywitz, S. J. Frost, P. Skudlarski, R. T. Constable, C. M. Lacadie, K. E. Marchione and J. C. Gore (1999). The cerebellum's role in reading: A functional MR imaging study. American Journal Neuroradiology, 20, 1925-1930.

Gabow, S. L. (1977). Population structure and the rate of hominid brain evolution. Journal of Human Evolution, 6, 643-665.

Gall, F. J. (1968). Anatomie et physiologie du systèm nerveux en général, et du cerveau en particular. Excerpted and translated in The human brain and spinal cord: A historical study illustrated by writings from antiquity to the twentieth century. E. Clarcke and C. D. O'Malley (Eds.), Berkeley and Los Angeles, University of California Press (Originally published 1812, Paris, Schoell).

Gannon, P. J., A. R. Eden and J. Laitman (1988). The subarcuate fossa and cerebellum of extant primates: Comparative study of a skull-brain interface. American Journal of Physical Anthropology, 77, 143-164.

Gannon, P. J., R. L. Holloway, D. C. Broadfield and A. R. Braun (1998). Asymmetry of chimpanzee planum temporale: Humanlike pattern of Wernicke's brain language area homolog. Science, 279, 220-222.

Gao, J.-H., L. M. Parsons, J. M. Bower, J. Xiong, J. Li and P. T. Fox (1996). Cerebellum implicated in sensory acquisition and discrimination rather than motor control. Science, 272.

Gardner, H. (1993). Frames of mind: The theory of multiple intelligences. New York: Basic Books.

________. (1999). Intelligence reframed. New York: Basic Books.

Gardner, R. A., B. T. Gardner and T. van Cantford (1989). Teaching sign language to chimpanzees. Albany, State University of New York Press.

Gazzaniga, M. S. (1967). Language after section of the cerebral commissures. Brain, 90. 131-148.

________. (1970). The bisected brain. New York: Appleton-Century-Crofts.
Gazzaniga, M. S. (1983). Right hemisphere language following brain bisection: A twenty year perspective. American Psychologist, 385, 525-537.

Gazzaniga, M. S., J. E. Bogen and R. W. Sperry (1962). Some functional effects of sectioning the cerebral commissures in man. Proceedings of the National Academy of Sciences (USA), 48, 1765-1769.

Geshwind, N. (1965). Disconnexion syndromes in animals and man. Brain, 88, 237-294; 585-644.

Geschwind, N. and W. Levitsky (1978). Human brain: Left-right asymmetries in temporal speech region. Science, 161, 186-187.

Gilissen, E., A. Dabringhaus, G. Schlaug, T. Schormann, H. Steinmetz and K. Zilles (1996a). Structural asymmetries in the cortical shape of humans and common chimpanzees: A comparative study with magnetic resonance tomography. Proceedings of the 3rd Joint Symposium on Neural Computation University of California, San Diego and California Institute of Technology, California Institute of Technology.

Gilissen, E., M.-T. Iba-Zizen, J.-L. Stievenart, A. Lopez, m. Trad, E. a. Cabanis and K. Zilles (1995). Is the length of the calcarine sulcus associated with the size of the human visual cortex? A morphometric study with magnetic resonance tomography. Journal of Brain Research, 36, 451-459.

Gilissen, E., H. Steinmetz, A. Dabringhaus, G. Schlaug, T. Schormann and K. Zilles (1996b). Evolution of the forebrain: A comparative magnetic resonance study of the hemispheric shape in common chimpanzees and humans. Proceedings of the 3rd Joint Symposium on Neural Computation, University of California, San Diego and California Institute of Technology, California Institute of Technology.

Gilissen, E. and K. Zilles (1995). The relative volume of the primary visual cortex and its intersubject variability among humans: A new morphometric study. Comptes Rendus de l'Académie des Sciences de Paris, 320 (Série 2a), 897-902.

________. (1996). The calcarine sulcus as an estimate of the total volume of the human striate cortex: A morphometric study of reliability and intersubject variability. Journal of Brain Research, 37(1): 57-66.

Goleman, D. (1995). Emotional intelligence: Why it can matter more than IQ. New York: Bantam Books.

Gould, S. J. (1966). Allometry and size in ontogeny and phylogeny. Biological Review, 41, 587-640.

________. (1978). Morton's ranking of races by cranial capacity. Science, 200, 503-509.

________. (1996). The mismeasure of man. New York and London: W.W. Norton & Company.

Gowlett, J. A. J. (1984). Mental abilities of early man: A look at some hard evidence. In R. A. Foley (Ed.), Hominid evolution and community ecology (pp. 167-192). London: Academic Press.

Gowlett, J. A. J. (1986). Culture and conceptualisation: The Oldowan-Acheulean gradient. In Bailey, G.N. and P. Callow (Eds.), Stone age prehistory: Studies in memory of Charles McBurney (pp. 243--260). Cambridge: Cambridge University Press.

________. (1996). Mental abilities of early *Homo*: Elements of constraint and choice in rule systems. In Mellars, P. and K. Gibson (Eds.), Modelling the early human mind (pp. 191-215). Cambridge: McDonald Institute for Archaeological Research.

Grafman, J., I. Litvan, S. Massaquoi, M. Stewart, A. Sirigu and M. Hallett (1992). Cognitive planning deficit in patients with cerebellar atrophy. Neurology, 42, 1493-1496.

Grasby, P. M., C. D. Frith, K. J. Friston, C. Bench, R. S. J. Frackowiak and R. J. Dolan (1993). Functional mapping of brain areas implicated in auditory-verbal memory function. Brain, 116, 1-20.

Greenfield, P. M. and E. S. Savage-Rumbaugh (1990). Grammatical combination in *Pan paniscus:* Processes of learning and invention in the evolution and development of language. In Parker, S.T. and K. Gibson (Eds.), "Language" and intelligence in monkeys and apes (pp. 540-578). New York: Cambridge University Press.

Habib, M., F. Robichon, O. Lévrier, R. Khalil and G. Salamon (1995). Diverging asymmetries of temporo-parietal cortical areas: A reappraisal of Geschwind/Galaburda theory. Brain and Language, 48, 238-258.

Haggard, P., J. Jenner, and A. Wing (1994). Coordination of aimed movements in a case of unilateral cerebellar damage. Neuropsychologia (Oxford), 32, 827-846.

Haines, D. E. (1986). The primate cerebellum comparative primate biology. In Swindler, E.R. and J. Erwin (Eds.), Comparative primate biology 1: Systematics, Evolution and Anatomy (pp. 491-535). New York: Alan R. Liss, Inc.

Hamilton, C. R. and B. A. Vermeire (1988). Complementary hemispheric specialization in monkeys. Science, 242, 1691-1694.

Harlow, J. M. (1868). Recovery from the passage of an iron bar through the head. Massachusetts Medical Society Publications 2, 327-347.

Harris, J. W. K. (1983). Cultural beginnings: Plio-Pleistocene archaeological occurrences from the Afar, Ethiopia. African Archaeological Review 1, 3-31.

Harris, J. W. K. and S. Semaw (1989). Further archaeological studies at the Gona River, Hadar, Ethiopia. Nyame Akuma, 31, 19-21.

Harrold, Francis B. (1989). Mousterian, Châtelperronian and early Aurignacian in Western Europe: Continuity or discontinuity? In Mellars, P. and C. Stringer (Eds.), The human revolution: behavioral and biological perspectives on the origins of modern humans (pp. 677-713). Edinburgh: Edinburgh University Press.

Harvey, P. H. and T. H. Clutton-Brock (1985). Life history variation in primates. Evolution, 39, 559-581.

Harvey, P. H., and J. R. Krebs (1990). Comparing brains. Science, 249, 140-145.

Haug, H. (1987). Brain sizes, surfaces, and neuronal sizes of the cortex cerebri: A stereological investigation of man and his variability and a comparison with some species of mammals (primates, whales, marsupials, insectivores, and one elephant). American Journal of Anatomy, 180, 126-142.

Hefner, H. E. and R. S. Heffner (1986). Effect of unilateral and bilateral auditory cortex lesions on the discrimination of vocalizations by Japanese macaques (Abstract). Journal of Neurophysiology, 56, 683-701.

Heilbroner, P. L. and R. L. Holloway (1989). Anatomical brain asymmetry in monkeys: Frontal, temporoparietal, and limbic cortex in *Macaca*. American Journal of Physical Anthropology, 80, 203-211.

Heillige, J. B. (1993). Hemispheric asymmetry. Cambridge MA, Harvard University Press.

Heim, J.-L. (1976). Les hommes fossiles de La Férrassie I. Archives de l'institut de Paléontologie Humaine. (Mémoire 35), 217-246.

________. (1989). La nouvelle reconstitution de crâne de La Chapelle-aux-Saints méthode et résultats.” Bulletin et Mémoires de la Société d'Anthropologie de Paris 1(1-2), 95-118.

Henneberg, M. (1990). Brain size/body weight variability in Homo sapiens: Consequences for interpreting hominid evolution. Homo 39 (3 & 4), 121-129.

Henning, I. and S. Clausen (1989). Cranial capacity in *Homo erectus*: Stasis or non-stasis, direction or trend. Hominidae. Proceedings of the 2nd International Congress of Human Paleontology (pp. 217-220). Milan: Editoriale Jaca Book.

Herrnstein, R. J. and C. Murray (1994). The bell curve. New York: The Free Press.

Heylighen, F. Web dictionary of cybernetics and systems. Heylighen, F. (Compiler and Editor), Principia Cybernetica Web. <http://pespmc1.vub.ac.be/ASC/INDEXASC.html> Last modified 2001, April.

Hiscock, M., L. C. Cole, J. G. Benthall, V. L. Carlson and J. M. Ricketts (2000). Toward solving the inferential problem in laterality research: Effects of increased reliability on the validity of the dichotic listening right-ear advantage. Journal of the International Neuropsychological Association, 6, 539-547.

Holloway, R. L. (1964). Some aspects of quantitative relations in the primate brain. Unpublished Doctoral Dissertation. University of California, Berkeley.

________. (1966). Cranial capacity, neural reorganization, and hominid evolution: A search for more suitable parameters. American Anthropologist, 68, 103-120.

________. (1967). The evolution of the human brain: Some notes toward a synthesis between neural structure and the evolution of complex behavior. General Systems, 12, 3-19.

________. (1969). Culture: A human domain. Current Anthropology, 10, 395-412.

________. (1972a). Australopithecine endocasts, brain evolution in the hominoidea, and a model of hominid brain evolution. In Tuttle, R. (Ed.), The functional and evolutionary biology of primates (pp. 185-204). Chicago and New York: Aldine-Atherton.

________. (1972b). New australopithecine endocast, SK 1585, from Swartkrans, South Africa. American Journal of Physical Anthropology, 37, 173-185.

________. (1973). New endocranial values for the east African early hominids. Nature, 243, 97-99.

________. (1975a). Early hominid endocasts: Volumes, morphology and significance. In Tuttle, R. (Ed.), Primate functional morphology and evolution (pp. 393-416). The Hague, Mouton.

________. (1975b). The role of human social behavior in the evolution of the brain. 43rd James Arthur Lecture at American Museum of Natural History (1973). New York: American Museum of Natural History.

________. (1976). Paleoneurological evidence for language origins. Annals of the New York Academy of Sciences, 280, 330-348.

________. (1978). Problems of brain endocast interpretation and African hominid evolution. In Jolly, C. (Ed.), Early hominids of Africa (pp. 379-401). London: Duckworth.

________. (1979). Brain size, allometry, and reorganization: Toward a synthesis. In Hahn, M.E., C. Jensen and B. C. Dudek (Eds.), Development and evolution of brain size: Behavioral implications (pp. 59-88). New York: Academic Press.

________. (1980). Indonesian "Solo" (Ngandong) endocranial reconstructions: Some preliminary observations and comparisons with Neandertal and *Homo erectus* groups. American Journal of Physical Anthropology, 53, 285-295.

________. (1981a). Culture, symbols, and human brain evolution: A synthesis. Dialectical Anthropology, 5, 287-303.

________. (1981b). “The endocast of the Omo 338-6 juvenile hominid: Gracile or robust *Australopithecus*?” American Journal of Physical Anthropology, 54, 109-118.

________. (1981c). Exploring the dorsal surface of hominid brain endocasts by stereoplotter and discriminant analysis. Philosophical Transactions of the Royal Society of London, (Series B), 292, 3-5.

________. (1983a). Cerebral brain endocast pattern of *A. afarensis* hominid. Nature, 303, 420-422.

________. (1983b). Human paleontological evidence relevant to language and behavior. Human Neurobiology, 2, 105-114.

________. (1984). The Taung endocast and the lunate sulcus: A rejection of the hypothesis of its anterior position. American Journal of Physical Anthropology 64, 285-288.

________. (1985). The past, present, and future significance of the lunate sulcus in early hominid evolution. In Tobias, P.V. (Ed.), Hominid evolution: Past, present, and future (pp. 47-62). New York: A. R. Liss.

________. (1988). 'robust' australopithecine brain endocasts: Some preliminary observations. Evolutionary history of the 'robust' australopithecines (pp. 97-106). F. E. Grine. New York: Aldine de Gruyter.

________. (1995). Toward a synthetic theory of brain evolution. In Changeux, J.P. and J. Chavaillon (Eds.), Origins of the human brain (pp. 42-60). Oxford, Clarendon Press.

________. (1996). Evolution of the human brain. In Lock, A. and C.R. Peters (Eds.), Handbook of human symbolic evolution (pp. 74-108). Oxford, Clarendon Press.

________. (1999). Hominid brain volume. Science, 283, 33.

Holloway, R. L. and M. C. De La Coste-Lareymondie (1982). Brain endocast asymmetry in pongids and hominids: Some preliminary findings on the paleontology of cerebral dominance. American Journal of Physical Anthropology, 58, 101-110.

Holloway, R. L. and W. H. Kimbel (1986). Endocast morphology of Hadar hominid 162-28. Nature, 321, 536.

Holloway, R. L. and D. G. Post (1982). The relativity of relative brain measures and hominid mosaic evolution. In Armstrong, E. and D. Falk (Eds.), Primate brain evolution: Methods and concepts (pp. 47-75). New York: Plenum Press.

Howell, F. C. (1960). European and northwest African Middle Pleistocene hominids. Current Anthropology, 1, 195-232.

Hublin, J.-J. (1992). Recent human evolution in northwestern Africa. Philosophical Transactions of the Royal Society of London (Series B) 337, 185-91

Hublin, J.-J., F. Spoor, M. Braun, F. Zonneveld and S. Condemi (1996). A late Neanderthal from Arcy-sur-Cure associated with Upper Palaeolithic artefacts. Nature, 381, 224-226.

Hutchins, E. (1995). Cognition in the wild. Cambridge: The MIT Press.
Iidaka, T., N. Sadato, H. Yamada and Y. Yonekura (2000). Functional asymmetry of human prefrontal cortex in verbal and non-verbal episodic memory as revealed by fMRI. Brain Research/ Cognitive Brain Research, 9, 73-83.

Inhelder, B. and J. Piaget (1958). The growth of logical thinking from childhood to adolescence. New York: Basic Books.

Isaac, G. (1972). Chronology and the tempo of cultural change during the Pleistocene. In Bishop, W.W. and J. Miller (Eds.), Calibration of hominoid evolution (pp. 381-430). Edinburgh: Scottish Academic Press.

________. (1976). Stages of cultural elaboration in the Pleistocene: Possible archaeological indicators of the development of language capabilities. Annals of the New York Academy of Sciences, 280, 275-287.

________. (1978, April). The food-sharing behavior of protohuman hominids. Scientific American, 90-108.

Ito, M. (1990). A new physiological concept on cerebellum. Revue Neurologique (Paris), 146, 564-569.

________. (1993). Movement and thought: Identical control mechanisms by the cerebellum. Trends in Neuroscience, 16, 448-454.

Jackson, J. H. (1875). Clinical and physiological researches on the nervous system (includes a reprint of "On the anatomical and physiological localisation of movement in the brain," from *Lancet*, 1873:184-185). London: Churchill.

Jelinek, A. L. (1977). The Lower Paleolithic: Current evidence and interpretations. Annual Review of Anthropology 6, 11-32.

Jenkins, I. H. and R. S. J. Frackowiak (1997). Functional studies of the human cerebellum with positron emission tomography. Revue Neurologique (Paris) 149, 647-53.

Jensen, A. R. (1995). Paroxysms of denial. In Jacoby, R. and Glauberman, N. (Eds.), The bell curve: History, documents, opinions (pp. 335-337). New York: Times Random House.

________. (1998). The *g* factor: The science of mental ability. Westport, CN, Praeger.

Jerison, H. J. Computer analysis of fossil brains: A research project. (1998, March). University of Wisconsin, Michigan State University, National Museum of Health and Medicine, National Science Foundation. <http://www.neurophys.wisc.edu/brain/index.html>.

________. (1973). Evolution of the brain and intelligence. New York and London: Academic Press.

________. (1982). Allometry, brain size, cortical surface, and convolutedness. In Armstrong, E. and D. Falk (Eds.), Primate brain evolution: Methods and concepts (pp. 77-84). New York: Plenum Press.

Jolicoeur, P. (1990). Bivariate allometry: Interval estimation of the slopes of ordinary and standardized normal major axes and structural relationships. Journal of Theoretical Biology, 144, 275-285.

Jolicoeur, P., P. Pirlot, G. Baron and H. Stephan (1984). Brain structure and correlation patterns in insectivora, chiroptera, and primates. Systematic Zoology, 33, 14-29.

Jones, E. G., P. R. Panger and T. M. Woods (1997). Maintenance of a somatotopic cortical map in the face of diminishing thalamocortical inputs (Abstract). Proceedings of the National Academy of Sciences (USA) 94,11003-11007.

Jonides, J., E. H. Schumacher, E. E. Smith, R. A. Koeppe, E. Awh, P. A. Reuter-Lorenz, C. Marshuetz and C. R. Willis (1998). The role of parietal cortex in verbal working memory. Journal of Neuroscience, 18, 5026-5034.

Kakei, S., J. Yagi, T. Wannier, J. Na and Y. Shinoda (1995). Cerebellar and cerebral inputs to corticocortical and corticofugal neurons in areas 5 and 7 in the cat. Journal of Neurophysiology, 74, 400-412.

Kandel, E. R. and R. D. Hawkins (1993). The biological bases of learning and individuality. Mind and brain: Readings from Scientific American (pp. 40-53). New York: W. H. Freeman and Company.

Kappleman, J. (1996). The evolution of body mass and relative brain size in fossil hominids. Journal of Human Evolution, 30. 243-276.

Karavanic, I. & Smith, F. H. (1998). The Middle/Upper Paleolithic interface and the relationship of Neanderthals and Early Modern Humans in the Hrvatsko Zagorje, Croatia. Journal of Human Evolution, 34, 223-248.

Karmiloff-Smith, A. (1996). Beyond modularity. Cambridge: The MIT Press.
Karmiloff-Smith, A., E. Klima, U. Bellugi, J. Grant and S. Baron-Cohen (1995). Is there a social module? Language, face processing, and theory of mind in individuals with Williams syndrome. Journal of Cognitive Neuroscience, 7(2): 196-208.

Kawashima, R., M. Matsumura, S. N., E. Naito, A. Waki, S. Nakamura, K. Matsunami, H. Fukuda and Y. Yonekura (1998). Regional cerebral blood flow changes in human brain related to ipsilateral and contralateral complex hand movements--a PET study. European Journal of Neuroscience, 10, 2254-2260.

Kay, R. F., M. Cartmill and M. Balow (1998). The hypoglossal canal and the origin of human vocal behavior. Proceedings of the National Academy of Sciences (USA), 95, 5417-5419.

Keeley, L. H. (1980). Experimental determination of stone tool uses: A microwear analysis. Chicago, Chicago University Press.

Keeley, L. H. and N. Toth (1981). Microwear polishes on early stone tools from Koobi Fora, Kenya. Nature, 293, 464-465.

Kein, J. (1991). The need for data reduction may have paved the way for the evolution of language ability in hominids. Journal of Human Evolution, 20, 157-165.

Kien, J. (1992). Remembering and planning: A neuronetwork model for the selection of behavior and its development for use in human language. In Haefner, K. (Ed.), Evolution of information processing systems (pp. 229-258). Berlin, Springer.

Keith, A. (1831). New discoveries relating to the antiquity of man. London: Williams and Norgate.

Killackey, H. P. (1995). Evolution of the human brain: A neuroanatomical perspective. In Gazzaniga, M.S. (Ed.), The cognitive neurosciences (pp. 1243-1254). Cambridge: The MIT Press.

Kim, H., S. C. Levine and S. Kertesz (1990). Are variations among subjects in lateral asymmetry real individual differences or random error in measurement?: Putting variability in its place. Brain and Cognition, 14, 220-242.

Kim, S.-G., K. Ugurbil and P. L. Strick (1994). Activation of a cerebellar output nucleus during cognitive processing. Science, 265, 949-951.

Kimbel, W. H., R. C. Walter, D. Johanson, K. E. Reed, J. L. Aronson, Z. Assefa, C. W. Marean, G. G. Eck, R. Bobe, E. Hovers, Y. Rak, C. Vondra, T. Yemane, D. York, Y. Chen, N. M. Evensen and P. E. Smith (1116). Late Pliocene *Homo* and Oldowan tools from the Hadar formation (Kada Hadar Member), Ethiopia. Journal of Human Evolution, 31, 549-561.

Kimura, D. (1993). Sex differences in the brain. Mind and brain: Readings from Scientific American (pp. 79-89). New York: W.H. Freeman and Company.

King, B. J. (1991). Social information transfer in monkeys, apes and hominids. Yearbook of Physical Anthropology, 34, 97-115.

Klatzky, R., B. McCloskey, S. Doherty, J. Pellegrino and T. Smith (1987). Knowledge about hand shaping and knowledge about objects. Journal of Motor Behavior, 19, 187-213.

Kleiber, M. (1947). Body size and metabolic rate. Physiological Reviews, 27, 511-541.

Klein, R. G. (1973). Geological antiquity of Rhodesian man. Nature, 244, 311-312.

________. (1992). The archeology of modern human origins. Evolutionary Anthropology, 1, 5-14.

________. (1999). The human career: Human biological and cultural origins. Chicago, The University of Chicago Press.

Klein, S. (1990). Human cognitive changes at the middle to upper Palaeolithic transition: The evidence of Boker Tachtit. In Mellars, P. (Ed.), The emergence of modern humans (pp. 499-516). New York: Cornell University Press.

Klekamp, J., A. Riedel, C. Harper and H.-J. Kretschmann (1987). A quantitative study of Australian aboriginal and Caucasian brains. Journal of Anatomy, 150, 191-210.

________. (1989). Morphometric study on the postnatal growth of non-cortical brain regions in Australian Aborigines and Caucasians. Brain Research, 485, 79-88.

Kochetkova, V. I. (1978). Paleoneurology. New York: Halsted Press.

Koechlin, E., G. Basso, P. Pietrini, S. Panzer and J. Grafman (1999). The role of the anterior prefrontal cortex in human cognition. Nature, 399, 148-151.

Kosslyn, S. M. (1994). Image and brain: The resolution of the imagery debate. Cambridge: The MIT Press.

Kosslyn, S. M. and O. Koenig (1992). Wet mind. New York: Free Press.

Krubitzer, L. (1995). The organization of neocortex in mammals: Are species differences really so different? Trends in Neuroscience, 18, 408-417.

Kuhl, P. K. (1983). The perception of auditory equivalence classes for speech in early infancy. Infant Behavior and Development 6, 263-285.

________. (1991). Perception, cognition and the ontogenetic and phylogenetic emergence of human speech. Plasticity of development (pp. 73-106). S. Brauth, W. Hall and R. Dooling. Cambridge: The MIT Press.

Kuhn, S., M. Stiner, D. Reese and E. Güleç. (2001). Ornaments of the earliest Upper Paleolithic: New insights from the Levant (Abstract). Proceedings of the National Academy of Sciences (USA), 10,1073.

Kujala, T., K. Alho and R. Naatanen (2000). Cross-modal reorganization of human cortical functions. Trends in Neuroscience, 23, 115-120.

LaBar, K. S., D. R. Gitelman, T. B. Parrish and M. Mesulam (1999). Neuroanatomic overlap of working memory and spatial attention networks: A functional MRI comparison within subjects (Abstract). Neuroimage, 10, 695-704.

Laberge, D. (1995). Computational and anatomical models of selective attention in object identification. In Gazzaniga, M.S. (Ed.), The cognitive neurosciences (pp. 649-664). Cambridge: The MIT Press.

Laitman, J. and R. C. Heimbuch (1982). The basicranium of Plio-Pleistocene hominids as an indicator of their upper respiratory systems. American Journal of Physical Anthropology, 59, 323-344.

Laitman, J., R. C. Heimbuch and E. S. Crelin (1979). The basicranium in fossil hominids as an indicator of their upper respiratory systems. American Journal of Physical Anthropology, 51, 15-34.

Laitman, J. and J. S. Reidenburg (1988). Advances in understanding the relationship between the skull base and larynx with comments on the origins of speech. Journal of Human Evolution, 3, 99-109.

Lakoff, G. and M. Johnson (1999). Philosophy in the flesh: The embodied mind and its challenge to western thought. New York: Basic Books.

Langer, J. (1993). Comparative cognitive development. In Gibson, K. and Ingold, T. (Eds.), Tools, language and cognition in human evolution (pp. 300-313). Cambridge: Cambridge University Press.

________. (2000). Heterochronic evolution of primate cognitive development. In Parker, S.T., J. Langer and M. L. McKinney (Eds.), Biology, brains and behavior (pp. 215-2360. Santa Fe, School of American Research.

Larson, C. F., D. Dodson and J. P. Ward (1989). Hand preferences and whole (*Galago senegalensis*). Brain, Behavior and Evolution, 33, 261-267.

Lashley, K. (1949). Persistent problems in the evolution of mind. The Quarterly Review of Biology, 24, 28-42.

Lashley, K. (1950). In search of the engram. Symposia of the Society for Experimental Biology, 4, 451-482.

Latimer, B. and J. Ohman (2001). Axial dysplasia in *Homo erectus* (Abstract). Journal of Human Evolution, 40, A12.

Le Gros Clark, W. E. (1938). The endocranial cast of the Swanscombe bones. Journal of the Royal Anthropological Institute, 68, 61-67.

________. (1947). Observations on the anatomy of the fossil Australopithecinae. Journal of Anatomy (London), 81, 300-333.

Leakey, M. D. (1971). Olduvai Gorge. Cambridge: Cambridge University Press.

Leiner, H. C., A. L. Leiner and R. S. Dow (1986). Does the cerebellum contribute to mental skills? Behavioral Neuroscience, 100, 443-454.

________. (1989). Reappraising the cerebellum: What does the hindbrain contribute to the forebrain? Behavioral Neuroscience, 103, 998-1008.

________. (1991). The human cerebro-cerebellar system: Its computing, cognitive, and language skills. Behavioral Brain Research (Amsterdam), 44, 113-28.

________. (1993). Cognitive and language functions of the human cerebellum. Trends in Neuroscience, 16, 444-454.

LeMay, M. (1976). Morphological cerebral asymmetries of modern man, fossil man, and nonhuman primate. Annals of the New York Academy of Sciences, 3499-3565.

________. (1985). Asymmetries of the brains and skulls of nonhuman primates. In Glick, S.D. (Ed.), Cerebral lateralization in nonhuman species. London: Academic Press.

LeMay, M., M. S. Billig and N. Geschwind (1982). Asymmetries of the brains and skulls of nonhuman primates. In Armstrong, E. and D. Falk (Eds.), Primate brain evolution; methods and concepts (pp. 263-278). New York: Plenum Press.

Leroi-Gourhan, A. (1958). Études du restes humain fossiles provenant des grottes d'Arcy-sur-Cure. Annales de Paléontologie (Vertébrés), 44, 97-140.

Leutenegger, W. (1982). Encephalization and obstetrics in primates with particular reference to human evolution. In Armstrong, E. and D. Falk (Eds.), Primate brain evolution: Methods and concepts (pp. 85-95). New York: Plenum Press.

________. (1987). Neonatal brain size and neurocranial dimensions in Pliocene hominids: Implications for obstetrics. Journal of Human Evolution, 16, 291-297.

Léveque, F. and B. Vandermeersch (1980). Découverte de restes humains dans un niveau Castelperronien à Saint-Césaire (Charent-Maritime). Comptes Rendus de l'Académie des Sciences de Paris (Series 2), 281, 18-189.

Levitt, P. (1995). Experimental approaches that reveal principles of cerebral cortical development. In Gazzaniga, M.S. (Ed.), The cognitive neurosciences (pp. 147-164) . Cambridge: The MIT Press.

Levy-Agresti, J. and R. W. Sperry (1968). Differential perceptual capacities in major and minor hemispheres. Proceedings of the National Academy of Sciences (USA), 6, 1151.

Leyton (Grünbaum), A. S. F. and C. S. Sherrington (1917 (1960)). Observations on the excitable cortex of the chimpanzee, orangutan and gorilla. 11, 135-222.

Lieberman, D. E. (1975). On the origins of language: An introduction to the evolution of speech. New York: MacMillan.

________. (1984a). The biology and evolution of language. Cambridge: Harvard University Press.

________. (1994a). Functional tongues and Neanderthal vocal tract reconstruction: A reply to Houghton (1993). American Journal of Physical Anthropology, 95, 443-452.

________. (1994b). Hyoid bone position and speech: Reply to Arensburg et al. (1990)). American Journal of Physical Anthropology, 94, 275-278.

Lieberman, D. E., O. M. Pearson and K. M. Mowbray (2000). Basicranial influence on overall cranial shape. Journal of Human Evolution, 38, 291-315.

Lieberman, P. (1984b). The biology and evolution of language. Cambridge: Harvard University Press.

Lieberman, P. and E. S. Crelin (1971). On the speech of Neanderthal man. Linguistic Inquiry, 2, 203-222.

Lieberman, P., J. Laitman, J. S. Reidenburg and P. J. Gannon (1992). The anatomy, physiology, acoustics and perception of speech: Essential elements in analysis of the evolution of human speech. Journal of Human Evolution, 23, 447-467.

Lotze, M., P. Montoya, M. Erb, E. Hulsmann, H. Flor, U. Klose, N. Birnbaumer and W. Grodd (1999). Activation of cortical and cerebellar motor areas during executed and imagined hand movements: An fMRI study. Cognitive Neuroscience, 11, 491-501.

Lovejoy, C. O. (1981). The origin of man. Science, 211, 341-350.

Lumley, H. de (1976). Les civilisations du Paléolitique Inférieur en Provence. In H. de Lumley (Ed.), La préhistoire française (1, Part 2, pp. 819-851). Paris, Éditions du CNRS.

Lumley, H. de and M.-A. de Lumley (1973). Pre-Neanderthal human remains from Arago cave in south-eastern France. Yearbook of Physical Anthropology,17, 162-168.

Lumsden, C. J. (1982). Neuronal group selection and the evolution of hominid cranial capacity. Journal of Human Evolution, 12, 169-184.

Luria, A. R. (1973). The working brain. New York: Basic Books.

________. (1980). Higher cortical functions in man. New York: Basic Books.

Lynn, R. (1994). Sex differences in intelligence and brain size: A paradox resolved. Personality and Individual Differences, 19, 21-28.

MacLarnon, A. (1993). The vertebral canal. In Leakey, R.E. and A. Walker (Eds.), The Nariokotome *Homo erectus* skeleton (pp. 359-390). Cambridge: Harvard University Press.

________. (1995). The distribution of spinal cord tissues and locomotor adaptation in primates. Journal of Human Evolution, 29, 463-482.

MacLeod, C., K. Zilles, A. Schleicher and K. Gibson (2000). The evolution of the dentate nucleus in *Hominoidea* (Abstract). American Journal of Physical Anthropology, (Supplement 30), 217.

MacNeilage, P. F., M. G. Studdert-Kennedy and B. Lindblom (1987). Primate handedness reconsidered. Behavioral and Brain Sciences, 10, 247-303.

Manger, P. R., T. M. Woods and E. G. Jones (1996). Plasticity of the somatosensory cortical map in macaque monkeys after partial amputation of a digit. Proceedings of the Royal Society of London (Series B), 263, 933-999.

Mania, U. (1995). The utilisation of large mammal bones in Bilzingsleben - a special variant of Middle Pleistocene man's relationship to his environment. Études et Recherches Archéologique de L'Université de Liège, 62, 239-246.

Marchant, L. F. and W. C. McGrew (1996). Laterality of limb function in wild chimpanzees of Gombe National Park: Comprehensive study of spontaneous activities. Journal of Human Evolution, 30: 427-443.

Marean, C. W. and S. Y. Kim (1998). Mousterian large-mammal remains from Kobeh cave: Behavioral implications for Neanderthals and early modern humans. Current Anthropology, 39 (Supplement): S79-S113.

Markowitsch, H. J. (1995). Anatomical basis of memory disorders. In Gazzaniga, M.S. (Ed.), The cognitive neurosciences (pp. 765-780). Cambridge: The MIT Press.

Martin, R. D. (1981). Relative brain size and basal metabolic rate in terrestrial vertebrates. Nature, 293, 57-60.

________. (1982). Allometric approaches to the evolution of the primate nervous system. Armstrong, E. and D. Falk (Ed.), Primate brain evolution: Methods and concepts (pp. 39-58). New York: Plenum Press.

________. (1983). Human brain evolution in an ecological context. Fifty-Second James Arthur Lecture on the Evolution of the Human Brain. New York: American Museum of Natural History.

________. (1990). Primate origins and evolution: A phylogenetic reconstruction. Princeton: Princeton University Press.

Matano, S. (2001). Brief communication: Proportions of the ventral half of the cerebellar dentate nucleus in humans and great apes. American Journal of Physical Anthropology, 114, 163-165.

Matano, S., G. Baron, H. Stephan and H. Frahm (1985a). Volume comparisons in the cerebellar complex of primates: II. Cerebellar nuclei. Folia Primatologica (Basel), 44, 182-203.

Matano, S. and E. Hirasaki (1996). Comparison of locomotor patterns and the cerebellar complex in Ateles and Macaca. Folia Primatologica (Basel), 6, 209-226.

________. (1997). Volumetric comparisons in the cerebellar complex of anthropoids, with special reference to locomotor types. American Journal of Physical Anthropology, 103,173-183.

Matano, S., H. Stephan and G. Baron (1985b). Volume comparisons in the cerebellar complex of primates. I: Ventral pons. Folia Primatologica (Basel), 44, 171-181.

Mathers, K. and M. Henneberg (1995). Were we ever that big? Gradual increase in hominid body size over time. Homo, 46(2), 141-173.

McBrearty, S. and J. Kingston. (1996, April). Environmental context of Rift Valley sites with evidence for Middle Pleistocene blade production in the Kapthurin Formation, Kenya. Paleoanthroplogy Society Abstracts. Paper presented at the annual meeting of the Paleoanthropology Society, New Orleans.

McGrew, W. C. (1992). Chimpanzee material culture. New York: Cambridge University Press.

McHenry, H. M. (1992a). Body size and proportions in early hominids. American Journal of Physical Anthropology, 87, 407-431.

________. (1992b). How big were early hominids? Evolutionary Anthropology, 1, 15-20.

________. (1994). Behavioral ecological implications of early hominid body size. Journal of Human Evolution, 27, 77-87.

McNaughton, B. L., J. J. Knierim and M. Wilson (1995). Vector encoding and the vestibular foundations of spatial cognition: Neurophysiological and computational mechanisms. In Gazzaniga, M.S. (Ed.), The cognitive neurosciences (pp. 585-596). Cambridge: The MIT Press.

Meignen, L. and O. Bar-Yosef. 1988. Variabilité technologique au Proche Orient: l'example de Kebara. In Otte, M. (Ed.), L'Homme de Néanderthal – La technique (pp. 81-95). Liège, ERAUL (31).

Mellars, P. (1989a). Major issues in the emergence of modern humans. Current Anthropology, 30, 349-385.

________. (1989b). Technological changes at the middle-upper Paleolithic transition: Economic, social and cognitive perspectives. In Mellars, P. and C. Stringer (Eds.), The human revolution (pp. 338-365). Princeton: Princeton University Press.

________. (1991). Cognitive changes and the emergence of modern humans in Europe. Cambridge Archaeological Journal, 1, 63-76.

________. (1996). The Neandertal legacy. Princeton: Princeton University Press.

________. (1998, June). Commentary on Neandertal Acculturation in Western Europe. D'Errico, F. Zilhão, M. Julien, D. Baffier, and J. Pelegrin. Cultural Anthropology, 39 (Supp.), S1-S44.

Middleton, F. and P. Strick. (1997). Dentate output channels: Motor and cognitive components. Progress in brain research. C. I. de Zeeuw, P. Strata and J. Voogd, Elsevier Science BV.

________. (2000). Basal ganglia and cerebellar loops: Motor and cognitive circuits. Brain Research. Brain Research Reviews (Amsterdam), 3, 236-250.

Mignault, C. (1985). Transition between sensorimotor and symbolic activities in nursery-reared chimpanzees (*Pan troglodytes*). Journal of Human Evolution, 14, 757-758.

Milton, K. (1981). Distribution patterns of tropical plant foods as an evolutionary stimulus to primate mental development. American Anthropologist, 83, 534-548.

________. (1988). Foraging behavior and the evolution of primate intelligence. In Byrne, R. and Whiten, A. (Eds.), Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes, and humans. Oxford, Oxford University Press.

Mithen, S. (1996a). On early Palaeolithic "concept-mediated marks," mental modularity, and the origins of art. Current Anthropology, 37, 666-669.

________. (1996b). The prehistory of the mind: The cognitive origins of art, religion and science. London: Thames and Hudson.

________. (2000). Mind, brain and material culture: An archaeological perspective. In Carruthers, P. and A. Chamberlain (Eds.), Evolution and the human mind: Modularity, language and meta-cognition (pp. 207-217). Cambridge: Cambridge University Press.

Mogilner, A., J. A. Grossman, U. Ribary, M. Joliot, J. Volkmann, D. Rapaport, R. W. Beasley and R. R. Llinás (1993). Somatosensory cortical plasticity in adult humans revealed by magnetoencephalography. Proceedings of the National Academy of Sciences (USA), 90, 3593-3597.

Mushiake, H. and P. Strick (1993). Preferential activity of dentate neurons during limb movements guided by vision. Journal of Neurophysiology, 70, 2660-2664.

Niewoehner, W. A. (2001). Behavioral inferences from the Skhul/Qafzeh early modern human remains. Proceedings of the National Academy of Sciences (USA), 10, 1073.

Noback, C. R. and N. Moskowitz (1962). Structural and functional correlates of "encephalization" in the primate brain. Annals of the New York Academy of Sciences, 102, 210-218.

Noble, W. and I. Davidson (1996). Human evolution, language and mind. Melbourne, Cambridge University Press.

O'Leary, D. D. and B. B. Stanfield (1985). Occipital cortical neurones with transient pyramidal tract axons extend and maintain collaterals to subcortical but not intracortical targets. Brain Research, 336, 326-333.

Oakley, K. P., P. Andrews, L. H. Keeley and J. D. Clark (1977). A reappraisal of the Clacton spear point. Proceedings of the Prehistoric Society, 43, 1-12.

Osherson, D., D. Perani, S. Cappa, T. Schnur, F. Grassi and F. Fazio (1998). Distinct brain loci in deductive versus probabilistic reasoning. Neuropsychologia(Oxford), 36, 369-376.

Pagel, M. D. and P. H. Harvey (1988). How mammals produce large-brained offspring. Evolution, 42, 948-957.

Painter, N. I. (1995). A large and enduring market. In Jacoby, R. and N. Glauberman (Eds.), The bell curve debate: History, documents, opinions (pp. 296-298). New York. Times Random House.

Pandya, D. N., B. Seltzer and H. Barbas (1988). Input-output organization of the primate cerebral cortex. Comparative Primate Biology 4: Neurosciences, 39-80.

Paradiso, S., N. C. Andreason, D. S. O'Leary, S. Arndt and R. G. Robinson (1997). Cerebellar size and cognition: Correlations with IQ, verbal memory and motor dexterity. Neuropsychiatry, Neuropsychology and Behavioral Neurology,10(1), 1-8.

Parker, S. T. (1990). Why big brains are so rare: Energy costs of intelligence and brain size in anthropoid primates. In Gibson, K. and S.T. Parker (Eds.), "Language" and intelligence in monkeys and apes. Comparative developmental perspectives (pp. 129-154). Cambridge: Cambridge University Press.

Parker, S. T. and K. Gibson (1979). A developmental model for the evolution of language and intelligence in early hominids. The Behavioral and Brain Sciences, 2, 367-408.

Parkins, E. J. (1997). Cerebellum and cerebrum in adaptive control and cognition: A review. Biological Cybernetics, 77, 79-87.

Passingham, R. E. (1975). Changes in the size and organization of the brain in man and his ancestors. Brain, Behavior and Evolution, 11, 73-90.

Pelegrin, J. (1991). Les savoir-faire: Une très longue histoire. Terrain, 16, 107-114.

Penhune, V. B., R. J. Zattore and A. C. Evans (1998). Cerebellar contributions to motor timing: A PET study of auditory and visual rhythm reproduction. Journal of Cognitive Neuroscience, 10, 762-765.

Perony, D. (1934). La Férrassie. Préhistoire, 3, 1-92.

Petersen, M. R., M. D. Beecham, S. R. Zolotow and W. C. Stebbins (1978). Neural lateralization of species-specific vocalizations by Japanese macaques. Science, 202, 324-327.

Petersen, S. E. and P. T. Fox (1988). Positron emission tomographic studies of the cortical anatomy of single-word processing. Nature, 331, 585-589.

Pettito, L. (1987). On the autonomy of language and gesture: Evidence from the acquisition of personal pronouns in American sign language. Cognition, 27, 1-52.

Phillipson, D. W. (1985). African archaeology. Cambridge: Cambridge University Press.

Piaget, J. (1952/1998). The origins of intelligence in children. Madison, CT: International University Press.

Pickering, S. P. (1930). Correlation of brain and head measurements, and relation of brain shape and size to shape and size of the head. American Journal of Physical Anthropology, 15, 2-51.

Pinker, S. (1990). Natural language and natural selection. Behavioral and Brain Sciences, 13, 707-784.

________. (1995). The language instinct. New York: Harper Perennial.

________. (1997). How the mind works. (London) New York: W.W. Norton & Company.

________. (1999). Words and rules: The ingredients of language. New York: Basic Books.

Plisson, H. (1988). Technologie et tracéologie des outils lithiques Moustériens en Union Soviétique: Les travaux de V.E. Shchelinskii. In L'Homme de Néandertal, Vol 4: La Technique (pp. 121-168). Liège: Etudes et Recherches Archéologiques de l'Université de Liège.

Posner, M. I. (1995). Attention in cognitive neuroscience: An overview. The cognitive neurosciences (pp. 615-624). M. S. Gazzaniga. Cambridge: The MIT Press.

Potts, R. (1988). Early hominid activities at Olduvai. New York: Aldine de Gruyter.

________. (1996). Humanity's descent: The consequences of ecological instability. New York: William Morrow and Company, Inc.

Price, C. J., D. W. Green and R. von Studnitz (1999). A functional imaging study of translation and language switching. Brain, 122((Pt 12)): 2221-2235.

Purves, D., G. J. Augustine and D. Fitzpatrick (1997). Definitions. Neuroscience. Sunderland, MA: Sinauer Associates, Inc.

Radinsky, L. (1972). Endocasts and primate brain evolution. The functional and evolutionary biology of primates. R. Tuttle. Chicago: Aldine-Atherton.

________. (1975). Primate brain evolution. American Scientist, 63, 656-663.

Révillion, S. (1993). Question typologique à propos des industries laminaires due Paléolithique Moyen de Seclin (Nord) et de Saint-Germain-des Vaux/Port-Racine (Manche): Lames Levallois ou lames non Levallois?” Bulletin de la Société Préhistorique Française, 90, 269-273.

Richards, M. P., Pettitt, P. B., Stiner, M. C. and Trinkaus, E. (2001). Stable isotope evidence for increasing dietary breadth in the European mid-Upper Paleolithic. Proceedings of the National Academy of Sciences (USA), 98, 6528-6532.

Richardson, K. (2000). The making of intelligence. New York: Columbia University Press.

Riedel, A., J. Klekamp, C. Harper and H.-J. Kretschmann (1989). Morphometric study on the postnatal growth of the cerebellum of Australian Aborigines and Caucasians. Brain Research, 499, 333-343.

Rigaud, J.-P. (1989). From the middle to the upper Paleolithic: Transition or convergence. In Trinkaus, E. (Ed.), The emergence of modern humans: Biocultural adaptations in the later Pleistocene (pp. 142-153). New York: Cambridge University Press.

________. (1997). Scenarios for the middle to upper Paleolithic transition: A European perspective. In Clark, G.A. and C. M. Willermet (Eds.), Conceptual issues in modern human origins (pp. 161-167). New York: Aldine de Gruyter, Inc.

Rigaud, J.-P. and J. F. Simek. (1987). The last pleniglacial in the south of France (24,000 – 14,000 years ago). In Soffer, O. (Ed.), The Pleistocene Old World: Regional perspectives (pp. 183-199). New York: Plenum Press.

Rightmire, G. P. (1976). Relationships of Middle and Upper Pleistocene hominids from sub-Saharan Africa. Nature, 260, 238-240.

________. (1986). Body size and encephalization in *Homo erectus*. Anthropos (Brno), 23, 139-149.

Rilling, J. K. and T. R. Insel (1998). Evolution of the cerebellum in primates: Differences in relative volume among monkeys, apes and humans. Brain, Behavior and Evolution, 52, 308-314.

Riva, D. and C. Giorgi (2000). The cerebellum contributes to higher functions during development: Evidence from a series of children surgically treated for posterior fossa tumours. Brain, 123 (Pt. 5), 1051-1061.

Roberts, A. C., P. Collins and T. W. Robbins (1996). The functions of the prefrontal cortex in humans and other animals. In Mellars, P. and K. Gibson (Eds.) Modelling the early human mind (pp. 67-80). Cambridge: McDonald Institute for Archaeological Research.

Robinson, T. E., J. B. Becker, D. M. Camp and A. Mansour (1985). Variation in the pattern of behavioral and brain asymmetries due to sex differences. In Glick, S.D. (Ed.), Cerebral lateralization in nonhuman species. London: Academic Press.

Robson Brown, K. A. (1993). An alternative approach to cognition in the lower Palaeolithic: The modular view. Cambridge Archaeological Journal, 3, 231-245.

Roder, B., W. Teder-Salejarvi, A. Sterr, F. Rosler, S. A. Hillyard and H. J. Neville (1999). Improved auditory spatial tuning in blind humans. Nature, 400, 162-166.

Roebroeks, W., J. Kolen and E. Resnsink (1988). Planning depth, anticipation and the organization of middle Palaeolithic technology: The 'archaic natives' meet Eve's descendants. Helinium, 28, 17-34.

Rolland, N. (1990). Middle Palaeolithic socio-economic formations in western Eurasia: An exploratory survey. In Mellars, P. (Ed.), The emergence of modern humans: An archaeological perspective (pp. 347-388). Edinburgh: Edinburgh University Press.

Ruff, C. B., E. Trinkaus and T. W. Holliday (1997). Body mass and encephalization in Pleistocene *Homo*. Nature, 387, 173-176.

Russ, J. C. (1999). The image processing handbook. Raleigh: CRC Press in cooperation with IEEE Press.

Sacher, G. A. and E. F. Staffeldt (1974). Relation of gestation time to brain weight for placental mammals: Implications for the theory of vertebrate growth. The American Naturalist,108, 593-615.

Salmon, D. P. and N. Butters (1995). Neurobiology of skill and habit learning. Current Opinion in Neurobiology, 5, 184-190.

Sackett, J. R. (1982). Approaches to style in lithic archaeology. Journal of Anthropological Archaeology, 1, 59-112.

Salomon, G., Ed. (1993). Distributed cognitions: Psychological and educational considerations. Cambridge: Cambridge University Press.

Savage-Rumbaugh, E. S., M. S. Romski, W. D. Hopkins and R. Sevcik (1989). Symbol acquisition and use by *Pan troglodytes, Pan paniscus* and *Homo sapiens*. In Heltne, G. and L. A. Marquardt (Eds.), Understanding chimpanzees. Cambridge: MA, Harvard University Press: 266-295.

Sawaguchi, T. (1988). Correlations of cerebral indices for "extra" cortical parts and ecological variables in primates. Brain, Behavior and Evolution, 32: 129-140.

________. (1989). Relationships between cerebral indices for "extra" cortical parts and ecological categories in anthropoids. Brain, Behavior and Evolution, 34: 281-289.

Schepers, G. W. H. (1946). The endocranial casts of the south African apemen. The South African fossil apemen: The Australopithecinae. Transvaal Museum Memoires, 2, 153-272.

Schick, K. D. and N. Toth (1993). Making silent stones speak: Human evolution and the dawn of technology. New York: Simon and Schuster.

Schlosser, R., M. Hutchinson, S. Joseffer, H. Rusinek, A. Saarimaki, J. Stevenson, S. L. Dewey and J. D. Brodie (1998). Functional magnetic resonance imaging of human brain activity in a verbal fluency task.

Journal of Neurology, Neurosurgery and Psychiatry (London), 64, 492-498.

Schmahmann, J. D. and D. N. Pandya (1995). Prefrontal cortex projections to the basilar pons in Rhesus monkey: Implications for the cerebellar contribution of higher functions. Neuroscience, 199, 175-178.

Schmahmann, J. D. and J. C. Sherman (1998). The cerebellar cognitive affective syndrome. Brain, 121 (Pt. 4), 561-579.

Schumacher, E. H., E. Lauber, E. Awh, J. Jonides, E. E. Smith and R. A. Koeppe (1996). PET evidence for an amodal verbal working memory system. Neuroimage, 3, 79-888.

Searle, J. R. (1984). Minds, brains and science. Cambridge: Harvard University Press.

Seidler, H., D. Falk, C. Stringer, H. Wilfing, G. B. Müller, D. zur Nedden, G. W. Weber, W. Reicheis and J. L. Arsuaga (1997). A comparative study of stereolithographically modelled skulls of Petralona and Broken Hill: Implications for future studies of middle Pleistocene hominid evolution. Journal of Human Evolution, 33, 691-703.

Seitz, R. J., A. G. Canavan, L. Yaguez, H. Herzog, L. Tellmann, U. Knorr, Y. Huang and V. Homberg (1994). Successive roles of the cerebellum and premotor cortices in trajectorial learning. Neuroreport, 5, 2541-4.

Seitz, R. J., Y. Huang, U. Knorr, L. Tellmann, H. Herzog and H. J. Freund (1995). Large-scale plasticity of the human motor cortex (Abstract). Neuroreport, 6, 742-744.

Semaw, S., P. Renne, J. W. K. Harris, C. S. Feibel, R. L. Bernor, N. Fesseha and K. Mowbray (1997). 2.5-million-year-old stone tools from Gona, Ethiopia. Nature, 385, 333-336.

Semendeferi, K. and H. Damasio (2000). The brain and its main anatomical subdivisions in living hominoids using magnetic resonance imaging. Journal of Human Evolution, 38, 317-332.

Semendeferi, K. and G. W. Van Hoesen (1997). The evolution of the frontal lobes: A volumetric analysis based on three-dimensional reconstructions of magnetic resonance scans of human and ape brains. Journal of Human Evolution, 32, 375-388.

Shanks, M. (1994). Commentary on "Symboling and the Middle-to-Upper Paleolithic transition." Current Anthropology, 35, 369-400.

Shea, J. J.(1989). A functional study of the lithic industries associated with hominid fossils in the Kebara and Qafzeh Caves, Israel. In Mellars, P. and C. Stringer (Eds.), The Human Revolution: Behavioral and Biological Perspectives on the Origins of Modern Humans (pp. 611-625). Princeton: Princeton University Press.

________. (1998). Neandertal and early modern human behavioral variablity. Current Anthropology, 39 (Supp.): S45-S78.

Sherrington, C. S. (1906). The integrative action of the nervous system. New Haven, Yale University Press.

Shtyrov, Y., T. Kujala, H. Lytinen, J. Kujala, R. J. Ilmoniemi and R. Naatenen (2000). Lateralization of speech processing in the brain as indicated by mismatch negativity and dichotic listening. Brain and Cognition, 43, 392-398.

Silveri, M. C., A. M. Di Betta, V. Filippini, M. G. Leggio and M. Molinari (1998). Verbal short-term store-rehearsal system and the cerebellum. Evidence from a patient with a right cerebellar lesion. Brain, 121 (Pt 11), 2175-2187.

Silveri, M. C., M. G. Leggio and M. Molinari (1994). The cerebellum contributes to linguistic production: A case of agrammatic speech following a right cerebellar lesion. Neurology, 44, 2047-2050.

Simmons, R. M. T. (1990). Role of the thalamus in the evolution of speech and language in man. In Sperber, G.H. (Ed.), From apes to angels: Essays in anthropology in honor of Phillip v. Tobias (pp. 229-244). New York: Wiley-Liss, Inc.

Smith, F. H. (1984). Fossil hominids from the Upper Pleistocene of central Europe and the origins of modern Europeans. In Smith, F.H. and F. Spencer (Eds.), The origins of modern humans: A world survey of the fossil evidence. New York: Alan R. Liss: 137-209.

Smith, F. H., E. Trinkaus, P. B. Pettit, I. Karavanik, and M. Paunovik. (1999). Direct radiocarbon dates for Vindija G_1 and Velika Pecina Late Pleistocene hominid remains. Proceedings of the National Academy of Sciences (USA), 96,12281-12286.

Smith, G. E. (1928). Endocranial cast obtained from the Rhodesian skull. Rhodesian man and associated remains (pp. 52-58). London: British Museum of Natural History.

Smith, R. J. (1996). Biology and body size in human evolution: Statistical inference misapplied. Current Anthropology, 37, 451-481.

Snell, O. (1891). Die abhänigigkeit des hinrgewichtes von dem körpergewicht und den geistigen fähgkeiten. Archive für Psychiatrisch Nervenkrankheiten, 23, 436-446.

Snyder, P. J., R. M. Bilder, W. Houwei, B. Bogerts and J. A. Lieberman (1995). Cerebellar volume asymmetries are related to handedness: A quantitative MRI study. Neuropsychologia (Oxford), 33, 407-419.

Soffer, O. (1989). The Middle to Upper Paleolithic transition on the Russian Plain. In Mellars, P. and C. Stringer, (Eds.), The human revolution: behavioral and biological perspectives on the origins of modern humans (pp. 714-737). Princeton: Princeton University Press.

Soffer, Olga. (1990). The Russian Plain at the Last Glacial Maximum." In Soffer, O. and C. Gamble (Eds.), The World at 18000 BP Volume 1: High latitudes (pp. 228-252). London: Unwin Hyman.

Sohnge, P. G., L. Visser and C. Van Riet Lowe (1937). "The geology and archaeology of the Vaal River basin. Union of South Africa Geological Survey (Memoire 35).

Sokol, R. R. and F. J. Rohlf (1981). Biometry. New York: Freeman.

Spearman, C. (1904). 'General intelligence' objectively determined and measured. American Journal of Psychology, 15, 201-293.

Spearman, C. (1927). The abilities of man: Their nature and measurement. New York: Macmillan.

Spelke, E. S. (1991). Physical knowledge in infancy: Reflections on Piaget's theory. In Carey, S. and R. Gelman (Eds.), Epigenesis of the mind: Essays in biology and knowledge. Hillsdale, NJ, Erlbaum.

Spoor, F. (1997). Basicranial architecture and relative brain size of STS 5 (*Australopithecus africanus*) and other Plio-Pleistocene hominids. South African Journal of Science, 93, 182-186.

Spoor, F., N. Jeffrey and F. Zonneveld (in press). Imaging skeletal growth and evolution (text adapted from that published in Development, Growth and

Evolution: implications for the study of the hominid skeleton. P. O'Higgins and M. Cohn. London: Academic Press). http://evolution.anat.ucl.ac.uk/image_grp/ImageFAQ.htm#CT_MRI_images.

Spoor, F., B. A. Wood and F. Zonneveld (1994). Implications of early hominid labyrinthine morphology for the evolution of human bipedal locomotion. Nature, 369, 645-648.

Springer, S. P. and M. S. Gazzaniga (1975). Dichotic testing of partial and complete split brain subjects. Neuropsychologia (Oxford), 13, 341-346.

Springer, S. P., J. Sidtis, D. Wilson and M. S. Gazzaniga (1978). Left ear performance in dichotic listening following commissurotomy. Neuropsychologia, 16, 305-312.

Stanfield, B. B. and D. D. O'Leary (1985). Fetal occipital neurones transplanted to the rostral cortex can extend and maintain a pyramidal tract axon. Nature, 313, 135-137.

Steklis, H. D. and S. Harnad (1976). From hand to mouth: Some critical stages in the evolution of language. Annals of the New York Academy of Sciences, 280, 445-455.

Stephan, H. (1972). Evolution of primate brains: A comparative anatomical investigation. In Tuttle, R. (Ed.), The functional and evolutionary biology of primates (pp. 155-174). Chicago and New York: Aldine-Atherton.

Stephan, H. (1988). Comparative size of brain and brain components. Comparative primate biology 1: Neurosciences (pp. 1-38). H. D. Steklis and J. Erwin, Alan R. Liss, Inc.

Stephan, H., R. Bauchot and O. J. Andy (1970). Data on size of the brain and of various brain parts in insectivores and primates. The primate brain (pp.289-297). C. R. Noback and W. Montagna. New York: Appleton-Century-Crofts.

Stephan, H., H. Frahm and G. Baron (1981). New and revised data on volumes of brain structures in insectivores and primates. Folia Primatologica (Basel), 35, 1-29.

Stewart, M. (1960). Indirect evidence of the primitiveness of the Swanscombe skull. American Journal of Physical Anthropology, 18, 363.

Stiner, M.C., N.D. Munro and T. A. Surovell. (2000). The tortoise and the hare: Small-game use, the broad-spectrum revolution, and Paleolithic demography. Current Anthropology, 41, 39-73.

Stout, D., N. Toth and K. Schick. (2000). Stone tool-making and brain activation: positron emission tomography (PET) studies. Journal of Archaeological Science, 27, 1215-1223.

Strait, D. S. (1999). The scaling of basicranial flexion and length. Journal of Human Evolution, 37, 701-719.

Straus, L. G. (1988). Explorations of the twilight zone: The early upper Paleolithic of Vasco-Cantabrian Spain and Gascony. In Hoffecker, J. F. and C. A. Wolf (Vol. Editors), The early upper Paleolithic: Evidence from Europe and the Near East (pp. 97-129). (BAR International Series).

________. (1994). Commentary on "Symboling and the Middle-to-Upper Paleolithic transition". Current Anthropology, 35, 369-400.

________. (1995). The Upper Paleolithic of Europe: An overview. Evolutionary Anthropology, 4, 4-16.

________. (1997). The Iberian situation between 40,000 and 30,000 b.p. In light of European models of migration and convergence. In Clark, G.A. and C.M. Willermet (Editors), Conceptual issues in modern human origins research (pp. 235-252). New York: Aldine de Gruyter, Inc.

Straus, L. G., J. L. Bischoff and E. Carbonell (1993). A review of the Middle to Upper Paleolithic transition in Iberia. Préhistoire Européenne, 3, 11-27.

Stiner, M.C., Munro, N.D., Surovell, T. A., Tchernov, E. and Bar-Yosef, O. Paleolithic population growth pulses evidenced by small animal exploitation. Science, 283, 190-194.

Strick, P. and F. Middleton (1994). Anatomical evidence for cerebellar and basal ganglia involvement in higher cognitive function. Science, 266, 458-461.

Stringer, C. (1974). Population relationships of later Pleistocene hominids. Journal of Archaeological Science, 1, 317-342.

Stringer, C.B. and Gamble, C. (1993). In search of the Neandertals. New York: Thames and Hudson.

Stringer, C. B. and J.-J. Hublin (1999). New age estimates for the Swanscombe hominid, and their significance for human evolution. Journal of Human Evolution, 37, 873-877.

Subramaniam, B., J. G. Hennessey, M. A. Rubin, L. S. Beach and A. L. Riess (1997). Software and methods for quantitative imaging in neuroscience: The Kennedy Krieger Institute Human Brain Project. In Kosloe, S.H. and M. F. Huerta (Eds.), Neuroinformatics: An overview of the Human Brain Project (pp. 335-360). Mahwah, NJ: Lawrence Erlbaum Associates.

Svoboda, J. (1987). Lithic industries of the Arago, Vértesszöllös, and Bilzingsleben hominids: Comparison and evolutionary interpretation. Current Anthropology, 28, 219-227.

________. (1998, June). Commentary on "Neandertal acculturation in Western Europe" , F. Zilhão, M. Julien, D. Baffier, and J. Pelegrin. Cultural Anthropology, 39 (Supp.),S1-S44.

Svoboda, J., V. Lozek and E. Vlcek. (1996). Hunters between East and West. New York: Plenum Press.

Symington, J. (1916). Endocranial casts and brain form: A criticism of some recent speculations. Journal of Anatomy and Physiology, 11 (Third series), 111-130.

Tague, R. G. and C. O. Lovejoy (1986). The obstetric pelvis of A. L. 288-1 (Lucy). Journal of Human Evolution, 15, 237-255.

Taylor, J. V. and R. Dibennardo (1980). Cranial capacity/cranial base relationships and prediction of vault form: A canonical correlation analysis. American Journal of Physical Anthropology, 53, 151-158.

Terman, L. M. (1916). The measurement of intelligence. Boston: Houghton-Mifflin.

Thach, W. T., H. P. Goodkin and J. G. Keating (1992). The cerebellum and the adaptive coordination of movement. Annual Review of Neuroscience, 15, 403-442.

Thieme, H. (1997). Lower Palaeolithic hunting spears from Germany. Nature, 385, 807-810.

Thoma, A. (1966). L'occipital de l'homme Mindélien de Vértesszöllös. L'Anthropologie, 70, 495-534.

Thomas, M. and A. Karmiloff-Smith (1998). *Quo vadis* modularity in the 1990s? Learning and Individual Differences, 10, 245-250.

Thurstone, L. L. (1938). Primary mental abilities. Psychometric Monographs 1.

Tobias, P. V. (1967). Olduvai Gorge. Cambridge: Cambridge University Press.
________. (1971). The brain in hominid evolution. New York: Columbia University Press.

________. (1975). Brain evolution in the hominoidea. In Tuttle, R. (Editor), Primate functional morphology and evolution (pp. 353-392). The Hague, Mouton.

________. (1980). *Australopithecus afarensis and A. africanus:* Critique and an alternative hypothesis. Palaentologica Africane 23, 1-17.

________. (1983). Recent advances in the evolution of the hominids with especial reference to brain and speech. Pontificae Academiae Scientiarum Scripta Varia, 50, 85-140.

________. (1987). The brain of *Homo habilis*: A new level of organization in cerebral evolution. Journal of Human Evolution, 16, 741-761.

Tooby, J. and L. Cosmides (1995). Mapping the evolved functional organization of mind and brain. In Gazzaniga, M.S. (Editor), The cognitive neurosciences (pp. 1185-1197). Cambridge: The MIT Press.

Toth, N. (1985). Archeological evidence for preferential right-handedness in the Lower and Middle Pleistocene, and its possible implications. Journal of Human Evolution, 14, 607-614.

________. (1987). The first technology. Scientific American, 256(4): 112-121.

Toth, N., K. D. Schick, E. S. Savage-Rumbaugh, R. A. Sevcik and D. M. Rumbaugh (1993). *Pan* the tool-maker: Investigations into the stone tool-making and tool-using capabilities of a Bonobo (*Pan paniscus*). Journal of Archaeological Science, 20, 81-91.

Tracy, J. I., S. H. Faro, F. B. Mohamed, M. Pinsk and A. Pinus (2000). Functional localization of a "time keeper" function separate from attentional resources and task strategy. Neuroimage, 11, 228-242.

Trinkaus, E. (1983). The Shanidar Neandertals.

________. (1992). Morphological contrasts between the Near Eastern Qafzeh-Skhul and Late Archaic human samples: Grounds for a behavioral difference? The evolution and dispersal of modern humans in Asia (pp. 227-294). T. Akakzawa, K. Aoki and t. Kimura. Tokyo, Hokusen-Sha.

Trinkaus, E., S. E. Churchill and C. B. Ruff (1994). Postcranial robusticity in *Homo*. II: Humeral bilateral asymmetry and bone plasticity. American Journal of Physical Anthropology, 93,1-34.

Trinkaus, E., S. E. Churchill, I. Villemeur, K. G. Riley, J. A. Heller and C. B. Ruff (1991). Robusticity versus shape: The functional interpretation of Neandertal appendicular morphology. Journal of the Anthropological Society of Nippon, 99, 257-278.

Trinkaus, E., C. B. Ruff and S. E. Churchill (1998). Upper limb versus lower limb loading patterns among Near Eastern Middle Paleolithic hominids. Neandertals and modern humans in west Asia (pp. 391-404). T. Akazowa, K. Aoki and O. Bar-Yosef. New York: Plenum.

Trinkaus, E. and F. Smith. (1985). The fate of the Neandertals. In Delson, E., ed. Ancestors: The hard evidence (pp. 325-333). New York: Alan R. Liss.

Ullman, M. T. (In press). The role of declarative and procedural memory in language (Abstract). Brain and Cognition.

van Dongen, H. R., C. E. Catsman-Berrevoets and M. van Mourik (1994). The syndrome of 'cerebellar' mutusm and subsequent dysarthria. Neurology, 44, 2040-2046.

Vandermeersch, B. (1981). Les Hommes Fossiles de Qafzeh (Israël). Oaris: C.N.R.S.

________. (1997). The Near East and Europe: Continuity or discontinuity? In Clark, G. A. and Willermet, C.M. (Editors), Conceptual issues in modern human origins research (pp. 107-116). New York: Aldine de Gruyter.

Vauclair, J. and J. Fagot (1988). Handedness and bimanual coordination in the lowland gorilla. Brain, Behavior and Evolution, 32, 89-95.

Verity, C. M., E. H. Strauss, P. D. Moyes, J. A. Wada, H. G. Dunn and J. S. Lapointe (1982). Long-term follow-up after cerebral hemispherectomy: Neurophysiologic, radiologic, and psychological findings. Neurology, 32, 629-639.

Villa, P. (1983). Terra Amata and the Middle Pleistocene archaeological record of southern France. University of California Publications in Anthropology. 13, 1-103.

Vygotsky, L. S. (1978). Mind in society: The development of higher psychological processes. Cambridge: Harvard University Press.

Watts, I. (1999). The origins of symbolic culture. In Dunbar, R., C. Knight and C. Power (Eds.), The evolution of culture (pp. 113-146). Edinburgh: Edinburgh University Press.

Weaver, A. H., T. W. Holliday, C. B. Ruff and E. Trinkaus (2000). The fossil evidence for the evolution of intelligence in Pleistocene *Homo*. In Nowell, A. (Ed.), In the mind's eye: Multidisciplinary perspectives on the evolution of human cognition (pp. 154-171). Ann Arbor, International Monographs in Prehistory.

Weber, G. W., J. Kim and H. Prossinger. Virtual anthropology, University of Vienna. <http://www.anthro.univie.ac.at/virtanth/virtanth.html>.Last update September 2000.

Weidenreich, F. (1943). The skull of Sinanthropus pekinensis. Palaeontologia Sinica (New Series D), 10, 1-486.

________. (1947). Some particulars of skull and brain of early hominids and their bearing on the problem of the relationship between man and anthropoids. American Journal of Physical Anthropology, 5, 4.

Weinert, H. (1931). Discussion of B. K. Schultz. Verh. Ges. Phys. Anthropol., 5: 39.

Welker, W. I. (1990). Why does the cerebral cortex fissure and fold? A review of the determinants of gyri and sulci. In Jones, E.G. and A. Peters (Eds.), Cerebral cortex Vol. 88 (pp. 3-136). New York: Plenum Press.

Wernicke, C. (1874). Der aphasisiche symptomenkomplex. Breslau, Cohn & Weigert.

Whallon, R. (1989). Elements of cultural change in the later Paleolithic. In Mellars, P. and C. Stringer, (Eds.), The human revolution: behavioral and biological perspectives on the origins of modern humans (pp. 433-453). Princeton: Princeton University Press.

White, D. D. (1998). The cerebellum in hominid evolution: Evidence from endocranial casts (Abstract). American Journal of Physical Anthropology, (Supplement 26), 231.

White, J. P. and H. I. Dibble (1986). Stone tools: Small-scale variability. Stone age prehistory: Studies in memory of Charles McBurney (pp. 47-53). G. N. Bailey and P. Callow. New York: Cambridge University Press.

White, L. E., G. Lucas, A. Richards and D. Purves (1994). Cerebral asymmetry and handedness. Nature, 368, 197-198.

White, R. E. (1982). Rethinking the Middle/Upper Paleolithic transition. Current Anthropology, 23, 169-192.

________. (1989a). Toward a contextual understanding of the earliest body ornaments. In Trinkaus, E. (Ed.), The emergence of modern humans: Biocultural adaptations in the later Pleistocene (pp. 211-231). New York: Cambridge University Press.

________. (1989b). Visual thinking in the ice age. Scientific American, 92-99.

________. (1989c). Production complexity and standardization in early Aurignacian bead and pendant manufacture: Evolutionary implications. In Mellars, P. and Stringer, C. (Eds.), The human revolution: Behavioral and biological perspectives in the origins of modern humans (pp. 360-399). Edinburgh: Edinburgh University Press.

________. (1996). On the evolution of human socio-cultural patterns. Handbook of human symbolic evolution (pp. 240-262). A. Lock and C. R. Peters. Oxford, Clarendon.

________. (1998, June). Commentary on "Neandertal Acculturation in Western Europe." Cultural Anthropology, 39 (Supp.), S1-S44.

Whiten, A. (1999). Parental encouragement in *Gorilla* in comparative perspective. In Parker, S. T., R. W. Mitchell, and H. L. Miles (Editors), The mentality of gorillas and orang utans (pp. 342-366). Cambridge: Cambridge University Press.

Wittleson, S. F., I. J. Glezer and D. L. Kigar (1995). Women have greater density of neurons in posterior temporal cortex. Journal of Neuroscience, 15, 3418-3428.

Wobst, H.M. (1976). Locational relationships in Paleolithic society. Journal of Human Evolution, 5, 49-58.

Wüllner, T. Klockgether, D. Peterson, T. Naegele and J. Dichgans (1993). Magnetic resonance imaging in hereditary and idiopathic ataxia. Neurology, 43, 318-325.

Wreschner, E. E. (1985). Evidence and interpretation of red ochre in the early prehistoric sequences. In P.V. Tobias, (Ed.), Hominid evolution: past, present and future (pp. 387-394). New York Alan R. Liss.

Wynn, T. G. (1979). “The intelligence of later Acheulean hominids. Man, 14, 371-391.

________. (1981). The intelligence of Oldowan hominids. Journal of Human Evolution,10, 529-541.

________. (1985). Piaget, stone tools and the evolution of human intelligence. World Archaeology,17, 32-43.

________. (1991a). Archeological evidence for modern intelligence. In Foley, R. A. (Ed.), The origins of human behavior. Cambridge: Unwin Hyman, Ltd.

________. (1991b). Tools, grammar, and the archaeology of cognition. Cambridge Archaeological Journal, 1, 191-206.

________. (1996). The evolution of tools and symbolic behavior. Handbook of human symbolic evolution (pp. 263-286). A. Lock and C. R. Peters. Oxford, Clarendon Press.

________. (2000). In Symmetry and the evolution of the modular mind. Evolution and the modern human mind; modularity, language and meta-cognition (pp. 113-139). Cambridge: Cambridge University Press.

Yerkes, R. M. (1917). The Binet version versus the point-scale method of measuring intelligence. Journal of Applied Psychology, 1: 111-122.

Zilles, K., E. Armstrong, K. H. Moser, A. Schleicher and H. Stephan (1989). Gyrification in the cerebral cortex of primates. Brain, Behavior and Evolution, 34, 143-150.

Zilles, K., H. Stephan and A. Schleicher (1982). Quantitative cytarchitectonics of the cerebral cortices of several prosimian species. In Armstrong, E. and D. Falk (Eds.), Primate brain evolution: Methods and concepts (pp. 177-201). E. Armstrong and D. Falk. New York: Plenum.

Zollikofer, C., M. Ponce de Léon and R. D. Martin (1998). Computer-assisted paleoanthropology. Evolutionary Anthropology, 6, 41-54.